



## Research

**Cite this article:** Glowacki L, von Rueden C.

2015 Leadership solves collective action problems in small-scale societies. *Phil. Trans. R. Soc. B* **370**: 20150010.

*Phil. Trans. R. Soc. B* **370**: 20150010.

<http://dx.doi.org/10.1098/rstb.2015.0010>

Accepted: 11 August 2015

One contribution of 13 to a theme issue 'Solving the puzzle of collective action through inter-individual differences: evidence from primates and humans'.

### Subject Areas:

behaviour, ecology

### Keywords:

leadership, collective action, pastoralists, foragers, cooperation

### Authors for correspondence:

Luke Glowacki

e-mail: [lukeglowacki@gmail.com](mailto:lukeglowacki@gmail.com)

Chris von Rueden

e-mail: [cvonrued@richmond.edu](mailto:cvonrued@richmond.edu)

# Leadership solves collective action problems in small-scale societies

Luke Glowacki<sup>1,2</sup> and Chris von Rueden<sup>3</sup>

<sup>1</sup>Department of Human Evolutionary Biology, and <sup>2</sup>Program for Evolutionary Dynamics, Harvard University, Cambridge, MA 02138, USA

<sup>3</sup>Jepson School of Leadership Studies, University of Richmond, Richmond, VA 23173, USA

Observation of leadership in small-scale societies offers unique insights into the evolution of human collective action and the origins of sociopolitical complexity. Using behavioural data from the Tsimane forager-horticulturalists of Bolivia and Nyangatom nomadic pastoralists of Ethiopia, we evaluate the traits of leaders and the contexts in which leadership becomes more institutional. We find that leaders tend to have more capital, in the form of age-related knowledge, body size or social connections. These attributes can reduce the costs leaders incur and increase the efficacy of leadership. Leadership becomes more institutional in domains of collective action, such as resolution of intragroup conflict, where collective action failure threatens group integrity. Together these data support the hypothesis that leadership is an important means by which collective action problems are overcome in small-scale societies.

## 1. Introduction

Humans are arguably the most successful vertebrate species. Our ability to cooperate on large scales is a key component of the success of our species, yet raises puzzling and difficult questions. What are the mechanisms that enable and sustain human collective action? How are we able to overcome conflicts of interest? How do societies maintain collective action as they grow in size and complexity?

Successful collective action is often attributed to effective leadership. We define leaders as individuals accorded differential influence within a group over the establishment of goals, logistics of coordination, monitoring of effort, or reward and punishment [1]. Leadership has received increasing attention in evolutionary models of human collective action [2–5], but their application to collective action in the field has been rare. We use ethnographic data to argue that leadership is a key means by which humans solve collective action problems. Our focus is on small-scale societies, where the scales of collective action are more representative of human evolutionary history, and most leader–follower interactions are *ad hoc* and occur in face-to-face contexts. How leadership occurs in small-scale societies has implications for the evolution of collective action and the origins of the institutional leadership that predominates in large-scale, politically complex societies.

First, we describe collective action problems generally and then discuss how resource ecology and social organization shape the particular collective action problems a society faces. Second, we present evidence of how leadership solves collective action problems. We argue that inter-individual differences, such as differences in body size or social connections, reduce costs for leaders and increase the efficacy of leadership. We then explore how leadership within small-scale societies can become less *ad hoc* and more institutional, where leadership is formally recognized by the community rather than negotiated with each collective action. We identify increasing wealth inequality, population density and intragroup conflict as sources of institutional leadership. Increasing wealth inequality and population density can provoke greater intragroup conflict, of a severity and frequency that threatens group integrity and places high personal costs on mediators. Under these conditions, institutional leadership can increase

the likelihood of successfully resolving within-group conflicts. We provide qualitative and quantitative data from two small-scale societies, the forager-horticulturalist Tsimane of lowland Bolivia and the nomadic pastoral Nyangatom of Ethiopia and South Sudan, to support these hypotheses.

## 2. Collective action and human societies

Collective action problems are common to group living social species [6]. They occur when one or more individuals incur costs to produce a collective good, which can be used by others, including ‘free-riders’ who did not contribute to its production. As it is individually advantageous to refrain from contributing to collective action while others contribute towards producing the collective good, free-riding has the potential to undermine collective action. This situation is called a collective action problem [7]. The production of collective goods does not always present collective action problems. In some cases, group members are equally motivated to contribute but are unsure how to coordinate their efforts, which can lead to coordination failure.

Across species, collective action problems occur in many different contexts, such as group foraging [8,9], migrations [10], intergroup conflict and territorial defence [11–13] and intragroup conflict resolution [14]. In some cases, collective action problems remain unsolved and the population or species is less able to exploit a particular resource [15].

Relative to other primates, humans are astonishingly adept at recognizing opportunities for mutual benefit [16], engaging in joint attention to communicate and act upon these opportunities [17] and solving collective action problems that arise. A large amount of theoretical and experimental work has been devoted to understanding the mechanisms that enable humans to solve collective action problems. These mechanisms include reciprocity [18], punitive sanctions [19–21], private incentives [22,23] and asymmetric benefits [6,7], among others. Punishment and reward may occur in the context of subsequent dyadic exchange as a result of the reputation individuals accrue from their participation in collective action [24–26]. Alternatively, contributions to collective action may be motivated by the benefits of signalling quality or cooperative intent to prospective mates or allies [27]. In dynamic social contexts among humans, more than one mechanism is probably important.

### (a) Collective action problems due to resource ecology and social organization

How individuals in human societies acquire resources often depends on the resolution of collective action problems. Many small-scale societies rely on hunting and gathering (foraging) as a primary means of producing food. However, foraging societies tend to experience substantial daily risk in food underproduction because of patchy and unpredictably acquired resources. Among foragers, the majority of hunting days are unsuccessful [28], and hunters are occasionally incapacitated due to injury or illness [29]. Thus, if individuals subsist entirely on their own returns, they and their dependents may not receive enough to eat on a given day. To buffer against this risk of food shortage, producers from different families exchange food, thereby decreasing variance in consumption over time [30–32]. Food sharing creates a

collective action problem because it would be individually beneficial for a potential hunter to refrain from hunting and sharing their returns while receiving gifts of food from other hunters. Despite the risk of free-riding, human societies do manage to solve this collective action problem. Reciprocity [33] and signalling of status [34,35] have been proposed as two processes that can explain why individuals hunt and share their catch despite the potential for others to shirk.

Sometimes collective action problems involve over-exploiting a resource rather than underproduction. Many environments have resources called commons that are readily available to all community members but susceptible to depletion. Examples of commons can include grasslands for grazing livestock, fruit trees and water sources. Without some means to manage access to these resources, overuse threatens to degrade the resource so that it is of limited value.

Societies frequently solve problems related to commons through their social organization. For instance, many East African pastoralists use grazing regimes and territorial sections with sanctions for violators in order to maintain dependable sources of grass for livestock [36,37]. Yet, the social organization of a society can produce its own collective action problems through increasing the potential for conflict within and between groups. Within-group conflicts can be particularly damaging if they escalate into feuds between kin groups or other coalitions that impose costs on the rest of the community, threatening individual and group survival [38]. Small-scale societies also commonly have intergroup conflict, whether through warfare [39,40] or resisting incursion by non-indigenous colonists and business interests [1,41]. Success in intergroup conflict can provide collective benefits to all members of the group, including territory, resources or deterrence, but individual participants pay opportunity costs and risk injury or death [39]. In order to generate these collective benefits, societies must find ways of overcoming the collective action problem [42,43].

The resolution of collective action problems allows societies to more successfully exploit their ecology. We will argue that a fundamental way societies do this is through leadership. However, leadership creates ‘second-order’ collective action problems when leaders experience opportunity costs, risk retaliation and expend more effort than other group members, who benefit from the disproportionate contribution of leaders to collective goods [1].

## 3. Leadership as a solution to collective action problems

Collective action often involves leaders, who have a larger role than other group members in the establishment of goals, logistics of coordination, monitoring of effort, dispute resolution, or reward and punishment. Leadership can vary along several dimensions. For instance, leadership can involve (i) passive influence versus active motivation of group members; or be (ii) distributed across multiple individuals versus concentrated in a single individual; (iii) based on persuasive reasoning versus coercion; (iv) situational versus institutional; and (v) achieved due to past actions or ascribed based on kinship or social identity. When leadership is ascribed, it also tends to be concentrated, to carry coercive power, and to be institutional, though these aspects of leadership do not necessarily have to covary.

Leaders can improve collective action by reducing the time to consensus and increasing the speed and flexibility of group action [16]. Task group experiments show that leadership emerges spontaneously and rapidly [44] and can improve group performance by facilitating the development of goals and an action plan [45]. Leader-based monitoring and sanctioning may reduce free-riding, by offering a clearer accounting of contribution levels, improving the efficiency of reward or punishment allocation and by limiting retaliatory actions among group members [16]. Results from public goods games indicate that a single punisher can improve group profits relative to an all punish condition [46], and leader-determined shares can improve team earnings relative to equal revenue sharing [47], even when equal revenue sharing is preceded by pre-play communication [48]. Leaders may increase contributions simply by setting a good example [3]. For example, in public goods games with sequential contributions, generous individuals who contribute first increase group contributions from others [49–51].

Leadership may not improve collective action problems in all contexts. When the costs to monitoring and sanctioning are minimal and group size is small, leadership may be inefficient relative to mutual monitoring and sanctioning [4]. Leadership can undermine cooperation if it is considered illegitimate or provokes fear of abuse of power, status envy or greater competition for rank [52]. Legitimacy means leaders have received collective approval [53]. In cases of real-world public goods, such as fisheries, legitimate leadership has been identified as the critical element in motivating compliance to regulations and curtailing resource exploitation [54]. Legitimacy also depends on the process by which leaders obtain their position. In a public goods game played with rural Ugandan farmers, elected leaders elicited greater contributions from group members than randomly appointed leaders [55].

### (a) Leadership in non-humans

Many examples of leadership in non-humans involve first-movers during group migration events, which provide collective benefits such as predatory avoidance. These individuals have greater incentive to move due to energetic demands [56], privileged information [57,58] or dominance [59], which enables differential exploitation of new resource patches [60,61]. Personality differences such as boldness are also associated with ‘first-movers’ independent of the immediate costs and benefits to leadership [62,63]. Gilby *et al.* [64] argue that a small number of individuals catalyse collective hunting among wild chimpanzees, not because they facilitate coordination but because of by-product benefits to worse hunters.

Sometimes leadership is more actively responsive to followers. Ravens use acrobatic displays to direct roost-mates to food sources [65], much like dances of honeybees [66]. But these situations lack significant conflicts of interest in which leaders actively coordinate and suppress free-riding, which is common among humans [67]. Policing of free-riding is evident in many species [68], including ants [69], and high-ranking primates in several species will police intragroup conflicts [14].

### (b) Leadership in small-scale human societies

Leadership is ubiquitous across human societies, even in small-scale societies where egalitarian norms limit status differentials or coercive authority [1]. Most leadership is

situational and confined to a particular context. Situational leadership often emerges during camp moves or group production. For instance, the !Kung of the Kalahari Desert recognized leaders during camp moves [70], rabbit drives by the Washoe of eastern California were coordinated by hunt leaders [71], whaling boats among Inuit off the Alaskan coast were directed by a captain [72] and Iglulik Inuit in northern Canada identified leaders who decided when group hunts were to be started and who oversaw the division of captured game [73]. Among the Yahgan of Tierra del Fuego, a leader emerged during whale feasts to coordinate the food division [74].

Small-scale societies with larger, more permanent settlements tend to have leadership that is more institutional, coercive and ascribed [75,76]. Two principal forces may affect the emergence of institutional leadership [77]. The first is access to monopolizable material wealth. Where resources are heterogeneously distributed, profitable resource patches can be defended by advantaged individuals or kin groups [78]. This privatization of resource patches potentiates patron–client systems [79,80]. Clients accept their subordinate economic position due to disincentives to dispersal, including lower concentration of productive habitat elsewhere and social (e.g. unfriendly neighbouring groups) or environmental (e.g. mountains, ocean, desert) barriers [81,82]. With the inter-generational transmission of property, inequality is maintained across generations [83], and wealthy kin groups codify their power through formal rules of inheritance and leadership. In the Pacific Northwest, chiefs and sub-chiefs inherited their titles and the rights to salmon runs via primogeniture, and they determined when and how commoners conducted salmon harvests [84]. Among the Chumash of the central California coast, hereditary chiefs controlled construction of seagoing *tomal* canoes, which they used to expand trade up and down the California coast. Chumash groups who lacked *tomals* also lacked hereditary chiefs [85]. Across human societies in general, the more that defensible material wealth determines production, the greater the political disparities [86].

The second factor affecting the institutionalization of leadership is the difficulty of collective action. Collective action problems become more frequent and difficult to solve as group size increases [7,87]. In larger, dense communities, the costs of monitoring for free-riding increase, and conflicts between group members tend to become more frequent [88,89]. Group members may prefer more institutional leadership when this helps solve the problems of life in large, dense communities [4,90,91]. For example, when Arapaho Indian bands agglomerated during the summer buffalo hunt, they elected a tribal chief to oversee production and to police crime; at other times of the year, bands were for the most part acephalous [71]. Institutional leadership can reduce the transaction costs of cooperation by homogenizing behaviour and social learning critical to coordination [92], streamlining decision-making [89], standardizing punishment and reward, and, perhaps most importantly, generating an *a priori* commitment of group members to leaders and their decisions.

Rarely is leadership in pre-state societies completely ascribed based on heredity; succession is generally subject to approval [93,94]. In addition, leaders’ offspring often acquired the privileged skill and social contacts that gave their fathers their power [95–97], blurring the line between leadership that is achieved versus ascribed.



### (c) Leadership as a collective action problem

The ubiquity of leadership and its ability to catalyse cooperation in experimental and ethnographic contexts suggests it is frequently advantageous to adopt leader–follower relationships as a solution to collective action problems [98]. However, leadership itself presents a collective action problem. When leaders actively coordinate, monitor, reward or punish, they incur costs that others do not. Dispute resolution has the potential to cause retaliation against those who mediate or arbitrate and to drag leaders into the conflicts of others. Leaders may be held more accountable for collective action failure, and leaders are sometimes expected to volunteer for dangerous tasks. For example, Yanomamo headmen took responsibility for patrolling the village perimeter for raiders [99]. Leaders also experience opportunity costs relative to non-leaders.

Inter-individual differences in endowment or in the expected gains from leadership are a common means by which informal leaders emerge, and can reduce the net costs of leadership [100]. For example, individuals with greater physical strength or coalitional support can mediate disputes or coordinate punishment with less risk of retaliation, less effort, and with greater efficacy [1,100]. Among the !Kung, ‘strong’ individuals who are valued social partners (good hunters, musicians, healers) tend to coordinate enforcement of social norms [101]. Heterogeneity in punishment cost across individuals makes it easier to stabilize altruistic behaviour in the provisioning of a public good [102], and experiments indicate that group members tend to tacitly agree on the individual who can punish at least cost as punisher [103] and believe that dominant individuals can punish more successfully and with lower risk of retaliation [104]. Even where group members are equally motivated, greater strength or coalitional support on the part of leaders may reduce the effort and time required to solicit the joint attention of group members and to generate consensus regarding an action plan [1]. Greater task-specific knowledge, which often covaries with age [105], can increase the efficiency of leader decision-making and followers’ commitment to leaders’ suggestions. Older individuals may also have more wisdom, which can be defined as general knowledge regarding interpersonal dilemmas and an ability to make appropriate judgements in the face of uncertainty [106]. In general, a motivation to pursue and compete for leadership is contingent on possession of traits that lower the costs and increase the efficacy of leadership [107].

Lower costs are not sufficient to stabilize leadership if leaders benefit no more than other group members from collective action. There are several mechanisms by which leaders may differentially benefit [1]. First, leaders may orchestrate collective actions that produce goods more beneficial to themselves and their kin [7]. For example, wealthy Barabaig pastoralists enforced conservation of grazing land because their larger herds stood to benefit the most [37]. Second, leaders may claim a tax for their services [4,80], through a greater share of the spoils [2] or through other normatively prescribed benefits such as rights to polygyny. Such taxation is typical of societies with more institutional leadership: Kwakiutl chiefs manage salmon fisheries and are given a share of followers’ production [84], and Chumash chiefs took a percentage of all debt repayments [108].

Leadership can also induce reciprocity in other currencies [5], including political support [109]. 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 [110]. Finally, 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 [27]. For example, Meriam turtle hunt leaders gave away most of their catch to neighbours or at feasts, not with an expectation of reciprocity but to demonstrate their qualities to potential mates and political allies [35]. Across small-scale societies, leadership tends to be motivated by the benefits of a prosocial reputation [77], whether these benefits accrue via reciprocity or signalling.

## 4. Tsimane and Nyangatom

We describe collective action problems and the role of leaders in collective action among two small-scale societies differing in ecology and social organization: the Tsimane forager-horticulturalists of Bolivia and the Nyangatom pastoralists of Ethiopia and South Sudan. In particular, we evaluate leadership during group food production (Tsimane), inter-group conflict (Nyangatom) and intragroup conflict resolution (Tsimane and Nyangatom). We test whether leaders in these contexts are older than most men and have more capital in the form of body size or social connections, and we describe when the Tsimane and Nyangatom rely on more institutional as opposed to informal leadership.

### (a) Tsimane

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 approximately 65% of their diet, hunting and fishing contribute approximately 25%, and foods purchased from merchants or town stores contribute the remainder. The Tsimane population is approximately 15 000 and is growing at 3.6% per year despite high infant mortality and high rates of infectious disease [111]. 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 approx. 25 000), in part because of the attraction of modern goods; proximity of healthcare, education and wage labour opportunity; and lower transportation costs for selling horticultural and forest products. These communities are also more likely to receive investment from government and non-governmental organization (NGO) projects such as schools and wells. Only in the late twentieth century were Tsimane villages given formal geographical 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 residing in the same or nearby households, in which parents, grandparents and siblings pool resources across generations [30]. On the other hand, unrelated community members will regularly visit each other to socialize and drink *shocdye’* (chicha), an alcoholic beverage fermented from manioc [112].

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 and group fishing

excursions. 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 individuals are collaborating with illegal loggers, collective action often fails.

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, help 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 for approximately 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. 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.

### (i) Collective fishing

Collective fishing by the Tsimane often involves *barbasco*, which are plants with poisonous compounds that 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 older children and adults of both sexes. 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 fishing leaders (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 leader is complete.

To assess who organizes *barbasco* events and why they do so, we draw on a database of food production by a representative sample of Tsimane households from several villages [1]. Between 2005 and 2009, each household was interviewed weekly over the course of a year, yielding names of participants and their fish catch for 40 multi-household *barbasco* events. On average, 5.45 individuals (range = 2–15) from 2.6 different households (range = 2–5) participated in each event. Fishing leaders were named in all events, and in nine of the events, multiple leaders were named. The ages and kin relatedness of all participants were ascertained from demographic interviews initially conducted in 2002 and updated annually thereafter [111].

As reported in von Rueden *et al.* [1], *barbasco* leaders 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 ordinary least squares regression model of age with organizer as predictor (1 = yes, 0 = no) and the average age of their *barbasco* group as a control. Women acted as organizer for 10 of 40 events, five of which included adult men as participants. On average, the households of organizers do not take home more fish than other participating households (Wilcoxon signed-ranks test  $z = 1.184$ ,  $p = 0.236$ ), even when this analysis is restricted to those 12 *barbasco* events where the leader or their spouse is unrelated to members of other participating households (Wilcoxon signed-ranks test  $z = 0.078$ ,  $p = 0.937$ ). Furthermore, only a quarter of household pairs ever directly reciprocated *barbasco* organization over the course of the year [1].

### (ii) Intragroup conflict resolution

Conflicts within Tsimane villages tend to concern disputes over land for horticultural purposes, accusations of theft or adultery, and stinginess in the context of social exchange. Conflicts tend to be resolved by the parties directly involved. For many of the conflicts that remain unresolved, third parties within the extended family or in the community (usually men) may step in to help mediate. Alternatively, community meetings may be organized by the *corregidor* and other influential individuals to try to generate consensus concerning the relative guilt of the parties in conflict. The community may decide to inflict punishment, usually verbal censure, community service (e.g. clearing village trails), or public whippings on rare occasions. At least one village has a *de facto* rule that the whipper not yet be a father so that the punished individual cannot take vengeance on the whipper's children [100]. In general, people prefer reconciliation to revenge and avoidance to direct confrontation. Households will often 'vote with their feet' by moving to a new village when they experience intractable conflict or little support from other village residents.

We test whether Tsimane conflict mediators or men who exercise leadership during community meetings are older than most men and have more capital, in terms of height, strength and social connections. During 2008 and 2009, data were gathered on conflicts and conflict mediation from interviews of all adult men from four villages ( $n = 195$ , aged 18+ years). These men ranked each other on informal political leadership ('whose voice carries more weight during village debates') by sorting photos of each other [113]. Men also reported their exchange partners, allies and conflicts with other villagers (including who mediated) from the past 6 months [113]. Clinicians employed with the Tsimane Health and Life History Project (<http://www.unm.edu/~tsimane>) measured men's height, shoulder and chest strength with a Lafayette Manual Muscle Tester, and grip strength with a Smedley III dynamometer. The strength measures were summed to create a composite measure.

The number of times a man has served as a mediator associates with his ranking on informal political leadership ( $r = 0.438$ ,  $p < 0.001$ ). Men who rank in the top 10% of political leadership were involved in 66% of all conflict mediations. Neither the frequency with which men mediate conflicts nor their informal political leadership covaries linearly with age (table 1). Rather, conflict mediation and political leadership have a quadratic relationship with age ( $p = 0.044$ ,  $p < 0.001$ , respectively), peaking at age 41 for political leadership. Average age of mediators was 36 years (range = 21–66).

**Table 1.** Pearson's correlations between measures of leadership and leader capital among Tsimane men ( $n = 195$ ).

leadership measure	age	strength	height	consang. kin	affinal kin	exchange partners	allies
no. conflicts mediated	0.062	0.109	0.211**	0.168*	0.169*	0.594**	0.866**
political leadership	0.113	0.190*	0.263**	0.167*	0.232**	0.499**	0.554**

\* $p < 0.05$ ; \*\* $p < 0.01$ .

**Table 2.** Mediation centralization and political leadership inequality across four Tsimane villages.

village	population	density ( $n \text{ km}^{-2}$ )	distance to market (km)	conflicts per man over past 6 months	mediation centralization <sup>a</sup>	political leadership inequality <sup>b</sup>
Virje	610	38	114	1.2	49	69
Jatata	87	133	101	0.5	65	64
Ton'tumsi	458	187	32	1.7	75	86
Jinac	124	231	47	1.5	86	88

<sup>a</sup>Per cent mediations by men in the top decile of political leadership within the village.

<sup>b</sup>Gini coefficients, weighted according to the maximum inequality obtainable from the leadership ranking method within each village [113].

Most men ( $n = 125$ ) never mediated a conflict over the past 6 months, including all but two of the 14 men in their 60s, 70s and 80s. In three of the four villages represented in the sample, the corregidor mediated more conflicts than others and is ranked highest on political leadership. Across a larger sample of villages ( $n = 34$ ), corregidores are on average 44 years old (range = 22–72), which is 5 years older than the average age of other adult men [1]. Only one Tsimane woman was reported as a mediator of men's conflicts, and no woman has yet been elected as corregidor.

Men who mediate more conflicts and who are recognized for their political leadership tend to be taller, have more consanguineal and affinal kin co-resident in the village, and are named more frequently as an exchange partner or ally (table 1). Political leadership, but not frequency of conflict mediation, associates significantly with strength (table 1). Of all these measures of leaders' capital, number of allies has the strongest relationship with leadership (table 1). Longitudinal data from one of the villages corroborates the importance of social support to leadership: larger and more skilled Tsimane men gained more social support over a 4-year period, and increase in social support (but not increase in size or skill *per se*) associated with increased political leadership over that same period [114].

The centralization of conflict mediation differs across the four Tsimane villages within the sample. By mediation centralization we mean the percentage of conflict mediations by men in the top decile of political leadership, which ranges from 49% to 86% of all mediations (table 2). Villages also differ in the distribution of informal political leadership, as assessed by village-specific Gini coefficients of men's rankings on political leadership (table 2). Gini coefficients are measures of inequality in which the actual distribution of a trait is compared with its uniform distribution. The political leadership Ginis are weighted according to the maximum inequality obtainable, given the leadership ranking method within each village. The ranking method did not differ qualitatively. Rather, in the two smaller villages, individuals were rated fewer times than in the two larger villages [113]. The

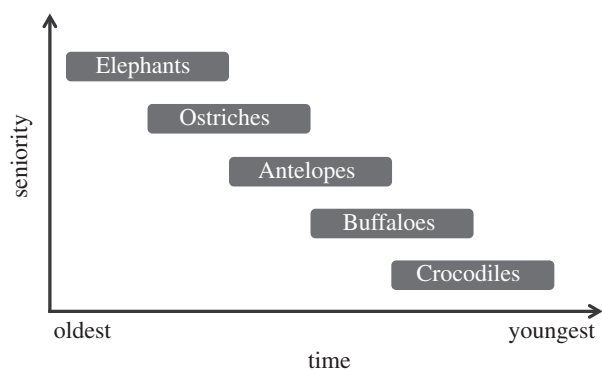
Gini coefficients in table 2 should be interpreted relative to one another rather than as absolute measures of inequality.

The two villages with the highest mediation centralization and greatest inequality in political leadership are closest to the market town of San Borja, have higher settlement density and have the most conflicts *per capita* (table 2). We speculate that market proximity and settlement density may provoke more frequent intra-community conflict, particularly over access to land for marketable horticultural goods. Furthermore, market proximity may increase exposure to external threats from loggers, ranchers and other colonists. By turning to a particular few men as mediators and leaders during community debates, community members are arguably demonstrating a demand for standardization and institutionalization of leadership, to more efficiently and effectively deal with increased intra- and intergroup conflict.

### (b) Nyangatom

The Nyangatom are nomadic agro-pastoralists numbering between 20 000 and 30 000 living along the common border of Ethiopia, South Sudan and Kenya [115,116]. They engage in a mix of livestock husbandry and horticulture as well as opportunistic hunting and gathering. Most Nyangatom are nomadic and reside in semi-permanent villages or mobile encampments centred around livestock. Semi-permanent villages usually have between 30 and 150 people and may be inhabited for several months to years. These villages occasionally relocate or dissolve and the composition of a village may change rapidly, sometimes doubling or halving in size based on the movements of the residents. The Nyangatom also reside in mobile livestock camps that relocate multiple times a year. Individuals commonly move between these camps and semi-permanent villages and other agriculturally productive areas. Young men are especially mobile and may change village residence numerous times a year.

The two defining features of Nyangatom identity are membership in one of seven territorial sections and, for men, belonging to a recognized generation set. Men inherit the



**Figure 1.** Current generation set system of Nyangatom. The Elephants are the oldest surviving generation while the youngest generation is informally referred to as Crocodiles.

territorial section of their father, while females are incorporated into the territorial section of their husbands upon marriage. Membership in a specific territorial section provides rights to territory used for grazing, horticulture and residence. In principle, Nyangatom individuals can reside anywhere in Nyangatom territory but in practice Nyangatom tend to reside within the areas belonging to their territorial section.

The generation set system affects daily life in numerous ways ranging from which persons an individual sits near to the order in which food is received at mealtimes. All Nyangatom men belong to one of several chronologically ordered generations that currently include the Elephants, Ostriches, Antelopes, Buffaloes and a yet unnamed generation informally referred to as the Crocodiles (figure 1). At any time, one senior generation known as ‘Fathers of the Country’ is recognized to have broad advisory authority over matters that affect the general welfare of the Nyangatom. The generation immediately following the Fathers of the Country is called the ‘Sons of the Country’ and they wield political and military might. Membership in a generation set is not determined by age; rather, individuals are assigned to the generation immediately following their father’s generation. As a result, large age differences may exist within a single generation set. However, the average age of members of more senior generations is older than the average age of subsequent generations. The Nyangatom also have a social category called ‘elders’ that is separate from the generation system and that signifies an individual has achieved a certain age and amount of social prominence within society. The generation system is distinct from the territorial sections, such that all Nyangatom men are members of the same generation system regardless of their territorial section.

The socio-ecological niche of the Nyangatom creates numerous collective action problems that must be solved for their survival. For instance, water is commonly acquired through hand-dug water holes that can reach 7 m in depth. Construction of these waterholes requires multiple individuals to coordinate digging them, yet in principle any person can use them. Villages are stockaded by thorn fences that provide protection to all individuals in the village against predators and potential enemies. The construction of village fences usually requires at least several individuals to cut brush, transport it to the village and build the fence. Finally, livestock are usually driven *en masse* to new areas requiring many unrelated individuals to herd and guard livestock other than their own.

The Nyangatom generally solve collective action problems such as these through their social organization. For instance,

waterholes are managed by one patrilineal family and the family head delegates the construction of it and limits access to it to family and close friends; village fences are constructed collectively but the woman residing closest to a particular section of fence is tasked with being responsible for it. She will generally recruit her co-wives and younger sisters to assist her in its construction and maintenance; and livestock movements are partly coordinated by members of the same territorial section even if they are not the owners of the livestock.

Informal leadership is common in Nyangatom society. For instance, communal ceremonies usually involve the ritual slaughter of livestock for consumption. Prior to the ceremony several individuals will take a leadership role and seek out donations from participants as well as plan logistic details such as the day and location of the event. Similarly, when herds of livestock are being driven near the territory of enemy groups who may try to steal them, several men will act as scouts to locate suitable and safe grazing areas before the herds are driven into the area.

### (i) Intergroup conflict

We focus on how informal leadership solves high-risk collective action in the form of intergroup conflict. Similar to many cultures in the borderlands of East Africa, the Nyangatom have violent intergroup conflict with several neighbouring ethnic groups [117]. The primary type of conflict is the raid, in which a group of individuals attempts to seize livestock from other groups. While many raids have fewer than 20 participants, some raids called ‘battle raids’ involve hundreds of warriors. The aim of battle raids is to capture livestock and kill enemies using overwhelming force, and participants face a risk of being killed or injured on each raid [43]. Successful battle raids can result in the creation of public goods such as deterrence and access to new territory. We focus on understanding how leadership facilitates collective action on battle raids.

Battle raids create a unique collective action problem due to the risks for participants and the scale of participation, which involves hundreds of participants many of whom are unrelated to each other. Battle raids generally occur after a serious provocation by an enemy group resulting in the community having public discussions about the appropriate course of action. If there is community support for a battle raid, one or more men take a leadership role in organizing the raid. Leadership on battle raids is not a formal or permanent office and the authority of the leaders is situational and confined to the context of the raid.

Leaders solve several problems necessary for the raid to occur. Leaders generate community support for the raid and attract participants by publicly discussing the need for a raid. They will make impassioned arguments about the social utility of a raid to motivate men to join. Leaders also recruit participants by sending messengers to other villages requesting assistance. Leaders also direct the ritual aspects of warfare through consultation with religious diviners. Finally, leaders solicit community support, especially through donations of livestock to feed the warriors while they wait for the battle raid to begin. When the battle raid finally occurs, battle leaders both plan the location and time of attack as well as take more active roles in conflict. Leaders commonly lead the warriors into battle and are sometimes among the last of the warriors to retreat.



We focus on answering the following questions to better understand how battle leaders facilitate collective action: Are battle leaders more experienced or knowledgeable than other men? Do battle raiders have more social connections than men of comparable ages? Finally, do battle leaders pay higher costs than other participants through their participation? Our data were obtained from long-term ethnographic fieldwork among the Nyangatom between 2009 and 2014 (see Glowacki & Wrangham [117] for more details on this sample). Our sample of battle leaders consists of nine men who each led at least one battle raid and were of the appropriate ages to participate in conflict.

We use age as a proxy for experience, evaluating whether battle raid leaders are older than other participants. Because the Nyangatom are a preliterate society, individuals do not know their ages; nonetheless the generation set system allows a comparative ordering of individuals by age when they differ in generations. Although generations overlap, members of more senior generations are usually older than members of more junior generations. Using data on a specific battle raid in 2010, where all available adult males ( $n = 127$ ) were interviewed about their participation in this specific raid, we found that participants came from five territorial sections and encompassed three generations listed in descending order of age: Ostrich ( $n = 42$ ), Antelope ( $n = 69$ ) and Buffalo ( $n = 16$ ). We treat these participants as a representative distribution of the generations of battle raid participants during the study period. Of the nine battle leaders in our sample, two were from the Antelope generation and seven were from the Ostrich generation, and none were from the Buffaloes. The concentration of battle leaders belonging to the senior Ostrich or Antelope generations while none belonged to the Buffalo generation provides support for battle leaders generally being older than participants as a whole ( $\chi^2 = 33, p < 0.001$ ).

To establish whether battle leaders have more social connections than comparable men who are not battle leaders, we used a status-ranking task that involved asking subjects to make status judgements of battle leaders compared with other men. Because all battle leaders were elders we compared battle leaders with 21 elders who had not previously led a battle raid. In this task, adult male community members were asked to sort battle leaders and non-leaders into one of three categories for status: low, medium or high. Status was operationalized as a well-known, respected person in the community. A score of 1–3 was assigned to each status judgement, respectively, and the scores of each subject were summed allowing us to rank individuals by status. We found that battle leaders had higher status than elders who had not ever led a battle raid ( $Z = 2.6, p = 0.01$ ). However, these results are confounded by the possibility that higher status for battle leaders may be a result of leading a battle raid and not a reason why a person was able to become a battle leader. Emic accounts indicate that although participating in warfare is a pathway to increased status, battle raid leaders must be well-connected and respected in order to mobilize several hundred participants for risky combat. Little-known individuals or those with poor reputations are unlikely to be able to mobilize community support and recruit enough participants for a battle raid.

Finally, although battle leaders are responsible for coordinating many of the logistical requirements they also are reported to have a more active role in conflict and to lead other men into the fight. Using a sample of leaders ( $n = 9$ )

and non-leaders ( $n = 118$ ), we used a logistic regression model to determine whether battle raid leadership was associated with dying in a battle raid. During the study period, three of the nine battle leaders died while leading a battle raid and four of 118 non-leaders also died during battle raids. The increased death rate for battle leaders supports the proposition that leaders take greater risks in battles they lead and have a higher mortality rate as a result ( $Z = 3.1, p = 0.002$ ). However, the additional risk battle leaders take is not compensated by battle leaders having greater reproductive success. We analysed the reproductive success of battle leaders compared with other elders who had not previously led battles and found no differences in the number of wives and children of leaders compared with non-leaders [117]. One reason for this may be because the increased mortality rate of battle leaders reduces their opportunity to gain additional wives.

In sum, we find that battle leaders are generally older and have higher status than other participants. They also take greater risks during combat than other men resulting in a significantly higher mortality rate. These factors may contribute to the likelihood of success in battle raids. If leaders are well-connected they are better able to recruit participants and mobilize community support. By being willing to take greater risks in conflict, leaders may encourage greater participation during conflict where individuals are inclined to shirk due to the hazards of battle.

## (ii) Intragroup conflict resolution

We describe how the threat of intragroup conflict in Nyangatom society contributes to the emergence of institutional leadership. Compared with the Tsimane, the Nyangatom have greater wealth inequality and depend more on commons such as grazing areas and point water sources. Greater wealth inequality and more common pool resources have the capacity to create conflicts of interest giving rise to significant intragroup conflict. The ability to manage intragroup conflict is a matter of great importance for the Nyangatom in part because of the high degree of large-scale cooperation needed for intergroup conflict and managing large herds of livestock. Additionally, individuals and families cannot simply move away from conflict due to the fact that other groups occupy the surrounding territories with whom there may be hostile relationships. These create the need for institutions and the capacity to solve more serious collective action problems.

Intragroup conflict can be caused by personal disputes, grievances or serious offences such as theft. In most cases, disputants resolve their differences through informal mechanisms, such as discussion, or they remain unresolved and the two parties may actively avoid each other, including moving to separate villages. For serious offences, such as the theft of livestock, the victim and their family may try to exact compensation by making demands for payment of livestock from the culprit's family.

The social organization of the Nyangatom contributes to managing and mitigating intragroup conflict. For instance, access to territory for grazing is restricted to members of a specific territorial section thus limiting the potential number of individuals competing for limited resources. When conflicts do arise, members are more likely to know each other because of belonging to the same territorial section. Yet, serious conflicts sometimes occur that require formal leadership to resolve. Because livestock are highly valued, the theft of



livestock by another Nyangatom can create dangerous intragroup grievances. Similarly, because marriage in Nyangatom involves the transfer of a larger number of livestock, claims of adultery and requests for divorce have the potential to trigger destabilizing intergroup conflict.

The generation set system provides a means to resolve serious disputes because it functions as a form of institutional leadership. The senior generation known as the Fathers of the Country has the authority to arbitrate serious disputes that threaten to contribute to feuds or endanger group cohesion. This authority is recognized through a population-wide norm deferring to the judgement of members of this senior generation but there is not a particular leadership office for any individual from this generation.

The Fathers of the Country are usually only appealed to in rare cases such as when conflict threatens to significantly disrupt social life, and *ad hoc* means of resolution have failed. When the Fathers of the Country are asked to arbitrate, any member of their generation can act as arbitrator. It is membership in the Fathers of the Country that vests the members of that generation with advisory authority. In practice, individuals are unlikely to appeal to particular members of the Fathers of the Country that are viewed as unreliable.

The recommendations made by the Fathers of the Country are non-binding but individuals that do not comply are likely to receive sanctions from the community, including exclusion, beatings and the threat of supernatural punishment that might include death. Because the authority of the Fathers of the Country is recognized by the Nyangatom through a population-wide, normative commitment to their recommendations, the institution provides an effective form of leadership that can resolve serious collective action problems created through intragroup conflict.

## 5. Discussion

Leadership in small-scale societies has received little empirical study, despite its importance for understanding the evolution of human collective action and historical transitions in sociopolitical complexity. Among the Tsimane forager-horticulturalists of Bolivia and Nyangatom pastoralists of Ethiopia and South Sudan, we analysed the characteristics of leaders and the contexts in which leadership is more likely to be informal versus institutional. We argue that in large groups, or in domains where collective action is especially difficult, leadership is more likely to depend on institutions, such as formal positions or age hierarchies. In general, Tsimane and Nyangatom leaders tend to have more capital than other individuals, such as having greater physical formidability, more knowledge or more social connections. Having increased capital compared with non-leaders reduces the costs of leadership and can increase its efficacy.

Among the Tsimane, we evaluated the determinants of leadership for several domains of collective action. Leaders of fishing events range in age from young children to older adults, and occasionally include women. Tsimane conflict mediation and political leadership were associated with leaders being stronger, taller and having a greater number of exchange partners, allies and coresident kin.

These traits of leaders can improve collective action. In experimental collective action tasks among the Tsimane, larger and more socially connected leaders improved group

performance [1]. Physically formidable Tsimane leaders do not coerce or intimidate group members—otherwise they would experience ostracism from the community, as has been documented in many other egalitarian societies [118]. Rather, their body size may dissuade free-riding and better capture the attention of group members, increasing the efficiency of idea exchange, consensus-building and physical coordination [1]. However, height and strength are typically less important to a leader's influence than the strength of the leader's coalition [77,119]. Longitudinal data from one Tsimane village shows that larger and more skilled Tsimane men gained more social support over a 4-year period, and increase in social support (but not increase in size or skill *per se*) was associated with increased political leadership over that same period [114].

Among the Nyangatom, we focused on collective action in intergroup warfare and intragroup conflict. The Nyangatom have greater material wealth inequality than the Tsimane and intergroup conflict is common. These contribute to more serious intragroup conflicts and the need for greater within-group cooperation. Intergroup conflict depends on battle leaders initiating raids and coordinating logistics. Battle leaders are generally older than other participants but are not the oldest men in the society, probably due to the physical demands of participating in warfare. Battle leaders have more status and social connections but observations suggest they are not larger than other participants. One reason for this is that intergroup conflict is conducted with automatic weapons, limiting the advantage of body size. Body size also does not appear important for institutional leadership in intragroup conflict, which is arbitrated by members of a senior generation. Rather, leaders are deferred to on the basis of belonging to a specific generation that is collectively acknowledged to have authority to arbitrate disputes.

Relative to men, Tsimane or Nyangatom women exercise less political leadership. Across small-scale societies, women's leadership is limited by the sexual division of labour (including care of multiple dependent offspring) and lack of opportunity to build broad coalitions in the service of political goals [120,121]. Nonetheless, women frequently have important roles in decision-making even if their leadership is generally less formal or visible [122]. Among the Ju/'hoansi Bushmen, women initiate criticism of jealousy, stinginess, and other non-normative behaviour more frequently than men [101]. Many Tsimane women have an active voice in community meetings despite men dominating corregidor and inter-family conflict mediation roles. Tsimane women compete over social partners, and popularity as a social partner predicts women's reproductive success [123]. Among the Nyangatom, battle raids require the consensus of the community at large and will not occur without the support of prominent women. Women commonly leverage their social influence to dissuade individuals from participating in raiding, or to promote raiding in other contexts [124]. Women also have an important role in intragroup conflict resolution because they can more easily travel between families and villages experiencing tension. Similarly, women have primary roles in brokering factional disputes among Amazonian horticulturalists from Conambo, Ecuador [125]. Leadership by women is significantly understudied in small-scale societies, and more work is needed on the ways women exercise leadership in the face of constraints.

We tested whether Tsimane and Nyangatom leaders tend to have more capital because such inter-individual

differences can help resolve the second-order collective action problem of who leads. Larger body size or greater social connections on the part of leaders reduce the risk of retaliation when leaders mediate conflicts or coordinate punishment, and they make it easier for leaders to recruit participants or build consensus. Well-connected leaders may also suffer less from the loss of a social tie, such as an exchange partner, resulting from particular leadership decisions or collective action failure. In general, a motivation to pursue and compete for leadership is contingent on possession of traits that lower the costs of seeking and exercising leadership [107].

Lower costs may not be sufficient to resolve the second-order collective action problem of who leads if leaders do not benefit relative to followers. These benefits may accrue via greater valuation of the collective good, a greater share of the spoils, direct payment, or more indirectly via positive reputations. Among the Tsimane, we found no evidence that leaders of fishing events take home more fish than other participants [1]. Rather, households may contribute leadership to collective fishing when they lack food, which has similarity to 'first-movers' in non-human species, who act out of hunger or greater energetic demands [67]. Informal political leadership among the Tsimane associates with more surviving offspring, due in part to marrying young and drawing on greater social support [126]. Such support may accrue principally during times of need, such as crop failure [114]. Despite the fact that Nyangatom battle leaders have higher status and more social connections, they do not have greater reproductive success measured by their number of wives and children [117]. This may be because they are more likely to die in raids than other participants, thus reducing their ability to obtain additional wives.

The degree of monopolizable wealth in a society and the difficulty of inter-family collective action contribute to the emergence of institutional leadership [77,86]. The Nyangatom rely on institutions such as generation sets and territorial sections to collectively manage livestock and resolve disputes that erupt over its distribution. The Tsimane have a relative absence of monopolizable wealth, low frequency of collective action across extended families and few formal institutions supporting group life. The institution of the corregidor or village representative was implemented only in the past few decades and in large part through efforts of NGOs. However, Tsimane villages nearer to the local market town and that have greater population density and *per capita* conflict show evidence of increasing demand for more institutional leadership. In these villages, a smaller subset of the most influential men is sought after as mediators, and informal political leadership is more unequally distributed across community members. Residents of near-town villages may prefer more

uniform and less diffuse leadership, to more efficiently resolve conflict and coordinate responses to out-group threats and opportunities. The Tsimane present a unique opportunity to observe real-time changes in political inequality in a small-scale society. Theory-building concerning the origins of social complexity in human societies has tended to rely on archaeological evidence.

Among both the Tsimane and Nyangatom, the organization of group production, whether in the form of collective fishing or in intergroup warfare, tends to rely on temporary informal leadership, while conflict resolution is more likely to involve institutional leadership. The most probable explanation for this is that internal conflicts that occur within a society can trigger feuds or lead to group fission and undermine other collective action, including those activities necessary for subsistence. The potential costs of not solving intragroup conflict are greater than the costs of failing to assemble any particular collective fishing event or raiding party. A similar argument has been made concerning leadership in highland New Guinea, where the institutionalized display of material wealth organized by Big Men is rewarded more than *ad hoc* leadership during war. Such material displays signal to other communities an ability to collectively organize in warfare and deter aggression [127,128]. As small-scale societies globally become more integrated into market economies and experience new sources of intra- and intergroup conflict, there is a tremendous but fleeting opportunity to generate additional ethnography on the emergence of leadership and develop a more comprehensive theory of the causes of institutional leadership.

**Ethics.** The Institutional Review Boards of Harvard University and University of California at Santa Barbara approved the research conducted by L.G. and C.v.R., respectively.

**Data accessibility.** Tsimane and Nyangatom data are available by contacting L.G. (Glowacki@fas.harvard.edu) and C.v.R. (cvonrued@richmond.edu).

**Competing interests.** The authors have no competing interests.

**Funding.** Funding for Tsimane research 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). Funding for Nyangatom research was provided by the Wenner-Gren Foundation and the Harvard University Mind, Brain, and Behavior Initiative.

**Acknowledgements.** We thank two anonymous reviewers for helpful comments that improved the manuscript. C.v.R. would like to thank Michael Gurven and Hillard Kaplan, co-directors of the Tsimane Life History Project, as well as all Tsimane participants. L.G. would like to thank all Nyangatom participants and the administration of Nyangatom Woreda and the South Omo Zone, especially Lore Kakuta.

## References

1. von Rueden C, Gurven M, Kaplan H, Stieglitz J. 2014 Leadership in an egalitarian society. *Hum. Nat.* **25**, 538–566. (doi:10.1007/s12110-014-9213-4)
2. Gavrillets S, Fortunato L. 2014 A solution to the collective action problem in between-group conflict with within-group inequality. *Nat. Commun.* **5**, 3526. (doi:10.1038/ncomms4526)
3. Henrich J, Chudek M, Boyd R. 2015 The Big Man Mechanism: how prestige fosters cooperation and creates prosocial leaders. *Phil. Trans. R. Soc. B* **370**, 20150013. (doi:10.1098/rsth.2015.0013)
4. Hooper PL, Kaplan HS, Boone JL. 2010 A theory of leadership in human cooperative groups. *J. Theor. Biol.* **265**, 633–646. (doi:10.1016/j.jtbi.2010.05.034)
5. Price ME, Van Vugt M. 2014 The evolution of leader–follower reciprocity: the theory of service-for-prestige. *Front. Hum. Neurosci.* **8**, 363. (doi:10.3389/fnhum.2014.00363)

6. Nunn CL. 2000 Collective action, free-riders, and male extragroup conflict. In *Primate males* (ed. PM Kappeler), pp. 192–204. Cambridge, UK: Cambridge University Press.
7. Olson M. 1965 *The logic of collective action: public goods and the theory of groups*. Cambridge, MA: Harvard University Press.
8. Bailey I, Myatt JP, Wilson AM. 2013 Group hunting within the Carnivora: physiological, cognitive and environmental influences on strategy and cooperation. *Behav. Ecol. Sociobiol.* **67**, 1–17. (doi:10.1007/s00265-012-1423-3)
9. Hooper PL, Demps K, Gurven M, Gerkey D, Kaplan HS. 2015 Skills, division of labour and economies of scale among Amazonian hunters and South Indian honey collectors. *Phil. Trans. R. Soc. B* **370**, 20150008. (doi:10.1098/rstb.2015.0008)
10. Voelkl B, Portugal SJ, Unsold M, Usherwood JR, Wilson AM, Fritz J. 2015 Matching times of leading and following suggest cooperation through direct reciprocity during V-formation flight in ibis. *Proc. Natl Acad. Sci. USA* **112**, 2115–2120. (doi:10.1073/pnas.1413589112)
11. Van Belle S, Scarry CJ. 2015 Individual participation in intergroup contests is mediated by numerical assessment strategies in black howler and tufted capuchin monkeys. *Phil. Trans. R. Soc. B* **370**, 20150007. (doi:10.1098/rstb.2015.0007)
12. Willems EP, Hellriegel B, van Schaik CP. 2013 The collective action problem in primate territory economics. *Proc. R. Soc. B* **280**, 20130081. (doi:10.1098/rspb.2013.0081)
13. Willems EP, Arseneau TJM, Schleuning X, van Schaik CP. 2015 Communal range defence in primates as a public goods dilemma. *Phil. Trans. R. Soc. B* **370**, 20150003. (doi:10.1098/rstb.2015.0003)
14. von Rohr CR, Koski SE, Burkart JM, Caws C, Fraser ON, Ziltener A, van Schaik CP. 2012 Impartial third-party interventions in captive chimpanzees: a reflection of community concern. *PLoS ONE* **7**, e32494. (doi:10.1371/journal.pone.0032494)
15. Willems EP, van Schaik CP. 2015 Collective action and the intensity of between-group competition in nonhuman primates. *Behav. Ecol.* **26**, 625–631. (doi:10.1093/beheco/arv001)
16. Tooby J, Cosmides L, Price M. 2006 Cognitive adaptations for n-person exchange: the evolutionary roots of organizational behavior. *Manag. Decis. Econ.* **27**, 103–129. (doi:10.1002/mde.1287)
17. Tomasello M, Carpenter M, Call J, Behne T, Moll H. 2005 Understanding and sharing intentions: the origins of cultural cognition. *Behav. Brain Sci.* **28**, 675–735. (doi:10.1017/S0140525X05000129)
18. Fehr E, Fischbacher U, Gächter S. 2002 Strong reciprocity, human cooperation, and the enforcement of social norms. *Hum. Nat.* **13**, 1–25. (doi:10.1007/s12110-002-1012-7)
19. Boyd R, Richerson PJ. 1992 Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethol. Sociobiol.* **13**, 171–195. (doi:10.1016/0162-3095(92)90032-Y)
20. Fehr E, Gächter S. 2002 Altruistic punishment in humans. *Nature* **415**, 137–140. (doi:10.1038/415137a)
21. Yamagishi T. 1986 The provision of a sanctioning system as a public good. *J. Pers. Soc. Psychol.* **51**, 110–116. (doi:10.1037/0022-3514.51.1.110)
22. Oliver P. 1980 Rewards and punishments as selective incentives for collective action: theoretical investigations. *Am. J. Sociol.* **85**, 1356–1375. (doi:10.1086/227168)
23. Rand DG, Dreber A, Ellingsen T, Fudenberg D, Nowak MA. 2009 Positive interactions promote public cooperation. *Science* **325**, 1272–1275. (doi:10.1126/science.1177418)
24. Alexander RD. 1987 *The biology of moral systems*. New York, NY: Aldine de Gruyter.
25. Macfarlan SJ, Lyle HF. 2015 Multiple reputation domains and cooperative behaviour in two Latin American communities. *Phil. Trans. R. Soc. B* **370**, 20150009. (doi:10.1098/rstb.2015.0009)
26. Panchanathan K, Boyd R. 2004 Indirect reciprocity can stabilize cooperation without the second-order free rider problem. *Nature* **432**, 499–502. (doi:10.1038/nature02978)
27. Gintis H, Smith EA, Bowles S. 2001 Costly signaling and cooperation. *J. Theor. Biol.* **213**, 103–119. (doi:10.1006/jtbi.2001.2406)
28. Hill K, Hurtado AM. 2009 Cooperative breeding in South American hunter–gatherers. *Proc. R. Soc. B* **276**, 3863–3870. (doi:10.1098/rspb.2009.1061)
29. Sugiyama LS, Chacon R. 2000 Effects of illness and injury on foraging among the Yora and Shiwiari: pathology risk as adaptive problem. In *Human behavior and adaptation: an anthropological perspective* (eds L Cronk, N Chagnon, W Irons), pp. 371–396. New York, NY: Aldine.
30. Hooper PL, Gurven M, Winking J, Kaplan HS. 2015 Inclusive fitness and differential productivity across the life course determine intergenerational transfers in a small-scale human society. *Proc. R. Soc. B* **282**, 20142808. (doi:10.1098/rspb.2014.2808)
31. Winterhalder B. 1986 Diet choice, risk, and food sharing in a stochastic environment. *J. Anthropol. Res.* **5**, 369–392.
32. Ziker JP, Rasmussen J, Nolin DA. 2015 Indigenous Siberians solve collective action problems through sharing and traditional knowledge. *Sustainability Sci.* 1–11. (doi:10.1007/s11625-015-0293-9)
33. Jaeggi AV, Gurven M. 2013 Reciprocity explains food sharing in humans and other primates independent of kin selection and tolerated scrounging: a phylogenetic meta-analysis. *Proc. R. Soc. B* **280**, 20131615. (doi:10.1098/rspb.2013.1615)
34. Hawkes K, O'Connell J, Coxworth J. 2010 Family provisioning is not the only reason men hunt. *Curr. Anthropol.* **51**, 259–264. (doi:10.1086/651074)
35. Smith EA, Bird RB, Bird DW. 2003 The benefits of costly signaling: Meriam turtle hunters. *Behav. Ecol.* **14**, 116–126. (doi:10.1093/beheco/14.1.116)
36. McCabe JT. 2004 *Cattle bring us to our enemies: Turkana ecology, politics, and raiding in a disequilibrium system*, xvii, 301 pp. Ann Arbor, MI: University of Michigan Press.
37. Ruttan LM, Mulder MB. 1999 Are east African pastoralists truly conservationists? *Curr. Anthropol.* **40**, 621–652. (doi:10.1086/300086)
38. Otterbein K. 1968 Internal war: a cross-cultural study. *Am Anthropol* **70**, 277–289. (doi:10.1525/aa.1968.70.2.02a00040)
39. Wrangham R, Glowacki L. 2012 Intergroup aggression in chimpanzees and war in nomadic hunter–gatherers. *Hum. Nat.* **23**, 5–29. (doi:10.1007/s12110-012-9132-1)
40. Gat A. 1999 The pattern of fighting in simple, small-scale prestate societies. *J. Anthropol. Res.* **55**, 563–583.
41. Corry S. 2011 *Tribal peoples for tomorrow's world*. Alcester, UK: Freeman Press.
42. Glowacki L, Wrangham R. 2013 The role of rewards in motivating participation in simple warfare. *Hum. Nat.* **24**, 444–460. (doi:10.1007/s12110-013-9178-8)
43. Mathew S, Boyd R. 2011 Punishment sustains large-scale cooperation in prestate warfare. *Proc. Natl Acad. Sci. USA* **108**, 11 375–11 380. (doi:10.1073/pnas.1105604108)
44. Stein RT. 1975 Identifying emergent leaders from verbal and nonverbal communications. *J. Pers. Soc. Psychol.* **32**, 125–135. (doi:10.1037/h0076842)
45. Pescosolido AT. 2001 Informal leaders and the development of group efficacy. *Small Group Res.* **32**, 74–93. (doi:10.1177/104649640103200104)
46. O'Gorman R, Henrich J, Van Vugt M. 2009 Constraining free riding in public goods games: designated solitary punishers can sustain human cooperation. *Proc. R. Soc. B* **276**, 323–329. (doi:10.1098/rspb.2008.1082)
47. van der Heijden E, Potters J, Sefton M. 2009 Hierarchy and opportunism in teams. *J. Econ. Behav. Organ.* **69**, 39–50. (doi:10.1016/j.jebo.2008.09.007)
48. Hamman JR, Weber RA, Woon J. 2011 An experimental investigation of electoral delegation and the provision of public goods. *Am. J. Polit. Sci.* **55**, 737–751. (doi:10.1111/j.1540-5907.2011.00531.x)
49. Gächter S, Nosenzo D, Renner E, Sefton M. 2012 Who makes a good leader? Cooperativeness, optimism, and leading-by-example. *Econ. Inq.* **50**, 953–967. (doi:10.1111/j.1465-7295.2010.00295.x)
50. Guth W, Levati MV, Sutter M, Van der Heijden E. 2007 Leading by example with and without exclusion power in voluntary contribution experiments. *J. Public Econ.* **91**, 1023–1042. (doi:10.1016/j.jpubeco.2006.10.007)
51. Potters J, Sefton M, Vesterlund L. 2007 Leading-by-example and signaling in voluntary contribution games: an experimental study. *Econ. Theory* **33**, 169–182. (doi:10.1007/s00199-006-0186-3)
52. Anderson C, Brown CE. 2010 The functions and dysfunctions of hierarchy. *Res. Organ. Behav.* **30**, 55–89. (doi:10.1016/j.riob.2010.08.002)
53. Blau P. 1964 *Exchange and power in social life*. New York, NY: Wiley.
54. Gutierrez NL, Hillborn R, Defeo O. 2011 Leadership, social capital and incentives promote successful



- fisheries. *Nature* **470**, 386–389. (doi:10.1038/nature09689)
55. Baldassarri D, Grossman G. 2011 Centralized sanctioning and legitimate authority promote cooperation in humans. *Proc. Natl Acad. Sci. USA* **108**, 11 023–11 027. (doi:10.1073/pnas.1105456108)
56. Fischhoff IR, Sundaresan SR, Cordingley J, Larkin HM, Sellier MJ, Rubenstein DI. 2007 Social relationships and reproductive state influence leadership roles in movements of plains zebra, *Equus burchellii*. *Anim. Behav.* **73**, 825–831. (doi:10.1016/j.anbehav.2006.10.012)
57. Foley C, Pettorelli N, Foley L. 2008 Severe drought and calf survival in elephants. *Biol. Lett.* **4**, 541–544. (doi:10.1098/rsbl.2008.0370)
58. Reeb SG. 2000 Can a minority of informed leaders determine the foraging movements of a fish shoal? *Anim. Behav.* **59**, 403–409. (doi:10.1006/anbe.1999.1314)
59. Peterson RO, Jacobs AK, Drummer TD, Mech LD, Smith DW. 2002 Leadership behavior in relation to dominance and reproductive status in gray wolves, *Canis lupus*. *Can. J. Zool.* **80**, 1405–1412. (doi:10.1139/z02-124)
60. King AJ, Douglas CMS, Huchard E, Isaac NJB, Cowlishaw G. 2008 Dominance and affiliation mediate despotism in a social primate. *Curr. Biol.* **18**, 1833–1838. (doi:10.1016/j.cub.2008.10.048)
61. Overdorff DJ, Erhart EM, Mutschler T. 2005 Does female dominance facilitate feeding priority in black-and-white ruffed lemurs (*Varecia variegata*) in southeastern Madagascar? *Am. J. Primatol.* **66**, 7–22. (doi:10.1002/ajp.20125)
62. Harcourt JL, Sweetman G, Johnstone RA, Manica A. 2009 Personality counts: the effect of boldness on shoal choice in three-spined sticklebacks. *Anim. Behav.* **77**, 1501–1505. (doi:10.1016/j.anbehav.2009.03.004)
63. Kurvers RHJM, Prins HHT, van Wieren SE, van Oers K, Nolet BA, Ydenberg RC. 2010 The effect of personality on social foraging: shy barnacle geese scrounge more. *Proc. R. Soc. B* **277**, 601–608. (doi:10.1098/rspb.2009.1474)
64. Gilby IC, Machanda ZP, Mjungu DC, Rosen J, Muller MN, Pusey AE, Wrangham RW. 2015 'Impact hunters' catalyse cooperative hunting in two wild chimpanzee communities. *Phil. Trans. R. Soc. B* **370**, 20150005. (doi:10.1098/rstb.2015.0005)
65. Wright J, Stone RE, Brown N. 2003 Communal roosts as structured information centres in the raven, *Corvus corax*. *J. Anim. Ecol.* **72**, 1003–1014. (doi:10.1046/j.1365-2656.2003.00771.x)
66. Lindauer M. 1957 Communication among the honeybees and stingless bees of India. *Bee World* **38**, 3–14; 34–39. (doi:10.1080/0005772X.1957.11094964)
67. King AJ, Johnson DDP, Van Vugt M. 2009 The origins and evolution of leadership. *Curr. Biol.* **19**, R911–R916. (doi:10.1016/j.cub.2009.07.027)
68. Singh M, Boomsma J. 2015 Policing and punishment across the domains of social evolution. *Oikos* **124**, 971–982. (doi:10.1111/oik.02064)
69. van Zweden JS, Furst MA, Heinze J, D'Ettoire P. 2007 Specialization in policing behaviour among workers in the ant *Pachycondyla inversae*. *Proc. R. Soc. B* **274**, 1421–1428. (doi:10.1098/rspb.2007.0113)
70. Marshall L. 1960 Kung Bushman bands. *Africa* **30**, 325–354. (doi:10.2307/1157596)
71. Lowie RH. 1948 Some aspects of political organization among the American aborigines. *J. R. Anthropol. Inst.* **78**, 11–24. (doi:10.2307/2844522)
72. Spencer RF. 1959 *The North Alaskan Eskimo: a study in ecology and society*. Washington, DC: US Government Printing Office.
73. Weyer EM. 1932 *The eskimos*. New Haven, CT: Yale University Press.
74. Gusinde M. 1937 *The Yanama: the life and thought of the water nomads of Cape Horn*. Vienna, Austria: Anthropos.
75. Johnson A, Earle T. 2000 *The evolution of human societies*. Stanford, UK: Stanford University Press.
76. Kelly RL. 1995 *The foraging spectrum: diversity in hunter-gatherer lifeways*, xvi, 446 pp. Washington, DC: Smithsonian Institution Press.
77. von Rueden C. 2014 The roots and fruits of social status in small-scale human societies. In *The psychology of social status* (eds J Cheng, J Tracy, C Anderson). New York, NY: Springer.
78. Dyson-Hudson R, Smith EA. 1978 Human territoriality: an ecological reassessment. *Am. Anthropol.* **80**, 21–41. (doi:10.1525/aa.1978.80.1.02a00020)
79. Boone J. 1992 Competition, conflict, and development of social hierarchies. In *Evolutionary ecology and human behavior* (eds EA Smith, B Winterhalder), pp. 301–337. New York, NY: Aldine de Gruyter.
80. Smith EA, Choi JK. 2007 The emergence of inequality in small-scale societies: simple scenarios and agent-based simulations. In *The model based archaeology of socio-natural systems* (eds T Kohler, VD Leeuw), pp. 105–119; 241–244. Santa Fe, NM: SAR Press.
81. Carneiro R. 1970 A theory of the origin of the state. *Science* **169**, 733–738. (doi:10.1126/science.169.3947.733)
82. Kennett D, Winterhalder B, Bartruff B, Erlandson J. 2009 An ecological model for the emergence of institutionalized social hierarchies on California's Northern Channel Islands. In *Pattern and process in cultural evolution* (ed. S Shennan), pp. 297–314. Berkeley, CA: University of California Press.
83. Mulder MB *et al.* 2009 Intergenerational wealth transmission and the dynamics of inequality in small-scale societies. *Science* **326**, 682–688. (doi:10.1126/science.1178336)
84. Boas F. 1921 *Ethnology of the Kwakiutl, based on data collected by George Hunt*. Washington, DC: US Government Printing Office.
85. Arnold J. 2010 The role of politically charged property in the appearance of institutionalized leadership: a view from the North American Pacific Coast. In *The evolution of leadership: transitions in decision making from small-scale to middle-range societies* (ed. J Kanter), pp. 121–146. Santa Fe, NM: SAR Press.
86. Kaplan HS, Hooper PL, Gurven M. 2009 The evolutionary and ecological roots of human social organization. *Phil. Trans. R. Soc. B* **364**, 3289–3299. (doi:10.1098/rstb.2009.0115)
87. Boyd R, Richerson PJ. 1988 The evolution of reciprocity in sizable groups. *J. Theor. Biol.* **132**, 337–356. (doi:10.1016/S0022-5193(88)80219-4)
88. Alberti G. 2014 Modeling group size and scalar stress by logistic regression from an archaeological perspective. *PLoS ONE* **9**, e91510. (doi:10.1371/journal.pone.0091510)
89. Johnson GA. 1982 Organizational structure and scalar stress. In *Theory and explanation in archaeology* (eds C Renfrew, M Rowlands, BA Segraes-Whallon), pp. 389–421. New York, NY: Academic Press.
90. Diehl MW. 2000 Some thoughts on the study of hierarchies. In *Hierarchies in action: cui bono?* (ed. MW Diehl), pp. 11–30. Carbondale, IL: Southern Illinois University Press.
91. Service E. 1962 *Primitive social organization: an evolutionary perspective*. New York, NY: Random House.
92. Spisak B, O'Brien M, Nicholson N, Van Vugt M. 2015 Niche construction and the evolution of leadership. *Acad. Manage. Rev.* **40**, 291–306. (doi:10.5465/amr.2013.0157)
93. Feinman GM, Neitzel J. 1984 Too many types: an overview of sedentary prestate societies in the Americas. *Adv. Archaeol. Method Theory* **7**, 39–102. (doi:10.1016/b978-0-12-003107-8.50007-4)
94. Lewis H. 1974 *Leaders and followers: some anthropological perspectives*. Reading, MA: Addison-Wesley.
95. Price D. 1981 Nambiquara leadership. *Am. Ethnol.* **8**, 686–708. (doi:10.1525/ae.1981.8.4.02a00020)
96. Werner D. 1981 Are some people more equal than others? Status inequalities among the Mekranoti Indians of central Brazil. *J. Anthropol. Res.* **37**, 360–373.
97. Wiessner P. 2010 The power of one? Big men revisited. In *The evolution of leadership: transitions in decision making from small-scale to middle-range societies* (eds J Kanter, K Vahn, J Earkins), pp. 195–222. Santa Fe, NM: SAR Press.
98. Van Vugt M, Hogan R, Kaiser RB. 2008 Leadership, followership, and evolution: some lessons from the past. *Am. Psychol.* **63**, 182–196. (doi:10.1037/0003-066X.63.3.182)
99. Chagnon NA. 1983 *Yanomamo: the fierce people*. New York, NY: Holt, Rinehart and Winston.
100. von Rueden C, Gurven M. 2012 When the strong punish: why net costs of punishment are often negligible. *Behav. Brain Sci.* **35**, 43–44. (doi:10.1017/S0140525X11001427)
101. Wiessner P. 2005 Norm enforcement among the Ju/'hoansi bushmen. *Hum. Nat.* **16**, 115–145. (doi:10.1007/s12110-005-1000-9)
102. de Weerd H, Verbrugge R. 2011 Evolution of altruistic punishment in heterogeneous populations.



- J. Theor. Biol.* **290**, 88–103. (doi:10.1016/j.jtbi.2011.08.034)
103. Przepiorka W, Diekmann A. 2013 Individual heterogeneity and costly punishment: a volunteer's dilemma. *Proc. R. Soc. B* **280**, 20130247. (doi:10.1098/rspb.2013.0247)
104. Gordon DS, Madden JR, Lea SEG. 2014 Both loved and feared: third party punishers are viewed as formidable and likeable, but these reputational benefits may only be open to dominant individuals. *PLoS ONE* **9**, e110045. (doi:10.1371/journal.pone.0110045)
105. Schniter E, Gurven M, Kaplan H, Wilcox N, Hooper PL. 2015 Skill ontogeny among Tsimane forager-horticulturalists. *Am. J. Phys. Anthropol.* **158**, 3–18. (doi:10.1002/ajpa.22757)
106. Baltes PB, Smith J. 1990 Towards a psychology of wisdom and its ontogenesis. In *Wisdom, its nature, origins, and development* (ed. RJ Sternberg), pp. 87–120. Cambridge, UK: Cambridge University Press.
107. Lukaszewski AW, von Rueden CR. 2015 The extraversion continuum in evolutionary perspective: a review of recent theory and evidence. *Pers. Indiv. Differ* **77**, 186–192. (doi:10.1016/j.paid.2015.01.005)
108. Hudson T, Underhay E. 1978 *Crystals in the sky: an intellectual odyssey involving Chumash astronomy, cosmology, and rock art*. Socorro, NM: Ballena Press.
109. Patton JQ. 2005 Meat sharing for coalitional support. *Evolution and human behavior* **26**, 137–157. (doi:10.1016/j.evolhumbehav.2004.08.008)
110. Boone JL, Kessler KL. 1999 More status or more children? Social status, fertility reduction, and long-term fitness. *Evol. Hum. Behav.* **20**, 257–277. (doi:10.1016/S1090-5138(99)00011-2)
111. Gurven M, Kaplan H, Supa AZ. 2007 Mortality experience of Tsimane amerindians of Bolivia: regional variation and temporal trends. *Am. J. Hum. Biol.* **19**, 376–398. (doi:10.1002/ajhb.20600)
112. Hooper PL, DeDeo S, Caldwell Hooper AE, Gurven M, Kaplan HS. 2013 Dynamical structure of a traditional Amazonian social network. *Entropy* **15**, 4932–4955. (doi:10.3390/e15114932)
113. von Rueden C, Trumble B, Thompson M, Stieglitz J, Hooper PL, Blackwell A, Kaplan H, Gurven M. 2014 Political influence associates with cortisol and health among egalitarian forager-farmers. *Evol. Med. Public Health* **1**, 122–133. (doi:10.1093/emph/eou021)
114. von Rueden C. 2011 The acquisition of social status by males in small-scale human societies (with an emphasis on the Tsimane of Bolivia). PhD dissertation, University of California, Santa Barbara, CA, USA.
115. Glowacki L. 2015 Incentives for war in small-scale societies. PhD dissertation, Harvard University, Cambridge, MA, USA.
116. Tornay S. 1981 The Nyangatom: an outline of their ecology and social organization. In *Peoples and cultures of the Ethio-Sudan borderlands* (ed. ML Bender), pp. 137–178. East Lansing, MI: African Studies Center, Michigan State University.
117. Glowacki L, Wrangham R. 2015 Warfare and reproductive success in a tribal population. *Proc. Natl Acad. Sci. USA* **112**, 348–353. (doi:10.1073/pnas.1412287112)
118. Boehm C. 1999 *Hierarchy in the forest: the evolution of egalitarian behavior*. Cambridge, MA: Harvard University Press.
119. von Rueden C, Gurven M, Kaplan H. 2008 The multiple dimensions of male social status in an Amazonian society. *Evol. Hum. Behav.* **29**, 402–415. (doi:10.1016/j.evolhumbehav.2008.05.001)
120. Low B. 1992 Sex, coalitions, and politics in preindustrial societies. *Polit. Life Sciences* **9**, 1–18.
121. Vandermassen G. 2008 Can Darwinian feminism save female autonomy and leadership in egalitarian society? *Sex Roles* **59**, 482–491. (doi:10.1007/s11199-008-9478-3)
122. Lee R. 1982 Politics, sexual and nonsexual, in an egalitarian society. In *Politics and history in band societies* (eds E Leacock, R Lee). New York, NY: Cambridge University Press.
123. Rucas S. 2015 Cooperation drives competition among Tsimane women in the Bolivian Amazon. In *The Oxford Handbook of Women and Competition* (ed. M Fisher). Oxford, UK: Oxford University Press.
124. Glowacki L, Gönc K. 2013 Customary institutions and traditions in pastoralist societies: neglected potential for conflict resolution. *Conflict Trends* **2013**, 26–32.
125. Browser B, Patton J. 2010 Women's leadership: political alliance, economic resources, and reproductive success in the Ecuadorian Amazon. In *The evolution of leadership: transitions in decision making from small-scale to middle-range societies* (eds KJ Vaughn, JW Eerkens, J Kanter), pp. 51–71. Santa Fe, NM: SAR Press.
126. von Rueden C, Gurven M, Kaplan H. 2011 Why do men seek status? Fitness payoffs to dominance and prestige. *Proc. R. Soc. B* **278**, 2223–2232. (doi:10.1098/rspb.2010.2145)
127. Roscoe P. 2009 Social signaling and the organization of small-scale society: the case of contact-era New Guinea. *J. Archaeol. Method Theory* **16**, 69–116. (doi:10.1007/s10816-009-9062-3)
128. Roscoe P. 2000 New Guinea leadership as ethnographic analogy: a critical review. *J. Archaeol. Method Theory* **7**, 9–126. (doi:10.1023/A:1009512726844)