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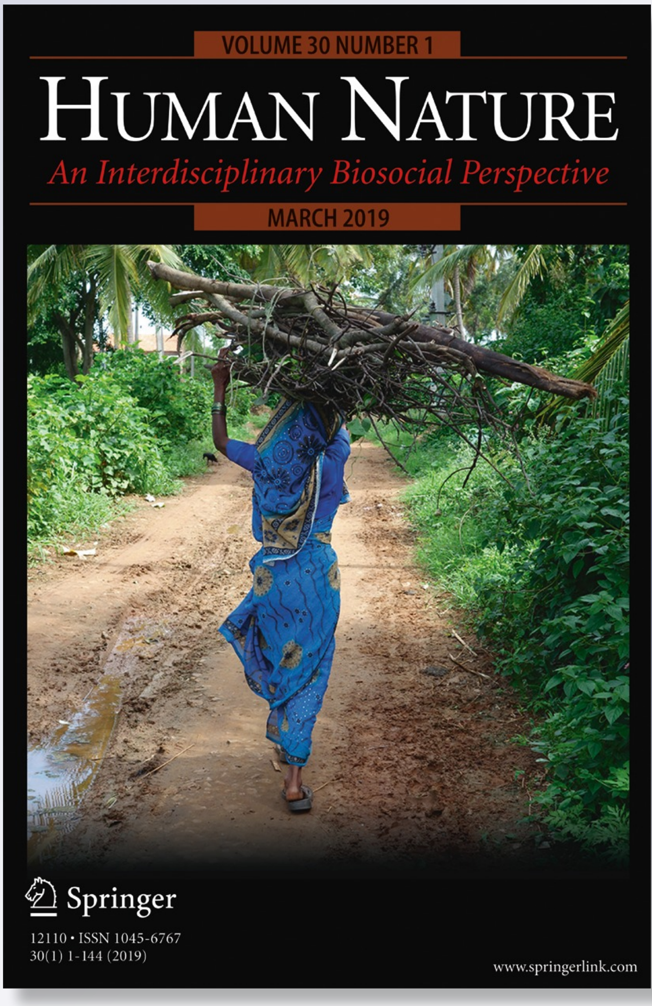

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Evolutionary Models of Leadership

Tests and Synthesis

Zachary H. Garfield[1] · Robert L. Hubbard[1] · Edward H. Hagen[1]

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Abstract
This study tested four theoretical models of leadership with data from the ethnographic record. The first was a game-theoretical model of leadership in collective actions, in which followers prefer and reward a leader who monitors and sanctions free-riders as group size increases. The second was the dominance model, in which dominant leaders threaten followers with physical or social harm. The third, the prestige model, suggests leaders with valued skills and expertise are chosen by followers who strive to emulate them. The fourth proposes that in small-scale, kin-based societies, men with high neural capital are best able to achieve and maintain positions of social influence (e.g., as headmen) and thereby often become polygynous and have more offspring than other men, which positively selects for greater neural capital. Using multiple search strategies we identified more than 1000 texts relevant to leadership in the Probability Sample of 60 cultures from the Human Relations Area Files (HRAF). We operationalized the model with variables and then coded all retrieved text records on the presence or absence of evidence for each of these 24 variables. We found mixed support for the collective action model, broad support for components of the prestige leadership style and the importance of neural capital and polygyny among leaders, but more limited support for the dominance leadership style. We found little evidence, however, of emulation of, or prestige-biased learning toward, leaders. We found that improving collective actions, having expertise, providing counsel, and being respected, having high neural capital, and being polygynous are common properties of leaders, which warrants a synthesis of the collective action, prestige, and neural capital and reproductive skew models. We sketch one such synthesis involving high-quality decision-making and other computational services.

Keywords Leadership · Prestige · Dominance · Collective action · Neural capital · Cross-cultural

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Leadership is ubiquitous across human societies (Brown 1991; Lewis 1974; Van Vugt 2006), and in the absence of clear leadership situational leaders quickly emerge (Campbell et al. 2002). Despite the evidence that leadership is a human universal, there is no unified theory of leadership. For more than a century, social scientists, economists, biologists, corporate researchers, and political scientists have contributed to a diverse body of literature on leadership, each with a unique perspective and unique goals (Bass and Stogdill 1990). More recently, however, scholars from a range of disciplines have adopted evolutionary theory to help unify findings on leadership (Cheng et al. 2014; Smith et al. 2016).

There is increasing interdisciplinary consensus on the distinction between the closely related concepts of high status/prestige, which is an individual's value based on subjective evaluations by the group, and influence/leadership, which involves objectively shaping the views or behaviors of others (Blader and Chen 2014; Kantner 2010). Von Rueden et al. (2014) define leaders as individuals who are accorded differential influence within a group over the establishment of goals, logistics of coordination, monitoring of effort, and reward and punishment. Van Vugt et al. (2008) suggest the functions of leadership are to motivate individuals to contribute to a shared goal and coordinating the execution of group goals.

From an evolutionary perspective, the phenomenon of leadership presents several problems. In most evolutionary models of behavior, agents evolve to maximize individual fitness and are often in conflict with other agents. Cooperation can evolve through a variety of mechanisms (Nowak 2006) but is most commonly thought to emerge if the agents are close genetic relatives (Hames 2015) or engage in reciprocal altruism (Kurzban et al. 2015). In most human societies, however, most individuals appear to surrender some autonomy to another individual—a leader—who is not necessarily a close genetic relative or exchange partner. If there are adaptations for leadership and for followership, then, over human evolution, the average fitness benefits of assuming the leadership role must have exceeded the average fitness costs, and the average fitness benefits of assuming the follower role must also have exceeded the fitness costs. The challenge, then, is to identify the fitness benefits and costs of both leadership and followership.

The Ethnography of Leadership

Evolutionary theories of leadership often draw inspiration from the ethnographic record. Many anthropologists have noted that in the small, kin-based societies that are often argued to be the best models of ancestral societies, leaders commonly gain influence through some combination of (1) physical threats and intimidation, (2) respect for special skills and abilities, and (3) generosity, resource distribution, and indebtedness (Cohen and Middleton 1967; Hoebel 1954; Kracke 1978). Moreover, leadership is more often achieved than ascribed (Kantner 2010; Smith et al. 2016), in contrast to more complex societies, in which ascribed leadership roles are more important (Earle 1997; Linton 1936).

Both ascribed and achieved statuses are probably important in all societies, however (Wiessner 2010).

Mead (1935), the first to define leaders in small-scale societies as "big men," noted the dual role of aggression and intimidation coupled with respect and admiration. Mead found that the horticultural Melanesian Arapesh had little organized leadership. Nevertheless, especially violent men were feared and had a profound influence on the community. Complex ceremonial life, on the other hand, required skilled leadership by the most capable and respected men (Mead 1935). Sahlins (1963) further elaborated on Melanesian big men, describing ascendancy to the social role as result of a series of political maneuverings and competitive displays in culturally valued skills.

Some leaders in foraging populations also rely on aggression, fear, and skill. Powerful Ona shamans in Tierra del Fuego, for example, though without formal positions of leadership, asserted authority using threats of ritual attack and occasional displays of severe physical aggression (Gusinde and Schütze 1937). Among the Tagemiut Eskimos of the Alaskan coast, sea mammal hunts were led by an *umialik*, a skilled and knowledgeable boat owner (Spencer 1959). Successful *umialit* continually competed with other contending leaders by demonstrating competence in hunting, generosity, intelligence, and good decision-making (cited in Lewis 1974; Pospisil 1964).

Some studies of hunter-gatherers call into question the importance, or even existence, of leaders. Among the! Kung, for instance, individuals in the formal headmen role primarily coordinated access to important resources, were expected to be generous, rarely competed to achieve or maintain influence, and avoided any perception they profited from their role. Yet they were often too young, old, or weak to offer generalized leadership, such as mediating disputes and providing counsel. Instead, these responsibilities fell to individuals with desirable personal qualities including exceptional intelligence, force, skill in hunting, social skills, and strong moral character (Marshall 1960). Among the Comanche, great importance was placed on individual freedom, yet leadership emerged during large-scale hunts and in warfare (Hoebel 1954). Even in the most egalitarian societies, however, such as Congo Basin foragers where individual autonomy is highly valued, the advice of elders and other respected individuals is given extra weight (Moïse 2014).

Another consistent ethnographic finding is the positive relationship between male social status and increased reproductive success (Gurven and von Rueden 2006; Smith 2004; von Rueden and Jaeggi 2016; von Rueden et al. 2010).

Comparative Studies of Leadership

Leadership behavior is common across many nonhuman animal species (Dyer et al. 2009). Smith et al. (2016), for example, systematically compared eight nonhuman mammalian species and eight small-scale societies in four domains of leadership: movement, food acquisition, conflict resolution, and between-group interaction. Each leadership domain was evaluated along five dimensions: distribution, emergence, power, benefits, and generality.

Smith et al. (2016) identified some commonalities in human and nonhuman leadership, including that leadership is largely achieved rather than inherited, and the fitness benefits of being a leader are typically similar to the fitness benefits of being a follower. In within-group conflict resolution and between-group interactions, power tends to be concentrated in a few individuals, whereas it is more diffuse in other domains, such as movement. One difference is that in humans, food acquisition is more often a group activity involving leaders, but in animals it is usually an individual activity without leaders. Another difference is that human leaders tend to lead in only one domain (e.g., conflict resolution) but nonhuman leaders typically lead in multiple domains. The Smith et al. (2016) study offers important insights but is limited by the small sample of human and nonhuman societies and their subjective ratings.

Evolutionary Theories of Leadership

The consistency with which ethnographers characterize leadership in small-scale human societies, and its parallels to patterns of leadership in nonhuman species, has inspired development of multiple evolutionary theoretical models of leadership (von Rueden and Van Vugt 2015).

One group of theories seeks the roots of at least some aspects of human social status and leadership, including the reproductive skew of high-status men, in the dominance hierarchies of our primate relatives (e.g., Barkow 1989; Chapais 2015; Hamstra 2014; Henrich and Gil-White 2001; Sapolsky 2005; Tiger 1970; Tiger and Fox 1971). A second group of theories proposes that leaders help solve problems that impede the evolution of collective actions, such as coordination and free-riding (e.g., Gavrilets and Fortunato 2014; Gavrilets et al. 2016; Glowacki and von Rueden 2015; Hooper et al. 2010; Price and Van Vugt 2014; Tooby et al. 2006; Van Vugt and Kurzban 2007). A third group of theories links prestige and leadership to gene-culture coevolution, with prestige and leadership roles related to cultural mastery and, in some theories, reproductive success (e.g., Barkow 1989; Henrich and Gil-White 2001; Henrich et al. 2015; Neel 1980; Richerson and Henrich 2012; Richerson et al. 2016). The preceding theories tend to emphasize universal components of leadership, whereas a fourth group of theories attempts to explain cross-cultural variation in leadership and hierarchy in reference to socioecological variation (e.g., Johnson and Earle 1987; Kaplan et al. 2009; Mattison et al. 2016; Price 1995; Price and Feinman 2010).

Study Goals

Most evolutionary models of leadership have been formulated and tested using data from only a few different cultures. Here we evaluate evolutionary models of leadership using ethnographic evidence from 58 traditional societies that vary substantially in levels of social complexity and subsistence strategy.

Testing a theory involves systematically evaluating its predictions with empirical evidence. It would be impractical to test every evolutionary theory of leadership. We therefore focused on four theories that highlighted elements of leadership that are common across many evolutionary theories of leadership yet made specific predictions that we could evaluate using existing ethnographic records. These were (1) the Hooper et al. (2010) theory of leadership in collective actions, which is based on a game-theoretical model and included elements, such as punishing free-riders, that appear in several similar theories; (2) the dominance model (Cheng et al. 2013; Henrich and Gil-White 2001), which emphasizes physical formidability, a key factor in primate dominance hierarchies; (3) the prestige model, which emphasizes cultural mastery and respect (Cheng et al. 2013; Henrich and Gil-White 2001); and (4) Neel's (1980) neural capital and reproductive skew model, which emphasizes the reproductive success of intelligent, knowledgeable leaders in small-scale societies.

Because these models purport to explain the evolution of the universal phenomenon of leadership, a model would be well supported if its key features are widespread in the ethnographic record and would lack support otherwise.

Hooper et al.'s Collective Action Model of Leadership

Hooper et al. (2010) provide a game-theoretical model that includes key components from the extensive theoretical literature on the emergence of leadership in collective actions (CA) (e.g., Gavrilets and Fortunato 2014; Gavrilets et al. 2016; Glowacki and von Rueden 2015; Price and Van Vugt 2014; Tooby et al. 2006; Van Vugt and Kurzban 2007). Within groups, willing individuals compete by offering a "tax rate"—the price they will charge the group for assuming the leadership role. The individual offering the lowest tax rate is chosen as leader. The leader then reduces the payoff of defectors in the CA, at a personal cost. Hooper et al. demonstrate that in certain conditions effective leadership can minimize the risk of failure in CA due to free-riding or inadequate organization. Their results suggest autonomous individuals will prefer having a leader and will voluntarily allow leaders to receive a share of returns rather than pursue collective activities in the absence of clear leadership. This trade-off is related to group size. In larger groups when there are high returns from cooperation and leaderless cooperation becomes problematic, a leadership role is an optimal solution for efficient CA. In the presence of a leader, individuals do not have to pay the cost of monitoring free-riders and are more motivated to contribute to a collective good. Although Hooper et al. (2010) do not discuss sex differences, since sanctioning free-riders might involve physical punishment, this model arguably implies that leaders would usually be men (the physically more formidable sex).

Under this CA model, leadership emerges in response to increasing group size, and leaders will increase performance in cooperative activities, sanction free-riders as necessary, are usually male, and receive a payoff from leadership services.

The Dominance Model of Leadership

Several theorists have argued that dominance-style leadership based on fear and aggression is homologous to high rank in nonhuman primate dominance hierarchies (Barkow 1989; Henrich and Gil-White 2001; Tiger and Fox 1971). Tiger and Fox (1971) were among the first to propose that human societies could be best understood in light of our primate heritage, specifically a heritage involving male dominance hierarchies that regulated access to fertile females and resources (see also Tiger 1970). Such dominance hierarchies have solid theoretical foundations in evolutionary game theory (Drews 1993; Maynard Smith and Parker 1976) and are associated with reproductive skew (Johnstone 2000; Vehrencamp 1983).

Tiger and Fox viewed human politics as a "breeding system" (1971:25). Leaders are dominant and, typically, older males who command "attention," a construct they borrow from a primatologist (Chance 1967), and who control the distribution of resources in the group. Barkow (1989) and Henrich and Gil-White (2001) similarly agreed that, like alpha males among nonhuman primates, dominant human leaders use force and intimidation to influence others.

Under the dominance model, leaders will be feared and have superior fighting ability, have a dominant personality and a reputation that promotes submission, be male, and have or strive for coercive authority over followers.

The Prestige Model of Leadership

In contrast to the relatively clear analogy, and perhaps homology, of human use of force and intimidation to dominance hierarchies in nonhuman animals, the evolution of status and leadership based on respect and persuasion is a conundrum.

According to Barkow (1989; Barkow et al. 1975), prestige is exapted dominance. Because paternal investment in offspring is high in humans, men competed to acquire the skills and knowledge (i.e., prestige) that would increase their ability to provision, and therefore be attractive to, women. Across diverse populations, men who are socially identified as having high prestige have greater reproductive success (Gurven and von Rueden 2006; Van Vugt 2006; von Rueden and Jaeggi 2016).

Henrich and Gil-White (2001) agree with Barkow that prestige is a human innovation that is closely related to symbolic culture and the acquisition of important skills. They disagree with Barkow, however, that prestige is exapted dominance based on sexual selection: why should men defer to other men who are skilled at providing resources to women? Henrich and Gil-White (2001) instead suggest that prestige processes are the result of psychological adaptations favoring enhanced cultural transmission. Because of variation in levels of skill in learned behaviors, individuals benefit by identifying the most skilled and emulating them. To better emulate the skilled, individuals must increase their proximity to them, and they do this by freely conferring their deference and prestige. Henrich and Gil-White (2001) suggest that younger individuals should emulate older individuals of the same sex, so prestige processes should operate in both sexes. The Henrich and Gil-White (2001) model, however, does not directly explain the well-documented mating success of prestigious men (e.g., von Rueden and Jaeggi 2016).

Because the Henrich and Gil-White (2001) model has been much more influential than the Barkow (1989) model, we chose to test the former (but the Neel model, discussed below, overlaps with both, and our data therefore will provide some insight into the Barkow model).

Under the prestige model, leaders will be respected and likable, have expertise, provide counsel to followers, be preferentially emulated, be male and female, and be expected to produce positive outcomes for followers.

The Relationship between Dominance and Prestige

Tiger and Fox (1971), Barkow (1989), and Henrich and Gil-White (2001) agree that dominance and prestige are both important in human societies, a view with a long history in anthropology (Kracke 1978), and one which appears in other disciplines, such as sociology. Weber (1978) distinguished coercive power (influencing others without their consent) from authoritative power (influencing others with their consent), for example, and identified charismatic authority, which is similar to prestigious-style leadership, as one of three types of legitimate exercise of power. Dominance and prestige-based strategies are not mutually exclusive or specific to individuals, but personalities, cultural values, and/or ecological settings might predispose societies to having prestigious or dominant leaders (Boehm 1993; Henrich and Gil-White 2001; Laustsen and Petersen 2017; Price and Van Vugt 2014; Spisak et al. 2012).

Some argue that dominance and prestige styles of leadership are behaviorally and cognitively distinct (Cheng et al. 2010, 2013; Henrich and Gil-White 2001). Chapais (2015), however, takes issue with that claim. Chapais (2015) points to many aspects of prestige that have homologues in nonhuman primates, especially the prosocial strategies, such as grooming and food sharing, that chimpanzees and other primates use to build coalitions and alliances, which would be homologous to the generosity and prosociality of prestigious leaders; the social competence necessary to use these alliances to maintain and increase rank, which would be homologous to the competence of experts; and the attraction of lower-rank individuals to higher-rank individuals, which would be homologous to the attraction of neophytes to experts. Among the Tsimane' forager-horticulturalists, von Rueden et al. (2014) found that elected and task-group leaders scored higher than nonleaders on measures of physical dominance, knowledge, trustworthiness, generosity, and number of adult kin, suggesting both dominance and prestige are integral to leader emergence and effectiveness in this small-scale society.

We treat dominance and prestige as separate models in order to determine the degree of theoretical overlap from the ethnographic record.

Neel's Neural Capital and Reproductive Skew Model of Leadership

Most contemporary discussions of the positive association of social status and mating success highlight the strong selection on status *striving*—a male motivation to increase status (e.g., Grammer 1996; Gurven and von Rueden 2006; von Rueden and Jaeggi 2016; Wiessner 2002). James Neel, a major figure in twentieth-century genetics and an early collaborator of Napoleon Chagnon, instead emphasized the strong sexual selection on leadership *qualities* (Chagnon 1988; Neel 1980; Neel et al. 1964), a point acknowledged by later scholars (e.g., von Rueden and Jaeggi 2016). Neel suggested that although physical abilities were important, *mental agility* was the most important quality predisposing an individual to leadership. Neel discussed a hypothetical quantity that "some will be tempted to equate to intelligence" (1980:285). But because he did not want to be "ensnared" by the word "intelligence," he termed it the Index of Innate Ability (IIA). Neel's discussion of leadership qualities and the IIA closely resemble the concept of embodied capital that is gaining currency in human behavioral ecology (e.g., Kaplan et al. 1995, 2000, 2003a, b). Embodied capital is organized somatic tissues and abilities, such as muscles, digestive organs, the immune system, skills, and knowledge. Kaplan and colleagues term the dimensions of embodied capital that are related to the brain, such as cognitive abilities and knowledge, *neural capital* (Kaplan et al. 2003a). If sexual selection favoring leaders with high neural capital characterized much of human evolution, it could explain encephalization in *Homo* (Neel 1980; Neel and Salzano 1967; Neel et al. 1964).[1]

Neel's theory is consistent with other theories and evidence connecting various measures of intelligence and cognitive skills with leadership (Boehm 2008; Fried 1967; Judge et al. 2004; Kaplan et al. 2000; Price and Van Vugt 2014; Roscoe 2007; Service 1964; Van Vugt and Kurzban 2007; Wilson et al. 1996) and is one of a variety of "social" intelligence hypotheses (e.g., Alexander 1990; Byrne and Whiten 1989; Flinn et al. 2005). It differs from most of them in that it emphasizes achievement of leadership roles based on skills and knowledge, rather than political machinations.

Neel's theory also differs from Miller's (1999) sexual selection theory for the evolution of intelligence. In Miller's theory, and unlike Neel's, there is selection for displays of cognitive abilities mainly to the extent that these serve as indicators of fitness to the opposite sex.

Although Neel's theory emphasizes mastery of culturally transmitted knowledge and skills, it differs from Henrich and Gil-White's (2001) theory because Neel also emphasized the connection with polygyny and male reproductive skew, which plays little direct role in Henrich and Gil-White's (2001) but has parallels with Barkow's (1989) sexual selection model of prestige. In Neel's theory, however, there is selection for neural capital because it helps men achieve leadership roles, not because it increases men's ability to provision women per se.

Under Neel's neural capital and reproductive skew model of leadership, leaders will be intelligent, knowledgeable men, will be polygynous, and will have greater mating opportunities, higher-quality mates, and larger families relative to nonleaders (Neel 1970, 1980; Neel and Salzano 1967; Neel and Sang 1994).

Theoretical Overlap in Models under Evaluation

The four theoretical models are not mutually exclusive but are nevertheless distinct. Each is uniquely vulnerable to a lack of evidence for key predictions. For example, the prestige and neural capital and reproductive skew models both emphasize knowledge and skill, but only the latter would be weakened by lack of evidence for reproductive success. The Hooper et al. (2010) model would not be weakened by lack of evidence of leader reproductive skew, skills, knowledge or dominance but, unlike the other models, would be weakened if there were no evidence for sanctioning free-riders (for example). The dominance model would be weakened by lack of evidence for fear and aggression, unlike the other models.

[1] In various publications Neel uses the term "eugenic." In her obituary of Neel, historian Susan Lindee (2001:504) writes: "Neel wanted to understand the forces driving human evolution, in order to assess how those forces had changed. This was in some ways a classic 'eugenics' question, as Neel recognized, justified by concerns that higher mutation rates and reduced selection pressure could lead to an overall decline in the fitness of the human gene pool. . . . He had a eugenic agenda, if eugenics is understood as the effort to promote policies and practices that preserve the health of the human gene pool. Yet most of his eugenic proposals, such as widespread access to prenatal testing and genetic counseling, would no longer be considered 'eugenic' primarily because they have been re-framed as benefiting individuals, rather than the state or the species."

Methods

We evaluated the cross-cultural support for these four theoretical models using the electronic Human Relations Area Files (eHRAF). The eHRAF is a digitized subset of the HRAF, a large database of ethnographic documents from nearly 400 cultures. Some of the documents are complete texts of ethnographies, such as *Yanomamo* and *Veiled Sentiments*; others are journal articles, and still others are diaries and personal journals. We restricted data collection to the 60-culture Probability Sample Files (PSF) subset of the eHRAF. The PSF is a stratified random sample that includes one randomly selected culture from 60 geographically diverse areas (Naroll 1967).

The eHRAF can be searched by keyword and also by codes from the Outline of Cultural Materials (OCM) (Murdock et al. 2008). The OCM is a hierarchically organized set of more than 700 topics, such as "status role and prestige," "social stratification," and "mortality," each of which is assigned a numeric code. Each paragraph in the eHRAF that discusses a topic in the OCM is assigned the code for that topic. Most paragraphs are assigned multiple codes. This allows researchers to find paragraphs relevant to, for example, prestige, even if they do not contain a keyword such as "prestige" or "prestigious."

We searched the PSF subset of the eHRAF using 16 OCM codes and seven keywords relevant to leadership for both men and women.[2] This search returned 14,081 paragraphs. Because many of the OCM topics were fairly general (e.g., "social stratification"), most of the paragraphs did not contain information specific to leadership. We therefore reviewed each paragraph for information specific to leadership, which, following von Rueden et al. (2014) and Van Vugt (2006), we defined as individuals occupying a special position in the decision-making hierarchy and who have disproportionate influence over group goals and decisions. After review, we determined that 1212 paragraphs (henceforth *text records*) from 321 documents contained information relevant to leadership.

We analyzed the text records in three interrelated ways: (1) by computing word frequencies of each text record, (2) by having two independent coders read and code each text record on a series of variables that operationalized our four theories, and (3) using data on each culture, such as mode of subsistence.

Term-Document Matrix

Word frequencies encode a surprising amount of the semantic information in a document (Landauer and Dumais 1997; Turney and Pantel 2010). We therefore computed the frequencies of all "informative" words in each text record by removing all punctuation and English stop words (uninformative words such as *the, is, at*), stemming the remaining words (reducing inflections such as plurals and past tenses to the root, or stem, words), and then generating a term-document matrix, in which the columns were all the unique word stems (terms), rows were the text records (documents), and the values in each cell were the frequencies of each word stem in each text record (most

[2] eHRAF search query: ((Cultures = (Any Culture)) AND (((Subjects = ('157' OR '554' OR '555' OR '557' OR '558' OR '571' OR '573' OR '578' OR '622' OR '626' OR '627' OR '628' OR '643' OR '665' OR '701' OR '851')) AND (Text = (leader* OR follower* OR headman OR headmen OR bigman OR bigmen OR chief)))))

values were 0; i.e., the matrix was sparse). These word frequencies, which were computed independently of our four theoretical models, provide a compact representation, literally in the ethnographers' own words, of the semantic content of each text record.

Operationalization of Coding Variables

We operationalized our four theoretical models of leadership using 24 variables.

The Hooper et al. (2010) CA model was operationalized with five variables: (1) the ability of leaders to increase performance in CA through supervision, (2) whether leaders receive a share of returns from CA, (3) whether leaders sanction free-riders, (4) if leadership emerges as a result of group size, and (5) if followers express preference for leaders in large but otherwise egalitarian cooperative groups.

The dominance model was operationalized with eight variables from the dominance-prestige scale (Cheng et al. 2010): whether the leader (1) asserts authority over followers, (2) is feared, (3) employs aggression, (4) is physically stronger than followers, (5) has a dominant or forceful personality, (6) has a reputation for dominance, (7) avoids dominance by others, and (8) is known for superior fighting ability.

The prestige model was operationalized with seven variables from the dominance-prestige scale (Cheng et al. 2010): whether leaders are (1) respected, (2) likable, (3) have expertise, (4) provide counsel, (5) are emulated, and (6) are expected to succeed. We added a measure of (7) family-level prestige, given the importance of kinship in traditional societies.

Neel's neural capital and reproductive skew model (Neel 1980; Neel and Salzano 1967) was operationalized with four variables: whether the leader (1) is described as intelligent or knowledgeable, (2) is polygynous, (3) has a bigger nuclear family relative to followers, and (4) has higher-quality mates than followers. These variables also apply to other sexual selection accounts of prestige (Barkow 1989; Tiger and Fox 1971).

All 1212 text records were coded on each of these 24 variables by two independent coders (ZG, RH). For each text record, a variable was coded as 1 if the text record had evidence for that variable, −1 if it had evidence against that variable, and 0 if there was no evidence either way. We also coded the sex of leaders in each text record as *male*, *female*, *both*, or *unknown*. Representative ethnographic paragraphs for each variable are available in the ESM (Table S3).

Interrater reliability was evaluated using statistics that equal 0 when agreement is that expected by chance and 1 when there is complete agreement. Across all cells, simple rater agreement was 94%; Cohen's $\kappa = 0.36$; Gwet's AC_1, which is the conditional probability that two raters will agree given that no agreement will occur by chance (Gwet 2014), was 0.94; and Bangdiwala's $B = 0.94$ (Munoz and Bangdiwala 1997). See the supplementary information for a discussion of the low κ value. To produce a consensus data set, all discrepancies between raters were jointly recoded to produce the final data matrix.

This coding process produced very little negative evidence for most model variables, with less than 1% (0.72%) of all coding equal to −1. In order to use logistic regression and other statistical methods that require variables to be dichotomous, we recoded the few −1 values as follows. For the nine variables in which the ratio of −1 values to +1 values was at least 10% or more, we created nine new complementary variables that equaled +1 precisely when the original variable equaled −1, and 0 otherwise. We then set −1 values in the original variables to 0. This produced three *anti-dominance model* variables, three *anti-prestige model* variables, and three *anti-collective action model* variables. To avoid creation of spurious "anti" variables with, e.g., a single non-zero value, all other −1 values, which were less than 1/10 of 1% (0.07%) of all coded values, and less than 10% (9.6%) of the original number of −1 s, were set to 0 (The text record ID numbers of these records are in Table S2, and the full text is available in Table S3).

After coding all text records on all variables, some text records had no evidence for any variable (all variables = 0). We eliminated these text records, resulting in a final data set of 1000 text records from 300 documents covering 58 cultures.

Table 1 displays the final variable operationalization with all 33 variables, along with counts of the dichotomous coding of 1 for evidence for and 0 for no evidence.

Model Scores

For each of the four theoretical models (collective action, dominance, prestige, and neural capital and reproductive skew) and the associated *anti* models (anti-collective action, anti-prestige, and anti-dominance) we computed a "score" indicating the level of support for each model. We computed a score for each individual text record and also for each culture. We illustrate this computation using the prestige model, which was operationalized by seven variables (see Table 1). The text record model score was the proportion of model variables scored as 1. For example, if, in a particular text record, there was evidence for 3 of the 7 variables of the prestige model, the prestige model score for that record would be 3/7 = 0.43.

We computed a similar score at the culture level. We illustrate this with the Akan culture, which had 33 records. Our data on the prestige model in the Akan culture therefore comprises a 33 × 7 matrix of 0s (no evidence) and 1s (evidence for), or a total of 231 data points. The model score was the proportion of these data points equal to 1. In this case, there were 37 1s, for a prestige model score of 37/231 = 0.16 in the Akan. Model scores were computed similarly for each model in each culture.

Statistical Analyses

A term-document matrix can be analyzed in a number of ways and allows for textual analysis of the raw ethnographic data, independent of variable operationalizations or researcher coding. To convey some of the semantic content of the text records as they related to the four theoretical models (but not to formally test any hypotheses), we estimated the association of word frequencies in each text record with each of the four model scores. Because we had thousands of unique word stems, we used lasso regression as a variable selection technique, which is especially useful when the number of predictors is much greater than the number of cases (i.e., $p >> n$) (Tibshirani 1996; Zou and Hastie 2005). Lasso regression has a penalty or shrinkage term, λ: larger values of λ retain more variables in the model, at the risk of over-fitting, whereas smaller values of λ decrease the number of predictors retained in the model, at the risk of under-fitting. The optimal value of λ can be estimated with cross-validation (Tibshirani 1996; Zou and Hastie 2005). We used the glmnet package (Friedman et al. 2010) to fit lasso regression models to determine which words best predicted each of

Table 1 Model variables, operational definitions, and counts of evidence for each variable.

Model	Variable	Operational definition	Evidence for (Count of 1s)	No evidence (Count of 0s)
Dominance	Aggression	The leader uses coercive control, aggression, or threats of violence.	41	959
	Assert authority	The leader asserts authority over unwilling others, or has power over followers.	140	860
	Avoid dominance	The leader actively avoids being controlled by others.	43	957
	Fear	The leader instills fear in followers.	42	958
	Fighting	The leader demonstrates or is known for superior fighting ability.	71	929
	Personality	The leader has a forceful or dominant personality.	24	976
	Reputation	The leader's reputation for dominant behavior leads followers to be submissive.	16	984
	Strong	The leader is seen as physically stronger than most followers.	18	982
Anti-dominance	Anti-aggression	The leader is unable, prevented from, or sanctioned for using or attempting to use coercive control, aggression, or threats of violence.	14	986
	Lacking coercive authority	The leader is unable to assert authority over unwilling others or have power over followers.	83	917
	Non-dominant personality	The leader has a personality that is not forceful or dominant.	23	977
Prestige	Counsel	The leader provides valued opinions or is sought out for counsel.	239	761
	Emulated	Followers emulate the leader.	18	984
	Expertise	The leader demonstrates expert knowledge or has unique talents and abilities.	265	735
	Family	The leader gains prestige or influence based on family level prestige.	116	884
	Followers expect success	Followers have an expectation of success of the leader.	56	944
	Likable	The leader is likable.	32	968
	Respected	The leader is respected, admired, or held in high esteem.	255	745
Anti-prestige	Lacking family-level prestige	The leader does not gain prestige or influence based on family level prestige.	12	988
	Unlikable	The leader is unlikable.	19	981
	Not respected	The leader is not respected, admired, or held in high esteem.	28	972

Table 1 (continued)

Model	Variable	Operational definition	Evidence for (Count of 1s)	No evidence (Count of 0s)
Neural capital & reproductive skew	Better mates	The leader has higher quality mates relative to followers.	12	988
	Big family	The leader has a larger (nuclear) family size relative to followers.	16	984
	Intelligent or knowledgeable	The leader has high intelligence, above average knowledge, or high cognitive abilities.	143	857
	Polygynous	The leader is polygynous.	78	922
Collective action	Cooperative activities	Followers prefer a leader in large, otherwise egalitarian, groups during cooperative activities.	17	983
	Group size	Leadership emerges in response to group size in collective activities.	13	987
	Payoff	The leader receives a share of productivity from collective activities.	143	857
	Performance	The leader functions to increase performance and group coordination in collective action through supervision.	132	868
	Sanction free-riders	The leader sanctions against free-riding in collective activities.	16	984
Anti-collective action	Leaderless cooperation	Followers do not prefer a leader in large, egalitarian groups during cooperative activities.	2	998
	No sanctioning	The leader does not sanction against free-riding in collective activities.	3	997
	Egalitarian large group	Leadership is absent among large cooperative groups.	4	996

See the ESM (Table 3) for example ethnographic paragraphs for each variable our four model scores for each text record. Because the model scores were counts, we used Poisson errors.

We analyze data from our researcher-coded operationalized variables at the text record level and at the culture level. Our first test was simply to assess the proportion of text records and cultures that had evidence for each of our theoretical variables. At the text record level, hierarchical cluster analysis was then used to identify natural groupings of all our coded variables. If variables from a model clustered together, and separately from the other variables, that would lend support to the theoretical cohesiveness of that model. If, on the other hand, variables from different models clustered together, that would suggest theoretical models may need revision or that clusters had identified components of a novel theoretical model.

At the culture level, we investigated whether support for each theory of leadership varied by important anthropological dimensions of culture, such as mode of subsistence, region, and levels of complexity. The eHRAF categorizes each culture on subsistence type. We slightly modified the eHRAF subsistence typology by collapsing "hunter-gatherers" and "primarily hunter-gatherers" into a single category, "hunter-gatherers," and by collapsing "agro-pastoralists" and "pastoralists" into a single "pastoralists" category. We renamed the eHRAF's "Other" subsistence category, which is applied to societies with various combinations of hunting, fishing, gathering, pastoralism, and horticulture or intensive agriculture, as "mixed." This produced a subsistence classification with five groups: Hunter-gatherers, Pastoralists, Horticulturalists, Agriculturalists, and Mixed.

The eHRAF does not score or evaluate cultures on, for example, "complexity," or other theoretical variables. We therefore drew on a different database, the Standard Cross-Cultural Sample (SCCS; Murdock and White 1969), which scores 186 cultures on a large number of qualitative or quantitative variables, such as kinship system, levels of male aggression, and social stratification. Fifty of these cultures are the same as, or very similar to, cultures in the PSF. We added the "region" (Gray 2003) and the "cultural complexity score" (Murdock and Provost 1973) variables from the SCCS to our database of eHRAF text records.

At the culture level, generalized linear models were used to identify the degree to which mode of subsistence, region, and cultural complexity predicted the proportion of evidence for each theoretical model. A substantial effect of any of these variables on support for a model would suggest that the model was specific to, a particular region or level of complexity, for example, and therefore not a cross-cultural universal.

We would judge a theoretical leadership model to be well-supported if there was evidence for each of its variables in a wide range of cultures, these variables clustered together but separately from those of other models, and if support did not depend strongly on culture-level variables such as region or complexity. We caution that a lack of ethnographic support for a variable or model does not *necessarily* imply the model is false; instead, lack of support might indicate, for example, a lack of interest on the part of ethnographers. Thus, the contribution of our study is to assess the extent to which key features of each model are supported or unsupported by the ethnographic record as represented in the eHRAF.

All analyses were conducted with R version 3.3.3 (2017-03-06) (R Core Team 2016).

Results

The geographic distribution of the cultures in our sample is displayed in Fig. 1, with cultures labeled by mode of subsistence and represented by a symbol proportional to the number of documents that provide ethnographic texts for that culture (for details, see Table S1).

The 1000 text records from 300 unique documents describing 58 cultures were generally short, with a median word count of 148, a mean of 165, and standard deviation of 100.5. The vast majority of text records pertained to male leadership (89.8%, 898 text records) and very few pertained to female leadership (2.5%, 25 text records). In 7 instances (0.7%) text records pertain to both males and females, and in 69 text records (6.9%) sex was unknown.

Textual Analysis

After removing stop words and stemming, our term-document matrix had 9253 columns (terms) and 975 rows (text records). For each lasso regression model, we used tenfold cross-validation to choose the λ parameter that minimized deviance. We then plotted all the non-zero coefficients for each model. The most predictive words for each model epitomize the semantic content of the text records with high scores for that model. In some cases, these words have clear links to model operationalization, but in other cases they reveal new insights about the models. For example, "fear" is the best predictor of the dominance model score and it was one of the variables in the dominance model, but "war" is the second-best predictor, yet it was not a dominance model variable (Fig. 2).

Text Record Level Results

For each of the 33 coded theoretical variables, we computed the percentage of text records that provided support, estimating standard errors using a binomial generalized linear mixed effects model with a random intercept for author nested within culture. The most strongly supported variables were *respected*, *expertise*, and *counsel* from the prestige model; *assert authority* from the dominance model; *lack of coercion* from the

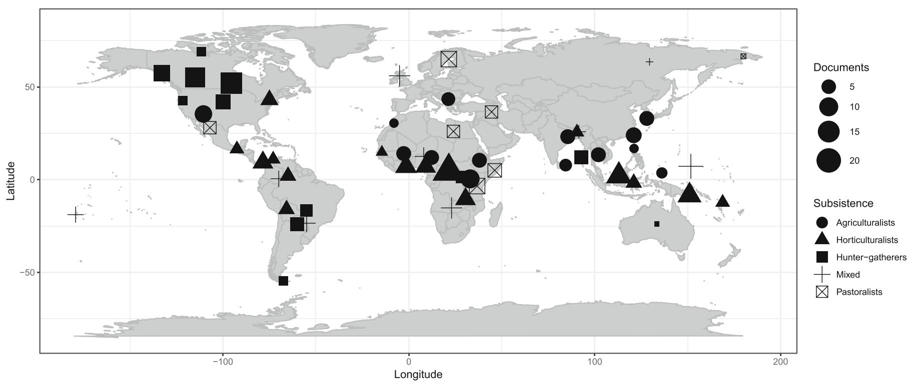

Fig. 1 Geographic distribution of cultures in the sample. Each symbol is one culture. The size of the symbols indicates the number of documents (not text records) describing that culture

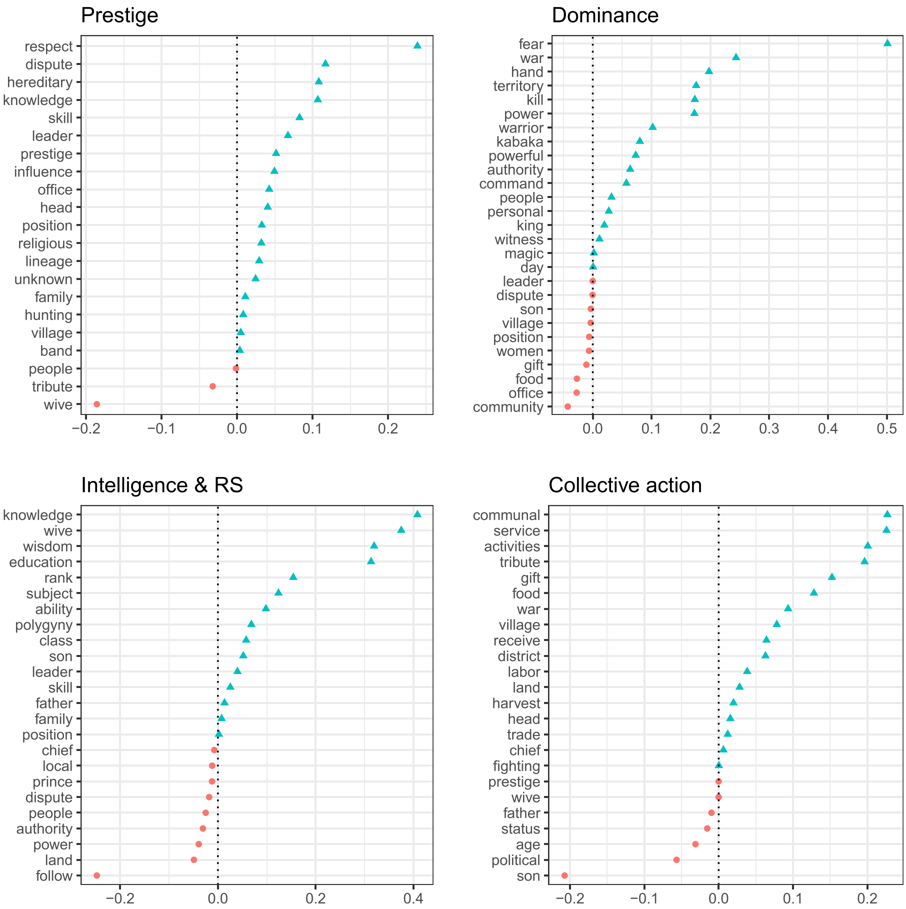

Fig. 2 Lasso Poisson regression coefficients, which indicate the words whose frequencies in each text record best predicted the model scores in each text record. Coefficients estimated with glmnet package using cross-validation to determine the optimal value of lambda (Friedman et al. 2010). Blue triangles are positive predictors; red circles are negative predictors

anti-dominance model; *performance* and *payoff* from the CA model; and *intelligent or knowledgeable* from the neural capital and reproductive skew model. See Fig. 3.

Figure 3 also illustrates variation in the text-level data of supporting evidence for each theoretical model. The prestige model was more strongly supported than the others. Among the anti-models, the anti-dominance model was most strongly supported. There was very little evidence supporting the anti-collective action model and no evidence against the neural capital and reproductive skew model, hence no associated anti-model.

Cluster Analysis of All Model Variables

We computed the distance between two variables as $1 - \mathrm{cor}\ (v_i,\ v_j)$ so the distance between highly correlated variables is close to 0, that between uncorrelated variables is close to 1, and that between anticorrelated variables

Fig. 3 Variable support, grouped by theoretical model. Green triangles represent the percent of text records with evidence for that variable. Blue squares represent the mean text record score for each model among female leaders only. Purple crosses represent the mean text record score for each model among all text records. Red circles represent the percent of cultures with at least 1 text record containing evidence for that variable. Bars are 95% confidence intervals. See text for details

is close to 2. We then used the pvclust package (Suzuki and Shimodaira 2006, 2015) to cluster the variables using the matrix of all pairwise distances and the Ward agglomeration algorithm. Hierarchical cluster analysis is sensitive to the choice of distance metric (here, correlation) and agglomeration algorithm (here, Ward agglomeration). Other choices of distance (e.g., Euclidean, Manhattan) and agglomeration (e.g., average, complete) would generate different clusters.

Figure 4 displays the dendrogram from this analysis, along with two estimates of significance for how strongly each cluster 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).

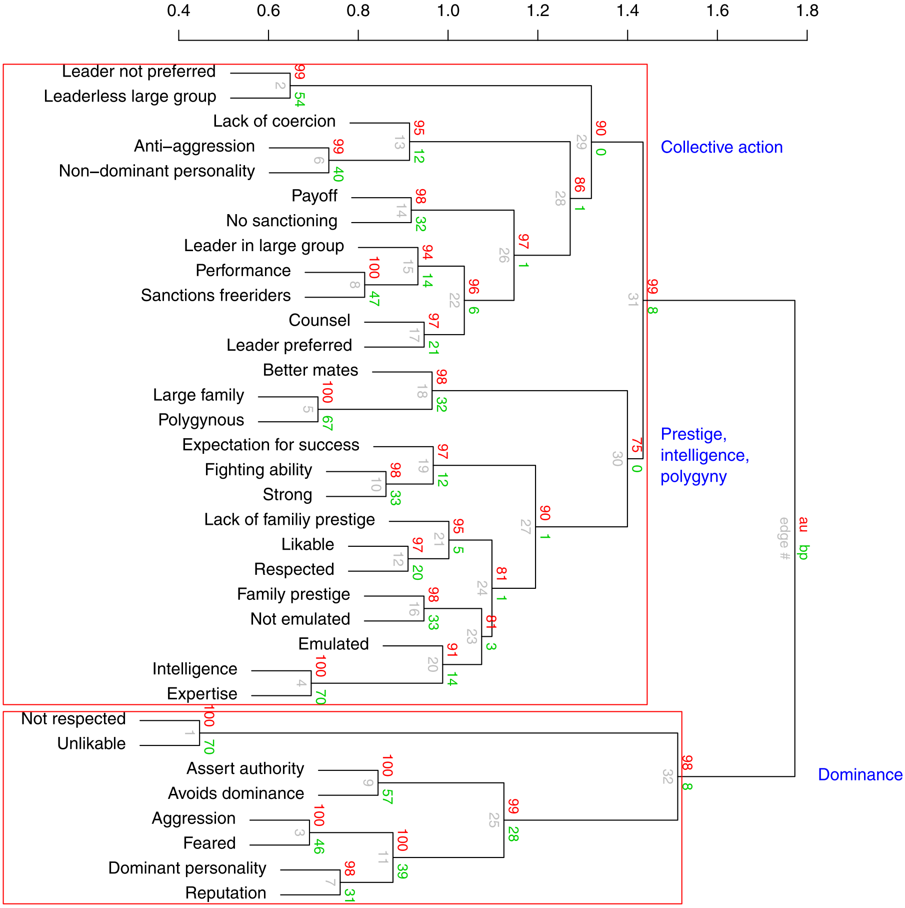

Fig. 4 Cluster analysis dendrogram of all theoretical variables. Red numbers are the approximately unbiased (au) p-values for each edge, and green numbers are the bootstrap probabilities (bp). Red rectangles demark the two top-level statistically significant clusters. For details, see Suzuki and Shimodaira (2006)

The analysis suggested two or three models of leadership rather than four. The top cluster had two main subclusters: one composed primarily of CA and anti-dominance model variables, similar to our Hooper et al. CA model, and the other combining most variables of the prestige model and neural capital and reproductive skew model. The bottom cluster contains six of seven dominance-model variables and two of three anti-prestige model variables, similar to our dominance model.

Culture-Level Results

To calculate the percentage of cultures that provided support for a particular theoretical variable, we deemed a culture to support a variable if at least one record from that culture supported that variable. We estimated standard errors using a cluster bootstrap. The most strongly supported variables, which were documented in more than 50% of cultures, were *respected*, *counsel*, *expertise*, and *family prestige* from the prestige model; *assert authority* and *fighting ability* from the dominance model; *lack of coercion* from the anti-dominance model; *payoff* and *performance* from the CA model; and, *intelligent or knowledgeable* from the neural capital and reproductive skew model. See Fig. 3.

We then fit four generalized linear models (GLM) with binomial errors and probit links to evaluate if the scores for our four models varied by region, complexity, or mode of subsistence. The Standard Cross-Cultural Sample (SCCS) (Murdock and Provost 1973) provided culture region and a quantitative index of cultural complexity, the eHRAF provided culture subsistence type, and the weights were the total cell counts for each theoretical model.

Model selection relying on AICc suggested *cultural complexity* be removed from all models (Table S5). Because *subsistence* was a significant predictor across all models, and *region* was significant in two models, we report models with *region* and *subsistence* as covariates. Tables 2 and S4 present ANOVAs and coefficients, respectively, of the four GLMs, and Figs. 5 and 6 plot all effects.

The dominance model score was predicted only by *subsistence*, with hunter-gatherers scoring lowest and horticulturalists highest. The prestige model score was predicted by both *subsistence* and *region*; hunter-gathers and pastoralists scored higher than other subsistence types, and African cultures scored lowest, with high scores from East Eurasian, South American, and Insular Pacific cultures. The neural capital and reproductive skew model was predicted by *subsistence*, with pastoralists scoring lower than other subsistence types. The CA model was predicted by *subsistence* and *region*, with higher scores in East Eurasian, Insular Pacific, and North American cultures; cultures with the *mixed* subsistence classification also score higher than others.

Discussion

Across cultures, leaders commonly enhanced performance in collective actions and received some sort of compensation (2/5 variables of the CA model); were nearly universally respected, had expertise, and provided counsel, and less frequently inherited prestige from their families (4/7 variables of the prestige model); were able to assert

Table 2 ANOVAs of the generalized linear regression models (binomial family, probit links) of the proportion of evidence for each theoretical model of leadership vs. region and subsistence type. For regression coefficients and summary statistics, see Table S4

Model	Term	LR.χ^2	df	p
Dominance	Region	9.6	5	0.087
	Subsistence	26.6	4	2.4e-05
Prestige	Region	27.2	5	5.2e-05
	Subsistence	24.2	4	7.2e-05
Neural capital & reproductive skew	Region	9.5	5	0.092
	Subsistence	19.7	4	0.00056
Collective action	Region	21.3	5	7e-04
	Subsistence	13	4	0.011

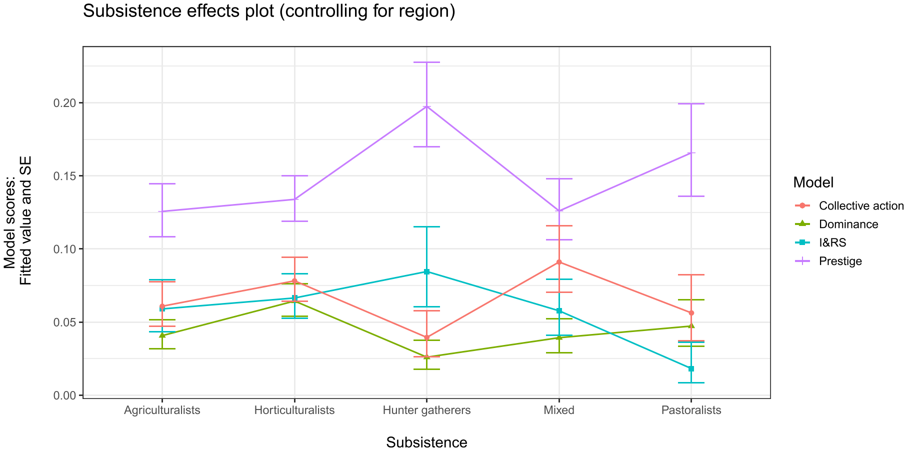

Fig. 5 The effects of subsistence on the scores of each of the four models of leadership (controlling for region). Each colored line represents one theoretical model. Bars are 95% CIs. Effects computed from the GLMs using the effects package (Fox 2003)

authority (1/8 variables of the dominance model) and, somewhat paradoxically, were *unable* to assert authority (1/3 variables of the anti-dominance model); and had high intelligence or knowledge (1/4 variables of the neural capital and reproductive skew model). See Fig. 3. In addition, 89.8% of the text records described male leaders, consistent with the CA, dominance, and neural capital and reproductive skew models, but not necessarily with the prestige model.

Thus, some aspects of each model were common across cultures, some aspects of each model were rare across cultures, and no single model adequately characterized all dimensions of leadership across all cultures. In addition, support for all models exhibited some statistically significant variation by mode of subsistence (Fig. 5), and

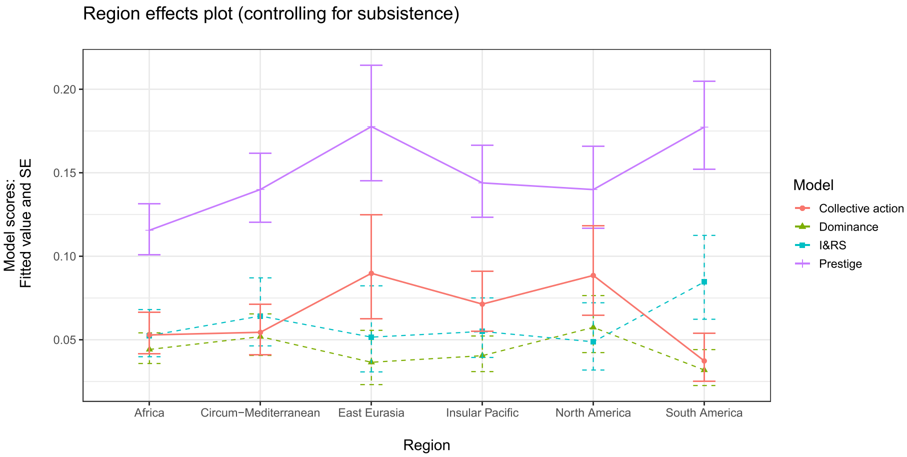

Fig. 6 The effects of region on the scores of each of the four models of leadership (controlling for subsistence). Each colored line represents one theoretical model. Bars are 95% CIs. Effects computed from the GLMs using the effects package (Fox 2003). Solid lines: significant effects. Dotted lines: non-significant effects

support for the prestige model and CA model exhibited some statistically significant variation by region (Fig. 6). However, the levels of variation by subsistence and region were generally small. Taken as a whole, each model captures some nearly universal aspect of leadership, at least as leadership is represented in the ethnographic record.

Collective Action Model

Terms that were positively associated with the CA model score included *communal*, *services*, *activities*, *tribute*, *gift*, and *food*, which align with the theoretical elements of collective actions. The negative predictors, such as *son*, *political*, and *status*, were much more enigmatic but hint at a distinction between leadership in communal collective actions vs. political leadership and prestige. See Fig. 2.

In support of the CA model, leaders often increased performance in collective activities, consistent with observational studies (Glowacki and von Rueden 2015), and were often rewarded for doing so. There was support for the CA model in all subsistence groups and regions, but with significant variation: support was somewhat higher in the Mixed subsistence category and somewhat lower in South America (Tables 2 and S4; Figs. 5 and 6). Cluster analysis revealed a close relationship between the CA model and the anti-dominance model (Fig. 4). This linkage is consistent with theories suggesting prosociality on the part of the leader is critical in motivating followers to contribute to collective goods and facilitating cooperation (Henrich et al. 2015). The strong overall male bias also supports the predicted male bias of the CA model, as does the fact that none of the 25 text records describing female leaders had any evidence for sanctioning free-riders.

Even among male leaders, however, our ethnographic data did not provide strong support for the sanctioning role of leaders in collective actions, and the female model score was about the same as the overall (mostly male) model score. See Fig. 3. This undermines many theories of leadership in which the central function of leaders is to avert a tragedy of the commons by punishing free-riders (Boyd and Richerson 1992; Frank 2003; Hooper et al. 2010; King et al. 2009; Kohler et al. 2012; Tooby et al. 2006). Our results are inconsistent with much experimental evidence documenting a willingness to support punishment of free-riders and the role of leaders in enforcing social norms in a variety of cooperative contexts (Fehr and Gächter 2000; Guala 2012; O'Gorman et al. 2009; Price et al. 2002; Van Lange et al. 2014). Systematic evidence from small-scale societies also promotes the role of leaders in sanctioning free-riders (Price 2003; Wiessner 2002).

Nevertheless, our data suggest a greater focus is warranted on theories of leadership in which punishment plays little or no role (e.g., Henrich et al. 2015; Kiyonari and Barclay 2008). One such theory was put forward by Gavrilets and Fortunato (2014, and consistent with Olson 1956): when there is a high level of between-group competition, and high-ranked individuals within groups receive a disproportionate share of group benefits, then high-ranked individuals will contribute more to the CA and tolerate rather than punish free-riders. We did not assess levels of between-group conflict, however, so we cannot directly test this model.

The Dominance Model

Terms that were positively associated with the dominance model score included *fear*, *war*, *hand*, *territory*, and *kill*. Although our coding scheme for dominance included *fear*, *aggression*, and *fighting ability* (Table 1), it did not specifically include warfare. This analysis therefore suggests that dominance-based leadership might be associated with warfare cross-culturally. Terms that were negatively associated included *community*, *office*, and *food*, which might distinguish this model from collective actions other than warfare. See Fig. 2.

The overall male bias in leadership supports the dominance model, and among the 25 instances of female leadership, there was no evidence for *aggression*, *fighting ability*, or *strong*.

Within the dominance model, the variable *asserts authority* had the most supporting evidence, and the variables *fighting ability*, *feared*, and *aggression* were also fairly well supported. Support for the other variables of this model, including physical strength (*strong*) and submission to reputation (*reputation*), however, was relatively low. See Fig. 3.

Richards (1940:106) describes the leadership style of Bemba chiefs and illustrates the dominance model:

> Much of [a chief's] power also rested in the old days on force. A chief practised savage mutilations on those who offended him, injured his interests, laughed at him or members of his family, or stole his wives. A number of these mutilated men and women still survive in Bemba country to-day. Command over the army and over the supply of guns also lay in the chief's hands and there is no doubt that the greatness of the Bena nandu rested to a large extent on fear. The people explain that the royal family were named after the crocodile because they are like crocodiles that seize hold of the common people and tear them to bits with their teeth.

The Prestige Model

Terms that were positively associated with the prestige model score included *respect*, *dispute* (which suggests dispute resolution is important for this style of leadership), *hereditary*, *knowledge*, and *skill*, most of which align with the theoretical components of prestige. Terms that were negatively associated included, interestingly, *wives* and *tribute*. See Fig. 2.

There was significantly greater evidence for the prestige model than for other models, and significantly greater support for the anti-dominance than for the anti-prestige component. Furthermore, certain components of the prestige model were more supported than others. Prestigious leaders were more likely to be described as having expertise, being respected, and being sought out for providing counsel, and less often described as being likable or expected to succeed. The strong male bias in leadership is not clearly predicted by the prestige model as formulated by Henrich and Gil-White (2001), and indeed, the prestige model score among the few female leaders was about the same as among all text records. See Fig. 3. A representative example of the prestige model is from Rogers and Taylor (1981:233) on the Ojibwa:

> The position of leader appears to have been based on his ability to secure for his followers abundant trade goods, to excel as a hunter, and to command superior religious knowledge. Nevertheless, such individuals were charismatic, not autocratic leaders. Their followers could sever their allegiance at will.

One critical aspect of the prestige model formulated by Henrich and Gil-White (2001) is that less prestigious individuals show respect toward, or defer to, more prestigious individuals so as to increase their proximity to them with the aim of better copying or emulating their superior skills. In these data, we found only limited evidence for this prediction: the *emulated* variable was the least documented component of the prestige model and was among the least supported variables in all of our a priori models (Fig. 3). In our 1000 text records we had only 18 supporting cases, one of which is this passage by Apter (1967:214) from the Ganda:

> Clan and tradition in these affairs served a direct political purpose. The most progressive chiefs had also been the religious stalwarts. The tradition of religious austerity and strong character had been exemplified by Sir Apolo, and to a large extent he served as a model for Nsibirwa.

In addition, characteristic ethnographic examples of the prestige model, such as the following text from Radcliffe-Brown (1922:45) on the Andamans, emphasize leaders' expertise and followers' desire to be in close proximity to leaders:

> [Respected] qualities are skill in hunting and in warfare, generosity and kindness, and freedom from bad temper. A man possessing them inevitably acquires a position of influence in the community. His opinion on any subject carries more weight than that of another even older man. The younger men attach themselves to him, are anxious to please him by giving him any presents that they can, or by helping him in such work as cutting a canoe, and to join him in hunting parties or turtle expeditions.

Nevertheless, despite support in other studies (e.g., Henrich and Henrich 2010, 2007; for review, see Richerson and Henrich 2012), our ethnographic data do not provide strong support for the social learning component of the prestige model. A similar eHRAF study of learning in 23 hunter-gatherer societies based on 146 text records from 77 documents (Garfield et al. 2016) found only two discussions of prestige-biased learning, one involving young Aleut men learning various aspects of sea mammal hunting from recognized experts in particular domains (e.g., marksmanship, weather forecasting) and another involving young Ojibwa girls learning to tan hides from women with good reputations for this task. Although we have little doubt that mentoring relationships were critical in human evolution, we suspect they would usually form between juveniles and adults, perhaps helping explain age-based status distinctions (as noted by Henrich and Gil-White 2001), rather than those that exist among adults. Indeed, Garfield et al. (2016) found that the large majority of cases of social learning involved either vertical or oblique transmission (i.e., from older to younger individuals), rather than the horizontal transmission that is predicted by the emulation model of prestige.

Neural Capital and Reproductive Skew Model

Terms that were positively associated with the neural capital and reproductive skew model included *knowledge*, *wives*, *wisdom*, and *education*, consistent with the theoretical components of this model. Terms that were negatively associated included *follow[ers]*, *land*, *power*, and *authority*, which might distinguish this type of leadership from dominance-style leadership. See Fig. 2.

Intelligent or knowledgeable was the most frequently cited component of the neural capital and reproductive skew model of leadership (>70% of all cultures), consistent with many theoretical models and observational studies (see Judge et al. 2004). Neel's discussions conceive of cognitive capacities broadly (and vaguely; Neel 1970), in reference to his hypothetical IIA, "a quantitative trait certainly related to intelligence, based on the additive effects of alleles at many loci" (Neel 1980:285). Neel also suggests leaders will have, "intellects and physiques which in that culture are superior" (Neel and Salzano 1967:563), but that compared with physical strength, mental agility is more important (Neel 1980). Our operationalization of this model included having above-average knowledge (Table 1) and therefore also supports the prestige model as conceptualized by Barkow et al. (1975) and Henrich and Gil-White (2001).

The strong male bias supports this model, and leaders were also frequently polygynous (in >40% of all cultures), which is consistent with many other studies (e.g., Chaudhary et al. 2015; von Rueden and Jaeggi 2016). There was limited evidence, however, that leaders had higher-quality mates or larger families than other men, and the female model score was about the same as the overall model score. See Fig. 3.

A linear model predicting evidence for Neel's model identified subsistence type as the only significant predictor, with pastoralists scoring lower than other subsistence types (Fig. 5). This finding is inconsistent with other quantitative studies of pastoral societies which have documented strong associations between increased status and leadership on the one hand and economic and reproductive success on the other (Borgerhoff Mulder et al. 2010; Glowacki and Wrangham 2013; Næss et al. 2010). Pastoral societies are the least represented subsistence mode in the PSF sample (7 of 60), however, so sample bias or ethnographer bias may be influencing this result. Aside from this caveat, evidence for this theoretical model as a whole is not biased toward any level of subsistence or geographic region.

The following example of the Eastern Toraja of Indonesia from Adriani and Kruijt (1950:385) typifies the role of superior knowledge in attaining a leadership role:

> In a group of men from a village community who go to war, there is only one tadoelako, who has the leadership, who determines when the people will break camp and when the people will come to a halt; who instructs the men who are going to spy on the enemy and who picks the moment that the attack will take place. He ascribes his power and his influence to the fact that he knows how to interpret the instructions that the ancestors-gods give in all sorts of signs. If one does not obey the tadoelako, then one is rebelling against the gods. It is not

> primarily courage that is asked of the tadoelako, but knowledge of all sorts of signs that appear and the interpretation of them. We have known tadoelako who were not courageous, but were respected by everyone because of their great knowledge and wisdom.

In small-scale societies, polygynous status is an indicator of leadership roles and serves to signal social distinction, as Vecsey (1983:163) describes among the Ojibwa:

> One of the symbols of religious leadership prestige was polygyny . . . the specialists tended to be exceptional hunters because of their rapport with the manitos and their hunting success enabled them to support large families. Male leaders took more than one wife to help tan the hides of slain animals and perform other domestic tasks. More to the point, male leaders took extra wives to show the community their ability to support them.

Across Theoretical Models

Exploratory hierarchical cluster analysis suggests interesting relationships across theoretical models (see Fig. 4). We identify three distinct clusters. The bottom cluster contains most of the dominance model variables. Thus, the aggressive, dominance style of leadership appears to stand apart from other leadership styles, as many have emphasized (Barkow 1989; Cheng et al. 2013; Henrich and Gil-White 2001; Kracke 1978), perhaps because dominance in humans is homologous to dominance in nonhuman primates whereas many argue that prestige is unique to humans (Barkow 1989; Henrich and Gil-White 2001; Mead 1935; Tiger and Fox 1971).

The top cluster contains two subclusters. The upper subcluster consists of mainly CA variables, and the lower subcluster mainly prestige, neural capital, and polygyny variables. Not too surprisingly, prestige and polygyny cluster together, along with the variables *expertise* and *intelligent or knowledgeable*, which indicates that a synthesis of the prestige and neural capital and reproductive skew models is warranted. Also interesting is that the prestige subcluster contains the *fighting* and *strong* variables, which belong to the dominance model, but not the *aggression* and *assert authority* variables. This relationship is consistent with the findings of von Rueden et al. (2014), which identified an association between physical strength and size with leadership in collective actions among the Tsimane', an egalitarian society with limited opportunity for dominance-based influence. Laboratory evidence suggests physically formidable leaders are often preferred by followers because of their enhanced abilities to facilitate group cooperation (Lukaszewski et al. 2016). These results indicate that *physically* formidable individuals are not necessarily leaders because of intrasexual *physical* aggression, competition, or coercion. Perhaps, as Chapais (2015) has suggested, dominance and prestige overlap in a necessary respect for physical strength and fighting ability independent of aggression and fear-based submission.

This division between the prestige–neural capital–polygyny and CA subclusters is a hint that leaders of collective actions do not necessarily acquire prestige and political influence, and prestigious political leaders do not necessarily lead collective actions. Supporting a distinction, von Rueden et al. (2014) found that leadership among the

Tsimane' was more distributed in collective fishing groups than among political leaders. In many small rural farming communities, members form labor exchange groups. One individual is appointed "chief-for-a-day," and he or she coordinates the CA to, e.g., clear a field, build a home, or harvest a crop. This leadership role does not extend to other aspects of village life. Although it is thought that members participate in exchange for help on a future project of their own (Moore 1975), one study found that men might participate to improve their reputations as cooperative partners with other men; importantly, these reputations did *not* predict association with a conjugal partner (Macfarlan et al. 2012). The separate clustering of prestige and polygyny variables from CA variables is also consistent with results from the organizational literature that leaders are distinct from managers (Keohane 2010; Zaleznik 1977).

On the other hand, the difference in branch lengths between the prestige–neural capital–polygyny and CA subclusters is very small, and the subcluster AU values are 75 and 90, respectively, indicating these subclusters are closely related. The demands of CA in small-scale societies are highly varied and include organizing within-group activities, such as a dance (Evans-Pritchard 1928), as well as confronting serious between-group threats, which can involve military strategizing and leading in battle (Glowacki and Wrangham 2013; Hollis and Eliot 1905). Among the Iban, for example, Cramb (1986:7) explains the relationship between personal prestige and organizing collective action:

> [T]he very success and prestige of the great pioneers, warleaders, and farmers depended on their ability to maintain a solidary and cooperative group of followers and associates. In the Iban scheme of values, individual achievement was inextricably linked with the ability to inspire and organize collective action. The likelihood of attaining a high degree of cooperation was enhanced by the fact that group members aligned themselves with a particular leader as a matter of free choice and on the basis of shared goals (Freeman 1981).

Prestige-Style Leadership Is Still a Conundrum

Our cluster analysis (Fig. 4) indicates that well-supported elements of the prestige model, the neural capital and reproductive skew model, and the CA model should be synthesized. This means a theory of prestige-style leadership must explain (1) the importance of skill, expertise, knowledge, and intelligence to the acquisition of prestige; (2) the increased reproductive success of prestigious men; (3) the influence of prestigious individuals over group decisions and the expectation that they will improve group outcomes; and (4) the respect and deference afforded prestigious adults. In addition, based on other research, such a theory should also explain (5) the generosity of prestigious adults in small-scale societies (e.g., Boehm 1999; Peterson 1993).

None of the models tested here satisfy all five criteria. We agree with Neel that the higher reproductive success of male leaders would represent steady sexual selection for the evolution of traits that others value in leaders, such as intelligence and abilities to acquire skills and knowledge, which could explain encephalization in *Homo* (Neel 1980; Neel and Salzano 1967; Neel et al. 1964). Yet Neel did not explain the causal connections between these traits, achieving prestige and leadership roles, and obtaining wives. With the exception of Barkow, in fact, few models of prestige-style leadership directly address leader mating success. The Henrich and Gil-White (2001) model does not explain the lopsided male bias in prestige-style leadership.

Male leaders' mating success could be explained by several knock-on benefits of prestige and leadership (Wiessner 2002), such as leaders' improved ability to provision mates (Barkow 1989), their higher genetic quality (Arden et al. 2009; Miller 2000), or the increased benefits they receive from group members in times of need (Gurven et al. 2000; Sugiyama 2004). Given the importance of intelligence, knowledge, and expertise to female reproduction, it is not clear, though, why there is such a strong male bias in prestige-style leadership in the first place. We therefore think it is theoretically worthwhile to consider if prestige-style leadership traits, in and of themselves, provide direct benefits to mates of both sexes.

High-Quality Decision-Making and Other Computational Services: Toward a Solution to the Conundrum of Prestige

Our solution to the conundrum of prestige is based on theories that conceptualize prestige as a reputation for providing valuable goods and services to others (e.g., Arnold 1996; Barclay 2011; Barkow 1989; Gurven et al. 2000; Henrich and Gil-White 2001; Price and Van Vugt 2014; Stanish 2004; Sugiyama 2004; Tooby and Cosmides 1996; von Rueden et al. 2008, 2010). Regarding prestige-style leadership specifically, we make two contributions to this theoretical foundation.

First, all human communities comprise overlapping groups of kin and non-kin, typically with a nested structure—for example, an unrelated male and female cooperate for years to raise their joint offspring within a family, multiple families are nested within a local residence group that might persist for anywhere from a season to a lifetime, and multiple residence groups are nested within larger, long-lasting regional groups (Birdsell 1958; Brown 1991; Kantner 2010; Murdock 1949; Rodseth et al. 1991; Roscoe 2009). Although there are incentives to cooperate at each level, there are potential conflicts of interest at each level. Unlike much previous literature on the evolution of leadership, we propose that prestige-style leadership could help resolve conflicts and improve outcomes at *every* level of social organization, including the family level. We submit that one reason for the apparent male bias in leadership in the ethnographic record is that the importance of leadership within and between families is not widely recognized, and women might often assume these leadership roles. We therefore agree with von Rueden et al. (2018) that widespread sex differences in leadership are probably due to the sexual division of labor and sex differences in formidability, not sex per se, but with the critical addition that these factors have predisposed men to lead at certain levels of social organization, and women to lead at others (cf. Bowser and Patton 2010). Once family leadership is taken into account, the sex difference in leadership could diminish, disappear, or even reverse.

Second, we provide the missing connections in Neel's model between intelligence and knowledge (neural capital), achieving leadership roles, and mating success. Brains comprise suites of evolved computational mechanisms that provide invaluable benefits to the individual. The evolution of language afforded unprecedented opportunities for individuals to provide some of these valuable computational services to others, which we propose is an important set of services underlying prestige. Mentoring (Henrich and

Gil-White 2001) would be one such computational service, as would providing information about, and insightful analysis of, recent events (Hess and Hagen 2006, 2017).

High-quality decision-making that benefits others, we propose, is a core computational service offered by prestige-style leaders. Optimal decision-making involves maximizing individual utility (for review, see Hagen et al. 2012). Whereas a nonhuman primate's brain arguably optimizes decisions for the individual only, we propose that a human's brain has the ability to optimize decisions for the both the individual and, optionally, others. Solving CA problems would be important examples of such a service (Glowacki and von Rueden 2015; Hooper et al. 2010; Price and Van Vugt 2014; Van Vugt and Kurzban 2007), but so would offering counsel and advice.

We highlight one type of decision-making service that we term *joint utility optimization* (JUO), in which a prestige-style leader is able to find a mutually beneficial option that she and most or all group members have incentives to choose, mitigating or avoiding the public goods problems of leadership discussed by Price and Van Vugt (2014). Optimizing individual utility can be computationally demanding. Jointly optimizing the utility of multiple individuals over the combinations of all their options would often require exceptional knowledge and computational abilities (neural capital) and also involves collaborative information processing and decision-making abilities (e.g., Hess and Hagen 2017; Wilson et al. 2004).

We propose that there was selection for JUO and other decision-making and computational services at all levels of human social organization. Parents invest in an offspring for up to two decades, and much of this investment fuels brain growth and development (Kaplan et al. 2000). With their immature cognitive abilities, infants and young children must rely on parents for many critical decisions; thus, mothers and fathers provide JUO and other computational services to their children. Because the brain continues to develop during adolescence and into early adulthood (Lebel and Beaulieu 2011), even adolescents and young adults might benefit from their mother's and father's mature decision-making mechanisms and greater knowledge and experience. In many hunter-gatherer and other traditional societies, for instance, parents play key roles in their offsprings' long-term mate choices (e.g., arranged marriages) (Walker et al. 2011). Given mothers' leading role in childcare across the mammals, initial selection for JUO and other computational services might have been in females (cf. Piantadosi and Kidd 2016).

Long-term mateships create additional selection pressures for JUO and other computational services, which explains why women would prefer mates who are good decision-makers, above and beyond their ability to provide more resources or genetic benefits. Long-term mateships involve two unrelated individuals with a joint interest in one or more offspring, but also numerous potential conflicts over, for example, residence patterns, investment in offspring from previous mateships, investment in the genetic kin of one mate vs. kin of the other mate, and other mating opportunities (Dyble et al. 2015; Hewlett 1991; Low 2003). Women who marry men that excel at finding JUO solutions and otherwise make good decisions will avoid costly conflicts and thus have higher fitness than other women. In addition, such men will be able to influence the decisions of the residence and regional groups in ways that align with the interests of their own families. By the same token, men who marry women that are also good decision-makers will do better than other men. Hence, the quality decision-making and other computational services hypothesis predicts selection for such adaptations in both men and women.

In summary, computationally demanding JUO capabilities and other decision-making and computational services—neural capital that is specific to humans—evolved to maximize benefits and minimize conflicts within and between families, local residence groups, and the larger regional political alliances that resulted from exchange of marriage partners, resulting in the prestige-style leadership that is now so common across cultures and contributing to encephalization in *Homo*.

Limitations

Because there is no single HRAF OCM code for leadership we used several OCM codes and keywords to cast a wide net, compiling a large number of ethnographic texts relevant to leadership. A consequence of this approach is that many texts provided only limited or no evidence on the particular models we tested here. At the same time, it is possible that our eHRAF search query missed important texts relevant to these models.

Additionally, our data are only as good as the source material. The vast majority of sources received high ratings on a quality evaluation scale, but these data are based on the topics ethnographers chose to write about. Therefore, absence of evidence for specific variables, such as emulation of prestigious individuals or the sanctioning of free-riders by leaders, is not strong evidence for the absence of the phenomenon. Furthermore, there are many evolutionary models of leadership that we did not test here.

Theories on the evolution of leadership in collective action focus on small-scale, egalitarian societies, which are probably more congruent with the vast majority of human evolutionary history. In testing the CA model of leadership described here, we rely on data from traditional societies encompassing a diverse range of cultural complexity. In highly stratified, complex societies leaders may receive a return or payoff from cooperative labor yet be very removed from the CA itself. It is unclear to what extent data on leadership in collective actions in complex stratified societies illuminate evolutionary models of collective actions in small-scale societies.

Lastly, there is a general male bias in the ethnographic record, especially regarding leadership and status striving (Quinn 1977; Rosaldo et al. 1974), and male political leaders are the norm cross-culturally (Low 2005; Pasternak et al. 1997). Given the extreme bias toward descriptions of male leadership in our data, and the lack of detailed descriptions of specific leaders, our results should be assumed to apply mainly to cultural models of male leadership in traditional societies.

Concluding Remarks

We found that leaders increased performance in collective actions and received benefits, but there was little evidence for sanctioning free-riders. Our results supported dominance and prestige leadership styles, with followers disfavoring the first and favoring the second, but found only limited evidence that prestigious leaders are emulated by their followers. Leaders demonstrated high expertise, intelligence, and knowledge (neural capital), and were often polygynous, but did not clearly have larger families or better mates.

Neel's argument that leadership played a key role in selecting for high neural capital in humans is compelling (Neel 1970, 1980; Neel and Salzano 1967; Neel and Sang 1994; Neel et al. 1964). Drawing on the work of Neel and many others, we sketched one model for this idea involving high-quality decision-making and other computational services: those who earn a reputation for making good decisions in multiple domains that benefit others as well as themselves will be chosen as leaders and mates.

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