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

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A B S T R A C T

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; Moïse, 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

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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 (Knauft 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; Knauft 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, Codding, & 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 multiethnic 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.

We collected four sets of data from each participant: (1) self-reported demographic and economic information, (2) anthropometric measures, (3) freelisted members of the community who the participant thought would be ideal models from whom to learn important skills, and (4) freelisted 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 freelists 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 freelisted 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 ($rank/rank_{max}$). 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*

[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 later (Luke Glowacki and Scott Calvert, personal communications).

[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.

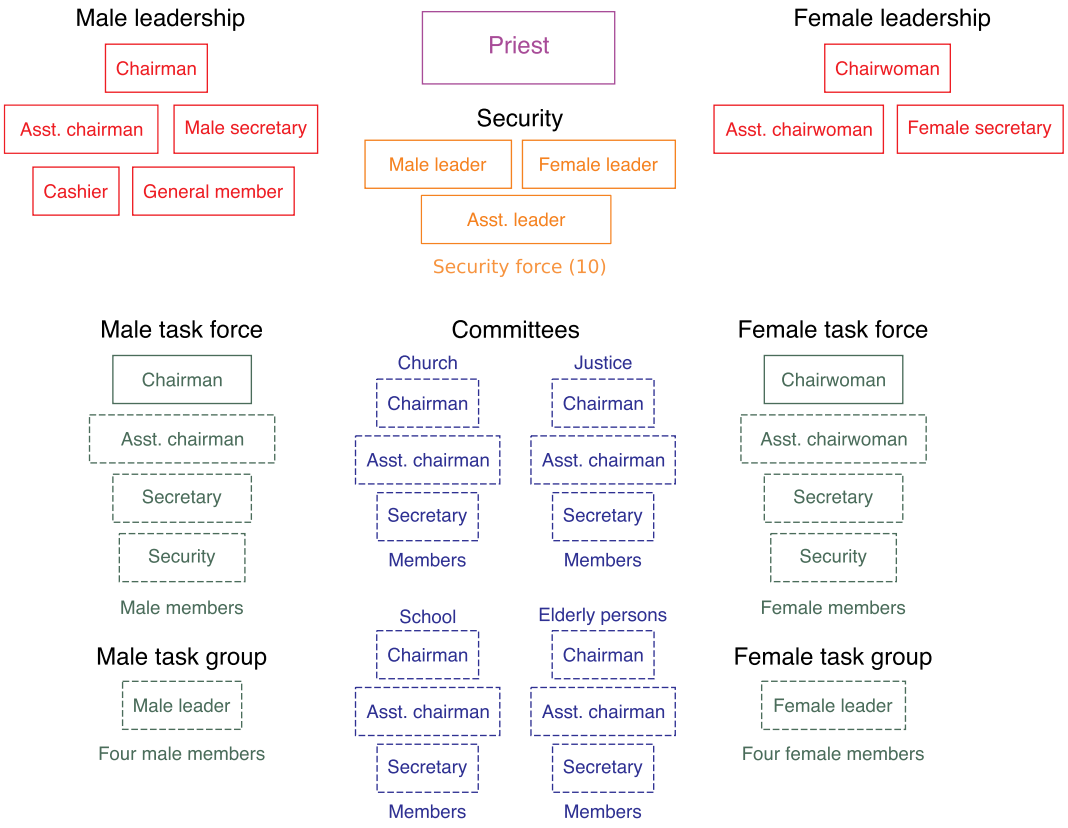

Fig. 1. The Chabu Kebele leadership system. Each box is one leader. Solid border: Major leader. Dashed border: Minor leader.

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

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

and for logistic regression:

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

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 $\lambda \to \infty$, the coefficients β_j are "shrunk" to 0. Thus, when λ is small, the βs 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 βs 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 under-fitted. 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. Loot 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, $0 \leq \alpha \leq 1$:

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

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 metanalaysis 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):

$$Leadership\ \ status \sim \text{Bernoulli}(p_i)$$
$$\text{logit}(p_i) = \beta_0 + \beta_1 Prestige_{EST,i} + \beta_2 Dominance_{EST,i} + \beta_3 Sex_i + \beta_4 Age_i$$
$$Prestige_{EST,i} \sim N\,(Prestige_{OBS,i}, Prestige_{SE,i})$$
$$Dominance_{EST,i} \sim N\,(Dominance_{OBS,i}, Dominance_{SE,i})$$

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 (*ɗoku*), 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 a 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 (*sòtā*) 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 leaders[4]; 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 ($\overline{\alpha} = 0.65$) than on male traits ($\overline{\alpha} = 0.75$) 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 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 where 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

[4] We 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.

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

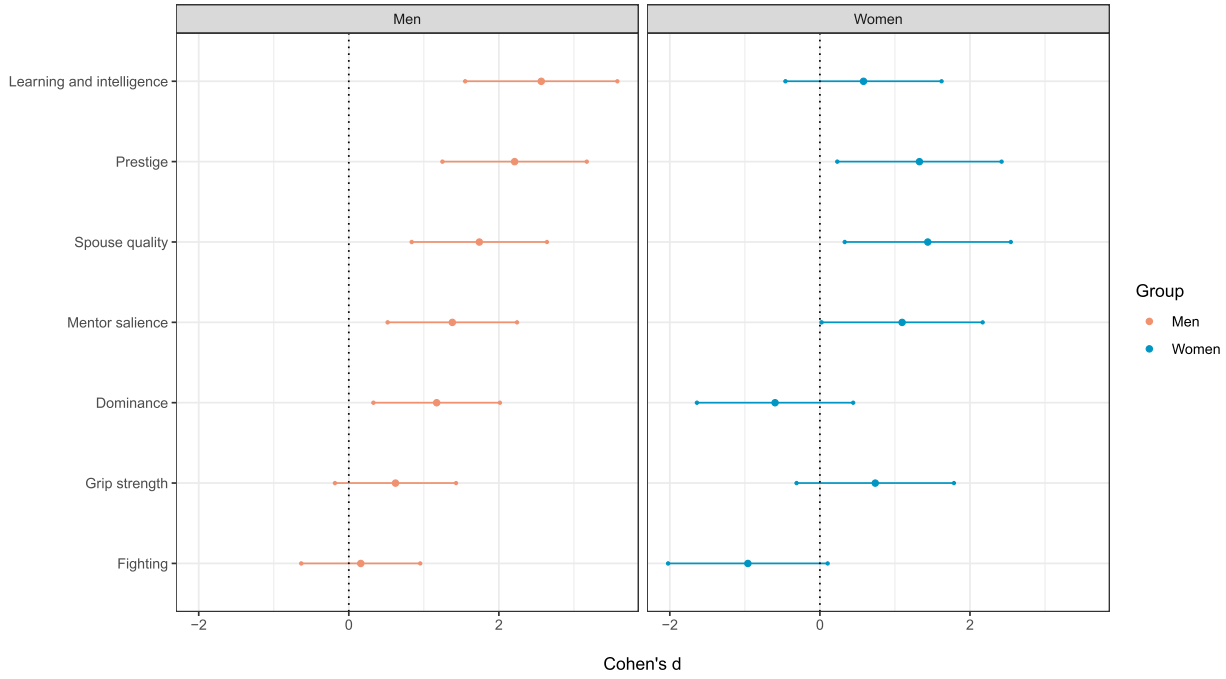

Fig. 2. Preregistered tests. Bivariate comparisons of elected leaders vs. non-leaders on mean values of hypothesized leadership traits. Tested within men only (n = 34) and within women only (n = 26). Values are Cohen's d; bars represent 95% CI. See Supplementary Information for details on preregistration.

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

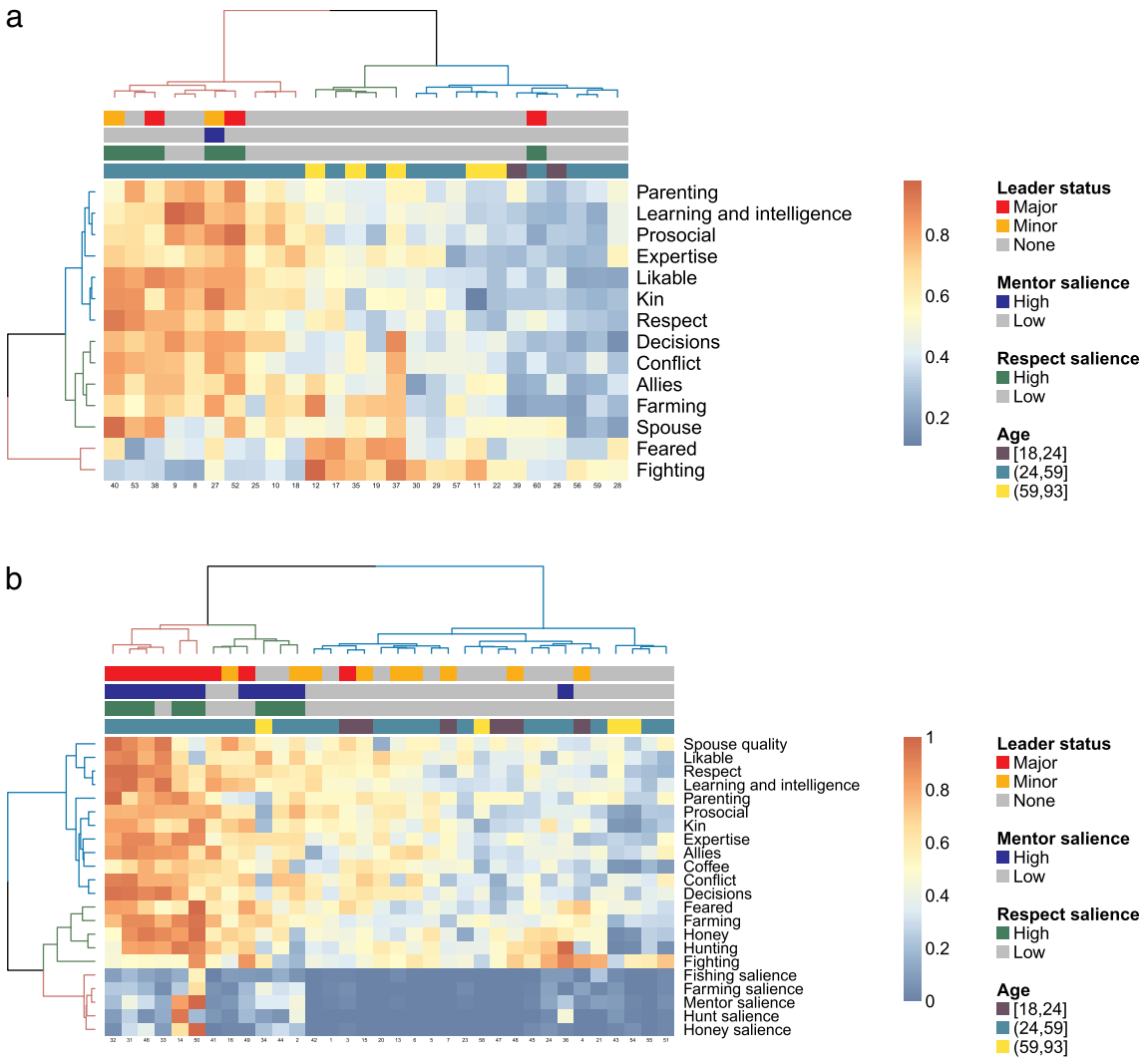

Fig. 3. Cluster analysis of peer-rated leadership traits. A. Female participant ratings. B. Male participant ratings. Colors in each cell represent the mean peer rating of each participant (columns) on each trait (rows). Columns are annotated with each participant's leadership status, mentor salience (above or below average), and age. Distance between row vectors computed with 1 − 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.)

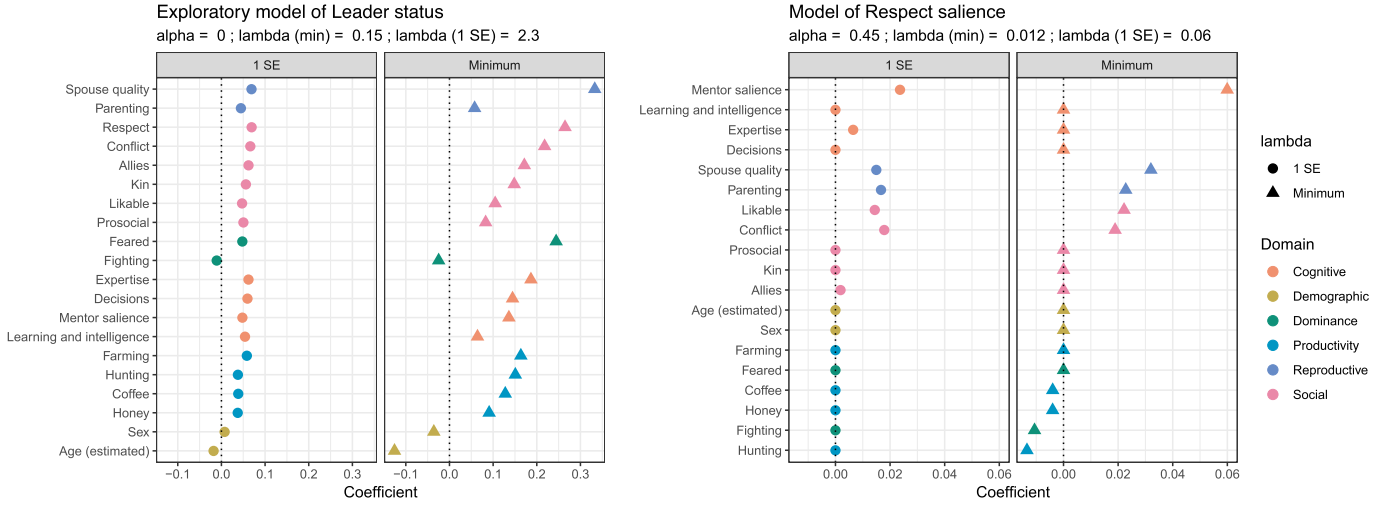

Fig. 4. Elastic net regressions. A. Leader status as a function of all peer-rated variables controlling for age and sex. Coefficients are log odds. B: Respect salience score as a function of peer-rated variables (excluding Respect) controlling for age and sex. Coefficients are standard linear regression 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.

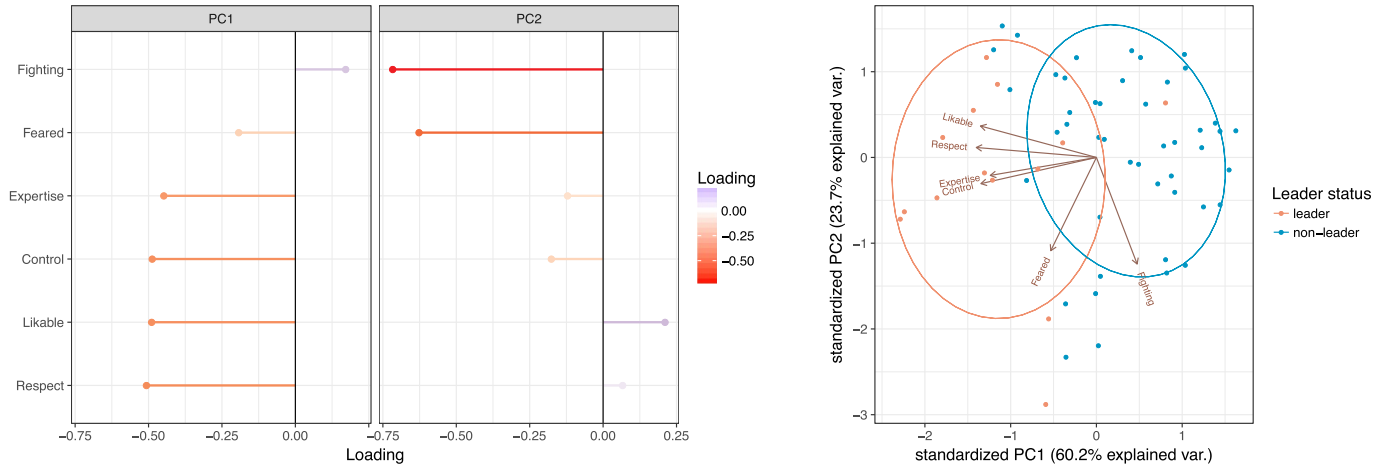

Fig. 5. Variable loadings (left) and biplot (right) of a PCA of the prestige and dominance variables. Variables were centered and scaled by one standard deviation. Each point in the biplot is one participant.

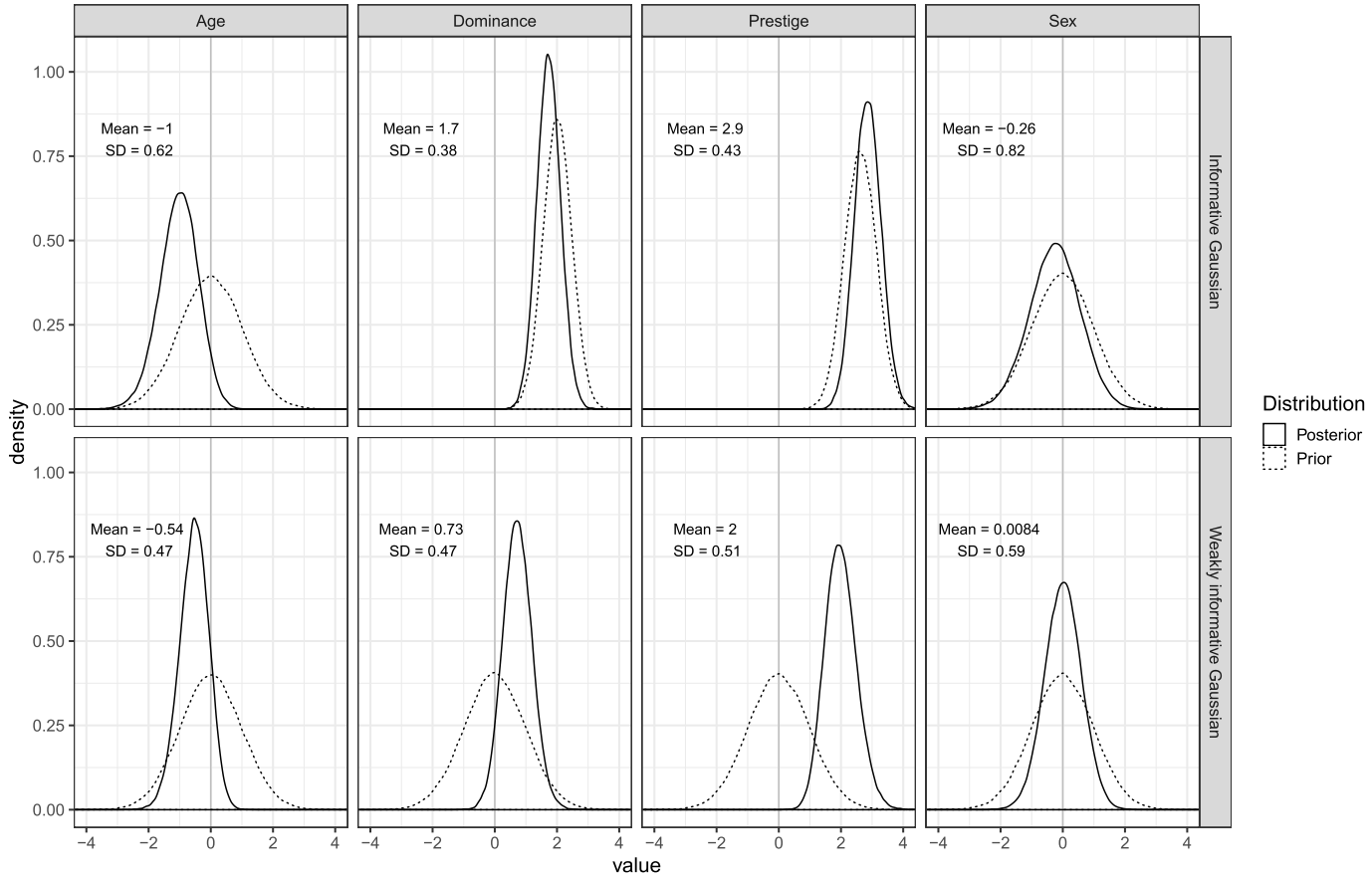

Fig. 6. Posterior distributions (solid lines) under two different sets of prior distributions (dotted lines). All variables were centered and scaled by one standard deviation. Coefficient distributions are log odds.

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 $\hat{R} > 1.000$, 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 freelisted 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 pvclust 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 − *cor*. Clusters agglomerated with the Ward algorithm.

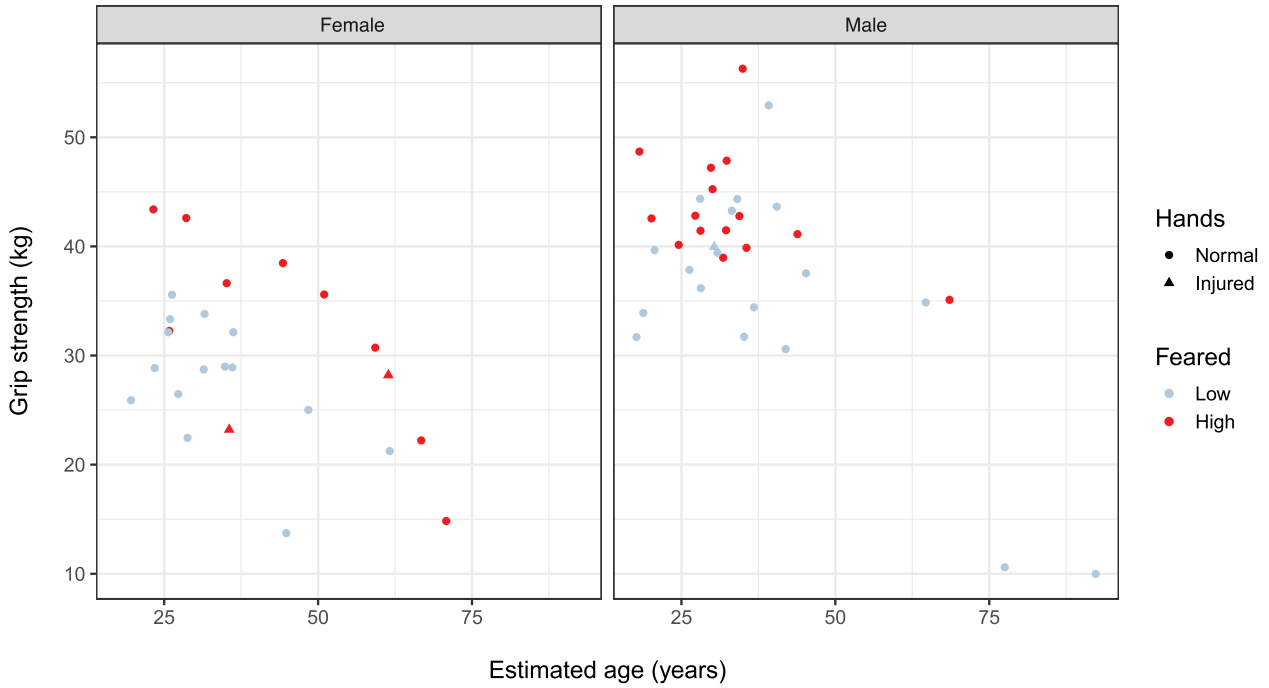

Fig. 8. Feared (greater or less than the mean) vs. age and grip strength, by sex. Three individuals had injuries to their right hands and were therefore tested using their left hands only. A small amount of jitter was added to distinguish overlapping points.

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, & Stieglitz, 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 freelisting 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 Stieglitz (2014). Our *Fighting* variable is based on peer-rated propensity for verbal *and* physical fighting, however, whereas Von Rueden, Gurven, Kaplan, and Stieglitz (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; Knauft 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, & Stieglitz, 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 preditors were endogenous, imperfectly operationalized, and imperfectly meaured. 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, & Stieglitz, 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 colinearity 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.

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Appendix A. Supplementary data

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

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