LEADERSHIP, PRESTIGE, AND SOCIAL LEARNING
ACROSS TRADITIONAL SOCIETIES

By

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A dissertation submitted in partial fulfillment of the requirements for the degree of

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LEADERSHIP, PRESTIGE, AND SOCIAL LEARNING
ACROSS TRADITIONAL SOCIETIES

Abstract

by Zachary Hughes Garfield, Ph.D.
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Evolutionary approaches to leadership are reinvigorating and unifying a diverse field. Influential evolutionary theories in anthropology have increasingly linked human leadership with prestige and social learning. Until very recently, many such theories have been inadequately supported with evidence from traditional societies.

Evolutionary anthropologists often rely on a broad range of evidence. Recent advances in genetics and emerging views of leadership in nonhuman species provide an opportunity to revise existing theories. An extensive review of evidence and theories on leadership, prestige and social learning suggested informational-based leadership – a form of “prestige” – occurs across diverse taxa; cumulative, complex culture may be uniquely human, but prestige-based leadership is not.

Using the electronic Human Relations Area Files (eHRAF) social learning in the ethnographic record among hunter-gatherers was assessed. Results suggested oblique and vertical transmission appear at similar rates and various forms of teaching are the most common processes of social learning. Vertical and oblique social learning are predominantly characterized
by teaching, whereas horizontal social learning is primarily through collaborative learning. Approximations of age reveal a developmental pattern in which social learning of miscellaneous skills characterizes infancy, subsistence skills dominate childhood, and the social learning of religious beliefs are most frequent during adolescence.

A novel field study revealed similarities between male and female elected leaders in a small-scale, egalitarian society, with the exception of aggressiveness which characterized male leaders but seemed to preclude women from leadership positions. This study also provided the first test of the prediction that prestigious leaders should be the target of biased social learning; results suggested a measure of biased social learning is only a modest predictor of leader status but was a strong predictor of being respected.

Evolutionary frameworks of leadership should account for the full range of human cultural diversity. Collectively, these works highlight the importance of incorporating evolutionary approaches into leadership studies generally and provide novel systematic results from traditional societies relevant to existing theoretical models on leadership, prestige, and social learning.
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Dedication

This dissertation is dedicated to the memory of my brother, Seth Thomas Potts, and the time we spent together in Washington.
CHAPTER ONE: INTRODUCTION

Anthropology has long history of focusing on patterns of leadership and followership and the qualities of leaders observed across traditional societies (e.g., Morgan, 1877; Mumford, 1909). The ethnography of egalitarian hunter-gatherers and other small-scale societies revealed the importance of achieved and prestige-based leadership positions across diverse societies (Levi-Strauss, 1948; Lewis, 1974). The ethnography of chiefdoms and more politically complex societies revealed both diversity and commonalities in institutionalized leadership across more socially stratified populations (Cohen & Middleton, 1967; Ottenberg, 1971).

Drawing on the ethnographic record, anthropological theories often closely link the nature of leadership to group-level social, economic, and political structures and/or individual-level social learning, economic, and reproductive strategies (Boehm, 1993; Johnson & Earle, 1987). Influential theories have associated leadership, prestige, and social learning, often emphasizing a critical relationship between social influence, i.e. leadership, and culture change, i.e. social learning (Barkow, 1989; Henrich & Gil-White, 2001; Richerson & Henrich, 2012). Researchers across the social and biological sciences have similarly contributed to a sizeable literature on leadership and social learning.

More recently, evolutionary anthropologists and psychologists have turned to evolutionary theory to unify theoretical models, incorporate diverse bodies of evidence, and develop novel, holistic theories on the evolutionary origins, functions, variation, and cross-cultural patterning of leadership and followership across human societies (Cheng & Tracy, 2014; Hooper, Kaplan, & Boone, 2010; Kantner, Vaughn, & Eerkens, 2010; Kaplan, Hooper, & Gurven, 2009; Van Vugt, 2006; von Rueden & van Vugt, 2015). Multiple theoretical models of
leadership, prestige, and social learning have emerged in recent years, but such theories largely remain untested with empirical data from traditional societies.

In association with an extensive review of relevant evidence and theories, comparative and field-based research was conducted to assess evolutionary theories and to provide systematic empirical data from traditional societies on leadership, prestige, and social learning, with an emphasis on synthesis and generating novel insight.

Evolutionary anthropology is unique in the diverse sources of evidence scholars rely on, which includes ethnographic reports from diverse contemporary societies, cross-cultural analyses, fossil evidence, genetic evidence from contemporary and ancestral sources, animal models and ethology, and experimental and psychological data. Incorporating such diverse evidence into research programs is challenging. Garfield, von Rueden, & Hagen, (2019) provide a comprehensive review of evidence and theories on political leadership from within evolutionary anthropology and (1) suggest a broad phylogenetic distribution and deep evolutionary history of prestige and informational-based leadership, (2) outline relationships between ecology, culture, and leadership, (3) suggest a process of inter and intra-generational social learning underlies individual strategies for social mobility and group-level political structure, and (4) suggest an evolutionarily informed view of leader-follower dynamics should be broadly incorporated into research investigating group living, such as on cooperation and mating.

A social learning component is likely associated with many if not all aspects of culture change and cultural variation. Despite a sizable theoretical literature (e.g., Cavalli-Sforza, Feldman, Chen, & Dornbusch, 1982) and many fieldwork-based case studies (e.g., Reyes-García et al., 2009), a systematic and comparative framework on the specific modes and processes of social learning across cultural domains remained unaddressed. The nature of social learning
among egalitarian hunter-gatherers is of particular interest given theoretical models of culture change and social behavior and organization frequently draw on select ethnographic examples from contemporary hunter-gatherer populations. Garfield, Garfield, & Hewlett, (2016) provide the first systematic, comparative analyses of hunter-gatherer social learning relying on the ethnographic record. Descriptive results revealed the importance of teaching across hunter-gatherers, speaking to an active debate between cultural anthropologists and psychologists who suggest a lack of active teaching among foragers (Lancy, 2010; Lancy & Grove, 2010), and cognitive psychologists and evolutionary biologists who suggest a broader conceptualization of ‘teaching’ reveals the universal importance of guided instruction across cultural domains (Csibra & Gergely, 2011; Kline, 2015). Garfield et al. (2016) also suggest teaching is largely through oblique and vertical social learning, prestige-biased social learning is less frequent than many theories suggest, and cultural values and kinship norms – which include age-graded social distinctions, culturally valued knowledge and skills, and gender-roles – are most often socially learned during adolescence among ethnographically described hunter-gatherers.

A major deficit in the leadership literature is a lack of empirical studies among small-scale societies. Furthermore, no study – in small-scale societies or otherwise – had investigated the relationship between leadership, prestige, and social learning, despite growing theoretical interest (Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013; Henrich, Chudek, & Boyd, 2015; Richerson & Henrich, 2012). Garfield & Hagen (2019) compare female and male elected leaders to non-leaders among the Chabu, a population of Ethiopian forager-horticulturalists with a history of egalitarianism. Results revealed a high degree of collinearity of traits theoretically related to leadership, but not often analyzed in a single study. Social learning preferences were only weakly predictive of leader status, but strongly predictive of being respected. Male and
female leaders generally displayed a similar phenotypic profile, with the exception of aggressiveness which characterized male elected leaders but not female elected leaders.

All three papers in this dissertation are co-authored papers that have been published or accepted by a peer-reviewed journal or edited volume. The first review paper, titled “The evolutionary anthropology of political leadership”, by Z Garfield, C Von Rueden, and E Hagen has been published in The Leadership Quarterly. Author contributions were as follows. Review design: Z.H.G., E.H.H., C.V.R. Manuscript preparation: Z.H.G., E.H.H. All authors discussed manuscript content and provided comments.

The second paper, an empirical study titled “A cross-cultural analysis of hunter-gatherer social learning” by Z Garfield, M Garfield, and B Hewlett, was published in the edited volume Social Learning and Innovation in Contemporary Hunter-Gatherers: Evolutionary and ethnographic perspectives. Author contributions were as follows. All authors contributed to study design. Study management: Z.H.G. and B.S.H. Data collection: Z.H.G. and M.J.G. Data coding: Z.H.G. and M.J.G. with minor coding by B.S.H. Manuscript preparation: Z.H.G. All authors discussed study execution and results and commented on the manuscript.

The third paper, an empirical study titled “Investigating evolutionary models of leadership among recently settled Ethiopian hunter-gatherers” by Z Garfield and E Hagen, has been accepted for publication in a 2019 special issue of The Leadership Quarterly on the evolution and biology of leadership. Author contributions were as follows. Data collection: Z.H.G. Both authors contributed to study design, management, analysis, and manuscript preparation.
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CHAPTER TWO:
THE EVOLUTIONARY ANTHROPOLOGY OF POLITICAL LEADERSHIP

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Abstract:

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

Leadership Studies in Anthropology:

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

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

Leadership is a complex, multifaceted phenomenon and researchers and theorists often focus on only a few specific dimensions. It can (1) involve passive influence versus active motivation of group members; (2) be distributed across multiple individuals versus concentrated in a single individual; (3) be based on persuasive reasoning versus coercion; (4) be situational versus institutional; and (5) be achieved on the basis of previous accomplishments or ascribed according to kinship or social identity (Smith et al., 2016; von Rueden et al., 2014). When
leadership is ascribed, it also tends to be concentrated, to carry coercive power, and to be institutional, though these aspects of leadership do not necessarily covary (Wiessner, 2010). A major strength of evolutionary anthropological theories of leadership is the diversity of evidence they tend to incorporate, including (1) evidence of status hierarchies and leadership in nonhuman primates and other animals, (2) paleoanthropological and genetic evidence for the evolution of modern humans from ape and early human ancestors, and (3) a large body of ethnographic reports on leadership across hundreds of different cultures. We first review these sources of evidence, and then discuss classes of theories for the evolution of leadership in humans, some of which also draw on psychological and developmental evidence from Western and non-Western societies.

**Dominance, Knowledge, and Leadership in Nonhuman Animals:**

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

**Dominance hierarchies and leadership**

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

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

**Leadership in primates**

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

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

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

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

*Leadership in social carnivores*

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

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

Among bush dogs (Speothos venaticus), leaders prompt individuals to follow with pronounced “rallying” displays, and will actively regroup individuals to maintain coordinated movement; such leaders are less likely than non-leaders to be the recipients of conspecific aggression, and lower ranking individuals behaviorally demonstrate submission via signals of deference (Macdonald, 1996). Leaders among African wild dogs (Lycaon pictus), primarily initiate and lead in cooperative hunting (Frame, Malcolm, Frame, & Lawick, 1979) and leaders are responsible for initiating subsistence efforts (Wilson, 1980).

Leadership based on information and consensus rather than formidability

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

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

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

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

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

**Dominance and Knowledge Across Hominin Evolution:**

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

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

The Pliocene, which began 5.3MYA and ended 2.6MYA, was marked by a cooling climate, reductions in forest habitats occupied by apes, and expansions of grasslands. During this phase, our ancestors had ape-sized brains and were bipedal, the latter indicating greater adaptation to a terrestrial environment. Social organization, let alone leadership, is difficult to infer from the fossil record. Foley and Gamble (2009) speculate that, based on the shift to patchier and more dispersed plant resources, these early hominins had larger day ranges and feeding parties likely separated and congregated more frequently than forest dwelling apes. Nevertheless, they conclude that their behavior was well within the normal expectations for ape social behavior and organization, including the presence of dominance hierarchies.

Australopithecines, which first appeared around 4MYA, exhibited substantial sexual body-size dimorphism, indicating male-male physical competition and polygyny (Plavcan, 2012b; Puts, 2010). Hence, the patterns of leadership among ancestral hominins were probably not too dissimilar to those of chimpanzees, gorillas, and baboons described earlier, and therefore were likely based on both dominance and knowledge.

The first members of genus Homo appear around the beginning of the Pleistocene, c. 2.6MYA, which was characterized by a further cooling of the climate and a transition from patchy, plant-based resources to nutrient dense, predictable animal-based resources (Kaplan, Hill, Lancaster, & Hurtado, 2000; Marean, 2016). Early Homo might also have been markedly sexually dimorphic, although the evidence is far from clear (Plavcan, 2012a). Most primates are sexually dimorphic to some degree, however (Kappeler & Van Schaik, 2004). In modern humans, body dimorphism is modest – men weigh about 15% more than women – but this is
greater than gibbons and a number of strictly monogamous and polyandrous primate species (Plavcan, 2012b). Human upper body strength, on the other hand, is highly sexually dimorphic and in over 90% of chance encounters between an adult man and woman, the man would have greater upper body strength (Pheasant, 1983; Plavcan, 2012b). Intrasexual contest competition was likely a strong selection pressure on male reproduction across human evolution (Puts, 2010) and at least some polygyny presumably characterized our early hominin ancestors for millions of years. Again, this suggests that male dominance hierarchies, based in part on physical formidability, probably played some role in the social organization of Homo, with dominant males often assuming leadership roles.

Multiple lines of evidence suggest the subsistence strategy of Pleistocene hominins centered on cooperative hunting of large-game (Bunn & Ezzo, 1993; Hoppe, 2004; Rodríguez-Hidalgo, Saladié, Ollé, & Carbonell, 2015; Smith et al., 2012). Comparative archaeological analyses of faunal remains at Plio-Pleistocene hominin sites and behavioral studies of contemporary carnivore hunting, suggest that human ancestors exploited a niche within the predatory guild of social carnivores in between top predators and confrontational scavengers (Stiner, 2002), a strategy which may have emerged from adaptations resisting predation of social carnivores (Willems & van Schaik, 2017). The cooperative hunting of contemporary hunter-gatherers has many commonalities with the hunting strategies of social carnivores including cacheing, transportation, systematic processing of carcasses, and widespread sharing within the local group (Brantingham, 1998). Leadership in cooperative hunting likely has deep evolutionary roots with components derived from a primate heritage, adaptation to a social carnivory niche, and human-specific adaptations (Smith et al., 2012; Stiner, 2002).
The earliest known fossil specimen of our species, *H. sapiens*, is dated to about 300,000 years ago in north Africa (Richter et al., 2017). Traditionally, it was thought that there was a punctuated cultural explosion or “revolution” in symbolic material culture, such as decorations, ornamentation, and art sometime after 100,000 years ago (Dunbar, 2007). Contemporary consensus in paleoanthropology, however, suggests a more gradual process of cognitive and cultural development from 300,000 years ago to the expansion of *H. sapiens* out of Africa to Eurasia c. 100,000 years ago, (Foley, Martin, Lahr, & Stringer, 2016; Kimbel & Villmoare, 2016; Mcbrearty & Brooks, 2000); a mixture of punctuated and gradual developments across features of the human phenotype is possible, though (Shultz, Nelson, & Dunbar, 2012). Given the importance of dominance-based and information-based leadership observed among both nonhumans and humans, we can postulate both processes of leader emergence occurred among prehistoric humans. Increases in cognitive capacity and symbolic culture across hominin evolution putatively suggests an increased reliance on informational asymmetries and, consequently, prestige-based leadership, as documented next in the ethnographic evidence.

**Ethnographic Evidence:**

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

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

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

_Equalitarian hunter-gatherers_

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

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

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

The largest groups of hunter-gatherers still practicing a relatively traditional lifestyle are found in the Congo Basin. These populations, who subsist by trading meat and other wild forest products for cultivated foods grown by neighboring farmers, are known for their strong cultural emphasis on individual autonomy (Hewlett, 2014). Putnam (1948, p. 334) explains that among the Mbuti, for example, “there are no chiefs, councils, or any other formal governing bodies in a pygmy camp. In making any decisions concerning the whole camp, two factors are involved. The first of these is respect for older people...secondly,... every man in the camp is entitled to state his own views on any subject.” Decisions regarding group movement and hunting ground selection are often based on shared, group-wide consensus, reached after extended, acephalous discussions (Putnam, 1948; Turnbull, 1962, 1965). There are reports of increased deference towards highly respected individuals, however, in addition to respect and deference towards elders (Moïse, 2014).
Though Congo Basin hunter-gatherers lack an overarching political leader, there are various specialized leadership roles. Among the Aka, for example, these include camp leaders (*kombeti*), older men with greater influence over subsistence activities and movement; elephant hunters (*tuma*), who lead important hunting and seasonal rituals and oversee ritual training of young boys; and traditional healers (*nganga*), who provide a variety of specialized services to the community and maintain a special position of respect and influence (Hewlett, 1988). There is some evidence that these leaders are more likely to be polygynous and have more children (Chaudhary et al., 2016; Hewlett, 1988).

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

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

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

Leadership among egalitarian horticulturalists

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

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

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

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

*Leadership among non-egalitarian hunter-gatherers*

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

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

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

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

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

Leadership among pastoralists

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

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

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

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

The contexts and degree to which age-grades and other social structural features facilitate coordination in the absence of more traditional leadership is an important feature of pastoral political systems (Fukui & Turton, 1979; Glowacki & von Rueden, 2015). Among the Maasai of East Africa, for instance, chiefs and shamans maintained authority. The primary political force resided within age-grades of young warriors, however, and chiefs exerted only marginal influence over them (Hollis Sir & Eliot, 1905). Within age-grades, rank emerged based on physical strength and demonstrated bravery, and these individuals serve as leaders in warfare (Merker, 1910). Successful military leaders are treated with great respect and receive a number of privileged adornments to mark their status and accomplishments (Merker, 1910).
Among the Kurds in the Middle East, inter-village warfare and territoriality significantly shaped political systems and created opportunities for leadership. The initiation and successful execution of warfare was the prime pathway to political influence and status mobility (Barth, 1953). Though common people were rarely at risk of true danger, an atmosphere of violence characterized social life and Kurdish chiefs embodied cultural ideals of formidable warriors by being vengeful and courageous, yet generous (Masters, 1953).

Leadership among chiefdoms

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

Among the Maori of New Zealand, each clan (hapu) was governed by a chief from the hereditary class of leaders (rangatira), and a paramount chief (ariki) from the dominant clan was the leader of the chiefdom. Chiefs organized collective labor and controlled property use, oversaw ceremonies, and interfaced with other leaders (Best, 1924a, 1924b; Meijl, 2003). Chiefs were exceptionally wealthy but despite great influence ultimately lacked coercive authority (Firth, 1959).
Polynesian chiefs maintained firm economic control and increased their prestige through perceived generosity which in turn afforded chiefs greater social influence and authority over followers. Among the Tikopia, land was owned by the clan chief and disputes over rights to use land were common among clan members, though only rarely required the chief's involvement, which could involve severe punishment to reach resolution (Firth, 1939b, 1949). Chiefs were more knowledgeable than commoners and youth identified as potential heirs to the chieftainship received special instruction from elders and experts (Firth, 1939a, 1939b). In addition to high social rank, chiefs were expected to be highly technically skilled in activities such as farming and canoe construction (Firth, 1939b). Tikopian chiefs were also exceptionally skilled practitioners of black magic (tautuku) and the power of supernatural attack instilled fear among commoners (Firth, 1949). Ultimately, in Polynesia, the greater the productivity and intensification of subsistence, the more economic capital a chief had for distribution, and the greater their influence became (Sahlins, 1958).

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

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

**Ongoing ethnographic research on leadership in small-scale societies**

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

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

Leadership among the Chabu takes traditional and non-traditional forms. In many traditional activities, leadership is ephemeral, based on individual skill, and specific to certain tasks, such as house construction or group hunting (Dira & Hewlett, 2018). The Chabu are involved in the state-mandated Kebele system, however, under which they elect individuals to formal leadership positions, defer to their authority, and can be punishing for failing to do so. Leaders nevertheless reflect the egalitarian ethos in that they are respected for their knowledge and skills and avoid the use of aggression (Garfield & Hagen, 2019).

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

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

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

**Theoretical Forerunners to Evolutionary Models of Leadership:**

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

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

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

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

_Chiefs: capital & control_

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

One argument for the increased function and hierarchy of leadership among sedentary, non-egalitarian hunter-gatherers is that in these communities leaders provide a benefit in controlling the efficient flow of information concerning the temporal availability of critical resources and ensuring resources are appropriately distributed throughout the group (Ames, 1985). These models suggest that even among hunter-gatherers with an ethos of autonomy and
egalitarianism, followers will willingly relinquish some degree of individual autonomy when they perceive a benefit to themselves. This includes functions of economies of scale (Henrich & Boyd, 2008), seasonal variation influencing political hierarchy (Wengrow & Graeber, 2015), collective action in larger groups (Hamilton, 2000), and in the context of defensible resources (Smith & Choi, 2007). These models speak to the nature of leadership among hunter-gatherers and, in part, explain the gradations of leadership from egalitarian bands, to non-egalitarian complex hunter-gatherers, to more stratified non-foraging populations.

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

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

**Evolutionary Theories of Human Leadership:**

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

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

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

*Are human leaders alpha males in a dominance hierarchy?*

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

Boehm’s (1993) Reverse Dominance Hierarchy theory challenges this view. Boehm contends that whereas primate societies are characterized by a linear dominance hierarchy with priority of access to resources and social control vested in high ranking alphas, the social systems of egalitarian humans are characterized by systems of control with power ultimately vested in the
group. Despite social hierarchy, norms and leveling mechanisms limit the coercive ability of individuals. Faced with overly assertive leaders, followers have the freedom and ability to disband, depose leaders, or in extreme circumstances assassinate undesirable leaders (Boehm, 1993, 1999, 2008). Boehm’s theory is informative to the degree it also accurately describes patterns in the ethnographic record. The causative mechanisms, however, are problematic. For Boehm, followers maintain the egalitarian ethos purposefully (also see Boehm, 1982; Lee, 1979; Woodburn, 1982), which implicitly downplays the social and environmental conditions underlying egalitarianism. In focusing on the maximum costs followers are willing to accept from poor leadership, his theory overlooks the complexity of social trade-offs and the mutual benefits received by leaders and followers (Price & Van Vugt, 2014; von Rueden et al., 2014). Finally, there are circumstances within egalitarian societies where a dominance hierarchy model may be more applicable. Gusinde (1937), for instance, reports of powerful Ona shamans in Tierra del Fuego who lacked officially sanctioned positions of leadership, yet were able to control large groups of followers through the threat of ritual attack and sporadic displays of intense physical aggression. The Reverse Dominance Hierarchy theory has nevertheless been influential within anthropology and other fields (e.g., Hogan & Kaiser, 2005).

*Human leadership based on intelligence, knowledge, and skills*

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

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

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

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

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

Contemporary genetic evidence for sexual selection

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

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

Tentatively interpreting the results from Karmin et al. (2015) as evidence of male reproductive skew (Figure 2.1), there were approximately 3 reproducing females for every
reproducing male from 140 to 30 thousand years ago (KYA), with some fluctuation during the expansion of out Africa c. 80–50 KYA. This ~ 100 KYA time span might have been sufficient for sexual selection to have acted on the evolution of the psychological mechanisms underlying prestige, mating, and leadership-followership, especially if the pattern seen here extended even further into the past.

**Figure 2.1:** The temporal dynamics of the ratio of female (Nf) and male (Nm) effective population size in the last 140 KY. The ratios of the global accumulative Ne estimates of mtDNA (Nf) and Y chromosome (Nm) are plotted against the time (in thousands of years) back from the present (0). The BSPs estimates of Ne were obtained in BEAST using a piecewise-linear coalescence model. Source: Figure and caption from Karmin et al. (2015).

The dramatic increase in this ratio starting after the glacial maximum c. 20 KYA, peaking at > 16 in the early-to-mid Holocene, has been attributed to a combination of a transition to patrilineal social organization coupled with intensive warfare that would have killed many men in some patrilineages, leading to extinction of their Y-chromosome lineages, and hence low Nm.
Women, on the other hand, would not have been killed but instead would have joined the victors’ patrilineages (Zeng, Aw, & Feldman, 2018). These factors, combined with other sociocultural factors such as the emergence and expansion of inequality, concentrations of power and wealth, and social prestige have likely contributed to increased variance in reproduction among human males in the last 10,000 years (Heyer et al., 2012; Karmin et al., 2015; Webster & Wilson Sayres, 2016). The potential impact of sexual selection over this much shorter time period, however, is less clear.

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

Theories on leadership in the context of the evolution of collective action

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

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

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

The political inequality of particular human societies, relative to more egalitarian hunter-gatherer ancestors, are often shaped by rates of inter-group violence over the society's history (Johnson and Earle, 1987, Kaplan et al., 2009, Mattison et al., 2016), though hunter-gatherers engage in warfare (see Glowacki et al., 2017). In larger groups, particularly those facing greater internal or external conflict, encompassing larger territories, and relying on defensible resources, group members may willingly cede greater decision-making and sanctioning authority to leaders, given the functional benefits of leader-follower relationships in such contexts (Glowacki and von Rueden, 2015, Hooper et al., 2010, Service, 1964). Among pastoralists, for example, cross-cultural evidence suggests a high degree of intergenerational transmission of material wealth, owing to kin-based control and inheritance of herds, positive assortative mating between wealthy kin groups, and benefits from economies of scale in herd management and labor (Borgerhoff
Mulder et al., 2010). The defensibility of material resources, such as herds, grazing grounds, and water access, facilitates institutionalized leadership structures and heritability of economic and political influence (Glowacki & von Rueden, 2015). Such conditions are also often associated with high rates of inter-group conflict. Warfare has likely been a recurrent threat over human evolutionary history (Glowacki et al., 2017, Lopez, 2016) and represents a collective action dilemma often associated with strong leadership (Chagnon, 1988, Glowacki and Wrangham, 2013, Otterbein, 1997).

Kaplan et al. (2009) integrate several of the foregoing ideas. They suggest that certain universal features of human social structure, such as the inheritance of various forms of wealth, food sharing, cooperation, and risk-pooling, are a consequence of adaptations to a human-specific foraging niche involving the social learning of complex skills targeting high return but highly variable food sources, such as large game (see also Kaplan et al., 2000). The resource base in different subsistence systems will vary in their economies of scale – which promote various forms of managerial leadership – and in their defensibility – which promotes various forms of dominance hierarchies and social stratification. See Table 2.1.

Table 2.1: Cultural variation in dimensions of social organization, including leadership, summarized by categorization by subsistence base reproduced from Kaplan et al. (2009).
Gene-culture coevolutionary theories of leadership based on information, skills, and experience, and implications for human cooperation

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

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

Many studies in Western populations provide evidence that learners preferentially copy, and direct attention to, prestigious individuals and those that are high in the social hierarchy (Cheng et al., 2013, Cheng et al., 2010, Foulsham et al., 2010, Henrich and Henrich, 2007, Maner et al., 2008, Richerson and Henrich, 2012), which could indicate that variants in human culture facilitate cultural group selection for human cooperation, through, for example, social learning mechanisms and biases (including conformism and prestige biases), social norms and institutions, symbolic markers of groups and individuals, and complex social institutions.
According to this perspective, leadership stands to play a significant role in cultural group selection models as leaders can greatly facilitate the adoption of successful cultural norms, attract group members and promote prosocial behavior; these models also suggest that egalitarian social norms may facilitate large-scale cooperation in the absence of formal leadership roles (Henrich et al., 2015, Richerson et al., 2016).

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

**Evolutionary Psychological Approaches to Leadership:**

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

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

Leadership often stems from cooperation among leaders and followers. Comparative psychologists have looked for unique components of human cognition related to cooperation, prosociality, and social norms (Tomasello & Gonzalez-Cabrera, 2017). Infants as young as 18 months demonstrate capacities for cooperation including commitment to a joint goal, understanding their unique role, and providing assistance to fellow cooperators (Moll & Tomasello, 2007). In experimental games, chimpanzees are skilled in manipulating social relationships and information to receive an individual payoff, as are human children. Unlike chimpanzees, however, human children are able to engage in true cooperation by encouraging other individuals to cooperate, identifying their unique role in a cooperative task, and deferring or leading as necessary to maintain a cooperative activity (Warneken, Chen, & Tomasello, 2006). This suggests that learning the complex nature of nested spheres of cooperation and deference, which are central to leader-follower dynamics, constituted a strong selective pressure in the human lineage since the LCA with chimpanzees.
Building on attachment theory (Bretherton, 1992, LeVine and Norman, 2008), anthropologists have documented an effect of cultural variation in infant-caregiver relations on the development of selective trust and social relationships. Leadership necessarily involves the relinquishing of autonomy by followers (freely or coerced), a process often rooted in the trust of leaders by followers. The intimate nature of social life and child rearing among hunter-gatherers, which includes increased physical contact between caregivers and infants relative to small-scale farming communities and industrialized populations, is suggested to shape internal models of trust and social relationships (Hewlett, Lamb, Leyendecker, & Schölmerich, 2000). Across development, children are not indiscriminately trusting of social superiors, but selectively trust those who have previously provided reliable information and those who behave in ways more consistent with group-level norms (Harris & Corriveau, 2011). In support of the importance of social developmental environments, research within managerial contexts suggests that leaders who were undermined within the family through, for example verbal abuse, are more likely to exhibit abusive supervisory behaviors (Kiewitz et al., 2012). Parental figures are the first leaders children follow and these early experiences can impact behavioral models. Comparative analyses of social learning among hunter-gatherers suggest that parents actively teach children specific cultural values, including sharing norms and age-graded social distinctions (Garfield et al., 2016). This also suggests that social dominance and patterns of deference might function to facilitate informational exchange. For infants and children, learning the nuances of social hierarchy quickly and efficiently is critical. Also, such psychological processes suggest that the benefits of maintaining group cohesiveness, a function of leader-follower dynamics, are significant. Features of the social environment of children across development may ultimately
perpetuate the degree of community egalitarianism and provide children with cues of existing patterns of deference, ultimately influencing leadership and followership.

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

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

There is very little evidence on social dominance and leadership among children in small-
scale societies. In one study comparing children from an industrialized and a hunter-gatherer
setting, high status individuals initiated activities and organized collective behavior. Among
hunter-gatherers, however, lower ranking children were more likely to initiate collective
activities and to engage in physical contact with others compared to lower ranking children in
industrialized populations (Hold, 1980).

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

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

*Evolved leadership psychology in adults*

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

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

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

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

**Female Leadership and Sex Differences in Leadership:**

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

*Gender differences in leadership in the ethnographic record*

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

Egalitarian societies, which are often characterized by increased gender equality, do allow for increased female leadership relative to more socially stratified societies (Dahlberg, 1981, Dyble et al., 2015, Endicott and Endicott, 2008, Leacock, 1978). Draper (1975) documented that women among more mobile !Kung bands had greater political influence compared to more sedentary populations. Nevertheless, even in most egalitarian societies men tend to occupy positions of political leadership (Collier & Rosaldo, 1981). Women’s political influence appears to be restricted by the demands of motherhood and female work. Among the Mekranoti-Kayapo in the Brazilian Amazon, increased investments in child care are negatively associated with group level influence in that mothers with greater parenting demands are less influential than women with less or no parenting demands (Werner, 1984). Brown (1970) suggests that the division of labor and the local political structure in traditional societies are similarly shaped by maternal demands. The subsistence activities of women are more likely to be those that are more compatible with childcare (Brown, 1970, Pasternak et al., 1997). Such qualities include tasks that are located close to home and are compatible with frequent interruptions from needy children. While these activities prioritize successful parenting, they also
serve to restrict women's ability to play a larger and more active role in local politics, at least while women are in their child rearing years.

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

**Gender differences in leadership styles**

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

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

Theories on female leadership

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

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

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

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

Von Rueden et al. (2018) suggest that sex differences in leadership are a product of sexual selection, sexual division of labor, and their interaction. Sexual selection on body size and the demands of pregnancy and motherhood privilege male leadership (e.g., Eagly & Johnson, 1990), and sexual selection may have shaped status-striving motivation among men, more so than women, to involve violent competition (Daly & Wilson, 1988), large coalition building (Benenson, 2013, Low, 1992), and risky economic pursuits (Gurven and von Rueden, 2006, Hawkes, 1991). These sex differences in physiology, obligate parental investment, and motivation contribute to culturally-transmitted sexual divisions of labor that impose opportunity costs on women's ability to pursue political leadership. Among the Tsimane*, for example, gender per se does not strongly predict political leadership; instead, the male bias in leadership is due to a male bias in body size, access to education, number of cooperation partners, and contribution to the latter from the sexual division of labor (von Rueden et al., 2018).
As discussed earlier, Garfield et al. (2019) propose that high quality decision-making that benefits others is a critical element of prestige-style leadership. The male bias in leadership might therefore stem, in part, from a research bias in which leadership is defined as political leadership at higher levels of social organization, such as the residence group (e.g., a band or settlement) or political units comprising multiple settlements, but which ignores leadership within and between families. For the reasons outlined above, men more often lead at the higher levels of social organization but women more often lead within and between families within a residence group, making daily decisions for their children and the family as a whole. From this perspective, a greater proportion of women than men might occupy leadership roles. Systematic evidence reveals that autonomous decision making by mothers in a small-scale society was positively associated with better nutritional outcomes in offspring (Starkweather & Keith, 2018) and greater executive functioning and emotional control of mothers in a Western population was associated with positive outcomes among children (Crandall, Ghazarian, Deater-Deckard, Bell, & Riley, 2018). In fact, since high levels of parental investment in offspring from infancy until early adulthood 20 years later is one hallmark of the human species, with mothers (and fathers) making numerous decisions for their children, it might be the case that mothering (and fathering) is one of the evolutionary origins of human leadership.

Conclusion:

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

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

The path forward

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

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

Also, leadership and mating are probably more deeply intertwined than is recognized by either mainstream or evolutionary theorists. Other than Barkow (1989), who argued that leaders and other prestigious men can offer more resources to mates, and Neel (1980), who argued that the reproductive success of leaders resulted in strong sexual selection on intelligence, few theorists have attempted to synthesize theories of sexual selection with theories of leadership, despite the overwhelming evidence that in most human societies leaders and other prestigious men have increased reproductive success (Glowacki and Wrangham, 2015, Glowacki and Wrangham, 2013, von Rueden et al., 2011, von Rueden and Jaeggi, 2016). Given that leadership within families, the primary social unit of reproduction, has also been almost entirely ignored, and that women might often fill the family leadership role, it is likely that there are some unexpectedly deep connections between leadership by both men and women, and their relationships with the opposite sex. Garfield et al. (2019), for example, argue that the computational and other services leaders of both sexes provide to groups, including the family group, might be valuable to both sexes when choosing mates. Hence, there would be sexual selection for these computational abilities in both males and females.
The second major implication of an evolutionary approach to leadership is that in larger societies especially, some qualities we are evolved to value in leaders might increasingly be mismatched to the actual challenges leaders and their followers face. Many possible mismatches are provided by Van Vugt (2008), von Rueden and Van Vugt (2015), and Giphart and Van Vugt (2018). The relationships between leadership, physical formidability, and mating provide particularly clear examples. Leaders are often tall (Hamstra, 2014, Stulp et al., 2013), for instance, which suggests that physical formidability is a desirable leader quality even in organizations in which physical fighting plays no role and leader-follower relationships are rarely face-to-face. There also is likely an evolved male psychology that seeks to take advantage of leadership roles to pursue mating opportunities (Barkow, 1989, Schmitt, 2015, Tiger and Fox, 1971). In most small-scale societies, polygyny is socially acceptable and most group work is divided between the sexes. In Western societies, however, monogamy is the law of the land, there is less sexual division of labor, sexual relationships among members of the same organization can create huge conflicts of interest, and unwanted sexual attention can be devastating. Increasingly strong institutions and social norms might therefore need to be put in place to regulate consensual relationships within organizations and prevent unwanted sexual attention. In general, historically successful cultural institutions and norms are often those that help mesh evolved leadership and followership intuitions with the collective action problems of very large societies and organizations (Richerson & Henrich, 2012).

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

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CHAPTER THREE:
A CROSS-CULTURAL ANALYSIS OF HUNTER-GATHERER SOCIAL LEARNING

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Abstract:

Social learning among hunter-gatherers has been widely discussed in the literature and authors often draw on ethnographic cases to support theoretical models. In this study we report on the cross-cultural occurrence of various modes and processes of social learning in distinct cultural domains from the ethnographic record. To our knowledge this is the first systematic, cross-cultural study of hunter-gatherer social learning. We rely on the sample of hunter-gatherers in the electronic Human Relations Area Files (eHRAF) to generate our source of ethnographic texts. We have coded and analyzed 982 ethnographic texts from 23 diverse societies. Oblique and vertical transmission appear at similar rates. Various forms of teaching are the most common processes of social learning and account for more than half of all coded texts. Vertical and oblique social learning are predominantly characterized by teaching, whereas horizontal social learning is primarily through collaborative learning. Approximations of age reveal a general developmental pattern in which social learning of miscellaneous skills characterizes infancy, subsistence skills dominate early and middle childhood, and the social learning of religious beliefs are most frequent during adolescence. Across development we identify a reduction in the importance of vertical transmission in favor of oblique transmission, for subsistence skills in particular. These results highlight the importance of teaching in the ethnographic record of hunter-gatherer social learning and provide a systematic, cross-cultural, framework for theoretical models to rely on.

Introduction:

The primary goal of this study is to identify and analyze the cross-cultural occurrence of various modes and processes of social learning in distinct cultural domains among hunter-
gatherers. Understanding the lifeways of hunter-gatherers requires a broad, holistic perspective incorporating multiple methodological approaches. Even a cursory ethnographic review reveals immense diversity within (Draper and Cashdan 1988) and between hunter-gatherer societies (Cummings et al. 2014; Kelly 2013; Lee and Daly 1999). Comparative approaches utilizing data on multiple hunting and gathering societies have been informative (Boehm 2008; Ember 1978; Marlowe 2005) and provide important methodological tools to systematically investigate and better understand a wide sample of forager groups (Munroe and Gauvain 2010). We consulted ethnographic materials on hunter-gatherers in the electronic Human Relations Area Files (eHRAF) to determine the relationships between cultural domains, modes, and processes of culturally transmitted and acquired information with reference to established evolutionary theoretical models. Despite the limitations of ethnography-based comparative research, the ethnographic record of hunter-gatherers is a resource that should not go overlooked. The specifics of social learning among small kin group-based forager populations are likely to reveal the expression of psychological mechanisms that facilitate adaptive learning in these environments (Tooby and Cosmides 1990). An evolutionary account of social learning must incorporate the descriptive accounts of learning across a wide range of foraging populations (Bock 2010). This approach can provide insights about the universality of the acquisition of culture and also the degree to which the environment and cultural values shape social cues facilitating learning.

Social learning has been a widely discussed topic, and theoretical models have been developed from case studies and ethnographic research across diverse cultural settings (Cavalli-Sforza et al. 1982; Henrich and Broesch 2011; Hewlett and Cavalli-Sforza 1986; Reyes-García et al. 2009). We seek to further validate these models and provide cross-cultural data on the
prevalence of the components of social learning. To our knowledge this is the first HRAF investigation of cultural transmission among hunter-gatherer societies. This study utilizes the rich and detailed information ethnographers have produced and is intended to supplement field-based research on hunter-gatherer social learning (Hewlett et al. 2011; Reyes-García et al. 2009).

The Transmission and Acquisition of Culture:

Anthropologists have been interested in understanding the diversity and universality of cultural learning processes since the inception of the discipline (Munroe and Gauvain 2010; Mead 1964; Tylor 1871). Social learning is at the root of culture, and neither social learning nor culture is unique to humans (Box and Gibson 1999; Laland and Galef 2009; Perry 2011). Although a number of cultural behaviors have been identified among other species such as ground-living monkeys, apes, and particularly chimpanzees, human culture is cumulative in nature and clearly an outlier among social animals (Laland and Hoppitt 2003; Whiten 2011). Our capacity for cultural transmission and the complex methods by which we deliver social information is an important feature promoting these distinctions.

Cavalli-Sforza and Feldman define cultural transmission as the acquisition of a cultural trait or the units of culture that are learned and subject to evolutionary change, by one individual from another, and may involve lengthy processes of social learning (Cavalli-Sforza 1981). However, as the models of Cavalli-Sforza and Feldman have identified, cultural transmission is not restricted to dyadic relationships, but include many-to-one and one-to-many contexts of transmission (Cavalli-Sforza et al. 1982). We use this expanded definition, conceptualizing cultural transmission as the process of communicating socially learned information from one individual or group to another individual or group (Cavalli-Sforza 1981; Cavalli-Sforza et al. 1982). Models of cultural transmission have identified multiple mechanisms by which culture
spreads and revealed that patterns are often specific to cultural domains, such as religion or politics (Cavalli-Sforza et al. 1982).

Modes of cultural transmission specify the context of the acquisition of culture, who is transmitting culture, and who is acquiring culture. Theoretical models describing the transmission of culture have used systems of genetic transmission as a foundation and point of comparison (Dawkins 2006). Vertical transmission of culture involves children learning from their parents, a mode more congruent with genetic inheritance (Cavalli-Sforza 1981). Vertical transmission stems from attachment between parents and offspring and is predominant during infancy and early childhood (Bowlby 1973). The altriciality and close proximity of human infants to their parents allows internal working models of cultural traits to develop based on those of their parents (Hewlett et al. 2000). Among the Okiek, parents impart important knowledge during this time, and Huntingford (1951) notes that “up to the age when a child can be of some help to its parents, both boys and girls are mainly with their mother, who teaches them the business of eating and living in a hut. She corrects childish bad habits and makes them familiar with the ordinary customs and precautions of everyday life that have to be observed in Dorobo surroundings. The father corrects improper behaviour towards himself and the mother.” Vertical transmission is a low cost method of acquiring culture for infants and young children and limits innovations while promoting cultural conservation (Cavalli-Sforza et al. 1982). In stable environments vertical transmission is expected to be highly adaptive, especially within reproductively salient dimensions of culture, such as traits promoting fertility, survival, and reproduction (Boyd and Richerson 1985; Richerson and Boyd 2005).

Oblique transmission involves social learning between individuals of distinct generations or age groups typically from an older generation to a younger generation (Cavalli-Sforza 1981).
Oblique transmission may occur within an extended kin group or local population. Grandparents or aunts and uncles may pass on cultural variants to grandchildren or nieces and nephews; similarly, adults of a local community may pass on cultural knowledge to unrelated children. Among the Ojibwa religious knowledge is acquired obliquely, and “older people relate the tribal tales, sing the songs and perform the religious rites, and the children pick them up by association” (Burgesse 1944). Oblique transmission can also occur between age grades of children with adolescents transmitting cultural information to younger children. This mode of learning becomes more common during middle childhood and may occur bidirectionally as younger children and older children participate in each other’s social learning (Harris and Corriveau 2011). Culture change can occur rapidly when transmitted obliquely, and in changing and stochastic environments, oblique transmission is predicted to be highly adaptive as a wider range of cultural variants may be available to adopt if vertically acquired cultural traits may no longer be successful in new ecological contexts (Boyd and Richerson 1985; Richerson and Boyd 2005). In subarctic North America among the Chipewyans, acquiring sufficient subsistence skills and learning the local geography necessitate taking advantage of the experience of several older adults. Informants expressed, “it is generally the rule that a young man will trap with some older relative for at least 4 or 5 years before attempting to go out on his own. This means that by the time a man is in his early or middle twenties, he is thoroughly familiar with at least one and probably more trapping areas and is also skilled at other trapping activities” (Van Stone 1963).

There are multiple types of oblique transmission. Concerted transmission involves a group of older individuals formally or informally gaining consensus on the transmission of particular cultural variants (Cavalli-Sforza 1981; Hewlett and Cavalli-Sforza 1986). Concerted transmission often occurs during initiation rituals and formal aspects of cultural development,
such as when Aranda elders pass on the religious dimension of astronomical knowledge during initiation; Maegraith (1932) explains that “when they grow up and have undergone their ceremonial circumcision, they are taught the ‘truth’ about the tribal legends and names handed on to the boys. The old men also instruct the initiated boys in the movements, colour and brightness of the stars. . .the knowledge is handed down by the old men to the boys at their initiation, and is carefully concealed from the women, who know practically nothing about the stars.” Because a community of adults converge in agreement upon the content of cultural transmission, the opportunity for innovation in cultural variants that are concertedly transmitted obliquely is expected to be difficult and infrequent (Hewlett and Cavalli-Sforza 1986). Hence, the content of concerted transmission is generally consistent within a population, often within the context of age and gender, and is predicted to be highly conserved across generations and cultural evolution (Cavalli-Sforza 1981; Hewlett and Cavalli-Sforza 1986).

Several types of model-based oblique transmission involve differential transmission by specific types of individuals with specific qualities (Boyd and Richerson 1985; Richerson and Boyd 2005). Prestige-biased learning is commonly discussed in the literature and involves preferential social learning from models that receive freely conferred deference from other members of the community (Chudek et al. 2011). Prestigious individuals embody conceptions of success within a cultural context, and humans possess a psychological adaptation to prefer modeling the behavior and skills of identified experts within cultural domains (Henrich and Gil-White 2001), such as in the case of Aleut men acquiring the components of hunting skills; Shade (1948) relates that “the training of young men was conducted by recognized experts in their fields: weather forecasting, skin boat handling, marksmanship, and so forth. Out of such a background grew an easily recognizable respect for knowledge and authority.” Prestige-biased
Learning facilitates more accurate and rapid cultural transmission by streamlining the process of selecting potential models for skill acquisition and differentially spreading the most successful information or skills across the group and to younger generations (Henrich and Gil-White 2001).

Cultural transmission also occurs within an age group. Horizontal transmission involves social learning from individuals of the same generation, age group, or cohort, roughly within 4–5 years of age (Cavalli-Sforza 1981). Horizontal transmission becomes more frequent during middle childhood when children spend a majority of time in mixed-aged playgroups (Konner 2010). Culture change can occur rapidly in domains that are primarily transmitted horizontally, and in changing environments, a reliance on horizontal transmission can be highly adaptive (Boyd and Richerson 1985; Richerson and Boyd 2005).

Multiple processes of social learning have been defined to explain how culture is learned. Teaching is one process of social learning and multiple forms have been identified across diverse taxa. Caro and Hauser (1992) provide three criteria for defining teaching. Teaching involves, first, a knowledgeable individual modifying their behavior in the presence of a naïve individual; second, the knowledgeable individual incurs some cost or derives no immediate benefit by modifying their behavior; third, the naïve individual acquires knowledge or skills more rapidly or efficiently than they would have otherwise, or he or she acquires knowledge or skills it would not have learned at all in the absence of the knowledgeable individual’s modified behavior (Caro and Hauser 1992). The roles of various forms of teaching and their importance in traditional societies have been elaborately discussed. Cultural anthropologists have historically downplayed the importance of teaching in traditional societies (Lancy and Grove 2010; Tomasello et al. 1993); however, cognitive psychologists have purported that teaching is a universal feature of human psychology (Gergely and Csibra 2006). Evolved psychological mechanisms produce a
type of learning described as natural pedagogy, which involves social learning by recognition of explicit cues of generalizable knowledge within a given context (Csibra and Gergely 2011; Gergely and Csibra 2006). These psychological mechanisms facilitate the efficacy of both learning and teaching and increase the capacities for social learning beyond those of observation and imitation alone. Teaching also involves guided demonstration, positive and negative reinforcement, verbal explanation, and scaffolding (see Hewlett et al., Chap. 3 this volume; Konner 2010). One aspect of this contention, concerning the frequency and importance of teaching, stems from the operationalization and classification of teaching. While some authors have conceptualized teaching only in the strict formal sense, others have suggested teaching is multidimensional and methods of informal teaching are in fact classifiable as teaching (Kruger and Tomasello 1996). Recently, significant work has moved this debate forward by resolving discrepancies between approaches to define and study teaching. Klein (2015) provides a taxonomy of teaching and links processes of teaching to cultural adaptation; this framework predicts teaching to be highly frequent cross-culturally. A more comprehensive conception of teaching reveals the importance of the social learning process in traditional cultural settings (Hewlett et al. 2011).

Imitation has been regarded as the dominant process of acquiring cultural information. Observation and imitation is considered a requisite technique to ensure the reproduction and transmission of cultural variants (Gergely and Csibra 2006). Observation and imitation can often occur peripherally around teaching, yet represent a distinct process of social learning. Imitation, verbal instruction, and prosociality have been suggested as the suite of sociocognitive processes responsible for the cumulative nature of human culture (Dean et al. 2012). Observation and imitation involves the learner directly observing some skill or behavior and then attempting to
replicate the observed actions or behaviors. Imitation is a widespread process of social learning across many species; however, only human children incorporate a dimension of sociality when imitating actions. For young children, unlike the process of imitation documented among monkeys, imitation is not purely utilitarian and self-serving but is a collaborative process that develops social networks and potentially incorporates horizontal transmission throughout the process (Dean et al. 2012). The ability and propensity to imitate are deeply engrained in children’s psychology to the point that children imitate unnecessary actions when attempting to replicate behaviors to achieve a goal (Lyons et al. 2007). This overimitation has been found to be unique to humans and is the result of a highly developed sense of attributing causality to a series of actions involved in task completion (Lyons et al. 2007; however, see Berl and Hewlett 2015 for exceptions). Overimitation can be beneficial in allowing the child to calibrate a specific action over time to more efficiently complete a given task; however, overimitation is initially costly in that redundant unnecessary actions are weighted equally with essential actions (Lyons et al. 2007). Investigating the nature of overimitation among children in diverse cultural settings remains an important aspect of research on social learning. Field studies among hunter-gatherers (Hewlett et al. 2011) and reviews of ethnographic materials (MacDonald 2007) suggest that observation and imitation is the primary process of human social learning in traditional cultural settings.

The nature of child development and demography in hunter-gatherer society indicates that over the course of human evolutionary history, much of the social interaction that occurs during childhood takes place in the context of mixed-aged groups (Konner 2010). The community of children in small kin-based societies provides ample opportunity for collaborative learning experiences involving children of all ages. Collaborative learning consists of two
learners of approximately equal skill, knowledge, and cognitive ability responding to a problem and co-constructing a solution (Konner 2010; Tomasello et al. 1993). For example, among the Mbuti, “the children played house, learning the patterns of cooperation that would be necessary for them later in life. They also learned the prime lesson of egalitarianism, other than for purposes of division of labor making no distinction between male and female, this nuclear family or that” (Turnbull 1983). Collaborative learning often involves acquiring sociocultural skills or information through play, practice, or adopting social roles among a group of children and requires children to consider the perspective of others (Hewlett and Boyette 2012; Hewlett et al. 2011). In this study collaborative learning was identified in the form of children’s play, and we developed a distinction between play, role-playing, and rule-based play from ethnographic accounts.

The local environment provides opportunities and limitations for social learning, and both learners and teachers exploit the local ecology and materials to facilitate cultural transmission. Local enhancement involves a learner gaining knowledge or skills by being exposed to particular areas of the local environment by others. Often this occurs unintentionally as a byproduct of daily life as young children are encouraged to accompany their parents or adults while attending to various tasks (Konner 2010). Local enhancement requires direction, initiative, or intention on the part of the transmitter or facilitator, but at the proximate level, local enhancement may resemble individual learning as the child is given the opportunity to learn directly from environmental conditions (Heyes et al. 2000; Konner 2010). Local enhancement may be unintentional; however, stimulus enhancement involves the learner being directly given an object to facilitate learning about the use and manipulation of that object or as a model for other objects. Among the San stimulus enhancement is used to instill practices of social exchange, and
Wiessner (1978) describes, “symbolic training to do hxaro begins between the age of 6 months and a year when the maternal or paternal grandmother cuts off a child’s beads, washes him, puts the beads in the child’s hand, has him give them to some older relative and replaces them with new ones.” This process of learning also seems to be especially salient in the acquisition of subsistence skills as parents and other adults often give children miniature versions of important subsistence tools, such as bows and arrows or traps (MacDonald 2007).

These mechanisms of cultural transmission have been proposed as features of the process of acquiring culture and constitute aspects of an evolved culture acquisition device (Brown 1991; Konner 2010; Tomasello et al. 1993). By systematically examining the modes and processes of cultural transmission, a more fine-grained view of the process of culture acquisition emerges and allows us to inquire about specific aspects of social learning in hunter-gatherers.

Field studies among hunter-gatherers provide opportunities for systematic observational research on social learning. Egalitarian hunter-gatherers are populations without strict social hierarchy, hereditary classes, or significant wealth differences and live in ways socially more congruent with the vast majority of human evolutionary history (Boehm 1999). Investigating cultural transmission among hunter-gatherers is one approach to infer ancestral patterns of human social learning and also allows us to better understand how groups of contemporary foragers pass on their cultural knowledge. Hewlett et al. (2011) report on social learning from behavioral observation data among Congo basin egalitarian foragers and offer specific findings and predictions concerning modes and developmental parameters of cultural transmission. Generally, social learning occurs early in life, vertical transmission characterizes early childhood, and horizontal and oblique transmission become more dominant during middle
childhood (Hewlett et al. 2011). However, studies such as this among hunter-gatherers are rare, despite a vast ethnographic literature on hunter-gatherer lifeways.

Other researchers have utilized the rich and detailed ethnography of hunter-gatherers, which spans over 150 years, to investigate social learning and cultural transmission. MacDonald (2007) uses a comparative approach to analyze the development of hunting skill in traditional societies and identifies cross-cultural patterns that characterize the transmission of hunting techniques with reference to the parameters and predictions of life-history theory. MacDonald’s study provides a highly informative review of the ethnographic descriptions of learning to hunt; however, the process of selecting ethnographic sources and the sample of societies she reviews are not specified, and her study includes societies that utilize farming and other subsistence strategies.

As MacDonald explains, models of human evolution and of our species’ unique life-history strategy have emphasized the importance of large, difficult-to-acquire, packages of high-quality animal protein (Kaplan et al. 2000; MacDonald 2007). Therefore, understanding the process of learning to hunt may be generalizable to other domains of learning as well. MacDonald’s review suggests learning to hunt begins very young through vertical or oblique modes of transmission and often involves stimulus enhancement, where older individuals provide children with miniature versions of tools for play and experimentation (MacDonald 2007). Adults teach and guide children on the use of hunting tools in some contexts. MacDonald (2007, p. 390) notes that in several cases, “adults or older children provide hunting tools for the children to play with. . .and adults also offer advice on the peculiarities of the weapons and how to use them.” Providing hunting weapons to children allows for the development of important skills through play and also gives parents the opportunity to influence and direct children’s use
of these tools and hence the acquisition of subsistence-based knowledge and skills through teaching (MacDonald 2007). Additionally, hunters may target easier prey when accompanied by children to facilitate the demonstration of proper technique (MacDonald 2007). However, MacDonald suggests teaching and observation are infrequent processes of acquiring hunting skill and learning to manufacture hunting tools. MacDonald suggests collaborative learning, group play, and stimulus enhancement are the dominant processes of the development of hunting skill. MacDonald emphasizes the importance of the social context and kin relations among males and the transmission of hunting skills. Clearly a number of modes and processes are important in acquiring subsistence skills.

Kruger and Tomasello (1996) provide a review of the ethnography on social learning and identify three types of cultural learning: imitative learning, instructed learning, and collaborative learning. These distinct processes of social learning are situated in a developmental context and are dependent upon degrees of comprehension and intentional states of the learner. Imitative learning emerges early in development, followed by instructed and collaborative learning (Kruger and Tomasello 1996). Through their review of ethnographic materials, Kruger and Tomasello further define three types of intentional instruction. They conclude that expected learning, which involves a laissez faire approach where children learn information or skills on their own accord, occurs throughout development and is employed for simple or relatively unimportant tasks; guided learning occurs when adults believe children need assistance to acquire knowledge or skills and is used when tasks are moderately complex and often involves adults scaffolding children’s learning; designed learning is a more formal process of instruction and occurs when children are perceived to need insistent and direct instruction and is reserved for complex or highly valued cultural tasks, such as sitting or walking early on and subsistence
skills across development (Kruger and Tomasello 1996). Kruger and Tomasello predicted that all human societies demonstrate intentional teaching of children and surveyed ethnographic materials of a range of cultures including foragers, chiefdoms, and state-level societies. Their review provides important evidence that many diverse cultures engage in intentional instruction at least to some degree; however, their study is limited in that the ethnographic materials reviewed and the process of selecting their sample of cultures are not specified and not developed in a systematic manner (Kruger and Tomasello 1996).

Our study is distinct from the previous comparative research on cultural transmission in that we draw on a specific sample of the ethnographic record by relying exclusively on the eHRAF. In doing so we avoid researcher-introduced biases from nonsystematic sampling of cultures. Additionally, we restrict our analyses to hunter-gatherers to best characterize social learning among populations that subsist in ways more congruent with the majority of human evolutionary history. The eHRAF does not provide a complete or perfect sample of hunter-gatherers, but by limiting our searches to this data set, we avoid suppressing evidence or selecting ethnographic cases that would tend to support one theoretical perspective over another. Furthermore, the eHRAF has subject-coded ethnographic texts providing additional safeguards against biases in the collection of our target ethnographic data. By relying on the eHRAF, we are able to be confident that all ethnographic materials derive from valid and reliable sources with the vast majority produced by trained social anthropologists or ethnographers. This study is the first systematic analysis of social learning among hunter-gatherers designed to provide results useful in the mainstream approach to social learning in evolutionary anthropological studies today.
Cross-Cultural Methodology:

Currently the eHRAF database contains ethnographic information on over 280 cultures. The content of the eHRAF is subject coded at the paragraph level using the Outline of Cultural Materials (OCM) coding scheme. Our search was limited to 46 cultures with the eHRAF subsistence designation of hunter-gatherers. Three OCM codes were used in an advanced search to extract ethnographic information on cultural transmission: 867 Transmission of Cultural Norms, 868 Transmission of Skills, and 869 Transmission of Beliefs. We focus on egalitarian social structures. Equestrian hunter-gatherers of the North American plains and complex hunter-gatherers of the North American Pacific Northwest were excluded from data collection. This allows for more valid comparisons among hunter-gatherers between cultures and regions. Our search (after exclusions) generated 982 paragraphs in 153 documents from our final sample of 23 hunter-gatherer populations.

Ethnographic information was only extracted and recorded if the ethnographer explicitly provided either context or content of social learning. All extracted texts contained information suitable for classification into a cultural domain and a specific process of cultural transmission (e.g., teaching, observation and imitation); however, in many cases, the mode of transmission (e.g., vertical, oblique) was not clear. Ethnographic texts can be classified as cases or cultural models. Cases are instances where the ethnographer describes an observed action or event involving specific individuals at a specific time. Cultural models are ethnographic descriptions of social values, norms, or standards that the ethnographer may infer based on their expertise or may be related from one or more local informants. Cases and cultural models provide valuable

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1 Our sample includes the Okiek, San, and Mbuti from Africa; the Ainu, Andaman, Vedda, and Semang from Asia; the Aleut, Chipewyan, Copper Inuit, Innu, Kaska, Ojibwa, Mi’qmak, and Northern Paiute from North America; and the Aranda, Tiwi, Abipón, Siriono’, Warao, Bororo, Ona, and Yaghan from South America.
and viable ethnographic material and both types of textual information are used in this analysis. Overly general statements regarding cultural acquisition or learning were disregarded. Cultural models that were purely based on myths or fables were not included. Extracted texts were required to have at least a brief statement concerning what cultural information was transmitted. Data collection procedures produced 146 ethnographic texts (14.8% of total texts generated by search) suitable for coding and analysis.

Ethnographic texts were coded for each instance of cultural transmission. An individual text may yield multiple codes. Codes were first classified by cultural domain and then coded for both mode of transmission and process of transmission. Table 2.1 lists operational definitions used in coding ethnographic texts. Cultural domains were determined post hoc from collected ethnographic texts. Additionally, each code includes a measure of the age of the learner coded as infancy, early childhood, middle childhood, adolescence, childhood (general), and nonspecific. The sex of the learner was also coded as male; female; both, for cases that mention each sex; and general, for statements that apply to children generally without specific mention of either sex.

Two coauthors (ZG, MG) independently coded the 146 texts, and a third coauthor (BH) coded a sample of half of the texts and easily resolved the few coding discrepancies to reach unanimous consensus. Collaborative learning rule-based play was not used in the final coding results because it rarely occurred.

We have employed two methods of evaluating these data. One approach is to simply look at the frequency of unique domain mode process combinations for each culture, rather than the full set of generated codes. This allowed us to characterize and compare cultures more so than the ethnography of those cultures. Given the amount of ethnographic materials available for each culture varies, this process partially avoids biases in the quantity of ethnographic materials. For
example, Lorna Marshall (1957) describes the processes of learning subsistence skills among the San noting that “the adults do not let their children out of their sight. . .the adults pause to show them how to hold a digging stick, or a toy bow or drill, so that play and learning merge.” The following statements yield a code of subsistence skills and knowledge—teaching—demonstration—oblique. A similar code is generated from Richard Lee’s (1979) description noting that “around age 12 a boy starts accompanying his father, uncles, or older brothers on hunts. . .the boy becomes more active in shooting, with mongoose, genets, hares, and game birds as the main targets; during the winter months the young adolescent boy also builds snarelines, often under the guidance of his father or grandfather.” These two ethnographic texts would only contribute to one count of the subsistence skills and knowledge—teaching—demonstration—oblique permutation; however, other codes may stem from each of these texts. All reported frequency data was produced from this version of the data, which used only unique domain mode process combinations for each culture, ignoring age or sex distinctions. Results concerning developmental patterns or sex biases rely on the full set of generated codes.
Table 3.1: Operational definitions of coding scheme

<table>
<thead>
<tr>
<th>Domains</th>
<th>Knowledge or skills related to food acquisition, includes hunting, gathering, food processing, production and use of subsistence-related tools, knowledge of edible plants and animals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subsistence skills and knowledge</td>
<td>Knowledge or skills related to the spiritual, religious, or supernatural domain, includes folk mythology, ritual training, and initiation dealing with the supernatural</td>
</tr>
<tr>
<td>Religious beliefs and practices</td>
<td>Knowledge or skills related to general locomotion, basic operation of crafts (e.g., canoes), swimming, basic climbing, dancing, singing, basic tool use (not directly tied to subsistence, or manufacture), alloparenting, toilet training, and some domestic skills (not directly related to subsistence, e.g., sewing)</td>
</tr>
<tr>
<td>Language</td>
<td>Knowledge or skills concerning the physical environment, including nonedible plants, ethnobotany, medicinal plants, astronomy (non-spiritual, e.g., navigation, naming constellations), weather patterns, geographical knowledge</td>
</tr>
<tr>
<td>Ecology</td>
<td>Knowledge or skills involving production of useful items, including watercrafts, other transportation crafts, craft manufacture such as basketry, textile manufacture, tool manufacture, and building dwellings</td>
</tr>
<tr>
<td>Miscellaneous skills</td>
<td>Knowledge or skills concerning culturally preferred social behavior, including gender roles, morality, social norms (e.g., sharing, generosity), proper behavior between kin, kin terms, age-graded social distinctions, emotional behavior, and culturally preferred conduct</td>
</tr>
<tr>
<td>Manufacture (non-subsistence)</td>
<td>Knowledge or skills concerning culturally preferred social behavior, including gender roles, morality, social norms (e.g., sharing, generosity), proper behavior between kin, kin terms, age-graded social distinctions, emotional behavior, and culturally preferred conduct</td>
</tr>
<tr>
<td>Cultural values and kinship</td>
<td>Knowledge or skills concerning culturally preferred social behavior, including gender roles, morality, social norms (e.g., sharing, generosity), proper behavior between kin, kin terms, age-graded social distinctions, emotional behavior, and culturally preferred conduct</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Modes</th>
<th>Learning from individuals of the same generation, age group, or cohort within approximately 5 years of age (e.g., children–children, adult–adult)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Horizontal</td>
<td>Social learning between individuals of distinct generations or age groups (e.g., uncle to nephew, adult to child, adolescents to young children)</td>
</tr>
<tr>
<td>Oblique</td>
<td>Social learning from a culturally identified expert to member(s) of a different generation or age group</td>
</tr>
<tr>
<td>Oblique–prestige bias</td>
<td>Several adults agree upon what should be transmitted to an individual (usually in initiation context)</td>
</tr>
<tr>
<td>Oblique concerted</td>
<td>Children learning from their parents</td>
</tr>
<tr>
<td>Vertical</td>
<td>The context was not specific enough to justify coding, but some information of a domain and a process was mentioned</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Processes</th>
<th>Individuals of approximately equal age, skill, knowledge, and cognitive ability collectively contribute to the learning of a specific skill or knowledge</th>
</tr>
</thead>
<tbody>
<tr>
<td>Collaborative learning</td>
<td>Type of collaborative learning that involves the transmission, acquisition, or practice of cultural knowledge or skills through informal play or miscellaneous games</td>
</tr>
<tr>
<td>Collaborative learning play</td>
<td>Type of collaborative learning that involves individuals of similar age collectively playing social roles (e.g., play house, husband-wife)</td>
</tr>
<tr>
<td>Collaborative learning, role-playing</td>
<td>The learner gains knowledge or skills by interacting with the local environment because other individuals expose the learner to the setting or environment (e.g., parents take children gathering or walk through forest)</td>
</tr>
<tr>
<td>Local enhancement</td>
<td>The learner is given an object to facilitate learning how to use the object</td>
</tr>
<tr>
<td>Observation and imitation</td>
<td>The learner directly observes some skill or behavior and attempts to replicate the observed actions or behaviors</td>
</tr>
<tr>
<td>Teaching</td>
<td>An individual modifies his or her behavior specifically to impart knowledge, skills, or behaviors, to a learner, but there is insufficient information to code as demonstration or storytelling</td>
</tr>
<tr>
<td>Teaching—demonstration</td>
<td>Type of teaching where an individual demonstrates knowledge, skills, or behaviors, to a learner, and may offer feedback and examples during the process</td>
</tr>
<tr>
<td>Teaching—storytelling</td>
<td>Type of teaching where an individual actively imparts specific (within one of the defined domains) knowledge, skills, or behaviors to a learner by verbal communication of stories or metaphors</td>
</tr>
<tr>
<td>Individual learning</td>
<td>Individual exhibits repeated attempts to learn a skill or develop new skills or knowledge on his or her own. Includes trial and error and individual practice</td>
</tr>
</tbody>
</table>

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Results:

An important dimension of the eHRAF is the classification and evaluation of source ethnographies. This sample of ethnographic texts stems from 77 unique documents covering 23 hunting and gathering cultures. These documents were primarily authored by ethnographers or social anthropologists (62, constituting 80 %), with the remaining authored by other social scientists or professionals.

Frequency data can be evaluated across the entire sample or within each cultural domain. Due to variation in the ethnographic materials of each culture in the eHRAF, certain cultures or regions are overrepresented in this sample. In the frequency data, 30 % of the codes stemmed from eight North American societies, 26 % of codes came from three African societies, 13.3 % of codes came from two societies from Oceania, and 10 % of codes were from four Asian societies. Results in Table 3.2 reveal certain domains were more commonly discussed than others. The subsistence skills and knowledge domain was the most common and accounted for 37.6 % of all frequency codes. The cultural values and kinship domain accounted for 16.5 % of the distribution followed by the religious beliefs and practices domain which accounted for 13.8 %. The manufacturing and miscellaneous skills domains accounted for 12.8 % and 11.5 % of the frequency data, respectively. The ecology domain accounted for 6.4 % and the language domain for 1 %.

Across the entire sample, the frequencies of vertical and oblique transmission were the most common and appear at similar rates (37 % and 34 %, see Table 3.2 column totals). If the subcategories of oblique (prestige bias, concerted) are added to the more general oblique classification, oblique becomes the most frequent mode of transmission (43 %). Only three
instances (3.2 %) of oblique codes described young children learning socially from adolescents, and two cultural models (2.1 %) mentioned young children learned from adolescents or elders. Therefore, the vast majority (95 %) of oblique codes concern children’s social learning from adults. Horizontal transmission accounted for 10 % of the frequency data.

**Table 3.2:** Prevalence of modes of transmission (with number of cases in parentheses) by cultural domain

<table>
<thead>
<tr>
<th>Domains</th>
<th>Vertical</th>
<th>Horizontal</th>
<th>Oblique General</th>
<th>Concerted</th>
<th>Prestige bias</th>
<th>Unknown</th>
<th>Domain totals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subsistence skills and knowledge</td>
<td>39 % (32)</td>
<td>14.6 % (12)</td>
<td>32.9 % (27)</td>
<td>3.7 % (3)</td>
<td>0.2 % (1)</td>
<td>8.5 % (7)</td>
<td>82 cases</td>
</tr>
<tr>
<td>Religious beliefs and practices</td>
<td>23.3 % (7)</td>
<td>6.7 % (2)</td>
<td>36.7 % (11)</td>
<td>23.3 % (7)</td>
<td>0</td>
<td>10 % (3)</td>
<td>30 cases</td>
</tr>
<tr>
<td>Language</td>
<td>33.3 % (1)</td>
<td>0 %</td>
<td>66.7 % (2)</td>
<td>0 %</td>
<td>0 %</td>
<td>0 %</td>
<td>3 cases</td>
</tr>
<tr>
<td>Ecology</td>
<td>50 % (7)</td>
<td>0 %</td>
<td>21.4 % (3)</td>
<td>7.1 % (1)</td>
<td>7.1 % (1)</td>
<td>14.3 % (2)</td>
<td>14 cases</td>
</tr>
<tr>
<td>Miscellaneous skills</td>
<td>16 % (4)</td>
<td>12 % (3)</td>
<td>36 % (9)</td>
<td>8 % (2)</td>
<td>4 % (1)</td>
<td>24 % (6)</td>
<td>25 cases</td>
</tr>
<tr>
<td>Manufacture (non-subsistence)</td>
<td>57.1 % (16)</td>
<td>7.1 % (2)</td>
<td>28.6 % (8)</td>
<td>0 %</td>
<td>3.6 % (1)</td>
<td>3.6 % (1)</td>
<td>28 cases</td>
</tr>
<tr>
<td>Cultural values and kinship</td>
<td>36.1 % (13)</td>
<td>8.3 % (3)</td>
<td>41.7 % (15)</td>
<td>5.6 % (2)</td>
<td>0 %</td>
<td>8.3 % (3)</td>
<td>36 cases</td>
</tr>
<tr>
<td>Mode totals</td>
<td>37 % (80)</td>
<td>10 % (22)</td>
<td>34 % (75)</td>
<td>7 % (15)</td>
<td>2 % (4)</td>
<td>10 % (22)</td>
<td></td>
</tr>
</tbody>
</table>

The frequency data of processes of cultural transmission in Table 3.3 highlight the importance of teaching in the ethnographic record of hunter-gatherers. We have identified three distinct types of teaching, teaching–demonstration, teaching–storytelling, and a more general teaching classification. These three processes accounted for 58 % of the data; the general teaching process was the most frequent process accounting for 37 %, while teaching–demonstration and teaching–storytelling accounted for 12.8 % and 8.3 % of the data, respectively. Observation and imitation was the second most frequent process (22 %), followed by stimulus enhancement and local enhancement, which both accounted for 4 %. Collaborative
learning and collaborative learning play each accounted for 2.8 %. Collaborative learning, roleplaying, was noted in 2.3 % of cases. Individual learning was noted in 3.7 % of frequency data texts.

**Table 3.3:** Prevalence of processes of transmission (with number of cases in parentheses) by cultural domain

<table>
<thead>
<tr>
<th>Domains</th>
<th>Processes</th>
<th>Observation and imitation</th>
<th>Stimulus enhancement</th>
<th>Local enhancement</th>
<th>Collaborative learning</th>
<th>Teaching</th>
<th>Individual learning</th>
<th>Domain totals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subsistence skills and knowledge</td>
<td>23.2 % (19)</td>
<td>6.1 % (5)</td>
<td>7.3 % (6)</td>
<td>3.7 % (3)</td>
<td>6.1 % (5)</td>
<td>3.7 % (3)</td>
<td>28 % (23)</td>
<td>82 cases</td>
</tr>
<tr>
<td>Religious beliefs and practices</td>
<td>10 % (3)</td>
<td>3.3 % (1)</td>
<td>0 %</td>
<td>3.3 % (1)</td>
<td>3.3 % (1)</td>
<td>43.3 % (13)</td>
<td>10 % (5)</td>
<td>30 cases</td>
</tr>
<tr>
<td>Language</td>
<td>33.3 % (1)</td>
<td>0 %</td>
<td>0 %</td>
<td>0 %</td>
<td>0 %</td>
<td>66.7 % (2)</td>
<td>0 %</td>
<td>3 cases</td>
</tr>
<tr>
<td>Ecology</td>
<td>7.1 % (1)</td>
<td>0 %</td>
<td>21.4 % (3)</td>
<td>0 %</td>
<td>0 %</td>
<td>21.4 % (3)</td>
<td>21.4 % (5)</td>
<td>14 cases</td>
</tr>
<tr>
<td>Miscellaneous skills</td>
<td>24 % (6)</td>
<td>8 % (2)</td>
<td>0 %</td>
<td>4 % (1)</td>
<td>4 % (1)</td>
<td>24 % (6)</td>
<td>28 % (7)</td>
<td>25 cases</td>
</tr>
<tr>
<td>Manufacture</td>
<td>42.9 % (12)</td>
<td>0 %</td>
<td>0 %</td>
<td>0 %</td>
<td>0 %</td>
<td>46.4 % (13)</td>
<td>7.1 % (2)</td>
<td>28 cases</td>
</tr>
<tr>
<td>Cultural values and kinship</td>
<td>16.7 % (6)</td>
<td>2.8 % (1)</td>
<td>0 %</td>
<td>2.8 % (1)</td>
<td>0 %</td>
<td>58.3 % (21)</td>
<td>0 %</td>
<td>36 cases</td>
</tr>
<tr>
<td>Processes totals</td>
<td>22 % (48)</td>
<td>4 % (9)</td>
<td>4 % (9)</td>
<td>2.8 % (6)</td>
<td>2.8 % (6)</td>
<td>2.3 % (5)</td>
<td>37.2 % (81)</td>
<td>12.8 % (28)</td>
</tr>
</tbody>
</table>

The mosaic plot depicted in Figure 3.1 displays the relationship of mode of transmission by the process of social learning for the frequency data. Note that the proportions along the x-axis represent the number of observations of each level of mode of transmission. The y-axis represents the overall proportions of each process of social learning. In this plot the subcategories associated with teaching, collaborative learning, and oblique transmission have been collapsed into their respective single category. Figure 3.1 illustrates the high frequency of oblique and vertical transmission; teaching dominates vertical and oblique transmission, while collaborative learning is most common in horizontal transmission.

**Figure 3.1:** Distribution of mode of social learning by process of social learning
The second approach to data analyses involves the full set of generated codes, including age and sex classifications, rather than unique combinations of domain mode process. In this data set, each domain mode process code also contains an evaluation of the age and sex of the learner. This version of the data allowed us to investigate wider patterns of social learning with the goal of characterizing the content and context of transmission across the complete sample of all codes.

The ethnographic record is not ideal for identifying the age of the learner in the context of cultural transmission. However, in many cases the ethnographer does specify rough estimates of the developmental stage of social learners. Our data collection procedure did not target any particular age range but relied on texts coded by the mentioned OCM codes. We used this information to code a measure of age to each domain mode process code generated. In half of the coded texts (141, 50.2 %), the ethnographer provides a general evaluation mentioning that transmission of culture occurs during “childhood.” However, the remaining texts (140, 49.8 %)
do provide sufficient detail warranting a rough, but more specific evaluation of the age of the social learner. Besides the more general coding of childhood, we have coded age as infancy (10 instances), early childhood (44), middle childhood (27), adolescence (37), all ages (7), and nonspecific (15).

We investigated the relationship between the age of the learner and the domain of cultural transmission across all domains (Table 3.4). Here we excluded the general evaluations of childhood and all ages as well as instances where the age of the learner was not specified. In infancy miscellaneous skills were the primary domain of culturally acquired content; early childhood was associated with learning in the subsistence skills and knowledge domain; the subsistence skills and knowledge domain also dominated middle childhood although to a lesser degree; adolescence was associated with cultural transmission in the religious skills and beliefs domain more so than others.

**Table 3.4: Prevalence of domain frequencies by age of learner**

<table>
<thead>
<tr>
<th>Domains</th>
<th>Age evaluations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Infancy</td>
</tr>
<tr>
<td>Subsistence skills and knowledge</td>
<td>2</td>
</tr>
<tr>
<td>Religious beliefs and practices</td>
<td>0</td>
</tr>
<tr>
<td>Language</td>
<td>1</td>
</tr>
<tr>
<td>Ecology</td>
<td>0</td>
</tr>
<tr>
<td>Miscellaneous skills</td>
<td>6</td>
</tr>
<tr>
<td>Manufacture</td>
<td>0</td>
</tr>
<tr>
<td>Cultural values and kinship</td>
<td>1</td>
</tr>
<tr>
<td>Age totals</td>
<td>10</td>
</tr>
</tbody>
</table>
Table 3.5 displays the relationship between the age of the learner and the mode of cultural transmission within each domain. To examine developmental relationships, Tables 3.5 and 3.6 omit data with age coded as childhood, all ages, and unknown. In many cases frequencies were low and do not warrant reporting; however, a few interesting results emerge. In the subsistence skills and knowledge domain, oblique and vertical transmissions were approximately equivalent (20 and 21 instances, respectively) during childhood generally. During early childhood subsistence skills and knowledge-related cultural transmission were predominantly vertical (15 instances), whereas horizontal transmission (3) and oblique transmission (1) were relatively infrequent. During middle childhood there was a reduction in the relative importance of vertical transmission (7) with a slight increase in the importance of oblique transmission (4). This trend continues into adolescence where oblique transmission was the most frequent mode of subsistence-related cultural transmission, with oblique noted in five instances and oblique concerted noted twice. Vertical transmission was identified twice in adolescence. In the cultural values and kinship domain, vertical transmission is the most frequent in the more general coding of childhood (17), with oblique (9) and horizontal (5) transmission following.
Table 3.5: Relationship between age of learner and mode by cultural domain

<table>
<thead>
<tr>
<th>Age–mode</th>
<th>Domains</th>
<th>Subsistence skills and knowledge</th>
<th>Religious beliefs and practices</th>
<th>Language</th>
<th>Ecology</th>
<th>Miscellaneous skills</th>
<th>Manufacture</th>
<th>Cultural values and kinship</th>
</tr>
</thead>
<tbody>
<tr>
<td>Infancy, horizontal</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Infancy, vertical</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Infancy, oblique</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Early childhood, horizontal</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Early childhood, vertical</td>
<td>15</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>4</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Early childhood, oblique</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Middle childhood, horizontal</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Middle childhood, vertical</td>
<td>7</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Middle childhood, oblique</td>
<td>4</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Adolescence, horizontal</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Adolescence, vertical</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>3</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Adolescence, oblique</td>
<td>7</td>
<td>13</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>5</td>
</tr>
</tbody>
</table>

Table 3.6 depicts the relationship between the age of the learner and the associated processes of cultural transmission across all domains. Concerning the teaching process of cultural transmission, 48% of codes were associated with the more general age classification of childhood. The next most frequent association with teaching was adolescence, which accounted for 16% of all teaching codes. Teaching in middle childhood accounted for 12.9% and in early childhood accounted for 8% of all teaching codes. Observation and imitation was predominately linked to childhood generally (75% of all observation and imitation codes); however, early childhood also stands being associated with 52% of all observation and imitation codes.
### Table 3.6: Relationship between age of learner and process by cultural domain

<table>
<thead>
<tr>
<th>Age, process</th>
<th>Domains</th>
<th>Subsistence skills and knowledge</th>
<th>Religious beliefs and practices</th>
<th>Language</th>
<th>Ecology</th>
<th>Miscellaneous skills</th>
<th>Manufacture</th>
<th>Cultural values and kinship</th>
</tr>
</thead>
<tbody>
<tr>
<td>Infancy, observation and imitation</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Infancy, collaborative learning</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Infancy, teaching</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Infancy, stimulus enhancement</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Infancy, local enhancement</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Infancy, individual learning</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Early childhood, observation and imitation</td>
<td>10</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Early childhood, collaborative learning</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Early childhood, teaching</td>
<td>4</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Early childhood, stimulus enhancement</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Early childhood, local enhancement</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Early childhood, individual learning</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Middle childhood, observation and imitation</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Middle childhood, collaborative learning</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Middle childhood, teaching</td>
<td>9</td>
<td>4</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Middle childhood, stimulus enhancement</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Middle childhood, local enhancement</td>
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Evaluations of social learning patterns in reference to sex were coded as male, female, or both, as well as general statements without specific reference to sex. The following results concerning sex differences exclude the both and general evaluation and exclusively evaluate instances of male-specific and female-specific social learning. Investigating relationships between male and female-specific social learning carries implications for sex differences and
sex-patterned aspects of culture among hunter-gatherers. Across the domains, a few were biased toward males. The religious beliefs and practices domain included 24 (86%) instances of male-based social learning and 4 (14%) instances of female-based social learning. The subsistence skills and knowledge domain included 36 (58%) references to male-specific social learning and 26 (42%) references to female-specific social learning. The miscellaneous skills domain included 11 (73%) instances of male-based social learning and 4 (27%) instance of female-based social learning. The ecology domain was also male biased with five of seven (71%) total occurrences specific to males. The manufacturing domain was relatively equally distributed between the sexes with 14 (52%) concerning males and 13 (48%) concerning females. Female social learning constitutes the majority within the cultural values and kinship domain with 12 instances (60%) compared to 8 (40%) for male-specific social learning.

Concerning modes of social learning, males were more likely to acquire cultural information horizontally, noted in 12 instances (75%), and obliquely, noted in 49 instances (73%). Vertical transmission was relatively equal between the sexes with 39 (53%) instances of female-specific and 34 (47%) instances of male-specific vertical transmission.

Across processes of social learning, collaborative learning (all types) was in favor of males with ten instances (83%) compared to only two mentions of female-specific collaborative learning. Teaching also demonstrates a slight male bias across all subcategories. The sample included 65 (62%) instances of male-specific teaching and 40 (38%) instances of female-specific teaching. Observation and imitation was recorded equally between males and females with 14 occurrences each. Local enhancement was also approximately equal with four instances of female-specific and three instance of male-specific local enhancement. Stimulus enhancement
exhibits a male bias although there are few occurrences; of five occurrences of stimulus enhancement, four were specific to males.

**Discussion:**

The most interesting finding from this study is the importance of teaching across a wide range of cultural domains among hunter-gatherers. Teaching is the most common process of social learning in each domain. In the context of social learning, teaching has been defined as “as modification of one’s behaviour to facilitate learning of information, knowledge or skills in another” (Hewlett et al. 2011, p. 1169). Our operationalization of teaching is consistent with this definition. As previously discussed, cultural anthropologists have long downplayed the importance of teaching among hunter-gatherers (Lancy and Grove 2010; Mead 1930; Rogoff 1990; Rogoff et al. 2007). Western styles of formal education and concerted efforts by parents to teach their children in industrial settings are contrasted with a laissez faire approach toward development and instruction in traditional foraging populations (Lancy 2010). However, some authors have begun to deconstruct this long-standing distinction and have provided evidence against perspectives that promote the absence of teaching in small-scale societies (Hewlett et al. 2011; Klein 2015). Ultimately, teaching as defined in the social learning literature is likely a uniquely human trait and occurs only rarely among nonhuman animals if at all (Konner 2010). Teaching complex skills and ideas requires symbolic communication (Hauser et al. 2002; Pagel 2009; Pinker and Jackendoff 2005). Language and teaching are hallmarks of humanity and the idea that teaching is absent or lacking among hunter-gatherers is logically unsound and not supported by the ethnographic record (Kruger and Tomasello 1996; Tomasello 2009); this holds for our systematic study as well as other reviews of classic ethnographies and ethnographic settings (Hewlett et al. 2011; Konner 2010; Kruger and Tomasello 1996). Given the intimate
nature of hunter-gatherer social life, it is not surprising teaching dominates social learning. Cooperative breeding necessitates teaching young children by both kin and non-kin (Burkart et al. 2009). Our results indicate a high cross-cultural prevalence and importance of teaching supporting many researchers in the field (e.g., Kruger and Tomasello 1996; Klein 2015; Hewlett et al. Chap. 3, this volume).

Observation and imitation remains critical, and several ethnographers noted parents encourage observational learning, demonstrating tasks with limited verbal instruction. Condon (1983) explains among the Copper Inuit, “Young boys...are more likely to be taken out hunting and trapping with their fathers, at which time they are instructed in the finer details of hunting, trapping, cold-weather camping, snowmobile repair, etc. Instruction in these areas...tends to be a nonverbal process. Parents do not verbally instruct their children at various tasks, but expect them to learn through observation. In fact, the persistent asking of questions is regarded as ‘childish’.” However, this history of downplaying the importance of teaching among foragers may reflect a shortsighted conception of teaching overlooking the role of various forms of teaching, such as natural pedagogy, which is hypothesized to be a psychological adaptation that has evolved across hominid evolution (Csibra and Gergely 2011). The finding that teaching is more dominant in social learning among hunter-gatherers relative to observation and imitation could in part stem from the focus and attention of ethnographers. Teaching is an easily observable process that can garner the attention of the group. There are multiple forms of teaching that generally involve a process of interaction. Learning by observation may be less obvious. Despite the numerous accounts of observational learning in the ethnographic record, it may be that ethnographers simply documented teaching more frequently than observational learning. Additionally, ethnographers may have a cultural bias in favor of the importance of
teaching given the emphasis of this process of learning in Western culture. Regardless, these results reveal uniformity in ethnographic accounts; teaching is important and frequent among hunter-gatherers and has likely been a common process of social learning cross-culturally and throughout human evolution (Csibra and Gergely 2011; Kruger and Tomasello 1996; Thornton and Raihani 2008).

Consistent with Hewlett et al. (2011), vertical transmission appears to be an important mode of cultural transmission among hunter-gatherers, especially in early childhood. However, oblique transmission is nearly as common as vertical transmission, and the aggregate of oblique transmission and the two subcategories, concerted and prestige bias, outranks vertical transmission by 6.4%. This suggests across childhood and the life span oblique transmission dominates cultural learning. As cooperative breeders, we can expect oblique transmission to be important among hunter-gatherer groups (Hewlett et al. 2011). Ethnographic descriptions often mentioned a wide range of adults taking care to transmit cultural information. As soon as the child begins spending significant time outside the home and beyond the reach of parents, the frequency of oblique transmission increases. Concomitantly, collaborative horizontal transmission increases, primarily in the form of children’s play.

Surprisingly, prestige bias was infrequently mentioned and only in the subsistence skills and knowledge, miscellaneous skills, ecology, and manufacturing domains. Prestige-biased learning has been widely discussed and documented in observational research and is expected to be an important aspect of children’s social learning specifically and cultural adaptation generally (Chudek et al. 2011). Identifying and rewarding prestigious individuals, in a given cultural context, is an evolved psychological adaptation (Henrich and Gil-White 2001), and prestige is associated with greater reproductive success across many different populations (Hill 1984;
Reyes-García et al. 2008). Perhaps the overarching and vestigial conception of egalitarian hunter-gatherers lacking prestige systems has contributed to ethnographers overlooking the importance of skill performance-directed learning. The ethnographic record does not highlight the importance of prestige-biased social learning to the degree that observational research and the theoretical literature suggest.

Comparing the relative frequency of data in different cultural domains partially reveals the priority of ethnographers and the general content of the ethnographic record of social learning. The process of learning subsistence skills has been widely discussed in the ethnographic record. The foraging lifestyle has been of great interest and especially among cultural ecologists. The degree to which contemporary hunter-gatherers can inform us of evolutionary history has also promoted a focus on subsistence (Lee and DeVore 1968; Slocum 1975). Religious beliefs, manufacturing technology, and cultural values and kinship typically receive a section or chapter in the standard ethnographic format, and these domains are relatively equally discussed. It is surprising that the process of learning language is so rarely mentioned. Linguistics has long been a component of anthropology, and cognitive psychologists and symbolic anthropologists have focused heavily on the diversity and role of language; however, this is not reflected in this sample of ethnographies.

Subsistence skills and practices are highly vertically transmitted. Parents are the primary agents in the cultural transmission of subsistence skills during early childhood with other adults in the community participating in the cultural education of subsistence-based knowledge later in childhood and adolescence. This supports and helps to explain the perspective that subsistence skills remain stable across several generations (Hewlett and Cavalli-Sforza 1986). Additionally, transmitting knowledge about the local ecology and various manufacturing practices is
predominantly the responsibility of the parents. Along with the subsistence domain, these are the only cultural domains in which vertical transmission is the most common. This suggests transmission of these skills and information occurs early and is highly conserved across generations, which is consistent with Zarger’s findings on the nature of learning about the environment (Zarger 2010), but inconsistent with other research suggesting the acquisition of ethnobotanical knowledge is predominantly oblique (Reyes-García et al. 2009). This may be due to the wide geographic range of societies in this sample and variation in the importance of ecological and ethnobotanical knowledge.

The transmission of religious beliefs and practices is primarily from the community of adults to a younger generation and is often concerted in that many adults deliver a consensus cultural message; many initiation rituals fall into this category. Teaching, including teaching in the form of storytelling and demonstration, is the primary process by which children and adolescents acquire religious-based knowledge. Similarly, cultural values and knowledge concerning kinship systems and kin-specific behavior are most commonly transmitted obliquely. As children become older and begin to spend more time away from their nuclear family, they begin to acquire ideological cultural information from a wide range of adults and older children. Learning religious beliefs may be distinct from subsistence-based and ecological knowledge, but is likely equally important to be a successful member of society and integrate with the wider community.

These results examine several theories of cultural transmission (Boyd and Richerson 1985; Cavalli-Sforza et al. 1982; Hewlett and Cavalli-Sforza 1986; Richerson and Boyd 2005) and provide a foundational reference for further research investigating specific domains and processes in specific cultural contexts. Despite the low frequency of particular modes or
processes in this sample, our results speak to the suite of mechanisms of social learning. We emphasize that various modes and processes are not mutually exclusive and all are likely to be present in any human population. This study could be expanded to include more stratified traditional societies, in order to highlight the unique nature (or lack thereof) of hunter-gatherer social learning. We provide greater external validity to observational research and theoretical literature highlighting the importance of teaching across a wide range of cultures and cultural domains while also supporting the finding that vertical transmission is dominant early in life with various forms of oblique transmission being more important throughout life in hunting and gathering societies (Reyes-García et al. Chap. 4, this volume).

Acknowledgment:

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CHAPTER FOUR:
INVESTIGATING EVOLUTIONARY MODELS OF LEADERSHIP AMONG RECENTLY SETTLED ETHIOPIAN HUNTER-GATHERERS

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Abstract:

Humans are thought to have evolved in small, egalitarian hunter-gatherer societies. Evolutionary theories of leadership, which draw heavily on studies of contemporary hunter-gatherer and other small-scale societies, have proposed numerous traits that putatively characterize leaders in domains of sociality, productivity, reproduction, dominance, and cognition. We investigated many such traits among the Chabu, an Ethiopian population of former hunter-gatherers who now subsist on hunting, gathering, horticulture, and cash crops. There were strong positive correlations among most traits across domains, which, in turn, were positively associated with elected leader status among both women and men. Measures of prestige and dominance were largely independent, and although both predicted leader status, prestige was more important. Biased social learning was a modest predictor of leader status but a stronger predictor of respect. Revised evolutionary theories of leadership must account for the importance of women leaders and the strong covariation of traits.

Introduction:

For the vast majority of human evolutionary history, people lived as hunter-gatherers in small nomadic bands with a stochastic resource base and, based on analogy with contemporary hunter-gatherers, social structures likely characterized by a lack of inherited social distinctions, a cultural ethos of sharing, and a high degree of egalitarianism (c.f., Binford, 2001; Formicola, 2007; B. S. Hewlett, 2016; Kelly, 2013; Lee & Daly, 1999; Marlowe, 2005; Mattison, Smith, Shenk, & Cochrane, 2016; Vanhaeren & d’Errico, 2005). Putatively, it is in this broad socioecological 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; Sahliks, 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 always, prosocial in nature (Henrich et al., 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 (Knauff 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; Knauff 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, Von Rueden, & Hagen, 2019; Garfield, Hubbard & Hagen, 2019; Smith, Ortiz, Buhbe, & Van Vugt, 2018), 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, & 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 et al. (2003) concept of neural capital (Garfield et al., 2019). In brief, Garfield et al. (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 et al., 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 et al., 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, 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 et al., 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 et al., 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 & Gil-White (2001) pointed out, however, that this did not explain why men would defer to other prestigious men.

Henrich & 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, & Henrich, 2010; Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013; Henrich & Gil-White, 2001; Henrich et al., 2015; Richerson & Henrich, 2012). Henrich & 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 et al., 2013).

Experimental evidence from Western populations supports the distinction between dominance and prestige (Cheng et al., 2010, 2013). There is also significant cross-cultural evidence that leaders use both dominance and prestige-based strategies to achieve positions of
influence (Barkow, 1989; Garfield et al., 2019; Gurven & Von Rueden, 2006; Kracke, 1978; Tiger & Fox, 1971; Von Rueden et al., 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 et al., 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. An extensive analysis of over 1000 ethnographic accounts of leadership found little evidence that prestigious leaders served as models for social learning (Garfield et al., 2019). Yet absence of evidence is not evidence of absence. It could easily be the case that the limited ethnographic evidence for the Henrich & 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 et al., 2018, 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 et al., 2013; Henrich et al., 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 et al., 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 2,000 forager-horticulturalists who reside in the remote highland forest areas of Southwestern Ethiopia spanning the regional states of Oromia; Southern Nations, Nationalities and Peoples Region (SNNPR); and Gambela (Dira & Hewlett, 2017; Kibebe, 2015). Most scholarly work on the Chabu focused on classifying their language (often mistakenly identified as Shabo or Mekeyir), relying on informants from rural multi-ethnic villages (Bender, 1975; Ehret, 1992; Fleming, 1991; see Kibebe, 2015 for review). More recent linguistic analyses based on forest dwelling informants suggests Chabu is the sole remnant language of a previously undocumented African language phylum (Schnoebelen, 2009; Kibebe, 2015).

The Chabu have only recently been the focus of any systematic or ethnographic research (e.g., Dira & Hewlett, 2016, 2017, 2018; B. L. Hewlett, 2016). 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 & 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 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.

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

**Figure 4.1:** The Chabu Kebele leadership system. Each box is one leader. Solid border: Major leader. Dashed border: Minor leader.
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 & 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 & 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 Figure 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. This sample included 3 male Kebele leaders, 2 female Kebele leaders, highly

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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.
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 et al., 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 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).
### Table 4.1: Peer-rated variables in five domains, and participant prompts.

<table>
<thead>
<tr>
<th>Domain</th>
<th>Variable name</th>
<th>Participant prompt</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cognitive</td>
<td>Consistency in quality decision</td>
<td>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.</td>
</tr>
<tr>
<td>Cognitive</td>
<td>Level of expertise</td>
<td>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.</td>
</tr>
<tr>
<td>Cognitive</td>
<td>Learning and intelligence level</td>
<td>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</td>
</tr>
</tbody>
</table>
(Learning and intelligence) 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 people 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 people 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.

<table>
<thead>
<tr>
<th>Productivity</th>
<th>Hunting returns (Hunting)</th>
</tr>
</thead>
<tbody>
<tr>
<td>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.</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Reproductive</th>
<th>Parental (Parenting)</th>
</tr>
</thead>
<tbody>
<tr>
<td>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.</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Reproductive</th>
<th>Spousal quality (Spouse)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Some people have a better spouse than others. Better spouses might be better partners, better workers, better parents, or more attractive. Look at the photos and rank them based on the quality of the individual’s current spouse from highest quality to lowest quality.</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Social</th>
<th>Number of allies (Allies)</th>
</tr>
</thead>
<tbody>
<tr>
<td>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.</td>
<td></td>
</tr>
<tr>
<td>Social</td>
<td>Conflict resolution skill (Conflict)</td>
</tr>
<tr>
<td>Social</td>
<td>Kin investment (Kin)</td>
</tr>
<tr>
<td>Social</td>
<td>Level of likability (Likable)</td>
</tr>
<tr>
<td>Social</td>
<td>Prosocial investment (Prosocial)</td>
</tr>
</tbody>
</table>
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.

**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.

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(β). 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

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

and for logistic regression:

$$-\text{loglik}(\beta)/n + \lambda \ast \text{penalty}$$
There are two popular forms of penalized regression: ridge regression and lasso regression. For ridge regression the penalty is \( ||\beta||_2^2 = \sum_{j=1}^{p} \beta_j^2 \), where the \( \beta_j \) 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 \( \beta_j \) are “shrunk” to 0. Thus, when \( \lambda \) is small, the \( \beta \)'s are relatively unrestricted, which can result in a good fit to the current sample (low bias), but a poor fit on future samples (high variance); roughly, the model will tend to be over-fitted. When \( \lambda \) is large, the \( \beta \)'s tend to shrink toward 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 \( \lambda \) is typically found by minimizing 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 \( \alpha \), \( 0 \leq \alpha \leq 1 \):

\[
\text{penalty} = (1 - \alpha)/2||\beta||_2^2 + \alpha||\beta||_1.
\]
Thus, $\alpha = 0$ is the ridge penalty and $\alpha = 1$ is the lasso penalty. With intermediate values of $\alpha$, 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 cross-validation to find the optimum values of $\lambda$ and $\alpha$, i.e., ones that minimized cross-validation error. We also chose a second $\lambda$ 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 $\lambda$ and therefore decrease false positives. For both elastic net regression models we report coefficients from the optimal $\lambda_{\text{min}}$ model and the more conservative $\lambda_{\text{1se}}$ model.

*Bayesian regression*

Numerous studies have found that prestige and/or dominance are associated with leadership and increased social status (Cheng et al., 2010, 2013; Gurven & Von Rueden, 2006; Laustsen & Petersen, 2017; Price, 2003; Von Rueden et al., 2011, 2014) which is supported by a rich body of theory and ethnography (Barkow, 1989; Boehm, 1993; Garfield et al., 2019; Henrich & Gil-White, 2001; Henrich et al., 2015; 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 4.2). The first model used informative Gaussian priors derived from metanalyses 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, & others, 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 4.2.

Table 4.2: 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 Figure 4. Values are log odds.

<table>
<thead>
<tr>
<th>Prior</th>
<th>Intercept</th>
<th>Prestige</th>
<th>Dominance</th>
<th>Sex</th>
<th>Age</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weakly informative Gaussian</td>
<td>$N(0,1)$</td>
<td>$N(0,1)$</td>
<td>$N(0,1)$</td>
<td>$N(0,1)$</td>
<td>$N(0,1)$</td>
</tr>
<tr>
<td>Informative Gaussian</td>
<td>$N(0,1)$</td>
<td>$N(2.63,0.52)$</td>
<td>$N(2.01,0.46)$</td>
<td>$N(0,1)$</td>
<td>$N(0,1)$</td>
</tr>
</tbody>
</table>
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 (Figure S1). We therefore used an “errors-in-variables” model, also known as a Bayesian measurement error model, in which the predictors are a distribution of values with a mean, computed as the mean peer-rating for each trait for each individual, and a standard error of the mean (McElreath, 2018; Stefanski, 2000):

\[
\text{Leadership status} \sim \text{Bernoulli}(p_i) \\
\logit(p_i) = \beta_0 + \beta_1 \text{Prestige}_i + \beta_2 \text{Dominance}_i + \beta_3 \text{Sex}_i + \beta_4 \text{Age}_i \\
\text{Prestige}_i \sim N(\text{Prestige}_{\text{obs},i}, \text{Prestige}_{\text{SE},i}) \\
\text{Dominance}_i \sim N(\text{Dominance}_{\text{obs},i}, \text{Dominance}_{\text{SE},i})
\]

We centered and scaled all continuous variables by one standard deviation, and then fit both Bayesian models in R (R Core Team, 2017) using Stan and the rstan package (Stan Development Team, 2018). (Unfortunately, the elasticnet 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 & 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 as pigs and buffaloes and is a generally considered a risky strategy but is an efficient technique for strong and skilled hunters (see Dira & Hewlett, 2016, 2017). Dirba hunting is likely the most culturally salient domain of traditional leadership among the Chabu. A collective hunt is organized by the owner of hunting dogs who informs neighbors of plans to hunt the following day. Those interested will join. During the hunt, all hunters may act independently and disperse, radiating from and following the pack of hunting dogs. The hunt leader, however, may also direct and coordinate hunters once the dogs have identified the location of a prey animal. If the animal is first identified by a dog but speared by a hunter other than the hunt leader, the hunt leader has authority over the kill and the distribution of meat. If dogs were not involved in identifying the prey, the hunter who made the kill oversees the distribution of meat. In either case, meat is distributed equally among the hunters, who then share with kin, neighbors, and social partners.

The Chabu show some respect and deference towards elders (gutare) and acknowledge that some individuals within age and sex grades are more respected than others. Individuals earn respect by offering effective solutions to community dilemmas, such as resolving conflicts between village members (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; 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 $\alpha$, 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 ($\alpha = 0.65$) than on male traits ($\alpha = 0.75$) 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 Figure 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 4.3 for summary statistics.
Table 4.3: Summary statistics. A: Study variables for male data B: Study variables for female data

<table>
<thead>
<tr>
<th>A: Column</th>
<th>n</th>
<th>Min</th>
<th>Max</th>
<th>Mean</th>
<th>SD</th>
<th>Gini</th>
<th>Histogram</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (estimated)</td>
<td>34</td>
<td>18.000</td>
<td>93.000</td>
<td>36.353</td>
<td>16.457</td>
<td>0.221</td>
<td></td>
</tr>
<tr>
<td>Height</td>
<td>34</td>
<td>156.000</td>
<td>177.500</td>
<td>166.691</td>
<td>5.098</td>
<td>0.017</td>
<td></td>
</tr>
<tr>
<td>Grip strength</td>
<td>34</td>
<td>10.100</td>
<td>55.600</td>
<td>38.768</td>
<td>9.216</td>
<td>0.120</td>
<td></td>
</tr>
<tr>
<td>Prestige</td>
<td>34</td>
<td>0.223</td>
<td>0.924</td>
<td>0.515</td>
<td>0.188</td>
<td>0.208</td>
<td></td>
</tr>
<tr>
<td>Dominance</td>
<td>34</td>
<td>0.305</td>
<td>0.928</td>
<td>0.526</td>
<td>0.147</td>
<td>0.155</td>
<td></td>
</tr>
<tr>
<td>Mentor salience</td>
<td>34</td>
<td>0.000</td>
<td>0.273</td>
<td>0.042</td>
<td>0.064</td>
<td>0.705</td>
<td></td>
</tr>
<tr>
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<td>0.648</td>
<td>0.093</td>
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</tr>
<tr>
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</tr>
<tr>
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<tr>
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<td>0.232</td>
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<tr>
<td>Feared</td>
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<td>0.210</td>
<td>0.988</td>
<td>0.516</td>
<td>0.183</td>
<td>0.202</td>
<td></td>
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<tr>
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<td>0.514</td>
<td>0.206</td>
<td>0.222</td>
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<tr>
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<td>0.952</td>
<td>0.513</td>
<td>0.207</td>
<td>0.227</td>
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<tr>
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<td>0.504</td>
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<table>
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<th>n</th>
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<th>Max</th>
<th>Mean</th>
<th>SD</th>
<th>Gini</th>
<th>Histogram</th>
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<td>0.827</td>
<td>0.526</td>
<td>0.176</td>
<td>0.195</td>
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<td>0.531</td>
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<tr>
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<td>0.004</td>
<td>0.000</td>
<td>0.001</td>
<td>1.000</td>
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</tr>
<tr>
<td>Respect salience</td>
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<td>0.000</td>
<td>0.562</td>
<td>0.078</td>
<td>0.145</td>
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<td>0.874</td>
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<td>0.221</td>
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<td>0.524</td>
<td>0.177</td>
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<tr>
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<td>0.976</td>
<td>0.545</td>
<td>0.208</td>
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<tr>
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<td>26</td>
<td>0.235</td>
<td>0.970</td>
<td>0.527</td>
<td>0.199</td>
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</tr>
<tr>
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<td>0.525</td>
<td>0.223</td>
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<td>0.208</td>
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<tr>
<td>Respect</td>
<td>26</td>
<td>0.277</td>
<td>0.922</td>
<td>0.524</td>
<td>0.187</td>
<td>0.206</td>
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</tr>
<tr>
<td>Spouse quality</td>
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<td>0.198</td>
<td>0.953</td>
<td>0.531</td>
<td>0.181</td>
<td>0.191</td>
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<td>0.196</td>
<td>0.884</td>
<td>0.524</td>
<td>0.210</td>
<td>0.234</td>
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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 4.4, Figure 4.2A, 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 (Figure 4.2A). 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 (Figure 2B).
**Figure 4.2:** 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.

**Table 4.4:** Results of a priori tests of mean differences between leaders and non-leaders by sex with 95% CI.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Leader mean</th>
<th>Leader mean SE</th>
<th>Non-leader mean</th>
<th>Non-leader mean SE</th>
<th>Cohen’s d</th>
<th>95% CI Lower bound</th>
<th>95% CI Upper bound</th>
<th>Group</th>
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<td>Prestige</td>
<td>0.734</td>
<td>0.049</td>
<td>0.437</td>
<td>0.026</td>
<td>2.210</td>
<td>3.171</td>
<td>1.248</td>
<td>Men</td>
</tr>
<tr>
<td>Dominance</td>
<td>0.640</td>
<td>0.050</td>
<td>0.486</td>
<td>0.025</td>
<td>1.171</td>
<td>2.014</td>
<td>0.328</td>
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<tr>
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<td>0.060</td>
<td>0.529</td>
<td>0.037</td>
<td>0.159</td>
<td>0.952</td>
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<td>0.422</td>
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<td>3.579</td>
<td>1.551</td>
<td>Men</td>
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<tr>
<td>Spouse quality</td>
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<td>0.067</td>
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<td>0.026</td>
<td>1.739</td>
<td>2.640</td>
<td>0.839</td>
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</tr>
<tr>
<td>Trait</td>
<td>Men (Mean ± SD)</td>
<td>Women (Mean ± SD)</td>
<td>p-value</td>
<td>Description</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Mentor salience</td>
<td>0.098 ± 0.031</td>
<td>0.001 ± 0.0009</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Grip strength</td>
<td>42.889 ± 1.090</td>
<td>33.260 ± 1.497</td>
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<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Prestige</td>
<td>0.695 ± 0.079</td>
<td>0.717 ± 0.091</td>
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</tr>
<tr>
<td>Dominance</td>
<td>0.447 ± 0.040</td>
<td>0.554 ± 0.033</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Fighting</td>
<td>0.392 ± 0.034</td>
<td>0.581 ± 0.047</td>
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<td></td>
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</tr>
<tr>
<td>Learning and intelligence</td>
<td>0.620 ± 0.094</td>
<td>0.504 ± 0.043</td>
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<td></td>
<td></td>
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</tr>
<tr>
<td>Spouse quality</td>
<td>0.501 ± 0.000</td>
<td>0.504 ± 0.043</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tbody>
</table>

**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 Figure 4.3.
Figure 4.3A: Cluster analysis of peer-rated leadership traits. A. Female participant ratings. B. Male participant ratings. Colors in each cell represent the mean peer rating of each participant (columns) on each trait (rows). Columns are annotated with each participant's leadership status, mentor salience (above or below average), and age. Distance between row vectors computed with $1 - \text{cor}$. Distance between column vectors computed with the Euclidean metric. Clusters determined with the Ward agglomeration algorithm.

Figure 4.3B
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 $r = 0.58$ ($\text{min} = 0.075$, $\text{max} = 0.95$). See also Figures 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 (Figure 4.3A, 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 Figure 4.2).

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 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 (Figure 4.3), 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 $\lambda_{min}$ 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 $\lambda_{1se}$ model, most variables were equally strong positive predictors, consistent with the 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 Figure 4.4A. For coefficients, see Table S5A in the Supplementary Information.
In the Henrich et al. (2015) model, *Mentor salience* plays a central role in leadership, yet in our exploratory model of leader status, Figure 4.4A, 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, Figure 4.4B, Mentor salience was indeed the strongest predictor in the $\lambda_{\text{min}}$ model but was about equal to other social and reproductive variables, Spouse quality, Parenting, Likable, and Conflict, in the more conservative $\lambda_{1\text{se}}$ 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.
**Figure 4.4:** 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.

**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 et al., 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 Figure 4.5.
Figure 4.5: 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.

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 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 (Figure 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 were 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 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 Figure 4.6.

**Figure 4.6:** 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.
Table 4.5A: Weakly informative Gaussian prior model posteriors in log odds. All variables were centered and scaled by one standard deviation.

<table>
<thead>
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<th></th>
<th>Mean</th>
<th>Standard deviation</th>
<th>2.5%</th>
<th>97.5%</th>
</tr>
</thead>
<tbody>
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<td>(Intercept)</td>
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<td>0.492</td>
<td>-2.73</td>
<td>-0.81</td>
</tr>
<tr>
<td>Prestige</td>
<td>2.00</td>
<td>0.509</td>
<td>1.06</td>
<td>3.05</td>
</tr>
<tr>
<td>Dominance</td>
<td>0.73</td>
<td>0.467</td>
<td>-0.16</td>
<td>1.67</td>
</tr>
<tr>
<td>Age</td>
<td>-0.54</td>
<td>0.470</td>
<td>-1.51</td>
<td>0.33</td>
</tr>
<tr>
<td>Sex</td>
<td>0.01</td>
<td>0.593</td>
<td>-1.16</td>
<td>1.17</td>
</tr>
<tr>
<td>log-posterior</td>
<td>-83.09</td>
<td>7.922</td>
<td>-99.57</td>
<td>-68.68</td>
</tr>
</tbody>
</table>

Table 4.5B: Final informative Gaussian prior model posteriors in log odds.

<table>
<thead>
<tr>
<th></th>
<th>Mean</th>
<th>Standard deviation</th>
<th>2.5%</th>
<th>97.5%</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-2.07</td>
<td>0.558</td>
<td>-3.19</td>
<td>-1.00</td>
</tr>
<tr>
<td>Prestige</td>
<td>2.86</td>
<td>0.428</td>
<td>2.04</td>
<td>3.72</td>
</tr>
<tr>
<td>Dominance</td>
<td>1.74</td>
<td>0.381</td>
<td>1.00</td>
<td>2.50</td>
</tr>
<tr>
<td>Age</td>
<td>-1.03</td>
<td>0.624</td>
<td>-2.31</td>
<td>0.13</td>
</tr>
<tr>
<td>Sex</td>
<td>-0.26</td>
<td>0.819</td>
<td>-1.89</td>
<td>1.33</td>
</tr>
<tr>
<td>log-posterior</td>
<td>-79.49</td>
<td>7.905</td>
<td>-95.88</td>
<td>-64.87</td>
</tr>
</tbody>
</table>

*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 (Figure 4.7) 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 Figure S9 in the Supplementary Information for more detail.
**Figure 4.7:** Hierarchical cluster analyses of grip strength, height, and peer-rated variables.

Distance was $1 - \text{cor}$. Clusters agglomerated with the Ward algorithm.

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 Figure 4.8.
Figure 4.8: *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.

**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 (Figure 4.3).

Our more conservative elastic net regression model of leader status, $\lambda_{1se}$ (Figure 4.4A) found that the coefficients of most predictor variables were of similar positive magnitude. The less conservative model, $\lambda_{min}$, however, found that *Spouse quality, Respect, Conflict resolution,* and *Feared* had larger coefficients than other variables. This 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 et al., 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 et al., 2008, 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 Figure 4.2). 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 Figure 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 (Figure 4.4) and our Bayesian models (Figure 4.6). These results should encourage the incorporation of women into evolutionary theories of leadership. Garfield et al. (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. 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 et al., 2018; Smith et al., 2018; 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 (Figure 4.5), verifying the distinction between prestige and dominance (Barkow, 1989; Cheng et al., 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 et al., 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 (Figure S10 in the Supplementary Information), associations supported by our preregistered bivariate tests (Figure 4.2).
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 (Table 4.5A and B and Figure 4.6), 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 theories and empirical findings in both large-scale and small-scale societies (Barkow, 1989; Chapais, 2015; Cheng et al., 2013; Henrich & Gil-White, 2001; Kracke, 1978; Price & Van Vugt, 2014; Tiger & Fox, 1971; Von Rueden et al., 2011, 2014).

In support of biased learning towards leaders, a unique prediction of the Henrich & Gil-White (2001) model, Mentor salience was clearly associated with leadership in the bivariate test (Figure 2) and cluster analysis heatmaps (Figure 4.3), was a positive predictor of leadership in the exploratory elastic net model (Figure 4.4A), and was the strongest predictor of Respect salience in the less conservative $\lambda_{\text{min}}$ elastic net model (Figure 4.4B). 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 (Figure 4.4A), which does not support the special role of biased learning towards prestigious leaders as suggested by Henrich & Gil-
White (2001), Cheng et al. (2013), and Henrich et al. (2015). Furthermore, Figure 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 & Gil-White (2001) and Cheng et al. (2013).

Chabu leaders are not physically stronger than non-leaders nor are they more likely to fight with others (Figure 2), contrary to predictions of the dominance model, and inconsistent with Von Rueden et al. (2014). Our Fighting variable is based on peer-rated propensity for verbal and physical fighting, however, whereas Von Rueden et al. (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; Knauff 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 & Gil-White (2001). In men, greater grip strength is associated with being feared, whereas in women older age also plays a role (see Figure 8). We failed to find any effect of height associated with leadership (consistent with Von Rueden et al., 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 (Figures 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-equalitarian population, dominant women are less preferred as leaders than non-dominant women.

**Limitations and future research**

Our study had a cross-sectional design that assessed correlations between perceived traits and elected leader status. Our predictors were endogenous, imperfectly operationalized, and imperfectly measured. We therefore cannot determine cause and effect. We also did not measure actual decisions or instances of leadership. All participants belonged to a single large Chabu community. Our results therefore might not generalize to smaller Chabu communities, particularly the small extended family settlements (Dira & Hewlett, 2017). The strong correlation among most of our variables along with a relatively small sample size limited our ability to clearly discriminate which variables best predicted leader status. Finally, although leaders tended to be married to other leaders, we did not investigate the relationship between marriage and achieving leader status. These political couples warrant further research.
Our analysis of sex differences might have been biased because female leader status included major and minor leaders, whereas male leader status was limited to major leaders. Our decision to operationalize leaders status as such was based on (1) heatmaps in Figures 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. 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 et al., 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 et al., 2019, 2018; Smith et al., 2018), 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 et al., 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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doi:10.1016/j.evolhumbehav.2010.02.004

doi:10.1037/a0030398


doi:10.1098/rstb.2015.0010


techniques to identify the number of latent factors: A simulation and tutorial.

https://doi.org/10.31234/osf.io/gzcre


doi:10.1080/10705511.2016.1186549


Scholars across the social and biological sciences are increasingly focusing on leader-follower dynamics across diverse populations and species, often relying on evolutionary theory in formulating hypotheses and interpreting observations. Leadership is a multifaceted phenomenon and empirical studies and theoretical models often focus on specific dimensions, such as the emergence of leadership in collective actions, the qualities of group-level leaders including the reproductive skew and mating behavior of leaders, follower preferences and ‘voting’ patterns, or the services leaders provide in distinct contexts. Some theories of leadership are context specific, whereas other purport to capture universal features of leader-follower behavior.

The dominance-prestige model of leadership makes unique predictions on the qualities of leaders and variation in follower preferences and provides a theoretical account for the origins of human leadership (Barkow, 1989; Cheng, Tracy, Foulsham, Kingstone, & Henrich, 2013; Henrich & Gil-White, 2001). Prestige-biased learning is strongly implicated in culture change and the formation of social hierarchy across human evolution and in certain cultural contexts (Boyd & Richerson, 1985; Cavalli-Sforza & Feldman, 1981; Henrich, Chudek, & Boyd, 2015). Several theories on prestige and social learning have emerged in recent years, yet largely remain untested.

This dissertation advances the dominance-prestige model of leadership and models of prestige-biased social learning in three ways: (1) in reviewing the emerging literature on non-human animal leadership and paleoanthropological evidence and challenging the claim that prestige, defined as deference to individuals based on knowledge and expertise, is uniquely
human; (2) investigating the domains, modes, and processes of social learning, including prestige-biased social learning, cross-culturally among ethnographically described hunter-gatherers; (3) formally testing the dominance-prestige model of leadership, including the social learning component of leadership and prestige, among a small-scale relatively egalitarian society with male and female elected leaders. Collectively, this work integrates theoretical frameworks and provides novel empirical evidence supporting components of influential theoretical models, while also presenting new challenges to mainstream theories on leadership, prestige, and social learning.

Prestige is a ubiquitous and near universal component of human leadership (Garfield, Hubbard, & Hagen, 2019). For decades theorists have suggested “prestige” to be uniquely human and dependent upon symbolic and cumulative culture. Theories on the origins of prestige, i.e. the universal components of human leadership, must account for the many processes of leadership and followership which stem from informational asymmetries and knowledge-based deference documented across diverse taxa (Garfield, von Rueden, & Hagen, 2019). Systematic, cross-cultural evidence suggests prestige-biased learning may not be as frequent among hunter-gatherers as some theories suggest, even in the context of widespread active teaching (Garfield, Garfield, & Hewlett, 2016). Therefore, the prestige-biased learning account of social influence and social structure is likely incomplete and does not sufficiently explain the evolutionary origins of prestige-biased learning or prestige-based leadership. This dissertation did find both prestige and dominance to be associated with leadership in a small-scale, relatively egalitarian society, supporting the dominance-prestige model of leadership; however, it failed to find a strong association between leader status and social learning preferences (Garfield & Hagen, 2019). Furthermore, in the small-scale society investigated here, when social learning
preferences are biased towards leaders, those individuals can be characterized as both prestigious and dominant, contrary to the predictions of contemporary evolutionary theories on prestige, dominance, and social learning (e.g., Cheng et al., 2013; Henrich et al., 2015; Richerson & Henrich, 2012).

Results from this dissertation suggest a synthetic revision on the origins of prestige-based leadership is required. Garfield & Hagen (in preparation), building on theoretical review (Garfield et al., 2018), cross-cultural analyses (Garfield et al., 2016, 2019), and results on leadership among the Chabu (Garfield & Hagen, 2019), suggest the evolution of human prestige remains a conundrum and a complete theory on the evolution 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; (4) the respect and deference afforded to prestigious adults; and (5) the generosity of prestigious individuals in small-scale societies. The Computation Services model and Joint Utility Improvement hypothesis addresses these criteria, suggesting individuals that exhibit high-quality decision making and offer neural capital-based computational services that benefit themselves as well as others, will be chosen as leaders and preferred as mates (Garfield et al., 2019; Garfield & Hagen, in preparation).
REFERENCES:


https://doi.org/10.21237/C7clio3112453
Chapter Four Supplementary Information:

Data collection procedures

Height was measured in centimeters using a measuring tape from the base of the heel to the top of the head. Grip strength was measured in kilograms of pressure using the Cambry digital hand dynamometer following the NHANES protocol (Centers for Disease Control and Prevention, 2012). After a demonstration of use, participants provided right hand and then left hand measurements, three times sequentially. Our grip strength measure is the mean value of the highest recorded value of each hand (three participants with injured right hands only provided data using the left hand and the maximum value was used as the grip strength measure for these participants).

Age estimation

Like many small-scale, non-literate populations, the Chabu do not keep track of years or have a clear idea of their own age. They do however often know the relative ages of similarly aged individuals. Our age estimation was not calculated systematically. We considered the participant’s self-reported age, but primarily relied on relative comparisons, the insight of both research assistants, and a consideration of the participant’s sibship and number and ages of their offspring. Age estimates are likely accurate within 5 years and very close to the relative ranking in the true ages of participants. Future data collection procedures will employ more systematic age estimation (e.g., Diekmann et al., 2017).

Salience score computations

A salience score for an item in a list is based on its order in the list relative to the total number of items in the list, with the item mentioned first having the highest score:

\[
salience = \frac{\max(order) - order + 1}{\max(order)}
\]
We then calculated the composite \textit{Mentor salience} for each named individual in each domain as the sum of his or her salience scores divided by the total number of raters:

\[ \textit{Mentor salience} = \frac{\sum s}{N} \]

where \( s \) = the individual item salience scores, and \( N \) = the participant sample size. Individuals with high \textit{Mentor salience} scores were named first by multiple participants, and those with low \textit{Mentor salience} scores were named later and/or less frequently. Participants who were not named as models for learning in a given domain were given a score of 0 on salience for that domain. For men, we computed their total \textit{Mentor salience} score as the average of their four \( S \) scores. Only one woman had a non-zero \( s \) score. Because women only participate in one of the four economic activities – farming – we simply assigned her the farming \( s \) score as her \textit{Mentor salience} score. Participants who were not listed were assigned a \textit{Mentor salience} score of 0.

We similarly computed the \textit{Respect salience} score for each participant who was mentioned in respected-persons freelisting prompt and assigned participants who were not listed a \textit{Respect salience} score of 0.

\textit{Peer-ratings and rater agreement}

Reyes-García et al. (2016) demonstrate peer-ratings are an efficient and accurate method for producing quantitative data from local knowledge. Methods for photography-based peer ratings are varied in anthropological field research (Hess, Helfrecht, Hagen, Sell, & Hewlett, 2010; Konečná & Urlacher, 2017; Patton, 2005; Reyes-García et al., 2008; Von Rueden et al., 2018, e.g., 2008). Approaches include complete rankings, block designs, and other randomization techniques. Von Rueden et al. (2018), used 12 peer-raters for a sample of 152 participants producing three unique ratings for two measures. The methods study by Reyes-
García et al. (2016) used six raters to evaluate a block of 20 individuals. Our peer-rating method is similar and consistent with the general distribution of other methods. We used a pool of seven peer-raters for a sample of 60 participants (with rankings conducted separately by sex) and collected five full ratings for each participant on each of the 17 peer-rated measures.

In our peer-rating data collection, raters were shown an array of photographs on a digital LCD screen (using the application Shotwell from Ubuntu MATE 16 running on a Raspberry Pi 3) of either all male participants or all female participants. Next, participants were read the prompt for the measure being rated (See Table 1) and instructed to point to the photograph of the individual who was the “top” for the given trait. The identified photograph was recorded and removed from the array. The process was iterated until only a single photograph remained. A within-sex relative ranking was then calculated (bounded between 0 and 1) for each participant for each peer-rated trait from each of the seven raters.
Figure S1: Cronbach’s $\alpha$ for each peer-rated variable. Sex refers to the sex of the target (raters rated male targets separately from female targets). Women were rated on a subset of traits based on the Dominance-Prestige scale (Cheng et al., 2010) we initially intended to operationalize Dominance as a sum of Control, Feared, and Fighting. During both data collection and analysis, we noticed that Control ratings were correlated with the components of the Prestige variable (mean correlation = 0.76) rather than the other two components of the Dominance variable (mean correlation = 0.17. We suspect that our participants interpreted “control” as either a motivation to lead or having a position of authority, rather than a motivation to determine or coercively control others’ behavior. We therefore computed Dominance, based
on the *Feared* and *Fighting* ratings only, which we use in all analyses. Because of this ambiguity we dropped *Control* from all other analyses.

**Self-report measures, egalitarianism, and inequality**

We collected a number of self-report measures not included in the analyses of the study, including additional demographics and measures of household wealth. We define and report those measures here along with descriptive statistics and Gini coefficients in order to provide greater empirical context of the study population. We briefly discuss egalitarianism among the Chabu relying on these data and qualitative ethnographic results.

The demographic self-report structured interview included age, patrilineal clan, marital status, total number of marriages, polygynous marriages, co-wife status, number of offspring, and number of deceased children. The self-reported wealth measures included the number of houses owned, the number and size of their households’, maize and coffee fields, and the number of animals (dogs, chickens, goats or sheep) owned. Men also reported on hunting frequency (times per week), hunting methods used (use of dogs, traps, or both), and average weekly returns (in number of kills); fishing frequency per week and average weekly returns; and, the number of beehives owned and approximate seasonal harvests in kilograms. See Tables S1 and S2.
Table S1: Self-report sociodemographic and economic variables with operational definitions.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Operational definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of spouses</td>
<td>The current number of spouses of the participant.</td>
</tr>
<tr>
<td>Times married</td>
<td>The total number of lifetime marriages of the participant.</td>
</tr>
<tr>
<td>Children</td>
<td>The current number of offspring of the participant.</td>
</tr>
<tr>
<td>Number of houses</td>
<td>The current number of houses the participant owns, including residential structures and field structures.</td>
</tr>
<tr>
<td>Maize fields</td>
<td>The current number of maize fields belonging to the participant’s household.</td>
</tr>
<tr>
<td>Maize fields area</td>
<td>A quantitative estimation of total maize field area based on the sum of the three-level ordinal classification of “small” = 1, “medium” = 2, and “large” = 3.</td>
</tr>
<tr>
<td>Coffee fields</td>
<td>The current number of coffee fields belonging to the participants household.</td>
</tr>
<tr>
<td>Coffee fields area</td>
<td>A quantitative estimation of total coffee field area based on the sum of the three-level ordinal classification of “small” = 1, “medium” = 2, and “large” = 3.</td>
</tr>
<tr>
<td>Dogs</td>
<td>The current number of dogs owned by the household.</td>
</tr>
<tr>
<td>Chickens</td>
<td>The current number of chickens owned by the household.</td>
</tr>
</tbody>
</table>
Sheep and goats

The current number of sheep and goats owned by the household (includes livestock “owned” but not at the study site).

Hunt returns

Average weekly returns from all hunting efforts in carcasses per week.

Honey returns

Average seasonal returns from honey harvesting reporting in kilograms per season.

Beehives

The current number of beehives owned.

Table S2: Summary statistics. A: Self-report sociodemographic and economic variables for male data B: Self-report sociodemographic and economic variables for female data

<table>
<thead>
<tr>
<th>A: Column</th>
<th>n</th>
<th>Min</th>
<th>Max</th>
<th>Mean</th>
<th>SD</th>
<th>Gini</th>
<th>Histogram</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of spouses</td>
<td>34</td>
<td>0</td>
<td>2</td>
<td>0.91</td>
<td>0.51</td>
<td>0.26</td>
<td></td>
</tr>
<tr>
<td>Times married</td>
<td>34</td>
<td>0</td>
<td>5</td>
<td>2.26</td>
<td>1.16</td>
<td>0.29</td>
<td></td>
</tr>
<tr>
<td>Children</td>
<td>34</td>
<td>0</td>
<td>7</td>
<td>1.65</td>
<td>2.00</td>
<td>0.63</td>
<td></td>
</tr>
<tr>
<td>Number of houses</td>
<td>34</td>
<td>1</td>
<td>6</td>
<td>2.62</td>
<td>1.26</td>
<td>0.25</td>
<td></td>
</tr>
<tr>
<td>Maize fields</td>
<td>34</td>
<td>0</td>
<td>4</td>
<td>1.53</td>
<td>0.83</td>
<td>0.27</td>
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<tr>
<td>Maize fields area</td>
<td>34</td>
<td>0</td>
<td>12</td>
<td>4.35</td>
<td>2.51</td>
<td>0.30</td>
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</tr>
<tr>
<td>Coffee fields</td>
<td>34</td>
<td>0</td>
<td>7</td>
<td>2.06</td>
<td>1.41</td>
<td>0.35</td>
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</tr>
<tr>
<td>Coffee fields area</td>
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<td>12</td>
<td>5.29</td>
<td>3.45</td>
<td>0.37</td>
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</tr>
<tr>
<td>Dogs</td>
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<td>0</td>
<td>12</td>
<td>1.74</td>
<td>2.48</td>
<td>0.66</td>
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</tr>
<tr>
<td>Chickens</td>
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<td>37</td>
<td>7.15</td>
<td>8.30</td>
<td>0.56</td>
<td></td>
</tr>
<tr>
<td>Sheep and goats</td>
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<td>4</td>
<td>0.53</td>
<td>1.24</td>
<td>0.88</td>
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<tr>
<td>Hunt returns</td>
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<td>Honey returns</td>
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<td>250</td>
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<td>Beehives</td>
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<td>150</td>
<td>31.79</td>
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</table>

<table>
<thead>
<tr>
<th>B: Column</th>
<th>n</th>
<th>Min</th>
<th>Max</th>
<th>Mean</th>
<th>SD</th>
<th>Gini</th>
<th>Histogram</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of spouses</td>
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<td>1</td>
<td>0.85</td>
<td>0.37</td>
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<tr>
<td>Times married</td>
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<td>1</td>
<td>8</td>
<td>2.42</td>
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<tr>
<td>Children</td>
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<td>6</td>
<td>2.04</td>
<td>1.56</td>
<td>0.42</td>
<td></td>
</tr>
<tr>
<td>Number of houses</td>
<td>26</td>
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<td>5</td>
<td>2.23</td>
<td>0.91</td>
<td>0.20</td>
<td></td>
</tr>
<tr>
<td>Maize fields</td>
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<td>1</td>
<td>4</td>
<td>1.31</td>
<td>0.74</td>
<td>0.21</td>
<td></td>
</tr>
<tr>
<td>Maize fields area</td>
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<td>1</td>
<td>9</td>
<td>3.31</td>
<td>1.57</td>
<td>0.21</td>
<td></td>
</tr>
<tr>
<td>Coffee fields</td>
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<td>0</td>
<td>4</td>
<td>1.65</td>
<td>0.98</td>
<td>0.30</td>
<td></td>
</tr>
<tr>
<td>Coffee fields area</td>
<td>26</td>
<td>0</td>
<td>12</td>
<td>4.73</td>
<td>2.92</td>
<td>0.32</td>
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<tr>
<td>Dogs</td>
<td>26</td>
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<td>3</td>
<td>1.12</td>
<td>0.95</td>
<td>0.48</td>
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<tr>
<td>Chickens</td>
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<td>4.54</td>
<td>5.99</td>
<td>0.57</td>
<td></td>
</tr>
<tr>
<td>Sheep and goats</td>
<td>26</td>
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<td>9</td>
<td>0.73</td>
<td>2.01</td>
<td>0.92</td>
<td></td>
</tr>
</tbody>
</table>
Tables 4.3 and S2 report Gini coefficients for peer-rated and self-reported measures separately by sex, whereas Figures S2 and S3 display Gini coefficients for both sexes combined. Most peer-rated and self-reported traits have low Gini coefficients (e.g., Prestige, Dominance, Allies, Spouse quality), including important measures of material property and subsistence (e.g., Maize fields, Coffee fields, Number of houses).
**Figure S2:** Gini coefficients for peer-rated variables for all participants, male and female.

Women do not engage in hunting, honey collection, or coffee production, explaining the high coefficients for those variables.
**Figure S3:** Gini coefficients for anthropometric and self-reported sociodemographic variables for all participants, male and female. Women do not own beehives or engage in hunting or honey collection, explaining the high coefficients for those variables.

A few measures of material wealth, however, have relatively high Gini coefficients (e.g., *Hunting, Honey, Coffee, Dogs, Sheep and goats, Chickens*). The high Gini coefficients for *Hunting, Honey,* and *Coffee* in Figure S2 reflect the fact that women do not engage in these activities (and therefore have ratings = 0); the Gini coefficients for these variables calculated among men only (Table 4.3) are all < 0.30.
Concerning the variables with high Gini coefficients within sexes: high-investing male spear hunters have many dogs whereas less frequent hunters or hunters who specialize in trap hunting have fewer dogs, and, at the time of data collection, a disease had recently killed many community dogs; only one household had any sheep/goats (there were three) in the village and a few participants reported owning several sheep/goats which were with family at other villages or towns. The Gini coefficient for number of offspring for males is high. In our data three males have a second wife, 10 additional males were polygynously married in the past, and 6 women are co-wives.

In general, the Gini coefficients we have reported are consistent with those reported by Smith et al. (2010) for various measures of embodied, relational, and material wealth on a small sample of largely egalitarian hunter-gatherers.

In support of persistent egalitarianism among the Chabu, participants unanimously asserted in interviews that despite differences in levels of respect, no individual is of greater social status per se. Elders are only marginally respected and children are highly autonomous, suggesting some age-egalitarianism. There is an ethos of communal property; people assert their right to use other peoples’ belongings as desired. When an individual is in great need, for example of medical care, many community members promptly direct cash on hand towards the household of the person in need. Most food, all tobacco, and all locally brewed “beer” and honey wine are widely shared and there are cultural rules for these sharing practices. There is also a strong cultural ethos of personal autonomy, generally.

Various dimensions of egalitarianism are eroding in favor of increased inequality, however. Many households now have locks on their houses, though many people explain this is due to non-community members increasingly visiting the village. When a man clears some forest
area for a coffee plot, he assumes sole ownership of that plot. Women do not have direct ownership over plots, though it is a household asset; if the women leaves the marriage she has no rights to the plots or their returns. All honey and some meat are now sold at markets and to neighboring communities and hence are no longer subject to community sharing norms. The Kebele system is increasingly formalizing social distinctions.

**Preregistered predictions**

We preregistered seven bivariate mean difference tests between leaders and non-leaders and predicted leaders would score higher than non-leaders across all tests. We also preregistered four multiple regression models. However, these models included many predictors (some of which we were unable to collect the necessary data), and we did not achieve sufficient sample size to fit standard linear regression models to our data. We therefore do not report these models.

Based on the Dominance-Prestige scale (Cheng et al., 2010) we initially intended to operationalize Dominance as a sum of Control, Feared, and Fighting. During both data collection and analysis, we noticed that Control ratings were correlated with the components of the Prestige variable (mean correlation = 0.76) rather than the other two components of the Dominance variable (mean correlation = 0.17). We suspect that our participants interpreted “control” as either a motivation to lead or having a position of authority, rather than a motivation to determine or control others’ behavior. We therefore computed Dominance, based on the Feared and Fighting ratings only, which we use in all analyses. Because of this ambiguity we dropped Control from all other analyses.

We preregistered a measure of mating success to be based on peer-rated measures of spouse quality and sociosexuality. Questions about sociosexuality, however, were determined to
be culturally inappropriate during fieldwork. Therefore, our reported bivariate test focused on
mating success is simply a test of spouse quality (Spouse) (See Table 4).
The numerical values of the effect sizes depicted in Figure 2 are reported in Table 4.
Correlation structure of peer-rated and self-reported variables
Figures S4 and S5 display Pearson correlation coefficients between all quantitative study
variables for males and female separately.

Figure S4: Correlation plot and Pearson correlation coefficients for all study variables. Male
data.
number_of_houses
beehives

0.63

honey_returns 0.16 −0.09
hunt_returns 0.07 0.1 0.34
sheep_goats 0.31 −0.17 0.17 0.13
chickens −0.04 0.44 0.09 −0.14−0.04
dogs
coffee_area
maize_area
children

0.44 0.19 0.63 −0.02 0.02 0.14

0.17 0.02 0.42 0.22 0.03 0.53 0.39

0.42 0.33 0.23 0.18 0.29 0.32 0.17 0.22

−0.1 −0.09−0.22−0.35 0.2 −0.29−0.07 0.02 −0.03

times_married 0.18 0.26 −0.01 0.06 0.05

0 −0.08 0.42 0.02 0.01

spouse_number 0.19 0.35 0.02 0.1 −0.38 0.07 0.08 −0.04 0.08 0.08 0.32
Respect_salience 0.25 0.21 0.32

0

0.37 −0.18−0.28 0.29 −0.12 0

0.21 0.21

Pearson correlation
coefficients

Mentor_salience 0.64 −0.04 0.25 0.17 0.17 0.41 0.08 −0.22 0.04 −0.07 0.04 0.41 0.41
Coffee

Honey
Farming
Spouse
Respect
Prosocial
Parenting
Likable
Kin
Intelligence

0.42 0.3 0.05 −0.21−0.07 0.08 0.39 −0.03 0.09 0.28 0.27 −0.11 0.28 0.35

0.5

0.84 0.74 0.54 0.27 0.05 −0.01−0.09 0.08 0.43 0.06 0.14 −0.03 0.26 −0.02 0.43 0.43

0.0

0.76 0.62 0.64 0.72 0.58 0.12 0.11 0.11 0.26 0.5 0.01 −0.05 0.18 0.12

0

0.37 0.4

−0.5

0.48 0.46 0.27 0.48 0.15 0.49 0.07 −0.13 0.02 −0.24 0.04 −0.22−0.03 0.1 0.02 −0.09−0.05 0.05

−1.0

0.7 0.74 0.55 0.46 0.68 0.43 0.61 0.12 −0.1 0.23 −0.03 0.28 −0.15−0.08 0.33 −0.09−0.18 0.13 0.12

0.73 0.5 0.68 0.62 0.55 0.69 0.48 0.57 0.17 −0.05 0.12 0.2 0.44 −0.2 0.04 0.19 0.03 0.15 0.3 0.22

0.69 0.52 0.45 0.48 0.41 0.26 0.45 0.42 0.58 0.13 −0.19 0.4 −0.11 0.28 −0.24−0.26 0.26 −0.03−0.05 0.23 0.16

0.42 0.53 0.83 0.65 0.47 0.26 0.23 0.51 0.19 0.52 0.05 −0.2 0.13 −0.11 0.1 −0.06−0.08 0.35 −0.06 −0.1 −0.1 −0.15

0.44 0.55 0.84 0.66 0.53 0.67 0.72 0.61 0.74 0.52 0.57 0.15 −0.03−0.11 0.1 0.51 −0.15 0.12 0.28 0.18 0.11 0.3 0.29

0.71 0.76 0.56 0.76 0.92 0.77 0.75 0.6 0.46 0.63 0.41 0.6 0.16 −0.04 0.17 −0.03 0.24 −0.21 0.03 0.18 −0.1 −0.1 0.09 0.08

Fighting −0.14 0.08 −0.35−0.27−0.22−0.24−0.25 0.17 0.28 0.35 −0.04 0.14 −0.21 0.01 0.34 −0.35 0.3 0.21 0.28 0.23 −0.07 0.39 0.19 0.15 0.25
Feared
Expertise
Decisions
Conflict
Allies

1.0

0.73 0.44 0.14 0.05 0.03 −0.08 0.24 0.44 0.37 0.31 0.11 0.5 0.07 0.45 0.49

Hunting

0.28 0.6 0.66 0.37 0.31 0.49 0.56 0.39 0.7 0.55 0.41 0.4 0.62 0.6 0.23 0.15 0.04 0.24 0.46 −0.07 0.04 0.07 −0.01 0.1 0.24 0.3

0.58 −0.08 0.74 0.72 0.63 0.59 0.71 0.76 0.58 0.72 0.66 0.55 0.71 0.69 0.66 −0.01 0.06 0.1 −0.02 0.36 −0.06−0.18 0.31 −0.06 0.02 0.39 0.34

0.75 0.45 −0.29 0.85 0.64 0.72 0.71 0.79 0.82 0.69 0.6 0.49 0.41 0.64 0.4 0.62 0.21 0.06 0.34 −0.07 0.2 −0.24−0.18 0.26 −0.08 0.04 0.11 0.13

0.84 0.76 0.52 −0.21 0.77 0.65 0.58 0.59 0.73 0.74 0.61 0.54 0.46 0.35 0.53 0.43 0.62 0.08 0.19 0.33

0

0.17 −0.23−0.06 0.26 −0.13 0.18 0.27 0.07

0.68 0.8 0.72 0.44 0.02 0.74 0.67 0.59 0.59 0.73 0.65 0.65 0.64 0.58 0.52 0.68 0.47 0.56 0.07 0.1 0.08 0.16 0.28 −0.14−0.09 0.19 0.12 0.06 0.13 0.19

250


**Figure S5:** Correlation plot and Pearson correlation coefficients for all study variables. Female data.

Figure S6 depicts the structure of correlations among peer-ratings, and their correlation to leader status. Most variables are strongly positively correlated. *Hunting, Honey* and *Coffee* stand apart because only men engage in these activities, so women’s ratings were set to 0. *Fighting* stands apart because it is negatively correlated with most other variables. *Feared* stands apart because although it is positively correlated with most variables, it is also positively correlated with *Fighting*. The median correlation coefficient of all ratings except *Fighting* is $r = 0.58$ ($\text{min} = 0.075, \text{max} = 0.95$).
**Figure S6:** Correlation network plot of peer-rated variables for both sexes, plus leader status. The proximities of the points were determined using multidimensional clustering based on the magnitude and sign of the Pearson correlation coefficients. Coefficients with magnitudes less than 0.3 are not displayed.

**Figure S7A** depicts an Exploratory Graph Analysis (EGA) network plot of a Gaussian graphical model using graphical LASSO with extended Bayesian information criterion to select the optimal regularization parameter. EGA is a novel and highly accurate technique in network psychometrics for estimating the number of factors in correlated multivariate matrices (Martin, Massen, Šlipogot et al, 2019; Golino et al., 2018). EGA was conducted using the EGA package (Golino & Epskamp, 2017). Figure S7B depicts a Bootstrap EGA using the non-parametric technique (with resampling) on 10,000 samples. Bootstrap EGA techniques can be used to assess the stability of EGA as well as analyze the performance of individual items in the network (Christensen & Golino, 2019). The Boostrap EGA median network suggests the three dimensions suggested by the initial EGA are correct, though the networks are not identical. In the EGA network plot (Figure S7A) dimension 1 is a “neural capital-prestige-mating” dimension
and includes the variables Allies (Als), Decisions (Dcs), Intelligence and learning (Int), Conflict resolution (Cnf), Respect (Rsp), Likable (Lkb), and Spouse quality (Sps); dimension 2 is a “dominance-productivity” dimension and includes the variables Farming (Frm), Feared (Frd), and Fighting (Fgh); dimension 3 is a “social services and skills” dimension and includes the variables Kin investment (Kin), Prosocial investments (Prs), Parental investment (Prn), and Expertise (Exp). In the Bootstrap EGA network plot (Figure S7B) the dimensions are the same although numbered differently (dimensions 1 and 2 are reversed). Tables S3 and S4 report summary statistics of the Bootstrap EGA model which reveal moderate stability of a 3 dimension network. Figure S8 plots the item replicability on each of the three dimensions, illustrating that 7/14 items replicate in their designated dimensions ~75% of the time or more, 6/14 replicate in their designated dimension between ~50% and 75% of the time, with Intelligence and learning (Int) replicating on its designated dimension about 47% of the time.
**Figure S7:** EGA Partial GLASSO correlation network plots, A (left): EGA network. B (right): Bootstrapped EGA median network
Table S3: Bootstrap EGA Summary Table

<table>
<thead>
<tr>
<th>Number of boots</th>
<th>Median number of dimensions</th>
<th>Standard deviation of dimensions</th>
<th>Standard error of dimensions</th>
<th>Lower 95% CI of dimensions</th>
<th>Upper 95% CI of dimensions</th>
</tr>
</thead>
<tbody>
<tr>
<td>10000</td>
<td>3</td>
<td>0.75</td>
<td>0.009</td>
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</table>

Table S4: Bootstrap EGA dimensions likelihood

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<tbody>
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<td>2</td>
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<tr>
<td>3</td>
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</tr>
<tr>
<td>4</td>
<td>0.3181</td>
</tr>
<tr>
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<td>7</td>
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</tr>
<tr>
<td>8</td>
<td>0.0001</td>
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</tbody>
</table>
**Figure S8:** Item replication proportions for the specified dimensions using the itemConfirm function in the Bootstrap EGA network.
**PVClust results**

**Figure S9:** Bootstrapped p-values for hierarchical cluster analyses of peer-ratings and anthropometric variables for men and women. A larger AU value (red) indicates stronger support for that cluster.

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**Elastic net coefficients**

**Table S5A:** Coefficients of the elastic net logistic regression model of leader status. 1 SE model coefficients are from the $\lambda_{1se}$ model, and Minimum model coefficients are the $\lambda_{min}$ model. See Figure 4.4A.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Variable type</th>
<th>1 SE model</th>
<th>Minimum model</th>
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</thead>
<tbody>
<tr>
<td>Spouse quality</td>
<td>Reproductive</td>
<td>0.069</td>
<td>0.333</td>
</tr>
<tr>
<td>Respect</td>
<td>Social</td>
<td>0.069</td>
<td>0.265</td>
</tr>
<tr>
<td>Feared</td>
<td>Dominance</td>
<td>0.048</td>
<td>0.244</td>
</tr>
<tr>
<td>Category</td>
<td>Dimension</td>
<td>Value 1</td>
<td>Value 2</td>
</tr>
<tr>
<td>---------------------------</td>
<td>---------------</td>
<td>---------</td>
<td>---------</td>
</tr>
<tr>
<td>Conflict</td>
<td>Social</td>
<td>0.066</td>
<td>0.218</td>
</tr>
<tr>
<td>Expertise</td>
<td>Cognitive</td>
<td>0.062</td>
<td>0.187</td>
</tr>
<tr>
<td>Allies</td>
<td>Social</td>
<td>0.062</td>
<td>0.171</td>
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<tr>
<td>Farming</td>
<td>Material</td>
<td>0.058</td>
<td>0.164</td>
</tr>
<tr>
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<td>Material</td>
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<tr>
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<td>Social</td>
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<td>0.148</td>
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<td>Cognitive</td>
<td>0.060</td>
<td>0.144</td>
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<td>Cognitive</td>
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<tr>
<td>Coffee</td>
<td>Material</td>
<td>0.039</td>
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<td>Social</td>
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<td>0.091</td>
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<tr>
<td>Prosocial</td>
<td>Social</td>
<td>0.050</td>
<td>0.083</td>
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<td>Cognitive</td>
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<td>0.064</td>
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<td>Reproductive</td>
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<td>0.058</td>
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<td>Dominance</td>
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<tr>
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<td>Demographic</td>
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<tr>
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Table S5B: Coefficients of the elastic net regression model of respect salience. 1 SE model coefficients are from the $\lambda_{1se}$ model, and Minimum model coefficients are from the $\lambda_{min}$ model. See Figure 4B.

<table>
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<tr>
<th>Variable</th>
<th>Variable type</th>
<th>1 SE model coefficients</th>
<th>Minimum model coefficients</th>
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<tr>
<td>Mentor salience</td>
<td>Cognitive</td>
<td>0.024</td>
<td>0.060</td>
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<tr>
<td>Spouse quality</td>
<td>Reproductive</td>
<td>0.015</td>
<td>0.032</td>
</tr>
<tr>
<td>Parenting</td>
<td>Reproductive</td>
<td>0.017</td>
<td>0.023</td>
</tr>
<tr>
<td>Likable</td>
<td>Social</td>
<td>0.014</td>
<td>0.022</td>
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<td>Conflict</td>
<td>Social</td>
<td>0.018</td>
<td>0.019</td>
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<tr>
<td>Feared</td>
<td>Dominance</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td>Farming</td>
<td>Material</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>resources</td>
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<td></td>
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<tr>
<td>Sex</td>
<td>Demographic</td>
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<tr>
<td>Age (estimated)</td>
<td>Demographic</td>
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<td>Allies</td>
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<td>Kin</td>
<td>Social</td>
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<tr>
<td>Prosocial</td>
<td>Social</td>
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<td>Decisions</td>
<td>Cognitive</td>
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<td>Expertise</td>
<td>Cognitive</td>
<td>0.006</td>
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Learning and intelligence

<table>
<thead>
<tr>
<th>Material</th>
<th>Dominance</th>
<th>Prestige</th>
<th>n</th>
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</thead>
<tbody>
<tr>
<td>Coffee</td>
<td>0.000</td>
<td>-0.004</td>
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</tr>
<tr>
<td>Honey</td>
<td>0.000</td>
<td>-0.004</td>
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</tr>
<tr>
<td>Fighting</td>
<td>0.000</td>
<td>-0.011</td>
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<tr>
<td>Hunting</td>
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<td>-0.013</td>
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</table>

_Bayesian logistic regression: Prior selection from metanalytic techniques_

_Table S6:_ Cheng et al. dominance and prestige correlation coefficients with measures of leadership.

<table>
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<tr>
<th>Study</th>
<th>Leadership measure</th>
<th>Dominance r</th>
<th>Prestige r</th>
<th>n</th>
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<tbody>
<tr>
<td>Cheng et al. 2010</td>
<td>Peer-rated leadership</td>
<td>0.4</td>
<td>0.73</td>
<td>91</td>
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<tr>
<td>Cheng et al. 2013</td>
<td>Perceived influence</td>
<td>0.68</td>
<td>0.57</td>
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<tr>
<td>Cheng et al. 2013</td>
<td>Perceived agency</td>
<td>0.69</td>
<td>0.45</td>
<td>191</td>
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<tr>
<td>Cheng et al. 2013</td>
<td>Behavioral influence</td>
<td>0.17</td>
<td>0.17</td>
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<tr>
<td>Cheng et al. n.d.</td>
<td>Peer-rated influence</td>
<td>0.45</td>
<td>0.67</td>
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<tr>
<td>Cheng et al. n.d.</td>
<td>Peer-rated influence</td>
<td>0.35</td>
<td>0.72</td>
<td>840</td>
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</table>
**Table S7:** Comparison of logistic regression models of leader status using leave-one-out cross validation.

<table>
<thead>
<tr>
<th></th>
<th>elpd_loo</th>
<th>p_loo</th>
<th>looic</th>
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</thead>
<tbody>
<tr>
<td>Weakly informative Gaussian model Estimates</td>
<td>-21.40</td>
<td>4.63</td>
<td>42.79</td>
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<tr>
<td>Weakly informative Gaussian model SE</td>
<td>3.35</td>
<td>1.00</td>
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<tr>
<td>Informative Gaussian model Estimates</td>
<td>-20.31</td>
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<td>40.62</td>
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<tr>
<td>Informative Gaussian model SE</td>
<td>3.99</td>
<td>1.65</td>
<td>7.97</td>
</tr>
</tbody>
</table>

**Exploratory data analysis**

To determine if major and minor leaders had different relationships with *Prestige* and *Dominance*, and if these interacted with sex, we plotted the distribution of our participants in dominance-prestige space, color-coded by leader type, and separately by sex (Figure S10). Visual inspection suggested that female major and minor leaders were positively associated with *Prestige* but not *Dominance*, whereas male major leader status was positively associated with both variables, but male minor leaders did not associate with either variable.
**Figure S10: Dominance vs. Prestige.** Each dot is one participant. Contour lines represent 2-d kernel density estimates. Leader type denoted by color.