

Leadership in an Egalitarian Society

Christopher von Rueden · Michael Gurven ·
Hillard Kaplan · Jonathan Stieglitz

© Springer Science+Business Media New York 2014

Abstract Leadership is instrumental to resolution of collective action dilemmas, particularly in large, heterogeneous groups. Less is known about the characteristics or effectiveness of leadership in small-scale, homogeneous, and relatively egalitarian societies, in which humans have spent most of our existence. Among Tsimane' forager-horticulturalists of Bolivia, we (1) assess traits of elected leaders under experimental and naturalistic conditions and (2) test whether leaders impact or differentially benefit from collective action outcomes. We find that elected leaders are physically strong and have more kin and other exchange partners. Their ranks on physical dominance, kin support, and trustworthiness predict how well their groups perform, but only where group members have a history of collaborative interaction. Leaders do not take more of the spoils. We discuss why physically strong leaders can be compatible with egalitarianism, and we suggest that leaders in egalitarian societies may be more motivated by maintaining an altruistic reputation than by short-term rewards of collective action.

Keywords Leadership · Status hierarchy · Cooperation · Egalitarianism · Small-scale society

A defining feature of humans relative to other primates is our tendency to act upon opportunities for mutual benefit (Tomasello et al. 2005). Taking advantage of these opportunities often requires resolution of collective action problems, including (1) coordination and (2) free-rider problems. Coordination problems include how to resolve asymmetrical preferences of group members, efficiently divide labor to achieve

C. von Rueden (✉)

Jepson School of Leadership Studies, University of Richmond, 28 Westhampton Way, Richmond, VA
23173, USA
e-mail: cvonrued@richmond.edu

M. Gurven

Department of Anthropology, University of California, Santa Barbara, CA 93106, USA

H. Kaplan · J. Stieglitz

Department of Anthropology, University of New Mexico, Albuquerque, NM 87131, USA

collective goals, and divide spoils. Collective action can also be undermined by free-rider problems, leading to under-contribution (Olson 1965) or over-consumption of collective goods (Hardin 1968). Free-rider problems, like the logistical problems of coordination, are aggravated by increasing group size (Boyd and Richerson 1988; Olson 1965) and social heterogeneity (Bowles and Gintis 1998; Ostrom 1990).

Humans employ a number of mechanisms to overcome collective action problems. Language (Alvard and Nolin 2002; Smith 2003) and shared ethnic markers (McElreath et al. 2003) may have evolved in part to reduce the transaction costs of coordination. We possess a coalitional psychology that represents groups as enduring entities and values membership in them for its own sake, thereby reducing the transaction costs of coordinating *de novo* with each collective action opportunity (Tooby et al. 2006). Solutions to free-rider problems include punishment of defectors (Fehr and Gächter 2002; Ostrom et al. 1992; Yamagishi 1986) and/or rewarding of high contributors (Rand et al. 2009).

The burden of coordination, punishment, and reward, however, is not equally shared by all group members. We define *leaders* as individuals who are accorded differential influence within a group over the establishment of goals, logistics of coordination, monitoring of effort, and reward and punishment. Leadership can be distributed across multiple group members or concentrated in a single individual, and it can range from passive influence (e.g. “first movers”) to active coordination or motivation of followers. Studies of self-managing task groups find that leadership can improve group performance (de Souza and Klein 1995; Pescosolido 2001; Taggar et al. 1999) and that leadership emerges spontaneously and rapidly (Bales et al. 1951; Bass and Norton 1951; Stein 1975), particularly in emergency situations requiring fast and efficient collective action (Hamblin 1958; Samuelson et al. 1984). Leadership is an ethnographically ubiquitous phenomenon (Brown 1991; Lewis 1974). These observations suggest that humans have evolved motivations to adopt leader-follower relationships to facilitate collective action (Price and van Vugt 2014; van Vugt et al. 2008). However, leadership is not a panacea for collective action problems. When the costs to collective action are minimal and group size is small, leadership may be inefficient relative to mutual coordination, monitoring, and sanctioning (Hooper et al. 2010). Leadership may also be of less benefit when group members are related and have a history of face-to-face interaction, which reduces the difficulty of coordination and the risk of free-riding (Ostrom 1990). Leadership can also crowd out cooperation if it is considered illegitimate or if it provokes fear of abuse of power, status envy, or greater competition for rank (Anderson and Brown 2010).

An evolutionary account of the conditions that structure leader-follower dynamics requires consideration of leadership in small-scale human societies, whose kin-based communities, traditional food production systems, and relative lack of formal hierarchy are more representative of ancestral human societies. Among hunter-gatherers, leadership emerges when multiple households must coordinate foraging activities or camp moves. The !Kung identified leaders who have influence over camp move decisions (Marshall 1960) and group discussions (Shostak 1981); rabbit drives by the Washoe of eastern California were coordinated by hunt leaders (Lowie 1948); when the Yahgan of Tierra del Fuego congregated to feast on whale, a leader emerged who coordinated the proceedings and appointed a constable to enforce order (Gusinde 1937); whaling among Inuit off the Alaskan coast required coordination among a crew overseen by a

captain (Spencer 1959); Iglulik Inuit in northern Canada identified a leader who instigated camps moves, decided when group hunts were to be started, and who oversaw the division of spoils (Weyer 1932); and Plains Indian bands elected a tribal chief to oversee production and to police crime when they aggregated during the summer buffalo hunt (Lowie 1948). Leadership is also potentiated by warfare: 74% of foragers in the Standard Cross-Cultural Sample showed informal leadership during war (Hooper et al. 2010). Informal leaders in small-scale societies are instrumental in coordinating debate and building consensus in the face of warfare and other emergency situations (Boehm 1996).

While these and other ethnographies of small-scale societies provide considerable description of leadership, they lack the quantitative detail and sample size to evaluate the determinants of leader emergence and effectiveness. It is unclear whether characteristics of leaders are systematically different relative to other group members, whether groups with leaders outperform groups without leaders on the same task, and whether leaders are compensated with a larger share of group production. In this paper, we provide a quantitative study of leadership among Tsimane' forager-horticulturalists of Bolivia. The Tsimane' are an interesting test case because there are limited opportunities for leadership to emerge. Households experience political autonomy, collective action across extended families is infrequent, and warfare is not endemic. We ask the following questions: (1) What traits are preferred in leaders? (2) Does leadership affect group performance? and (3) Do leaders differentially reward themselves? We investigate these questions in two naturalistic settings (election of village representatives and group fishing events) and an experimental setting. In addition, we compare the traits and effectiveness of leaders across Tsimane' villages, which vary in population size, cooperative "character" based on villagers' history of interaction (see Gurven et al. 2008), and exposure to the market economy. The effect of context on the attributes and performance of leaders has long been of interest to psychologists (e.g., Fiedler 1967) but has rarely been studied outside of the traditional domains of leadership studies: the military and corporate bureaucracy. Our results bear on evolutionary models of leadership by testing whether groups profit with leaders and whether leaders are compensated by profiting more than others.

The paper is organized as follows. First, we theoretically motivate the predictions we test. Second, we describe our study population and methods. This paper is one of the first to bring quantitative data to bear on leadership using mixed methods (ethnographic, observational, and experimental) in a small-scale society. Third, we present our results and discuss their implications for the nature and importance of leadership in small-scale societies.

What Traits Are Preferred in Leaders?

Leaders are often chosen for possessing superlative, task-relevant knowledge (Bass 1990; Hollander 1964). Cross-culturally, older adults often fill leadership roles, in part because they have had more time to accrue such knowledge (Silverman and Maxwell 1978; Simmons 1945). Older individuals will also have more social support from adult offspring and other kin; individuals with the most kinship ties to other group members tend to hold leadership positions in traditional societies (Chagnon 1979; Hughes 1988;

Walker et al. 2013). However, age-related decline in physical condition can be detrimental to leadership acquisition, which is why older but not necessarily the oldest individuals are favored as leaders.

Leaders are often taller, stronger, or display more dominant behavior than their peers, whether in large-scale, democratic societies (Lord et al. 1986; Stulp et al. 2013) or small-scale societies such as the Xavante (Maybury-Lewis 1967) and Mekranoti of Brazil (Werner 1982), where warriorship was a traditional pathway to leadership. However, tall or physically strong leaders are not necessarily chosen for their physical dominance per se, particularly in small-scale, egalitarian societies where authoritarian behavior leads to censure, ostracism, or even execution (Boehm 1999). In more egalitarian societies, leaders who are physically dominant in terms of height or strength may be desired because they improve cooperation. Physical dominance may reduce the effort required by leaders to solicit the joint attention of group members, or enable them to coordinate punishment of defectors with less risk of retaliation and with greater efficacy (von Rueden and Gurven 2012). Physical dominance also signals hunting or other productive abilities.

The contribution of physical dominance to leadership emergence and effectiveness may partly explain why women tend to wield less political influence than men in traditional societies. Women's opportunity for leadership is also restricted by the sexual division of labor and by sex differences in coalition-building (Low 1992). Nevertheless, women often have a voice in community affairs in small-scale societies. In Amazonian horticulturalists from Conambo, Ecuador, women broker factional disputes within the village (Bowser and Patton 2010). Among the Mekranoti of Brazil, women act as heads of the women's society within each village, though neither they nor the men who act as village headmen wield any coercive authority (Werner 1982).

Since group members are wary of exploitation by leaders, particularly if they are physically dominant, trustworthiness is integral to leader emergence and effectiveness (Smith et al. 2007). To win the trust of followers, successful leaders act with generosity (Blau 1964; van Knippenberg and van Knippenberg 2005) and fairness (de Cremer and van Knippenberg 2002; Tyler and Blader 2000), which signals to followers their prosocial intentions and group commitment. Among Alaskan Inuit, inheritors of boats and whaling gear would not necessarily become captains without attracting a crew via generosity (Rainey 1947). Across Amazonian societies such as the Tsimane', meat-sharing generosity is an important determinant of coalitional support and political influence (Levi-Strauss 1944; Patton 2005; Stearman 1989; von Rueden et al. 2008). In addition to building trust, generosity grows leaders' political support by indebting others and by demonstrating superior wealth and power. The potlatch of the Pacific Northwest (Barnett 1938) and moka of highland New Guinea (Strathern 1971) enabled chiefs and big men to signal their material and social capital through grandiose displays of generosity.

Due to phenotypic correlation, the same individual may be superlative on many of the traits conducive to leadership. Headmen from the Mekranoti are not only tall and skilled warriors but are also generous and knowledgeable in food production and ceremonial affairs (Werner 1982). Likewise, headmen among the Kapauku of highland New Guinea are physically fit and brave in war as well as generous, wealthy, and eloquent (Pospisil 1963). A previous study of one Tsimane' village found that political influence accrues to a few men who are not only physically strong but also

knowledgeable, generous, and central hubs of the village kin and ally network (von Rueden et al. 2008). Here we assess Tsimane' leadership preferences by evaluating the traits of elected representatives (*corregidores*) from 34 villages as well as leaders elected in the context of a task group experiment (see “Methods”).

Prediction 1: Corregidores and task group leaders are superlative in terms of physical dominance, knowledge, generosity, trustworthiness, and number of adult kin.

The relative contribution to leader emergence of age, size, or other traits may depend on the context of collective action (Fiedler 1967). For example, older individuals are less likely to be selected as leaders in our experimental tasks, which reward agility and presented collective action problems with which participants had no previous experience. Age is also of less relevance to leadership when task knowledge is easily acquired. In Tsimane' society, group fishing with poisonous plant compounds (barbasco) is one of the few contexts in which households coordinate to engage in collective action, and the required plant knowledge and fishing skills are largely acquired by adolescence (Schniter 2009). We do not expect organizers of barbasco fishing to be older than other participants. However, older individuals should be preferred as *corregidores*, whose tasks can require wisdom and dispensing of advice regarding life's problems (see “Ethnographic Setting”).

Prediction 2: Corregidores are older than other adult villagers; task group leaders and barbasco organizers are no older than the average group member, given the task-specific demands.

The age of *corregidores* may depend on the market integration of their village. Older individuals are disfavored as leaders during times of institutional change and rapid informational obsolescence (Maxwell and Silverman 1970). Within a more market-integrated Tsimane' village, young and middle-aged men wield more political influence than older men, owing partly to the increasing importance of schooling and market-related knowledge for acquiring wealth and for interacting with outside political bodies (von Rueden et al. 2008). This knowledge includes Spanish fluency and wage labor experience with non-Tsimane' loggers, ranchers, or other colonists.

In more market-integrated villages, the opportunities and threats presented by interaction with outside groups may also privilege physical dominance in *corregidores* more than in other villages. In experimental settings with Western subjects, leaders possessing dominant traits are preferred during intergroup conflict (Halevy et al. 2012; Little et al. 2007; Spisak et al. 2012; Tigue et al. 2012), during which free-riding can be particularly damaging. Dominant leaders may be perceived as better representing their group's interests in negotiations with other groups; Lukaszewski et al. (2013) find that American men perceived as stronger were rated as more likely to achieve status in a work team, and this was mediated by perceptions of their within-group coordination and between-group representation abilities.

Prediction 3: Corregidores of more market-integrated villages are more likely to be young, educated, fluent in Spanish, and physically dominant.

Village size and heterogeneity may also pattern villagers' choice of leader. Larger Tsimane' villages present more difficult challenges for leaders, not only because there are more people to coordinate but because village residents are on average less closely related to each other (von Rueden 2011). Groups that are heterogeneous in terms of kinship, ethnicity, income, or other factors often experience more conflict, greater difficulty in coordination, and more free-riding, owing to fewer shared interests, less trust, and less history of interaction (Ruttan 2006; Williams and O'Reilly 1998). When group members experience less solidarity, they may prefer more dominant leaders with greater monitoring and punishment efficiency (van Vugt and de Cremer 1999). In order to win over a more distrustful electorate, corregidores in larger villages, and those who aspire to the position, may also have to be more generous to signal their prosocial intentions.

Prediction 4: Corregidores of larger villages with more heterogeneity in kinship are more likely to be physically dominant and generous.

Does Leadership Affect Group Performance?

We assess whether experimental groups who elect a leader complete collective action tasks faster than groups who do not, owing to improvement in coordination or, alternatively, discouragement of free-riding. Groups are composed of seven adult Tsimane' men who were asked to perform two different collective action tasks with which they had no prior experience (see "Methods"). We expect leadership to improve collective action in groups of seven since a mathematical model (Hooper et al. 2010), a comparison of group size with political organization across human societies (Johnson 1982), and task group experiments (Bass and Norton 1951) all identify 6 or 7 individuals as a critical point at which groups are more likely to adopt leadership in the resolution of collective action dilemmas. While leadership may arise in those tasks that are not preceded by an election, only elected leaders were explicitly given authority over the division of the spoils. Greater say over the division of spoils brings greater power to punish or reward. The spoils consisted of a monetary award that differed in amount depending on task completion time. Furthermore, groups who do not elect a leader prior to the task should experience greater coordination difficulty due to the initial negotiation of leader-follower dynamics.

Prediction 5: Groups who elect leaders complete tasks faster.

If individuals do not elect the most qualified leaders, or if aggrandizing but unqualified leaders self-nominate, group performance or productivity may suffer as a consequence. Group members usually prefer that they have a say over who becomes their leader, and elected leadership is typically more effective in maintaining cooperation than exogenously imposed leadership (Baldassarri and Grossman 2011; Durham et al. 1997; Rivas and Sutter 2011). Leader preferences may also "misfire" under evolutionary novel conditions; narcissistic and overconfident individuals are sometimes elevated to leader positions (Brunell et al. 2008) with potentially negative consequences for team

performance (Campbell et al. 2005), but this effect may be more common where group members are unacquainted and gregarious leaders are mistaken for generous leaders. Among the Tsimane', group members have known each other much of their lives. We predict that groups who elect as leader the most qualified from among their ranks will outperform other groups.

Prediction 6: Groups who elect stronger, more knowledgeable, more generous, more trustworthy, or more kin-supported leaders complete tasks faster than groups who elect less superlative leaders.

Do Leaders Differentially Reward Themselves?

When leaders coordinate, monitor, reward, or punish, they incur costs that others do not. Dispute resolution has the potential to drag leaders into others' conflicts, and leaders are expected to volunteer for dangerous tasks. For example, Yanomamo headmen took responsibility for patrolling the village perimeter for raiders (Chagnon 1983). For leadership to be an evolutionary stable strategy, leaders must differentially benefit in fitness relative to other group members to offset the costs of their efforts. Alternatively, group members could reap equal rewards and switch leadership roles over iterations of collective action to share costs. This latter possibility is less likely where there are significant individual differences in leadership ability or in the expected gains from leadership.

There are five mechanisms by which leaders may differentially benefit from collective action. The first two mechanisms provide more indirect, reputational benefits. First, leadership may induce reciprocity in other currencies, including political support (Frohlich et al. 1971; Patton 2005). These reciprocated benefits may accrue principally during times of need, such as conflict or food shortage, and thus leadership can act as a form of insurance (Boone and Kessler 1999). Second, effective leadership may serve as a costly signal of quality or cooperative intent, which motivates community members to reward leaders with sex, alliance, or deference because of the information these costly signals convey (Gintis et al. 2001). For example, Meriam turtle hunt leaders gave away most of their catch to neighbors or at feasts, not with expectation of reciprocity but to demonstrate their qualities to potential mates and political allies (Smith et al. 2003).

The final three mechanisms reward leaders more directly. First, effective leaders may find themselves, over the course of their lives, in more productive and successful collective actions relative to other individuals (Price 2003; Tooby et al. 2006). Second, leaders may orchestrate collective actions that produce goods more beneficial to themselves and their kin. For example, wealthy Barabaig pastoralists enforced conservation of grazing land because their larger herds stood to benefit the most (Ruttan and Borgerhoff Mulder 1999). Third, leaders may claim a tax for their services (Hooper et al. 2010; Smith and Choi 2007), through a greater share of the spoils or through other normatively prescribed benefits. Such taxation is typical of societies with more formalized, permanent leadership: Kwakiutl chiefs manage salmon fisheries and are given a share of followers' production (Boas 1921), Chumash chiefs took a percentage of all debt repayments (Hudson and Underhay 1978), and chieftanship in

general is often compensated with rights to polygyny, as among the Mekranoti (Levi-Strauss 1944). Leaders will be able to extract more from the collective good or charge a higher fee the more others depend on their services and are unable to seek alternative sources of leadership (Blau 1964; Emerson 1962).

Among the Tsimane', we investigate whether leaders differentially benefit from collective action via the fifth mechanism outlined above: claiming a larger share of the spoils. We assess the returns to leadership in the context of our experimental group tasks and barbasco fishing events.

Prediction 7: Leaders claim a larger share of the spoils than other group members.

We also compare the traits of leaders to their reward allocation decisions. Physically dominant individuals may be more tempted to act in their own interests at the expense of other group members; stronger men have a greater sense of entitlement and have less fear of reproach (Sell et al. 2012). Conversely, leaders known for their trustworthiness can be expected to act more charitably when dividing the spoils.

Prediction 8: The greater their physical dominance and the lower their trustworthiness relative to other group members, the larger the share of the spoils taken by leaders.

When collective action does not achieve its intended goals, leaders may reward themselves less than they would were collective action successful. Leaders assume responsibility for group coordination and the consequences of uncertain activities (Blau 1964), so group failure may mean leaders claim less direct compensation or else face greater losses in reputation and legitimacy. For example, canoe and net owners among Ponams take more fishing catch than other crew when the catch is large but may forgo shares when the catch is small (Carrier and Carrier 1983). In barbasco fishing events among the Tsimane', a small total fish catch may cause leaders' households to take a smaller share than otherwise. Similarly, task group leaders may allocate themselves a smaller payout relative to other group members the smaller the group's monetary reward. Such a decision on the part of leaders would suggest they value the indirect, reputational benefits of leadership in addition to the immediate gains.

Prediction 9: The fewer the spoils of collective action, the smaller the proportion of the spoils leaders claim in compensation.

Methods

Ethnographic Setting

The Tsimane' are forager-horticulturalists living in lowland forests of Bolivia along the Maniqui River and its tributaries. The cultivation of plantains, rice, corn, and sweet manioc constitute ~65% of their diet, hunting and fishing contribute ~25%, and foods purchased from merchants or town stores contribute the remainder. The Tsimane'

population is roughly 11,000 and is growing at more than 3% per year despite high infant mortality and high rates of infectious disease (Gurven et al. 2007). The Tsimane' are dispersed among approximately 95 villages, which range in size from 30 to 700 individuals. Larger communities tend to be closer to the market town of San Borja (population ~25,000), in part because of the attraction of modern goods; proximity of health care, education, and wage labor opportunity; and lower transportation costs for selling horticultural and forest products. These communities are also more likely to receive investment from government and NGO projects such as schools and wells. Only in the late twentieth century were Tsimane' villages given formal geographic boundaries; the extended family, not the community, remains the central unit of social organization. Food sharing and productive activities are mostly confined to extended families. On the other hand, unrelated community members will regularly visit each other to socialize and drink *shocdye'* (chicha), an alcoholic beverage fermented from manioc.

Collective action consisting of multiple adults from different extended families is infrequent in Tsimane' society. The Tsimane' have no documented history of intervillage warfare. Collective action does occur in such contexts as intra- and intervillage soccer matches, community trail maintenance, and group fishing excursions. Our analysis of the returns to group fishing focuses on barbasco fishing, in which plants with poisonous compounds (*vashi'*, *conofoto*, *chito'*) are introduced into a dammed section of a river or stream, asphyxiating the trapped fish. The fish are then easily shot with an arrow or even grabbed by hand. Barbasco fishing often involves multiple individuals from several households, including adults of both sexes and older children. Organization of barbasco events is an ad-hoc position requiring the recruitment of participants and the coordination of dam construction and procurement of the requisite plants prior to the event. Tsimane' organizers will sometimes entice participants with offers of *shocdye'*. In large events, many participants often arrive only after the initial damming and poisoning by the organizers is complete.

Villagers also hold occasional meetings, which are used to plan collective action on a larger scale, such as clearing of overgrowth from community trails in preparation for a village festival, or responding to incursion by illegal loggers or other colonists. When free-riding is particularly attractive, as is the case when certain individuals are in cahoots with illegal loggers, collective action often fails. Community meetings are also used to discuss intravillage disputes that were unresolved by the parties directly involved. Influential individuals will try to generate consensus concerning the relative guilt of the parties in conflict, and the community may decide to inflict punishment, usually verbal censure, community service (e.g., clearing village trails), or public whippings on rare occasions. However, no individual or group within a community maintains coercive authority over others. This includes the village *corregidor* (literally, "corrector"), who is elected to represent community interests to outside political bodies, mediate intravillage disputes, coordinate trail-clearing and other intravillage projects, and facilitate community meetings. Only men have been elected *corregidor*. Their tenure can be as short as a couple of months, though most *corregidores* hold their position on the order of 5 years.

Villages have only been electing *corregidores* since 1989 when an evangelical organization, the New Tribes Mission, helped the Tsimane' establish more structured political organization in the face of intensified conflict over natural resources,

exploitation by merchants, and increasing interaction with NGOs and government offices. Throughout the twentieth century, transition to more institutionalized leadership was common in small-scale societies who experienced greater demand to interface with the outside world (Lee and Daly 1999). Until renewed efforts at proselytizing the Tsimane' by New Tribes Mission and other religious organizations in the late twentieth century, shamans and other older men wielded the most influence within communities. Like these Tsimane' leaders of previous generations, *corregidores* are normatively constrained to lead via consensus-building rather than by fiat. *Corregidores* typically wield more influence than others, but political decision-making within communities is best described as consensus-based, in which open debate must ultimately lead to mutual agreement. Individuals who threaten open debate because they are aggressive or angry are criticized.

Experimental Collective Action Tasks

Groups of seven adult male participants were recruited at random from two Tsimane' villages in September 2009: Ton'tumsi (6 groups) and Virje (4 groups). These villages are both large (458 and 610 residents, respectively), but Virje has half the settlement density of Ton'tumsi and is four times the travel distance to San Borja. Across both villages, the average age of participants was 35.4 years (range=19 to 66), which is not significantly different from the average age (35.9, range=18 to 82) of all adult males from Ton'tumsi and Virje. The ten groups did not differ in terms of average age (Kruskal-Wallis $\chi^2=10.25$, $p=0.33$) or in the distribution of ages (nonparametric Levene statistic=1.22, $p=0.30$).

Each group of seven men performed two different tasks that require face-to-face interaction, dynamic problem solving, and physical coordination. Only one group was tested per day, and each group completed their two tasks back-to-back. They first performed the "Spider Web Game," which requires all group members to pass through a vertical web of ropes via holes in the web (Fig. 1a). These holes are approximately 60 cm high and 80 cm wide and form a 4×2 rectangular grid. The task has the following conditions: (1) no single hole in the web can be used by more than one person, and (2) once a group member reaches the other side of the web they cannot return to the starting side, unless (3) a group member touches one of the ropes, after which the whole team must

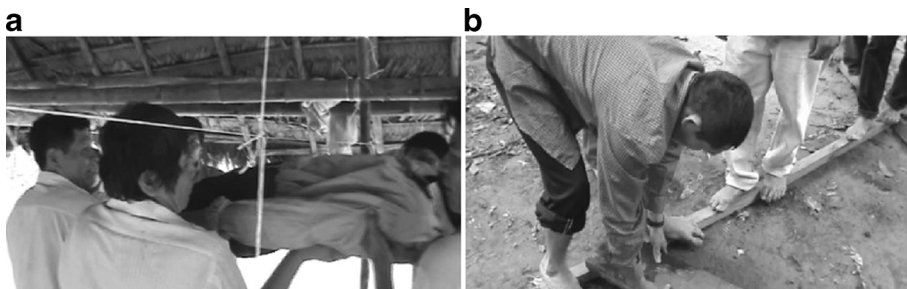


Fig. 1 Tsimane' participating in (a) Spider Web Game and (b) River Game

start the task over. To solve the task, one group member should crawl through a lower hole in the web, and then from the opposite side of the web, assist in passing other group members through higher holes in the web. The group must be careful to leave at least one lower hole unused for the last group member to pass through unaided.

The second task, the “River Game,” requires group members to travel from one point on a field to another point approximately 15 m away without touching the ground. At each group’s disposal are three 2-m-long, 30-cm-wide planks, and between the starting and ending points are ten bricks scattered at irregular intervals. To solve the task, groups must first lay a plank from the starting point to the first brick, walk together across the plank, lay a new plank that reaches to a more forward-positioned brick, walk onto that plank, and then retrieve the plank in the rear to use again (Fig. 1b). By repeating this method, they reach the end point. On two occasions, however, the group reaches a configuration of three bricks forming an isosceles triangle where the furthest brick (the vertex) is more than 2 m from either of the other two, nearer bricks. The solution is to lay a plank that connects the two nearer bricks and then by bisecting this plank with another plank they can reach the more distant brick. If at any point a group member touches the ground, the whole group must start the task again from the starting point.

All groups played both the Spider Web Game and the River Game. In the LEADER treatment condition, groups were asked to elect a leader who would “help the team” and “have say over the division of the reward”. In the NO LEADER control, groups were instead told that the division of spoils would be decided collectively among themselves and that no leader would be elected. We alternated with each group whether they elected a leader for the Spider Web Game or for the River Game. For each task, the rules were read to participants in Tsimane’ language by a Tsimane’ research assistant. This happened prior to a leader election. Participants were allowed to ask questions for clarification but were not told how to solve the tasks. The groups were also told they would be timed to see how fast they could complete the tasks. Completion of each task would provide each group a 20 boliviano (Bs) reward (approximately \$3 US), which would be doubled to 40 Bs if the task was completed in less than 10 min. Even if his group received the smaller reward for both tasks, a group member could expect to earn about 6 Bs for 30–60 min of his time. This is more than the roughly 5 Bs hourly earnings a Tsimane’ could expect from wage labor in 2009. After each task, groups were led to a table on which sat a pile of 1-B coins, which amounted to either 20 or 40 Bs depending on the group’s performance. In the LEADER condition, the leader was told he could distribute the coins as he wished; in the NO LEADER condition, groups were told they could divide the coins as they saw fit.

During the course of the tasks, CVR and the Tsimane’ research assistant recorded whether any participants slowed their group because of lack of motivation or negligence. Both CVR and the research assistant had to be in agreement for an individual to be considered problematic for their group. CVR also made film recordings of all the groups as they performed the tasks, which were later used to calculate the number of times group members spoke to each other or engaged in physical contact. If an individual paused in the midst of speaking for longer than 3 s, then we considered him to have initiated a new instance of verbal communication.

Traits of Task Group Leaders and Corregidores

Months prior to the experimental collective action tasks, all adult male residents of Ton'tumsi and Virje were evaluated on multiple traits, including the ability to win physical fights (i.e., physical dominance), trustworthiness, generosity in meat-sharing, and reputation for giving good advice. These measures are from assessments community members made of each other through a photo-ranking procedure (see von Rueden et al. 2008 for details). Ton'tumsi men photo-ranked each other in July 2009, and Virje men photo-ranked each other in July 2008. Participants' scores on the photo-ranked traits were transformed into ordinal ranks from 1 to 7, reflecting their score relative to the six other task group members. Participants were also assigned ordinal ranks for age and relatedness to the other group members. We estimated kin relatedness as the number of other men in the task group to which a group member or his wife was related, whether as a parent, sibling, or child. Aging and determination of kinship of all individuals is the result of demographic interviews first collected in 2003–2005 (Gurven et al. 2007) and updated annually thereafter.

In 2010, we were able to identify corregidores from 34 villages. Although these villages constitute only a third of all Tsimane' communities, the sample is representative in terms of village size and distance to San Borja. We assess corregidores' physical dominance by comparing their ages, heights, weights, and strength that year to other adult men (>21 years) from the 34 villages. Clinicians employed by the Tsimane' Health and Life History Project (THLHP: [http://www.unm.edu/~Tsimane'/'](http://www.unm.edu/~Tsimane'/)) measured the heights and weights of most adults from these communities, using a Seca stadiometer and a digital Tanita weigh scale. The Tanita scale was also used to estimate percent body fat. Shoulder, chest, and leg strength were measured with a Lafayette Manual Muscle Tester and grip strength was measured with a Smedley III dynamometer; we sum these values to create a composite strength measure. While visiting with clinicians, men also reported their years of schooling and Spanish fluency. We also compare corregidores with other men in terms of number of adult kin co-resident in the village (parents, siblings, or offspring over the age of 21), number of food-sharing partners, average meat calories given and received per day, and material wealth. Data on food-sharing is restricted to 9 villages where anthropologists affiliated with the THLHP conducted weekly food production interviews with a representative sample of households. Each household was interviewed for ~1 year between 2005 and 2009. A representative sample of households from 25 villages reported their physical assets during a single interview conducted between 2003 and 2010. These assets may include pots, domestic animals, guns, machetes, radios, bicycles, and 30 other goods. We calculate material wealth as the summed market value of these assets.

Informed consent was obtained from all Tsimane' prior to their involvement in the THLHP and obtained again for participants in particular studies affiliated with the THLHP, including the collective action tasks.

Barbasco Fishing

The household food production interviews include data on 94 barbasco fishing events. For each event, we recorded who had organized the barbasco event, who helped procure the poisonous plants, and who helped construct the dam. We restrict our

analysis to 40 barbasco events in which more than one household participated and fish return data are known for at least one member of each participating household. We analyze fish catch based on per capita household returns (household catch/ n household members with fish return data). On average, 5.45 individuals (range=2–15) from 2.6 different households (range=2–5) participated in each barbasco event. In nine of the events, multiple organizers were named, in which case we average their households' per capita returns.

We also test our predictions on two subsets of the multifamily barbasco events: (1) events for which fish catch data are available for all known participants ($n=17$) and (2) events in which the organizer and his spouse are unrelated to members of other participating households ($n=12$). These additional analyses allow us to check whether missing data or kin relatedness are unduly influencing our results.

Results

What Traits are Preferred in Leaders?

We find mixed support for prediction 1 (Corregidores and task group leaders are superlative in terms of physical dominance, knowledge, generosity, trustworthiness, and number of adult kin). Elected task group leaders from Ton'tumsi have more kin within their group relative to other group members (Table 1), and they are deemed more trustworthy, physically dominant, and knowledgeable (they are sought out for advice). Ton'tumsi task group leaders are not more likely to be rated as generous meat-sharers. Virje elected task group leaders do not rank significantly higher than their six other group members on any of these traits, according to Wilcoxon signed rank tests (Table 1).

Table 1 Trait rankings of elected task group leaders from the villages of Ton'tumsi and Virje, and comparison of leaders' traits with task completion time

Trait	Leaders' avg. rank ^a			Correlation with task completion time ^b		
	Ton'tumsi ($n=6$)	Virje ($n=4$)	Combined ($n=10$)	Ton'tumsi ($n=6$)	Virje ($n=4$)	Combined ($n=10$)
Trustworthiness	1.33**	4.50	2.60*	0.66*	0.32	0.77***
Kin relatedness	1.50**	2.50	1.90***	0.68*	0.26	0.72***
Physical dominance	1.67**	3.25	2.30**	0.93***	-0.32	0.59**
Knowledgeable	2.00**	3.00	2.40**	-0.17	0.00	0.17
Meat-sharing generosity	3.17	3.50	3.30	-0.67*	-0.20	-0.37
Age	3.50	3.75	3.60	-0.78**	0.32	0.22

^a Ranks within group of seven; significance estimated by Wilcoxon signed rank tests

^b Spearman's rho

* one-tailed $p < 0.10$, ** one-tailed $p < 0.05$, *** one-tailed $p < 0.01$

Analysis of the traits of corregidores from 34 villages corroborates physical dominance and kin relatedness as hallmarks of leadership (Table 2). In OLS regression models with corregidor status (1=yes, 0=no) as an independent variable and age, age², and village dummy variables as controls, corregidores are 2.78 kg heavier than other men ($p=0.026$), have 7.10 kg more muscle strength ($p=0.021$), have 0.96 more adult coresident kin ($p=0.048$), have 3.87 more meat-sharing partners ($p=0.048$), and they receive 2.1 times more meat calories per day from others than do other men ($p=0.038$). Even with an additional control for number of co-resident kin, corregidores report more meat-sharing partners ($b=3.677$, $p=0.061$) and receive more meat calories per day ($OR=2.087$, $p=0.037$). Corregidores are also wealthier ($p=0.009$); they average US \$1225 (SE=\$163) in material assets whereas non-corregidores average \$870 (SE=\$40). Corregidores are neither taller nor have a higher percent of body fat. They are not more likely to be educated or fluent in Spanish, nor do they give away more meat calories per day (Table 2). We do not evaluate corregidor trustworthiness since we lack this measure across the 34 village sample.

Given differences in sample coverage, inclusion of all our corregidor measures in a single model drops the number of corregidores we evaluate to only 5. Of those measures that associate significantly with corregidor status, we can compare strength and kin support without losing power ($n=517$, including 25 corregidores). A binary logistic regression model of corregidor status, with age and village dummy variables as controls, indicates independent effects of strength ($OR=1.044$, $p=0.013$) and kin support ($OR=1.188$, $p=0.025$).

We find mixed support for prediction 2 (Corregidores are older than other adult villagers; task group leaders and barbasco organizers are no older than the average group member). According to an OLS regression model of men's age, with corregidor status (1=yes, 0=no) as a predictor and village dummy variables as controls, corregidores are 5.6 years older ($p=0.029$) than other adult men (>21 years). The average age of corregidores is 44 but varies widely from 22 to 72. Task group leaders

Table 2 Regression analyses of traits of Tsimane' men, with corregidor status (1=yes, 0=no) as covariate^a

Dependent variable	<i>n</i> (all men)	<i>n</i> (corregidores)	<i>b</i>	Two-tailed <i>p</i>	OR	95 % CI
Height (cm) ^b	895	34	1.33	0.13	–	–
Weight (kg) ^b	895	34	2.78	0.03	–	–
Strength (kg) ^b	517	25	7.10	0.02	–	–
% Body fat ^b	844	34	0.51	0.48	–	–
Co-resident adult kin ^b	1032	34	0.96	0.05	–	–
Meat-sharing partners ^b	240	9	3.87	0.05	–	–
Material wealth (logUS\$) ^b	404	13	0.22	0.01	–	–
Meat cal received / day ^c	240	9	0.73	0.04	2.07	1.04–4.12
Meat cal given / day ^c	240	9	−0.06	0.86	0.93	0.47–1.87
Education (yrs) ^d	728	25	0.38	0.47	1.47	0.52–4.17
Spanish fluency ^d	739	25	0.46	0.34	1.58	0.62–4.05

^a Controlling for village dummy variables, age, and age²

^b Linear regression, ^c Negative binomial regression, ^d Binary logistic regression

are no older than other participants (Table 1). Barbasco organizers can be quite young (range=8–71). However, they are on average 4.9 years older than other participants ($p=0.017$), according to an OLS regression model of age with organizer as predictor (1=yes, 0=no) and the average age of their barbasco group as a control.

We find no support for prediction 3 (Corregidores of more market-integrated villages are more likely to be young, educated, fluent in Spanish, and physically dominant). As a proxy for market integration we use linear village distance (km) to San Borja. A linear regression of the ages of the 34 corregidores on distance indicates no tendency for residents of near-market villages to elect younger individuals as corregidor ($b=-0.066$, $p=0.506$). Corregidores' education, Spanish fluency, height, weight, and strength also do not increase in near-market villages.

We find little support for prediction 4 (Corregidores of larger, more heterogeneous villages are more likely to be physically dominant and generous). We measure village population size as the number of male and female residents over 21 years old. Because of positive skew in its distribution, we log village size prior to analysis. Corregidores of larger villages are neither younger ($b=-8.699$, $p=0.250$), taller ($b=4.079$, $p=0.279$), nor stronger ($b=16.891$, $p=0.140$) than corregidores in other villages, though the results are in the expected direction. As Fig. 2 illustrates, corregidores of larger villages are heavier ($b=13.354$, $p=0.026$). To determine the heterogeneity of kin relations within a village, we average residents' number of adult co-resident kin and divide by the total number of adult village members. This measure of kin relatedness fails to predict corregidores' age, height, weight, or strength. Neither population size nor the kin relatedness of villages predicts corregidor generosity, whether in terms of meat calories given to other households or number of meat- or labor-sharing partners.

Do Leadership or the Traits of Leaders Affect Group Performance?

We find mixed support for prediction 5 (Groups who elect leaders complete tasks faster). Across both Ton'tumsi and Virje, the election of a leader is not significantly related to completion time in either the Spider Web Game or the River Game (Wilcoxon signed-rank $z=1.244$, one-tailed $p=0.107$). Average completion time with

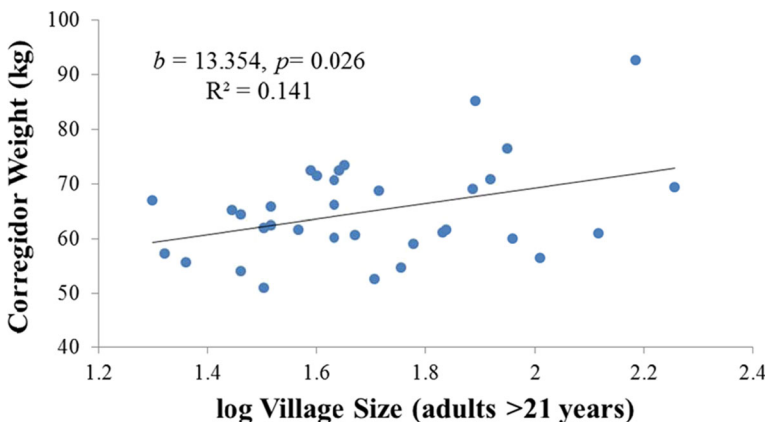


Fig. 2 Corregidores are heavier in more populous villages ($n=34$ villages)

and without an elected leader is 21.81 min (SD=19.67) and 22.76 min (SD=16.81), respectively. However, election of a leader is associated with a marginally faster completion time when the analysis is restricted to Ton'tumsi (Wilcoxon signed-rank $z=1.604$, one-tailed $p=0.058$). Election of a leader in Ton'tumsi improved completion time by 32% for the Spider Web Game and 22% for the River Game. If our sample size in Ton'tumsi were 14 groups rather than 12 our statistical power would have been sufficient to reject the null hypothesis. In Virje, on the other hand, election of a leader does not show any relationship to task completion time when results of both tasks are combined (Table 3).

Not only are the Ton'tumsi results more supportive of elected leaders improving task performance, but Ton'tumsi residents were in general much more adept at the tasks than Virje residents. On average, Ton'tumsi groups completed the tasks in 15.31 min (SD=5.81) whereas groups completed the tasks in 33.95 min (SD=21.63) in Virje (Mann-Whitney $U=16$, $p=0.012$). Six of the eight Virje completion times are slower than the slowest Ton'tumsi completion time. This is surprising given that kin relatedness was marginally higher within Virje groups (Mann-Whitney $U=3.5$, $p=0.065$). The average participant in Ton'tumsi and Virje had 0.4 and 1.1 related group members, respectively. Ton'tumsi and Virje groups also differed in their frequency of physical contact. During the tasks, Ton'tumsi participants initiated physical contact with each other 7.84 times/min (SD=2.25) compared with 2.26 times/min (SD=1.19) in Virje (Mann-Whitney $U=0$, $p=0.016$). The differences between Ton'tumsi and Virje task groups in frequency of verbal communication and in free-riding are less significant. Ton'tumsi participants spoke an average of 8.02 times/min (SD=3.53) compared with 5.41 times/min (SD=2.35) in Virje (Mann-Whitney $U=25$, $p=0.082$). Individuals identified as negligent or lacking motivation were observed in 13/20 tasks, with an average of 1.05 "free-riders" per group (range=0–3). Virje groups contained on average 1.50 free-riders compared with 0.75 per Ton'tumsi group (Mann-Whitney $U=27$, $p=0.115$).

Is the leader effect in Ton'tumsi driven by changes in group member coordination and motivation? Ton'tumsi groups with and without leaders do not differ in number of unmotivated or negligent individuals, frequency of verbal communication, or frequency and distribution of physical contact. There is evidence that elected leadership changes the distribution of communication across group members. Election of a leader in

Table 3 Group performance with and without elected leaders

Community	Task	No. of groups	Avg. completion time (min) w/o elected leader	Avg. completion time (min) w/elected leader	% Faster w/ elected leader	One-tailed p^a
Ton'tumsi	Web	6	16.96	11.61	32	
	River	6	13.66	10.70	22	
	Both	12	15.31	11.15	27	0.06
Virje	Web	4	33.21	57.92	-74	
	River	4	34.68	17.69	49	
	Both	8	33.95	37.80	-11	0.50
Both	Both	20	22.76	21.81	4	0.11

^a significance estimated by Wilcoxon signed-rank tests

Ton'tumsi is associated with increased inequality in who speaks (Wilcoxon signed-rank $z=1.992$, $p=0.046$). The distribution of speaking in groups with and without elected leaders produces Gini coefficients (measures of inequality) of 0.45 and 0.43, respectively. Leaders tended to talk relatively more, but not all non-leaders talked relatively less. At least one group member, often an individual considered for the leader position, increased their verbal communication in tandem with the leader.

We find support for prediction 6 (Groups who elect older, stronger, more knowledgeable, more generous, more trustworthy, or more kin-supported leaders complete tasks faster than groups who elect less superlative leaders). Across both villages, groups complete their tasks significantly faster if they elect a leader who is relatively more trustworthy (Spearman's $\rho=0.767$, one-tailed $p=0.005$), has more kin within the group (Spearman's $\rho=0.724$, one-tailed $p=0.009$), and is more likely to win a physical fight (Spearman's $\rho=0.585$, one-tailed $p=0.038$) (Table 1). These results are not driven by the intervillage differences in task completion time and leader trait rankings. Restricted to just Ton'tumsi, leaders' relative trustworthiness, number of intragroup kin, and fighting ability show large associations with faster task completion times (Table 1). We find no association between leaders' ranking on these traits and the number of free-riders in their groups, the frequency with which group members spoke or engaged in physical contact, or the distribution of speaking and physical contact across group members.

Are Leaders Differentially Rewarded from the Spoils of Collective Action?

We find no support for prediction 7 (Leaders claim a larger share of the spoils than other group members). Experimental results of division of spoils were similar across all groups and tasks for both villages, whether or not an elected leader determined the outcome. In each of the 20 reward divisions, six of the group members received an equal share of the reward and a seventh group member received a smaller share than the others. This suggests an equal distribution would have been preferred had the coins been divisible into seven equal amounts. On the 10 occasions elected leaders determined division of spoils, they allocated themselves the smaller share on five occasions. Three of the five occasions in which elected leaders did not allocate themselves the smaller reward, they gave the smaller share to free-riders. On average, the 10 elected leaders gave themselves 3.30 Bs per task ($SD=1.57$) whereas they gave each other group member 3.78 Bs ($SD=1.38$). This difference is not statistically significant (Wilcoxon signed-rank $z=1.287$, $p=0.198$). However, across all 20 reward divisions, elected leaders received significantly less income than other group members (Wilcoxon signed-rank $z=2.269$, $p=0.023$). Free-riders earned, on average, 3.35 Bs ($SD=1.07$) while every other group member earned 3.56 Bs ($SD=1.33$; $n=13$ tasks), though this difference is not significant (Wilcoxon signed-rank $z=0.035$, $p=0.972$).

In only 15/40 barbasco events did members of organizers' households take home more fish than participants from other households, and in nine events members of organizers' households received the least fish. On average, organizers' households received 6.30 kg of fish per person ($SD=5.52$). The average take per member of other participating households was 5.17 kg ($SD=7.78$). These average returns are not significantly different (Wilcoxon signed-rank $z=1.184$, $p=0.236$). A null result is also obtained when the comparison is restricted to those 17 barbasco events for which

complete fish catch data are known (Wilcoxon signed-rank $z=1.034$, $p=0.301$) or to those 12 events for which the organizer and his spouse are unrelated to members of other participating households (Wilcoxon signed-rank $z=0.078$, $p=0.937$). Organizers are not restricting their fish catch principally to benefit kin from other households.

In 22/40 events, at least one household did not contribute labor to organization of the event, procurement of the plants, or construction of the dam. These “free-riders” typically appeared as fish were harvested. On average, members of “free-rider” households received 5.46 kg of fish per event while members of other households received 6.04 kg (Wilcoxon signed-rank $z=0.049$, $p=0.961$). Fourteen of the free-rider households were closely related to at least one member of a contributing household. Analysis of the eight events in which free-rider households were unrelated to other participants also produces no difference in their fish catch (Wilcoxon signed-rank $z=0.420$, $p=0.674$).

We find no support for prediction 8 (the greater their physical dominance and the lower their trustworthiness relative to other group members, the larger the share of the spoils taken by leaders). Based on the 10 reward divisions managed by leaders elected during the task group experiment, leaders’ receipt of the smaller share is unrelated to their within-group ranking on physical dominance (Mann-Whitney $U=11.5$, $p=0.841$) or trustworthiness (Mann-Whitney $U=8.0$, $p=0.421$). We also find no support for prediction 9 (The fewer the spoils of collective action, the smaller the proportion of the spoils leaders claim in compensation). Elected leaders are no more likely to take the smaller share when their groups received the smaller payout (Spearman’s $\rho=0.218$, $p=0.545$). Similarly, the relative share of the fish catch claimed by members of barbasco organizers’ households does not vary with the average amount of fish caught per participant (Spearman’s $\rho=-0.108$, $p=0.508$).

If barbasco organizers do not gain any obvious advantages, what else might explain the greater costs leaders incur to make these fishing bonanzas possible? Since barbasco organization is not as time- or skill-intensive as other forms of leadership, such as tenure as *corregidor*, we suspected that households reciprocate the organization of barbasco events to share costs. Thirty-four pairs of households participated in more than one barbasco event together (mean=2.8, range=2–6) during which an individual from one of the households acted as organizer. However, only nine household pairs (26%) ever reciprocated the role of organizer. If our sample is restricted to those 12 household pairs who do not share close kin, only two households (17%) reciprocated barbasco organization. Regression analysis of all household pairs who cooperated in barbasco fishing ($n=51$) does not find evidence of direct reciprocity (Fig. 3).

We summarize our predictions and results in Table 4, which notes which predictions were tested on which forms of Tsimane’ leadership (experimental task group leader, village *corregidor*, or barbasco organizer).

Discussion

Dominance, Trustworthiness, and Support from Kin Are Integral to Leader Emergence

According to sociologist Peter Blau (1964), the dilemma of leadership is gaining ascendancy over others and simultaneously winning their approval. His observation

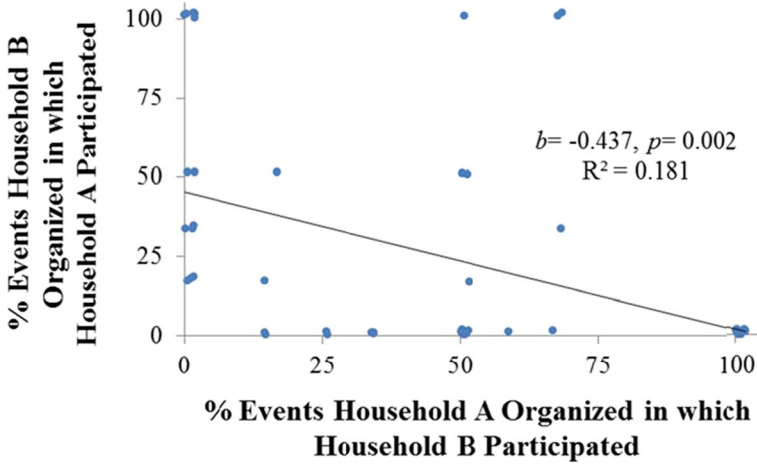


Fig. 3 Barbasco organizers do not directly reciprocate leadership ($n=51$ household pairs, data jittered)

accords with our finding that men who are physically dominant and who are rated as more trustworthy are elected as task group leaders in the village of Ton'tumsi. Elected representatives (*corregidores*) from 34 villages also tend to be physically dominant, based on their weight and strength relative to other adult men. In small-scale societies,

Table 4 Summary of predictions and results

Prediction	Type of leader evaluated ^a	Result
Leaders possess superlative attributes	T,C	Leaders are physically dominant, rated as more trustworthy, and have more kin and other exchange partners
Leaders are older than the average group member	T,C,B	Leaders are relatively older, but not when tasks are novel or require physical agility
Leaders of market-integrated villages are more physically dominant and more educated	C	No effect
Leaders of more populous, heterogeneous villages are more physically dominant	C	Leaders are heavier in more populous villages
Leaders improve group performance	T	Leaders are only effective where group members have a history of collaborative interaction
Leaders with superlative attributes are most effective	T	Leaders are more effective the higher they rank on physical dominance, trustworthiness, and kin support
Leaders take more of the spoils	T,B	Leaders take no more than other group members
More dominant leaders take more; more trustworthy leaders take less	T	No effect
Leaders take less the worse the group performs	T,B	No effect

^a T=experimental task group leader, C=village corregidor, B=barbasco organizer

preferences for physically dominant leaders are not restricted to warlike groups, such as the Yanomamo (Chagnon 1983), among whom prowess in battle has historically contributed to men's social status.

The support of kin is instrumental to gaining a leadership position (Chagnon 1979; Hughes 1988; Walker et al. 2013). Ton'tumsi task group leaders have more adult kin in their groups, and corregidores have more adult, co-resident kin than other men. Individuals who are central hubs of their group's kinship network may be more trusted than other individuals to pursue goals that benefit the majority of group members. In addition, individuals with more kin backing their decisions are more likely to get their way in conflicts with other aspiring leaders (Chagnon 1979). In Ton'tumsi, support from allies, whether kin or not, predicts political influence during community meetings more than any other attribute (von Rueden et al. 2008). We find independent effects of physical dominance and kin support on likelihood of being a corregidor.

We do not find evidence that Tsimane' leaders share meat more generously than other men. Elected task group leaders are no more generous meat-sharers than average. Corregidores have more meat-sharing partners than other men, but they tend to receive more than they give. These results contrast with our previous findings that high-status Tsimane' men are recognized as generous meat-sharers (von Rueden et al. 2008) and tend to receive fewer calories per day from other households (von Rueden et al. 2011). One possibility is that frequent leadership, more than social status more generally, carries opportunity costs with respect to hunting and other forms of traditional food production. Corregidores and those who aspire to be one may spend less time hunting and more time participating in wage labor, organizing community meetings, mediating disputes, and representing community interests in negotiation with NGOs and Bolivian government officials. The time demands of the office were cited by two former corregidores of Ton'tumsi as their reason for quitting the job.

Since we did not evaluate corregidores at the time of their election, it is possible that the traits we evaluated are more a consequence than a determinant of corregidor status. Although corregidores receive more gifts of meat than other men, we have reason to doubt that their physical dominance is principally a product of their position. The association of corregidor status with strength and body weight, but not with body fat, suggests that corregidores are heavier because of the electoral advantage of physical strength more than any short-term nutritional benefits to leadership. Furthermore, corregidor status does not eliminate the need to invest multiple hours a day in food production. Number of intravillage kin connections might increase for corregidores if their relatives immigrated opportunistically in hopes of nepotism, but in our experience no Tsimane' has cited this as a reason for migration. Mate search, conflict avoidance, and declining food availability are the more frequent motives for migration. The greater material wealth of corregidores may result in part from "skimming off the top" of group production, but our finding that leaders don't take more of the spoils in the experimental tasks and in barbasco fishing suggests otherwise. Rather, corregidores were likely chosen for their success in wage labor or sales of horticultural goods, which signals market acumen and experience in negotiating with outsiders.

In general, the variable tenure of corregidores influences the extent to which they are shaped by the office. We have detailed political history for two large and two small Tsimane' villages, which indicates that average corregidor tenure is 5.2 years (mode=3 years, range=2 months to 20 years). Since most corregidores do not exceed the

average tenure, the age difference we estimated between *corregidores* and other adult male villagers (5.6 years) is likely not far removed from their age difference when elected.

Dominance, Trustworthiness, and Support from Kin Are Integral to Leader Effectiveness

In the collective action experiment in Ton'tumsi, groups completed tasks faster if they elected a leader. However, elected leadership produced no observable change in group members' frequency of verbal communication, physical contact, or free-riding, which may have contributed to the improvement in group performance. We do find that Ton'tumsi groups with leaders display greater inequality in who speaks, which may have increased the efficiency of group coordination. Leadership can be particularly valuable where coordination is vulnerable to the "too many cooks in the kitchen" problem. Too many individuals vying for influence over group decisions can harm group performance (Groysberg et al. 2011; Ronay et al. 2012).

Not only did leadership improve group performance, but the preference for physically dominant, trustworthy, and kin-connected leaders appears to have maximized Ton'tumsi group members' collective returns. The higher the elected leaders rank on these traits, the faster the groups completed their tasks. A leader who is trustworthy motivates group members because they anticipate a fair distribution of work and of the spoils. Stronger, larger leaders may improve coordination by commanding joint attention, and they can thwart free-riding through more credible threats of punishment. Perhaps for these reasons, student task groups report lower confidence in their groups' effectiveness when they are not led by the most dominant group members (Zyphur et al. 2009). However, we detected no association between leaders' trait rankings and how group members interacted with each other, in terms of verbal communication, physical contact, or negligence. Our measures may be imprecise, or maybe we failed to measure more relevant indices of group coordination and motivation.

Leader Emergence and Effectiveness Depend on the Context

Unlike the experimental results in Ton'tumsi, election of a leader in Virje was unassociated with task completion time, elected leaders were not superlative on any of the traits we evaluated, and leaders' trait rankings bore no association with their groups' task completion time.

Why is Virje different? First, the tasks were novel to the participants and required creative problem-solving. When successful collective action requires creative problem-solving that depends on input from a broad range of ideas and perspectives, the benefits of leadership can be negated by the suppression of opinion expression (Surowiecki 2004). This can result from leaders monopolizing speaking time and followers not challenging leaders' perspectives (Anderson and Brown 2010). A recent study found that a group intelligence factor predicts the performance of groups of two to five individuals on a number of coordination tasks, and equality in conversational turn-taking increases group intelligence (Woolley et al. 2010). However, election of a leader in Virje is associated with no greater inequality in the frequency with which task group members spoke, relative to Ton'tumsi.

Second, election of a leader may have sparked status envy or resentment in Virje more than in Ton'tumsi. However, we find no effect of leader election on the number of group members who were negligent or unmotivated, either in Virje or Ton'tumsi.

Third, elected leaders may have had no effect in Virje because their job was too formidable. Relative to Ton'tumsi, Virje group members engaged in significantly less physical contact, and task completion time was significantly slower, for all tasks and conditions. This is despite the fact that average kin relatedness was higher in Virje groups than in Ton'tumsi groups. We believe that elected leaders improved performance in Ton'tumsi groups because community members' facility with collective action passed a threshold beyond which elected leaders could be instrumentally useful.

The discrepancy between Ton'tumsi and Virje task group performance is unsurprising in light of more general characteristics of these communities. Virje residents live at lower density (38 individuals per km²) relative to Ton'tumsi (74 individuals per km²), which may restrict opportunity for socializing and collective action across households. In addition, clusters of extended family members within Virje have recently threatened to splinter into different communities. Conflict between these family clusters resulted in the ousting of the previous corregidor after only a few months in office. The current corregidor is relatively ineffective. In private, one-on-one interviews conducted immediately after the experimental tasks, Ton'tumsi and Virje task group members were asked about two traits of their village corregidor: (1) his ability to resolve disputes and (2) his ability to recruit individuals to help clear community trails. They responded on a Likert scale ranging from 1=Unable to 5=Always able. Compared with Ton'tumsi task group members, Virje participants reported lower confidence in their corregidor's ability to resolve disputes (2.3 vs. 3.2, $t=3.602$, $p=0.001$) and to coordinate community trail-clearing events (3.0 vs. 3.4, $t=1.846$, $p=0.070$). According to several Virje residents, their current corregidor is a compromise candidate who is supported by the various intracommunity kin factions specifically because he won't accomplish much. When collective action isn't expected to be successful, such as when group members lack mutual trust, leaders who will cause the least dissension may be preferred over leaders who provide the most opportunity for success.

In addition to the effect of village "cooperative character" on our experimental results, we found that residents of more populous villages tend to elect heavier corregidores. We predicted that larger and more heterogeneous villages would elect more physically dominant leaders because such villages are at greater risk of intravillage conflict, coordination failure, and free-riding. Tsimane' villages vary substantially in population size and kin heterogeneity, from villages composed of two or three extended families to villages with seven hundred inhabitants with low average relatedness. However, village size is not significantly related to corregidor strength, and we found no effect of average kin relatedness of villagers on choice of corregidor. Given the political and economic autonomy of Tsimane' extended families, the difficulty of coordination and incidence of conflict across family clusters may not differ markedly between small and large villages. Alternatively, physical dominance may be of less value in conflict mediation than we suppose.

We predicted that villages closer to San Borja would prefer physically dominant corregidores to improve their bargaining power with outside political groups, loggers, and non-Tsimane' colonists. We also predicted that residents of villages closer to San Borja experience more market-related conflict and cooperation and so would opt for a

more educated and Spanish fluent corregidor. These predictions are not supported. Distance to San Borja may be a poor proxy for intervillage variation in market integration. Alternatively, Tsimane' villages may not differ enough in market integration for such variation to affect leader preferences. No village is so isolated that all of its residents lack formal education, experience of wage labor, or conflict with loggers and other colonists.

The type of collective action also patterns leader emergence. While both barbasco organizers and corregidores help resolve naturally occurring collective action problems, the organizers of barbasco fishing events differ significantly from corregidores. We found a relatively equal distribution of barbasco organization across participating households, and organizers are as young as 8 years of age. This suggests that individuals organize barbasco events when their households have greater food demand, irrespective of their leadership acumen. Leaders in non-human societies are often the first to move to a new resource patch because of hunger or greater energetic demands (King et al. 2009). Whereas most individuals may at some point expect to organize a barbasco event, few individuals ever become corregidor. In Ton'tumsi, only five men have been elected corregidor since the institution was created in 1989. It is also noteworthy that many women have acted as barbasco organizer, even in mixed-sex groups, whereas no woman has ever been elected corregidor. Formal political influence of women across traditional societies is rare because of subjugation, the sexual division of labor (including care of multiple dependents), and sex differences in coalition building (Low 1992). When leadership carries political influence and is skill- and time-intensive, leadership has typically been monopolized by men with superlative qualities.

Leaders Are Not Directly Rewarded

For leader-follower relationships to evolve as a solution to collective action dilemmas, leaders or their relatives must differentially benefit to offset the costs of leadership. We tested whether barbasco organizers or experimental task leaders claim a larger share of the collective good but found that not to be the case in either setting. Barbasco organizers took no more fish than others, even when they were unrelated to the other participants. The direct rewards of taking a larger share may be a small prize relative to maintaining or improving one's reputation or social status. For barbasco organizers, what is most at stake might be continued participation with other households in barbasco events. Although we found little evidence for direct reciprocation of barbasco organization, only 7 of 31 households who participated in more than three events had never had a household member act as organizer. Barbasco participants may be engaging in more generalized reciprocity, whereby a household organizes for some households and follows the lead of others. Furthermore, households appear to alternate "free-riding" with labor contribution across barbasco events. Of all households that participated in more than one event, none were free-riders across all events.

In the experimental tasks, elected leaders were careful to avoid seeming greedy when dividing the spoils. They solicited the assistance and opinions of group members during the reward division, and leaders' average returns were less than what they allocated to other group members. When asked by CVR why they chose or volunteered to award themselves less than others, leaders' responses included the following: "I

didn't want others to be angry," "I don't want them to think I am greedy," "I had hoped my team would perform better," and "I thought the others needed the money more." The last response suggests reputation is not the only motivator of leaders' allocation decisions. If leaders are wealthier than other group members, as we find with *corregidores*, the reward will have less marginal value to them. We predicted that leaders would be most likely to forfeit benefits when the collective good was smaller, as a reputation-saving strategy. However, we found no relationship between the payoffs to leaders and the performance of their groups, whether in the experimental tasks or *barbasco* fishing.

To maintain trustworthiness, legitimacy, and social support, leaders must carefully manage followers' perceptions of their fairness and generosity. Nambikwara chiefs who kept too many women as wives were perceived as domineering and caused families to leave for other bands (Levi-Strauss 1944). Among the Gitksan, individuals would move to new households after potlatches in which they felt their leader was not as generous as others (Adams 1973). The legitimacy of *corregidores* hinges on how they use their wealth; a past *corregidor* of Ton'tumsi was given money by villagers to start a local business, but his mismanagement of the business and purchase of personal, luxury items soon led to his being voted out of office.

While leaders who are generous with their time and treasure may suffer short-term losses, leaders who maintain reputations for magnanimity may net benefits over the long-run. For example, magnanimous leaders and their families may be given the most assistance during periods of illness, injury, or famine (Boone and Kessler 1999). Among the Ache hunter-gatherers of Paraguay, generous meat-sharers were most likely to be provisioned when sick or injured (Gurven et al. 2000). After occasional crop loss, only Ton'tumsi men who rank in the top 25% of political influence within the community reported receiving aid for their families from non-kin (von Rueden 2011), and politically influential Ton'tumsi men produce more surviving offspring, even after controlling for their food production skill, income, and support from close kin (von Rueden et al. 2011).

Conclusion

We evaluated Tsimane' leadership experimentally and in two naturalistic settings: organization of *barbasco* fishing and election of village representatives (*corregidores*). Although *corregidores* are a relatively new institution, many of the leadership functions they fulfill are not novel. Throughout Tsimane' history, influential community members have facilitated interhousehold meetings and mediated disputes. Tsimane' households are politically autonomous, as in other egalitarian societies, but this does not preclude emergence of leader-follower relationships. Egalitarianism does mean that leaders lack coercive authority, operate via consensus-building, and must carefully manage perceptions of their generosity and fairness or risk censure, ostracism, or even execution (Boehm 1999). The distribution of spoils in *barbasco* fishing and in our experimental tasks, and the role of trustworthiness in task leader emergence and effectiveness, accords with such egalitarian leadership.

Our study suggests that leadership efficacy depends on local cultural dynamics. In one of the two villages in which we ran our collective action experiment, group

performance was poor, elected task leaders rated average on all traits we evaluated, and the corregidor was evaluated as less capable. We attribute this to intervillage differences in trust and “cooperative character” because of village members’ history of interaction, an explanation that also accords with previous work among the Tsimane’ documenting intervillage differences in giving during Dictator Games (Gurven et al. 2008).

The more we understand the contexts that shape leader emergence and effectiveness in small-scale societies, the more insight we will gain into leadership in large-scale societies. Successful political candidates in modern democracies tend to be physically dominant in terms of height (Ellis 1994; Stulp et al. 2013) and more masculine in terms of their facial and vocal characteristics (Little et al. 2007; Tigue et al. 2012). The advantage of physical dominance in winning elections in modern nation states is at first glance irrational. Size or strength should not improve one’s political capital where contests do not depend primarily on brawn or physical intimidation. Our political psychology may be designed for the face-to-face collective action of small-scale societies and not the large-scale societies of recent human history. However, in neither small- nor large-scale societies should we expect physical fight outcomes to directly regulate leader emergence and effectiveness. The Tsimane’ elect leaders who are physically strong in part because such leaders can improve group coordination or motivation, not because the politics of Tsimane’ society is “red in tooth and claw.” Physically dominant Tsimane’ men accrue more influence in general because they attract more allies, both kin and non-kin (von Rueden et al. 2008). Even in small-scale societies such as the Yanomamo, where ferocity is admired and warriorship has historically contributed to social status, headmen do not command followers into action and their position depends upon the allegiance of kin and other allies (Chagnon 1983). 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, whether in war or peace.

Acknowledgments We thank the Tsimane’ who participated in this study, especially the communities of Ton’tumsi and Virje (names changed to maintain anonymity). Montserrat Soler, Curtis Atkisson, and two anonymous reviewers provided helpful comments on an earlier draft. We are also grateful to the Tsimane’ Health and Life History Project personnel. Funding was provided by grants from the National Science Foundation (BCS-0136274, BCS-0422690, and DDIG-0921429) and National Institutes of Health/National Institute on Ageing (R01AG024 119–01).

References

- Adams, J. W. (1973). *The Gitskan potlatch: Population flux, resource ownership, and reciprocity*. Toronto: Holt, Rinehart, and Winston.
- Alvard, M. S., & Nolin, D. A. (2002). Rousseau’s whale hunt? Coordination among big game hunters. *Current Anthropology*, 43(4), 533–559.
- Anderson, C., & Brown, C. E. (2010). The functions and dysfunctions of hierarchy. *Research in Organizational Behavior*, 30, 55–89.
- Baldassarri, D., & Grossman, G. (2011). Centralized sanctioning and legitimate authority promote cooperation in humans. *Proceedings of the National Academy of Sciences*, 108(27), 11023–11027.
- Bales, R., Strodtbeck, F., Mills, T., & Roseborough, M. (1951). Channels of communication in small groups. *American Sociological Review*, 16(4), 461–468.
- Barnett, H. G. (1938). The nature of the potlatch. *American Anthropologist*, 40(3), 3349–3358.

- Bass, B. M. (1990). *Bass & Stogdill's handbook of leadership: Theory, research, and managerial applications* (3rd ed.). New York: Free Press.
- Bass, B. M., & Norton, F.-T. M. (1951). Group size and leaderless discussions. *Journal of Applied Psychology*, 35(6), 397–400.
- Blau, P. M. (1964). *Exchange and power in social life*. New York: Wiley.
- Boas, F. (1921). *Ethnology of the Kwakiutl, based on data collected by George Hunt*. Thirty-fifth Annual Report of the Bureau of American Ethnology. Washington, DC: Smithsonian Institution.
- Boehm, C. (1996). Emergency decisions, cultural selection mechanics, and group selection. *Current Anthropology*, 37(5), 763–793.
- Boehm, C. (1999). *Hierarchy in the forest: The evolution of egalitarian behavior*. Cambridge: Harvard University Press.
- Boone, J. L., & Kessler, K. L. (1999). More status or more children? Social status, fertility reduction, and long-term fitness. *Evolution and Human Behavior*, 20, 257–277.
- Bowles, S., & Gintis, H. (1998). The moral economy of communities: structured populations and the evolution of pro-social norms. *Evolution and Human Behavior*, 19(1), 3–25.
- Bowser, B., & Patton, J. (2010). Women's leadership: political alliance, economic resources, and reproductive success in the Ecuadorian Amazon. In K. J. Vaughn, J. W. Eerkens, & J. Kantner (Eds.), *The evolution of leadership: Transitions in decision making from small-scale to middle-range societies* (pp. 51–71). Santa Fe: SAR Press.
- Boyd, R., & Richerson, P. J. (1988). The evolution of reciprocity in sizable groups. *Journal of Theoretical Biology*, 132(3), 609–617.
- Brown, D. (1991). *Human universals*. Boston: McGraw-Hill.
- Brunell, A. B., Gentry, W. A., Campbell, W. K., Hoffman, B. J., Kuhnert, K. W., & Demaree, K. G. (2008). Leader emergence: the case of the narcissistic leader. *Personality & Social Psychology Bulletin*, 34(12), 1663–1676.
- Campbell, W. K., Bush, C. P., Brunell, A. B., & Shelton, J. (2005). Understanding the social costs of narcissism: the case of the tragedy of the commons. *Personality & Social Psychology Bulletin*, 31(10), 1358–1368.
- Carrier, J. G., & Carrier, A. (1983). Profitless property: marine ownership and access to wealth on Ponam Island, Manus Province. *Ethnology*, 22, 133–151.
- Chagnon, N. (1979). Is reproductive success equal in egalitarian societies? In N. A. Chagnon & W. Irons (Eds.), *Evolutionary biology and human social behavior* (pp. 374–401). North Scituate, MA: Duxbury Press.
- Chagnon, N. (1983). *Yanomamo: The fierce people*. New York: CBS College Publishing.
- de Cremer, D., & van Knippenberg, D. (2002). How do leaders promote cooperation? The effects of charisma and procedural fairness. *Journal of Applied Psychology*, 87(5), 858–866.
- de Souza, G., & Klein, H. J. (1995). Emergent leadership in the group goal-setting process. *Small Group Research*, 26(4), 475–496.
- Durham, C. C., Knight, D., & Locke, E. A. (1997). Effects of leader role, team-set goal difficulty, efficacy, and tactics on team effectiveness. *Organizational Behavior and Human Decision Processes*, 72(2), 203–231.
- Ellis, L. (1994). The high and mighty among man and beast: how universal is the relationship between height (or body size) and social status? In L. Ellis (Ed.), *Social stratification and socioeconomic inequality* (Vol. 2, pp. 93–112). Westport, CT: Praeger.
- Emerson, R. M. (1962). Power-dependence relations. *American Sociological Review*, 27(1), 31–41.
- Fehr, E., & Gächter, S. (2002). Altruistic punishment in humans. *Nature*, 415(6868), 137–140.
- Fiedler, F. E. (1967). *A theory of leadership effectiveness*. New York: McGraw-Hill.
- Frohlich, N., Oppenheimer, J., & Young, O. (1971). *Political leadership and collective goods*. Princeton, NJ: Princeton University Press.
- Gintis, H., Smith, E. A., & Bowles, S. (2001). Costly signaling and cooperation. *Journal of Theoretical Biology*, 213(1), 103–119.
- Groysberg, B., Polzer, J. T., & Elfenbein, H. A. (2011). Too many cooks spoil the broth: how high-status individuals decrease group effectiveness. *Organization Science*, 22(3), 722–737.
- Curven, M., Allen-Arave, W., Hill, K., & Hurtado, M. (2000). "It's a wonderful life": signaling generosity among the ache of Paraguay. *Evolution and Human Behavior*, 21, 263–282.
- Curven, M., Kaplan, H., & Supa, Z. (2007). Mortality experience of Tsimane Amerindians of Bolivia: regional variation and temporal trends. *American Journal of Human Biology*, 19(3), 376–398.
- Curven, M., Zanolini, A., & Schniter, E. (2008). Culture sometimes matters: intra-cultural variation in pro-social behavior among Tsimane Amerindians. *Journal of Economic Behavior & Organization*, 67, 587–607.

- Gusinde, M. (1937). *The Yamana: The life and thought of the water nomads of Cape Horn*. The Fireland Indian, Vol. II. Vienna: Anthropos.
- Halevy, N., Chou, E. Y., Cohen, T. R., & Livingston, R. W. (2012). Status conferral in intergroup social dilemmas: behavioral antecedents and consequences of prestige and dominance. *Journal of Personality and Social Psychology*, *102*(2), 351–366.
- Hamblin, R. (1958). Leadership and crises. *Sociometry*, *21*(4), 322–335.
- Hardin, G. (1968). The tragedy of the commons. *Science*, *162*(3859), 1243–1248.
- Hollander, E. (1964). *Leaders, groups, and influence*. Oxford: Oxford University Press.
- Hooper, P. L., Kaplan, H. S., & Boone, J. L. (2010). A theory of leadership in human cooperative groups. *Journal of Theoretical Biology*, *265*(4), 633–646.
- Hudson, T., & Underhay, E. (1978). *Crystals in the sky: An intellectual odyssey involving chumash astronomy, cosmology, and rock art*. Socorro, NM: Ballena Press.
- Hughes, A. L. (1988). *Evolution and human kinship*. Oxford, UK: Oxford University Press.
- Johnson, G. A. (1982). Organizational structure and scalar stress. In C. Renfrew, M. Rowlands, & B. A. Segraves-Whallon (Eds.), *Theory and explanation in archaeology* (pp. 389–421). New York: Academic.
- King, A., Johnson, D., & van Vugt, M. (2009). The origins and evolution of leadership. *Current Biology*, *19*, R911–R916.
- Lee, R., & Daly, R. (1999). *The Cambridge encyclopedia of hunters and gatherers*. Cambridge: Cambridge University Press.
- Levi-Strauss, C. (1944). The social and psychological aspects of chieftanship in a primitive tribe: the Nambikwara. *Transactions of the New York Academy of Sciences*, *2*(7), 16–32.
- Lewis, H. (1974). *Leaders and followers: Some anthropological perspectives*. Reading, MA: Addison-Wesley.
- Little, A., Burriss, R. P., Jones, B. C., & Roberts, S. C. (2007). Facial appearance affects voting decisions. *Evolution and Human Behavior*, *28*, 18–27.
- Lord, R. G., De Vader, C. L., & Alliger, G. M. (1986). A meta-analysis of the relation between personality traits and leadership perceptions: an application of validity generalization procedures. *Journal of Applied Psychology*, *71*(3), 402–410.
- Low, B. S. (1992). Sex, coalitions, and politics in preindustrial societies. *Politics and Life Sciences*, *11*(1), 63–80.
- Lowie, R. H. (1948). Some aspects of political organization among the American Aborigines. *Journal of the Royal Anthropological Institute*, *78*(1–2), 11–24.
- Lukaszewski, A., Simmons, Z., Anderson, C., & Roney, J. (2013). Why are physically formidable people afforded higher social status in social groups? Strength as a psychophysical cue to in-group contribution capacity. San Luis Obispo, CA: Invited talk presented at the California Workshop on Evolutionary Social Sciences.
- Marshall, L. (1960). !Kung Bushman bands. *Africa*, *30*(4), 325–354.
- Maxwell, R. J., & Silverman, P. (1970). Information and esteem: cultural consideration in treatment of the aged. *Aging and Human Development*, *1*, 361–392.
- Maybury-Lewis, D. (1967). *Akwe-Shavante society: Social organization of a Brazilian tribe*. Oxford: Oxford University Press.
- McElreath, R., Boyd, R., & Richerson, P. J. (2003). Shared norms and the evolution of ethnic markers. *Current Anthropology*, *44*(1), 122–130.
- Olson, M. (1965). *The logic of collective action: Public goods and the theory of groups*. Cambridge: Harvard University Press.
- Ostrom, E. (1990). *Governing the commons: The evolution of institutions for collective action*. Cambridge: Cambridge University Press.
- Ostrom, E., Walker, J., & Gardner, R. (1992). Covenants with and without a sword: self-governance is possible. *The American Political Science Review*, *86*(2), 404–417.
- Patton, J. Q. (2005). Meat sharing for coalitional support. *Evolution and Human Behavior*, *26*, 137–157.
- Pescosolido, A. T. (2001). Informal leaders and the development of group efficacy. *Small Group Research*, *32*(1), 74–93.
- Pospispil, L. J. (1963). *The Kapauku Papuans of West New Guinea*. New York: Holt, Rinehart, and Winston.
- Price, M. E. (2003). Pro-community altruism and social status in a Shuar village. *Human Nature*, *14*(2), 191–208.
- Price, M., & van Vugt, M. (2014). The evolution of leader-follower reciprocity: the theory of service-for-prestige. *Frontiers in Human Neuroscience*, *8*, 363.
- Rainey, F. (1947). The whale hunters of Tigara. *American Museum of Natural History Anthropological Papers*, *41*(2), 231–283.

- Rand, D. G., Dreber, A., Ellingsen, T., Fudenberg, D., & Nowak, M. (2009). Positive interactions promote public cooperation. *Science*, *325*(5945), 1272–1275.
- Rivas, M. F., & Sutter, M. (2011). The benefits of voluntary leadership in experimental public goods games. *Economics Letters*, *112*(2), 176–178.
- Ronay, R., Greenaway, K., Anicich, E. M., & Galinsky, A. D. (2012). The path to glory is paved with hierarchy: when hierarchical differentiation increases group effectiveness. *Psychological Science*, *23*(6), 669–677.
- Ruttan, L. (2006). Sociocultural heterogeneity and the commons. *Current Anthropology*, *47*(5), 843–853.
- Ruttan, L., & Borgerhoff Mulder, M. (1999). Are East African pastoralists truly conservationists? *Current Anthropology*, *40*(5), 621–652.
- Samuelson, C. D., Messick, D. M., Rutte, C., & Wilke, H. (1984). Individual and structural solutions to resource dilemmas in two cultures. *Journal of Personality and Social Psychology*, *47*(1), 94–104.
- Schniter, E. (2009). *Why old age: non-material contributions and patterns of aging among older adult Tsimane (doctoral dissertation)*. Available from ProQuest (UMI No. 3390774).
- Sell, A., Hone, L. S. E., & Pound, N. (2012). The importance of physical strength to human males. *Human Nature*, *23*(1), 30–44.
- Shostak, M. (1981). *Nisa: The life and words of a !Kung woman*. Cambridge: Harvard University Press.
- Silverman, P., & Maxwell, R. J. (1978). How do I respect thee? Let me count the ways: deference towards elderly men and women. *Cross-Cultural Research*, *13*(2), 91–108.
- Simmons, L. W. (1945). *The role of the aged in primitive society*. London: Yale University Press.
- Smith, E. A. (2003). *Human cooperation: Perspectives from behavioral ecology*. In P. Hammerstein (Ed.), *Genetic and Cultural Evolution of Cooperation* (pp. 401–427). MIT Press.
- Smith, E. A., & Choi, J.-K. (2007). The emergence of inequality in small-scale societies: simple scenarios and agent-based simulations. In T. A. Kohler & S. E. Van der Leeuw (Eds.), *Model-based archaeology of socio-natural systems* (pp. 105–120). Santa Fe: SAR Press.
- Smith, E. A., Bliege Bird, R., & Bird, D. W. (2003). The benefits of costly signaling: Meriam turtle hunters. *Behavioral Ecology*, *14*(1), 116–126.
- Smith, K. B., Larimer, C. W., Littvay, L., & Hibbing, J. R. (2007). Evolutionary theory and political leadership: why certain people do not trust decision makers. *Journal of Politics*, *69*(2), 285–299.
- Spencer, R. F. (1959). *The North Alaskan Eskimo: A study in ecology and society*. Bulletin of the Bureau of American Ethnology 171. Washington, DC: Smithsonian Institution.
- Spisak, B. R., Dekker, P. H., Kruger, M., & Van Vugt, M. (2012). Warriors and peacekeepers: testing a biosocial implicit leadership hypothesis of intergroup relations using masculine and feminine faces. *PLoS ONE*, *7*(1), 1–8.
- Stearman, A. M. (1989). Yuqui foragers in the Bolivian Amazon: subsistence strategies, prestige, and leadership in an acculturating society. *Journal of Anthropological Research*, *45*(2), 219–244.
- Stein, R. T. (1975). Identifying emergent leaders from verbal and nonverbal communications. *Journal of Personality and Social Psychology*, *32*(1), 125–135.
- Strathern, A. (1971). *The rope of Moka: Big Men and ceremonial exchange in Mount Hagen, New Guinea*. London: Cambridge University Press.
- Stulp, G., Buunk, A. P., Verhulst, S., & Pollet, T. V. (2013). Tall claims? Sense and nonsense about the importance of height of US presidents. *The Leadership Quarterly*, *24*(1), 159–171.
- Surowiecki, J. (2004). *The wisdom of crowds: Why the many are smarter than the few and how collective wisdom shapes business, economies, societies, and nations*. New York: Knopf Doubleday.
- Taggar, S., Hackew, R., & Saha, S. (1999). Leadership emergence in autonomous work teams: antecedents and outcomes. *Personnel Psychology*, *52*(4), 899–926.
- Tigue, C. C., Borak, D. J., Connor, J. J. M. O., Schandl, C., & Feinberg, D. R. (2012). Voice pitch influences voting behavior. *Evolution and Human Behavior*, *33*(3), 210–216.
- Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences*, *28*, 675–735.
- Tooby, J., Cosmides, L., & Price, M. E. (2006). Cognitive adaptations for N-person exchange: the evolutionary roots of organizational behavior. *Managerial and Decision Economics*, *27*(2–3), 103–129.
- Tyler, T., & Blader, S. (2000). *Cooperation in groups: Procedural justice, social identity, and behavioral engagement*. Philadelphia: Psychology Press.
- van Knippenberg, B., & van Knippenberg, D. (2005). Leader self-sacrifice and leadership effectiveness: the moderating role of leader prototypicality. *Journal of Applied Psychology*, *90*(1), 25–37.
- van Vugt, M., & de Cremer, D. (1999). Leadership in social dilemmas: the effects of group identification on collective actions to provide public goods. *Journal of Personality and Social Psychology*, *76*(4), 587–599.

- van Vugt, M., Hogan, R., & Kaiser, R. B. (2008). Leadership, followership, and evolution: Some lessons from the past. *American Psychologist*, *63*(3), 182–196.
- von Rueden, C. (2011). *The acquisition of social status by males in small-scale human societies (with an emphasis on the Tsimane of Bolivia) (doctoral dissertation)*. Available from ProQuest (UMI No. 3495771).
- von Rueden, C., & Gurven, M. (2012). When the strong punish: why net costs of punishment are often negligible. *Behavioral and Brain Sciences*, *35*, 43–44.
- von Rueden, C., Gurven, M., & Kaplan, H. (2008). The multiple dimensions of male social status in an Amazonian society. *Evolution and Human Behavior*, *29*, 402–415.
- von Rueden, C., Gurven, M., & Kaplan, H. (2011). Why do men seek status? Fitness payoffs to dominance and prestige. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 2223–2232.
- Walker, R. S., et al. (2013). Living with kin in lowland horticultural societies. *Current Anthropology*, *54*(1), 96–103.
- Werner, D. (1982). Chiefs and presidents: a comparison of leadership traits in the United States and among the Mekranoti-Kayapo of central Brazil. *Ethos*, *10*(2), 136–148.
- Weyer, E. M. (1932). *The Eskimos*. New Haven: Yale University Press.
- Williams, K. Y., & O'Reilly, C. A. (1998). Demography and diversity in organizations: a review of forty years of research. *Research in Organizational Behavior*, *20*, 77–140.
- Woolley, A. W., Chabris, C. F., Pentland, A., Hashmi, N., & Malone, T. W. (2010). Evidence for a collective intelligence factor in the performance of human groups. *Science*, *330*(6004), 686–688.
- Yamagishi, T. (1986). The provision of a sanctioning system as a public good. *Journal of Personality and Social Psychology*, *51*(1), 110–116.
- Zyphur, M. J., Narayanan, J., Koh, G., & Koh, D. (2009). Testosterone-status mismatch lowers collective efficacy in groups: evidence from a slope-as-predictor multilevel structural equation model. *Organizational Behavior and Human Decision Processes*, *110*(2), 70–79.

Christopher von Rueden is assistant professor of leadership studies at the University of Richmond. He received his PhD from the University of California, Santa Barbara in 2011. He has worked with the Tsimane' forager-horticulturalists of Bolivia since 2005, investigating how status is acquired over the life course, the reproductive and health consequences of status, and the effects of socioecological change on status inequality.

Michael Gurven is professor of anthropology at University of California, Santa Barbara. He received his PhD from the University of New Mexico in 2000. He has conducted fieldwork in Paraguay and Bolivia with Ache and Tsimane' forager-horticulturalists. His research interests include intragroup cooperation and problems of collective action, and the application of life history theory to human health, longevity, development, and sociality. Since 2002, Gurven and Kaplan have co-directed the Tsimane' Health and Life History Project to develop theory and test implications of different models of human life history evolution.

Hillard Kaplan is a professor of anthropology at University of New Mexico. He received his PhD from the University of Utah in 1983. He has conducted fieldwork in Paraguay, Brazil, Botswana, and Bolivia. His research interests include evolutionary perspectives on life course development and senescence, and brain evolution. He has applied human capital theory towards explaining human life history evolution, and the proximate physiological and psychological mechanisms governing fertility and parental investment in both traditional, high-fertility, subsistence economies and modern, low-fertility, industrial societies.

Jonathan Stieglitz is a research assistant professor at the University of New Mexico. He has worked among Tsimane' forager-farmers of Bolivia since 2004. His research focuses on human sexual conflict, parent-offspring conflict, and reproductive and mental health.