

# Formation of raiding parties for intergroup violence is mediated by social network structure

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Intergroup violence is common among humans worldwide. To assess how within-group social dynamics contribute to risky, betweengroup conflict, we conducted a 3-y longitudinal study of the formation of raiding parties among the Nyangatom, a group of East African nomadic pastoralists currently engaged in small-scale warfare. We also mapped the social network structure of potential male raiders. Here, we show that the initiation of raids depends on the presence of specific leaders who tend to participate in many raids, to have more friends, and to occupy more central positions in the network. However, despite the different structural position of raid leaders, raid participants are recruited from the whole population, not just from the direct friends of leaders. An individual's decision to participate in a raid is strongly associated with the individual's social network position in relation to other participants. Moreover, nonleaders have a larger total impact on raid participation than leaders, despite leaders' greater connectivity. Thus, we find that leaders matter more for raid initiation than participant mobilization. Social networks may play a role in supporting risky collective action, amplify the emergence of raiding parties, and hence facilitate intergroup violence in small-scale societies.

warfare | social networks | collective action | pastoralists | emergence

ntergroup violence is common, worldwide, and harmful. Global annual deaths from large-scale warfare, for example, range from 0.5 to 1 million, and this does not include nonfatal physical and mental injuries (1). A diverse set of approaches has been used to study intergroup violence and warfare. Evolutionary models have credited collective violence with an important role in the development of modern human behavior (2-7), whereas cultural and ecological factors have been shown to influence small and largescale violence (8-13). More recently, there has been increased interest in understanding the dynamics of group-based violence and the social processes that can contribute to it in the setting of insurgent and terrorist groups (14, 15); for example, online records suggests small, self-organizing groups coalesce into larger groups preceding terrorist attacks (16). Warfare has also been studied as a collective action problem-because individuals must mobilize to engage in a group activity with shared gains (e.g., deterrence, territory) and individual risks (e.g., injury, death) (17, 18).

Despite these advances, fundamental questions remain about how violent groups are formed, and the extent to which they may self-organize and emerge organically. Theoretical work suggests interindividual differences may be important for initiating and sustaining risky collective action, but empirical evidence in humans supporting this is sparse (19, 20). Research in primate behavior provides some clues regarding the emergence of violent intergroup conflict. Wild chimpanzees engage in lethal coalitionary violence against other communities (21), and a few "impact" individuals show exceptional motivation to participate in intergroup interactions (22, 23). Similarly, other primate species show interindividual variation in initiating intergroup conflict, including lemurs (24) and vervet monkeys (25). In these cases, the initiative shown by such individuals appears responsible for promoting participation by others.

To understand how violence is initiated in self-organizing groups of humans, we explore the role of social structure in collective violence in a traditional, nonstate society. Such small-scale societies offer an appealing opportunity to answer questions regarding the emergence of collective violence because they are generally free from formal institutions regulating conflict, such as are found in modern nation states (26), and there is neither conscription nor formal institutional control over violence. Unfortunately, field data on collective violence in these contexts are rare. Most studies of intergroup violence in small-scale populations have focused on the mortality rate and demographic effects of warfare, rather than the social precursors (27–29).

Although social networks are known to facilitate solutions to collective action problems (30–32) and to have a role in the emergence of both cooperation (33, 34) and violence (35), prior work on the structure of social networks (36) and their role in the emergence of violence in evolutionarily relevant populations is limited. A study among the Yanomamö examined how coparticipation in lethal intergroup violence influenced alliances later in life, finding that men who participated together in a killing were likely to live together and exchange marriage partners (37). That study provided important evidence regarding how participation in an intergroup conflict can be used strategically to advance subsequent relationships among participants; however, it did not evaluate social networks or the group composition of raiding parties.

### Significance

The social network structure of a small-scale society is crucial to formation of raiding parties involved in violent between-group raids. We mapped the social networks among Nyangatom men in a defined area of Ethiopia and ascertained membership in 39 intergroup raiding parties over 3 y. Although a small set of leaders initiated raids, they were not especially crucial for the composition of the raiding parties; instead, aspects of social network structure served to determine group composition and to amplify group size, once a raid was initiated. Intergroup violence, like other forms of collective action, depends on social structure and not just individual agency. This is relevant to spontaneous violent activities in settings as diverse as revolutions, gangs, and terrorist groups.

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To address how social networks influence the emergence of violence, we mapped the social ties in a nonstate society in which groups engaging in violent intergroup raiding formed organically, analyzing the role of social networks in instigating and sustaining intergroup conflict. Using observations derived from long-term ethnographic fieldwork, coupled with detailed mapping of the social network of raiding-aged men, we present data from a complete set of 39 discrete intergroup conflict events among the Nyangatom, a society of nomadic agro-pastoralists inhabiting a remote region along the border of South Sudan and Ethiopia largely outside the reach of state institutions (38, 39).

# The Nyangatom

Many Nyangatom live in mobile cattle camps containing between 10 and 100 persons, and the population and number of these camps are not fixed (38). Depending on seasonal variation, camps may disband (with residents forming new camps) or they may aggregate and form larger villages. The Nyangatom also have semipermanent villages with dynamic membership, and movement between camps and villages is common. Livestock have a central place in the culture and diet of the Nyangatom and are necessary for many social exchanges, including marriage. To marry, a male is required to provide the family of the bride with bride wealth, often 30-60 cattle but sometimes as many as 100 cattle. Therefore, livestock are highly sought after, and violent conflict with other groups to obtain them is common (38-40). The Nyangatom also have a distinctive social organization involving sequential generation sets and age sets (38); most males engage in activities such as herding, socializing, and raiding with members of their age group, creating strong social bonds between members (38).

The primary type of intergroup conflict event for the Nyangatom is the raid (singular emojirimónu), in which a small group of men attempt to locate and seize livestock from other nearby ethnic groups, kill enemies they encounter when they can do so with minimal risk, and then escape unharmed. Casualties among members of raiding parties are unusual as they seek to minimize personal risk, but injuries and deaths of members of enemy groups are common, and fatalities among raiders are not unheard of. Successful raiders receive captured livestock (18, 39) and sometimes other social benefits, such as status, honorific names and scars, and public praise (9, 41). Raids generally begin with one or two individuals recruiting other participants, a process that typically takes several days. Raiding parties can also emerge when large groups of young men are congregated, such as during a ceremony. Individuals are not compelled to join a raiding party, and many young men elect not to join; and there are no formal sanctions for cowardice, desertion, or failure to participate (39).

#### Results

We used extensive semistructured interviews to collect information regarding intergroup conflict events that occurred between the Nyangatom and their neighbors. We comprehensively identified all 91 men residing in the study area who were of the appropriate age for raid participation ( $\sim$ 18–45 y) and established group composition for a complete set of all intergroup raids initiated during the study period (n = 39; *Methods*).

We measured a variety of attributes of potential raiders, including height, weight, kin relationships, and measures of paternal wealth (Dataset S1, Table S1). We also performed a comprehensive, sociocentric network study of this population of Nyangatom males. To measure friendship ties within this group, we used a gift task modeled on prior work with the Hadza huntergatherers of Tanzania (33) in which Nyangatom were asked to identify other study participants to whom they would like to give an anonymous gift.

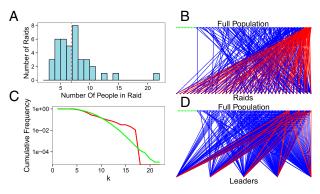
On average, there was one raid every 4.7 wk, and raids were generally nonoverlapping in time, with raiding forays typically lasting several days. Most of the population (78 of 91) participated

in at least one raid (mean participation, 2.9 raids; SD, 3.3). On average, about 7 men (SD, 3.4) participated in each raid (Fig. 1*A*); roughly 80% of raids in our sample were successful, resulting in an average of four head of livestock (including cattle, goats, and donkeys) being captured by each raider of a successful raid.

Measured individual-level characteristics were tested for association with raid participation in bivariate models without controls including the number of siblings, height, weight, and measures of paternal wealth (Dataset S1, Tables S2–S5). Although the number of siblings, weight, and paternal wealth were significant in bivariate models, none of these egocentric characteristics remains significant in a multivariate model (Dataset S1, Table S7). That is, we did not find evidence that these variables were independently relevant to whether a person went on a raid. However, a bootstrap analysis showed that the average weight of a leader is higher than that of a nonleader (P = 0.010), whereas neither the height (P = 0.468) nor the number of siblings (P = 0.364) is significantly different between leaders and nonleaders (*SI Methods*).

Fig. 1B shows a bipartite network of all 91 subjects and all 39 raids, with the five individuals identified as leaders on any raid shown in red. Leaders were clearly the most participatory, and all raids had at least one of these leaders. To complement the ethnographic data, we also used the raid participation data alone (Fig. 1B) to conduct a "minimal set analysis" to independently identify leaders (SI Methods). This analysis attempts to identify the smallest group of individuals at least one of whom participated in every raid. The procedure successfully identified all five individuals that were named as leaders on any raid by participants. These five individuals also participated in significantly more raids than expected due to chance (all  $P \ll 0.001$ ) as determined by a procedure where we randomly reassign the identities of those who participated in each raid while keeping the distribution of raid participation fixed (SI Methods). Intriguingly, these results show that leaders can be successfully identified from raid participation data alone without prior information on the roles of each participant. Because there was no raid that did not include at least one leader, these results also suggest that leadership has an important role in the formation of intergroup violence.

The social network of raiding-age Nyangatom men is shown in Fig. 2, with those who did not participate in any raids shown in green, those who participated in at least one raid in blue, and leaders shown in red. Node size corresponds to the number of raids



**Fig. 1.** (*A*) Distribution of raid sizes over a total of 39 raids. The dashed red line shows the mean. (*B*) Bipartite participant–raid network. Top nodes are people, and bottom nodes are raids. Each raid has at least one leader. (C) Degree distribution (cumulative frequency) of the friendship network (red) and the average distribution of  $10^3$  random networks with the same number of nodes and edges (green). The real distribution does not differ significantly from a random graph. (*D*) Participant–leader raid relation network. A leader (*Bottom*) is connected to an alter if the alter went on a raid with the leader.

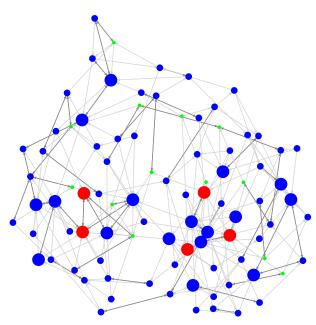


Fig. 2. Network of friendship ties in Nyangatom society determined using gift allocation task. Node size is proportional to raid participation (number of raids in which an individual participated). Dark gray arrows indicate reciprocal, two-way friendship ties, and light gray arrows are one-way ties. The age structure of the population is also visible, insofar as there is a rough demarcation visible here between the "northwest" and "southeast" regions of this network, with more ties within than between the two communities.

in which a person participated (larger indicates more raids). The mean number of incoming friendship nominations (in-degree) was 3 (SD, 2.7), and the range was 0–13.

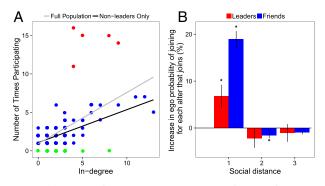
Although in-degree is associated with both wealth and number of siblings, the strongest predictor of the number of friendship nominations is leadership status. Leaders have more than twice as many friends (defined by receiving gifts) as nonleaders (5.2 vs. 2.4) and the difference is strongly significant (P = 0.01). Leaders also score significantly higher on a measure of network centrality, even when controlling for in-degree (P = 0.04) (*SI Methods*). This means that leaders not only have more friends but also that their friends tend to be more popular, meaning leaders also have more friends of friends as well.

We explored the ways the Nyangatom social network is similar to certain other social networks by measuring a comprehensive set of statistics (33). Although the cumulative degree distribution (Fig. 1C) does not appear to differ significantly from a random network (P = 0.76), a number of other important properties are shared with nonrandom social networks. Reciprocity (the probability that participant B names participant A as a friend, given that participant A names participant B) is significantly higher in the Nyangatom network (reciprocity, 0.37) than in a random network ( $P \ll 0.001$ ); that is, there are significantly more two-way friendship ties in the real network than a random network. In addition, at 0.17, transitivity (the probability that two of a participant's friends are friends with one another) is also significantly higher in the Nyangatom network than a random network with the same number of vertices and edges ( $P \ll 0.001$ ). Finally, there is also strong homophily (the tendency of people with similar characteristics to have social ties with one another) by age group (0.88,  $P \ll 0.001$ ) (Fig. S1) and by degree (0.10, P = 0.04). This homophily by age partly reflects the fact that the primary social interactions for males in Nyangatom society occur between members of the same age group; and our assessment of social ties also shows stronger connections within age groups than between age groups, thus supporting the validity of the gift-giving task as a measure of social connections among the Nyangatom.

Social network structure is highly relevant to the composition of raiding groups, and membership in raiding groups does not arise by chance. Fig. 3A shows that individuals with more social connections (i.e., higher degree) tend to go on more raids, even when we exclude the five leaders from the analysis and more popular nodes (those with higher degree) tend to go on more raids (Fig. S2). Each additional social connection is associated with an increase of 0.45 raids (SE, 0.17; P = 0.01) in the expected number of raids in which a subject participates. In fact, regression models that include indegree, height, weight, wealth, and number of siblings show that social relationship "capital" is more strongly associated with raid participation than physical or material capital (SI Methods). Although we expect that having more social connections leads to more invitations or pressure to participate in raiding parties, it is also possible that increased raiding contributes to a greater number of social connections. Although wealth is associated with participation, the association becomes insignificant when we exclude leaders from the model (SI Methods). Our measure of network indegree is the only variable that survives various model specifications.

However, the emergence of violent collective behavior is more nuanced than leaders simply being linked by friendship ties to nonleader "followers." We used regression analysis to evaluate the decision to join a raid, examining how this decision is associated with the total number of other people who join the raid, the number of one's friends in particular who participate, and the number of other leaders who participate (*SI Methods*). In these models, we treated each individual's decision to participate in each raid as the dependent variable, and we assessed how the presence of other potential raiders was associated with the probability that an individual would participate in a raid. To control for unobserved characteristics of individuals (e.g., their attitudes toward violence or risk, as well as other personality factors) and of raids (e.g., the distance to the raid target or the anticipated value of the raided items), we included in the model fixed effects for both individuals and raids.

Although raid size was not significantly associated with decisions to join raids, leader and friend participation was. Specifically, subjects were 6.8% (SE, 2.4%) more likely to join raids if they were directly connected by friendship to a leader in that raid. If, on



**Fig. 3.** (*A*) Number of times people joined raids as a function of social indegree. Regression lines are shown for the full population (gray) ( $R^2 = 0.32$ ) and excluding the leaders (black) ( $R^2 = 0.42$ ). People who participated in no raids are green, nonleader participants are blue, and leaders are red. (*B*) Increase in probability of joining a raid based on geodesic social distance to leaders and to nonleader friends. Lines denote 1 SE. The large positive coefficients on first-degree connections show that direct nonleader friends are more motivating than leader friends, and both are significant. The negative coefficient on second-degree connections provides evidence against cascades beyond 1 degree in raiding-party formation. Motivation did not extend significantly to third-degree friends.

the other hand, they were friends of friends with the leader (social distance 2) or friends of friends of friends (social distance 3), they were no more likely to join (Fig. 3B). This suggests that leaders may be able to mobilize their direct friendship contacts to join raids. However, further analysis yields the important observation that, if so, leaders are no more able to mobilize their friends than is anyone else in the population. Each nonleader friend who participated in a raid increased the likelihood that a person joined by 19.2% (SE, 1.4%), which is significantly higher than the boost in probability associated with leader friends participating ( $P < 10^{-5}$ ).

Although leaders appear to be less relevant than nonleaders for predicting any one decision to join a raid, recall that leaders are much better connected to the network. It is possible that leaders may have less effect per person, but a greater total effect because they are connected to more people. However, a test of this hypothesis fails. In a model where we regress total participation by a person's friends on a person's decision to join, their leadership status, and an interaction variable that indicates the effect of leadership on total mobilization, we find that significantly fewer people join when a leader joins than when a nonleader joins (P = 0.008) (*SI Methods*). In other words, the key motivating factor to join a raid once a raid is initiated is not leadership; it is friendship.

Social distance has an unusual relationship in the results for nonleader friends (Fig. 3B). After controlling for friend participation, each friend of a friend who participates in a raid actually decreases the likelihood a person will join by 1.6% (SE, 0.6%; P =0.006). This suggests that people just outside of a person's direct social network may actually slightly demotivate participation in raids; weak ties are apparently not useful for recruiting and may even be somewhat detrimental. This also suggests that the men indeed have different sorts of relationships with each other, even within a population of just 91 individuals. The significance of these associations survives models with various controls (*SI Methods*).

Finally, a model with sibling participation did not provide evidence for siblings being more or less likely than chance to raid with each other (P = 0.23) (*SI Methods*). Thus, it appears that kinship did not influence raiding-party composition, consistent with prior work with humans (37).

## Discussion

A rich picture appears regarding the role of leadership and social network structure in the emergence of collective intergroup violence in this evolutionarily relevant population. Leaders appear to matter mechanistically, functioning as focal points or as nucleation sites for raids among the Nyangatom. Although they participate most often (the five leaders are the top five participants, by number of raids), they are not particularly good at directly mobilizing other participants. Instead, nonleaders have a critical role in amplifying the size and specifying the composition of raids once leaders initiate their formation. Although leaders may instigate raids, they have no more influence than anyone else in promoting participation. Moreover, our analysis of individual decisions to participate in raids, using fixed-effects models, shows that social network structure is key even when controlling for the "push" of individual differences in the tendency to join raids and the "pull" of differences between raiding parties that may make some parties more appealing to join than others.

Our findings are also noteworthy because we did not uncover ethnographic reports of formal sanctioning for nonparticipants. However, it is possible that the withdrawal of a friendship tie is a form of sanction (31). If so, then, the pattern of friendships may itself depend on the willingness of men, at least occasionally, to join raids together. Work among the Yanomamö suggests that coparticipation in violence may result in subsequent formation of social bonds (37), and men commonly enlist in the military with friends and are often encouraged to do so in state-sponsored wars (42). Future research should include repeated measures of network structure to ascertain the extent to which collective violence also shapes the network.

One important limitation of our study is that our network measures only provide a snapshot of the social network at one point in time, leaving open the possibility that coraiding led to the formation of the social ties we observed rather than men opting to raid with their friends. Nevertheless, based on the ethnographic evidence collected, we think friendship is a primary mechanism that contributes to coparticipation in a raid. Among East African pastoralist societies such as the Nyangatom, young men engage in many collective activities together, such as herding and ceremonies, creating opportunities to meet other members of their age group. As a result, they form very tightly bound cliques early in adolescence that are an important part of social life. Raids are risky and raiders are commonly nervous before a raid; this may be why individuals choose to raid with their friends rather than with people they are not so well acquainted with (as our findings also document, even within a relatively small population of 91 people). Rather than acting primarily as a mechanism to generate friendships with unfamiliar individuals, raids may instead act to deepen friendships or be built upon them.

Important similarities and differences emerge between our results and behavioral data on collective violence in other primates. Among wild chimpanzees engaged in group border patrols and hunting, there is little indication that kinship influences the likelihood or effectiveness of such collective action (43). Among the Nyangatom, we also found no influence of sibling relationships on raiding-party composition, suggesting alternative mechanisms for generating participation. This is also consistent with the cognitive and social complexity of humans and with prior observational work regarding the role of social ties in the emergence of both collective violence (10, 37, 42, 44) and altruism in humans (31, 32, 45).

Although we find that participation in raiding is widespread throughout the population, there is also significant individual variation. A substantial portion of the population did not participate in any raids, whereas five individuals participated in more than 10 raids and most participated in slightly less than 3 raids. The fact that the initiation of raiding parties appears to depend on leaders who function as nucleation sites for raids and who attract other participants is consistent with research showing how individual variation within a population can contribute to the resolution of collective action problems (17, 20), including in risky, intergroup violence in both humans and chimpanzees (46). Leaders may alter the costs and benefits for others—either by reducing the costs of the raid to other participants (e.g., via setting the time of the raid or by scouting) or by exerting social pressure on others to join (18, 47–49).

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In sum, we find that leadership matters in initiating collective violence in this small-scale society, but that it is not an especially important factor with respect to who joins the raiding parties. However, violent group formation does not involve individuals simply copying the risky violent behaviors of other members of their group either; rather, social network structure matters in the formation of raiding parties and in the emergence of such structured violence. To the extent that Nyangatom raiding behavior mimics the general phenomenon of risky collective action, we have identified an important amplifying effect: a handful of motivated individuals, with distinctive network positions, coupled with a wider group of reinforcing individuals embedded within a network, can lead to population-level violent effects.

These results might be relevant to other informal contexts in which violence occurs, such as urban gangs (35), localized insurgencies (14, 50), revolutionary protests (10), or terrorist attacks (16). Many types of violence do not depend solely on the desires and actions of individuals or even dyads, and instead may at least partially emerge and be supported by the very social structure in which all individuals are embedded (51). These observations, finally, suggest two things with respect to the prospect of managing violence. On the positive side, attenuating the impact of a leader may prevent the original nucleation of the violence. However, on the negative side, once violence is switched on, people are likely to join from throughout the whole population, and so, once instigated, violence has a wide-reaching effect on the society.

#### Methods

Data were collected as part of an ongoing ethnographic study of the Nyangatom in which one of the researchers (L-G.) intermittently resided in the study area in Ethiopia between 2009 and 2012. We used semistructured interviews to collect information regarding intergroup conflict events that occurred between the Nyangatom and their neighbors, including the Turkana, Daasanach, and Suri.

We identified 91 men residing in the study area who were of the appropriate age to participate in raids (~18-45 y). We conducted interviews with each of these individuals, collecting data on their conflict history including both successful and unsuccessful raids; raiding-party composition was validated through peer reports. The presence of a raider on a raiding party was determined by an individual's participation in the raiding party for any portion of it; we did not measure desertion, and some individuals may have ceased their participation during the actual raid because they were afraid or for other reasons. Leadership was ascertained by cross-validated personal accounts elicited by questions about whether any person was a leader of the raid using two Nvanoatom terms for leader (singular *Ekarikor*): singular *Eketamunan*).

We also performed a comprehensive, sociocentric network study of the entire population of raiding-age Nyangatom males (n = 91). To measure friendship ties within this group, we used a gift task modeled on prior work with the Hadza hunter-gatherers of Tanzania (33) in which the Nyangatom subjects were asked to identify other study participants to whom they would like to give a gift of candy. Giving a gift is an important measure of friendship in most societies (52). We chose candy as the allocation currency because of its practical ease and because Nyangatom value it. Subjects were presented with three pieces of candy and shown photo sheets containing the facial portraits of study participants to whom an anonymous allocation could be given. They

- Lozano R, et al. (2012) Global and regional mortality from 235 causes of death for 20 age groups in 1990 and 2010: A systematic analysis for the Global Burden of Disease Study 2010. Lancet 380(9859):2095–2128, and erratum (2013) 381(9867):628.
- Böhm R, Rusch H, Gürerk Ö (2016) What makes people go to war? Defensive intentions motivate retaliatory and preemptive intergroup aggression. *Evol Hum Behav* 37(1):29–34.
- Bowles S (2009) Did warfare among ancestral hunter-gatherers affect the evolution of human social behaviors? Science 324(5932):1293–1298.
- Rusch H (2014) The evolutionary interplay of intergroup conflict and altruism in humans: A review of parochial altruism theory and prospects for its extension. Proc Biol Sci 281(1794):20141539.
- Rusch H (2014) The two sides of warfare: An extended model of altruistic behavior in ancestral human intergroup conflict. *Hum Nat* 25(3):359–377.
- Wrangham RW, Glowacki L (2012) Intergroup aggression in chimpanzees and war in nomadic hunter-gatherers: Evaluating the chimpanzee model. *Hum Nat* 23(1):5–29.
- Kelly RC (2005) The evolution of lethal intergroup violence. Proc Natl Acad Sci USA 102(43):15294–15298.
- Bohorquez JC, Gourley S, Dixon AR, Spagat M, Johnson NF (2009) Common ecology quantifies human insurgency. *Nature* 462(7275):911–914.
- Glowacki L, Wrangham RW (2013) The role of rewards in motivating participation in simple warfare. Hum Nat 24(4):444–460.
- Gould RV (1995) Insurgent Identities: Class, Community and Protest in Paris from 1848 to the Commune (Univ of Chicago Press, Chicago).
- Hsiang SM, Burke M, Miguel E (2013) Quantifying the influence of climate on human conflict. Science 341(6151):1235367.
- Lim M, Metzler R, Bar-Yam Y (2007) Global pattern formation and ethnic/cultural violence. Science 317(5844):1540–1544.
- Wiessner P, Pupu N (2012) Toward peace: Foreign arms and indigenous institutions in a Papua New Guinea society. Science 337(6102):1651–1654.
- Johnson N, et al. (2011) Pattern in escalations in insurgent and terrorist activity. Science 333(6038):81–84.
- Johnson NF, et al. (2013) Simple mathematical law benchmarks human confrontations. Sci Rep 3:3463.
- Johnson NF, et al. (2016) New online ecology of adversarial aggregates: ISIS and beyond. Science 352(6292):1459–1463.
- Gavrilets S, Fortunato L (2014) A solution to the collective action problem in betweengroup conflict with within-group inequality. Nat Commun 5:3526.
- Mathew S, Boyd R (2011) Punishment sustains large-scale cooperation in prestate warfare. Proc Natl Acad Sci USA 108(28):11375–11380.
- McAuliffe K, Wrangham R, Glowacki L, Russell AF (2015) When cooperation begets cooperation: The role of key individuals in galvanizing support. *Philos Trans R Soc Lond B Biol Sci* 370(1683):20150012.

were asked to indicate the three persons that they would like to receive the gift of candy and told they would not be identified as the donor. All 91 subjects (100%) participated, yielding a total of 273 social ties within this group, and distributions occurred only after all participants completed the task. We also measured a variety of attributes of the study participants including height, weight, and estimates of paternal wealth (*SI Methods*).

To explore associations between raid characteristics and raid participation, we evaluated linear regression models that estimated the association between an individual's decision to join a particular raid and various raid characteristics. The basic model is as follows:

#### $E[Y_{ir}] = \theta_i + \gamma_r + \beta x_{ir},$

where the dependent variable  $Y_{ir}$  is 1 if person *i* joins raid *r*, and 0 otherwise;  $x_{ir}$  is a vector of characteristics for participant *i* and raid *r*; and  $\theta_i$  and  $\gamma_r$  are individual and raid fixed effects, respectively. We report results of the linear model for more intuitive interpretation. The results are consistent in both sign and magnitude compared with generalized linear models. See *SI Methods* for further description of methods.

Approval for this study was obtained from the Harvard University Committee on the Use of Human Subjects; the South Omo Zone, Southern Nations, Nationalities, and Peoples' Region, Federal Democratic Republic of Ethiopia; and local elders. Informed consent was obtained from all participants.

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- 20. Gavrilets S (2015) Collective action problem in heterogeneous groups. Philos Trans R Soc Lond B Biol Sci 370(1683):20150016.
- Wilson ML, et al. (2014) Lethal aggression in Pan is better explained by adaptive strategies than human impacts. *Nature* 513(7518):414–417.
- Gilby IC, Eberly LE, Wrangham RW (2008) Economic profitability of social predation among wild chimpanzees: Individual variation promotes cooperation. *Anim Behav* 75(2):351–360.
- Gilby IC, Wilson ML, Pusey AE (2013) Ecology rather than psychology explains co-occurrence of predation and border patrols in male chimpanzees. *Anim Behav* 86(1):61–74.
- Nunn CL, Deaner RO (2004) Patterns of participation and free riding in territorial conflicts among ringtailed lemurs (*Lemur catta*). *Behav Ecol Sociobiol* 57(1):50–61.
- Arseneau TJM, Taucher A-L, van Schaik CP, Willems EP (2015) Male monkeys fight in between-group conflicts as protective parents and reluctant recruits. *Anim Behav* 110:39–50.
- 26. Boehm C (2012) Ancestral hierarchy and conflict. Science 336(6083):844–847.
- Beckerman S, et al. (2009) Life histories, blood revenge, and reproductive success among the Waorani of Ecuador. Proc Natl Acad Sci USA 106(20):8134–8139.
- Chagnon NA (1988) Life histories, blood revenge, and warfare in a tribal population. Science 239(4843):985–992.
- Hill K, Hurtado AM, Walker RS (2007) High adult mortality among Hiwi huntergatherers: Implications for human evolution. J Hum Evol 52(4):443–454.
- Kearns M, Suri S, Montfort N (2006) An experimental study of the coloring problem on human subject networks. *Science* 313(5788):824–827.
- Rand DG, Arbesman S, Christakis NA (2011) Dynamic social networks promote cooperation in experiments with humans. Proc Natl Acad Sci USA 108(48):19193–19198.
- Rand DG, Nowak MA, Fowler JH, Christakis NA (2014) Static network structure can stabilize human cooperation. Proc Natl Acad Sci USA 111(48):17093–17098.
- Apicella CL, Marlowe FW, Fowler JH, Christakis NA (2012) Social networks and cooperation in hunter-gatherers. *Nature* 481(7382):497–501.
- Fowler JH, Christakis NA (2010) Cooperative behavior cascades in human social networks. Proc Natl Acad Sci USA 107(12):5334–5338.
- 35. Papachristos AV (2009) Murder by structure: Dominance relations and the social structure of gang homicide. AJS 115(1):74–128.
- Perkins JM, Subramanian SV, Christakis NA (2015) Social networks and health: A systematic review of sociocentric network studies in low- and middle-income countries. Soc Sci Med 125:60–78.
- Macfarlan SJ, Walker RS, Flinn MV, Chagnon NA (2014) Lethal coalitionary aggression and long-term alliance formation among Yanomamö men. *Proc Natl Acad Sci USA* 111(47):16662–16669.
- Tornay S (1981) The Nyangatom: An outline of their ecology and social organization. *Peoples and Cultures of the Ethio-Sudan Borderlands*, ed Bender ML (Michigan State University, East Lansing, MI), pp 137–178.
  Glowacki L, Wrangham R (2015) Warfare and reproductive success in a tribal pop-
- Glowacki L, Wrangham R (2015) Warfare and reproductive success in a tribal population. Proc Natl Acad Sci USA 112(2):348–353.

- 40. Tornay S (1979) Armed conflicts in the Lower Omo Valley, 197011976. Warfare Among East African Herders, eds Fukui K, Turton D, Minzokugaku H (National Museum of Ethnology, Suita, Osaka, Japan), pp 97–117.
- 41. Glowacki L (2015) Incentives for war in small-scale societies. PhD dissertation (Harvard University, Cambridge, MA). 42. Costa DL, Kahn ME (2008) Heroes and Cowards: The Social Face of War (Princeton
- Univ Press, Princeton).
- 43. Langergraber KE, Mitani JC, Vigilant L (2007) The limited impact of kinship on cooperation in wild chimpanzees. Proc Natl Acad Sci USA 104(19):7786-7790.
- 44. Isakov A, Holcomb A, Glowacki L, Christakis NA (2016) Modeling the role of networks and individual differences in inter-group violence. PLoS One 11(2):e0148314. 45. Nowak MA (2006) Five rules for the evolution of cooperation. Science 314(5805):

SANG

- 1560-1563. 46. Gilby IC, et al. (2015) "Impact hunters" catalyse cooperative hunting in two wild chimpanzee communities. Philos Trans R Soc Lond B Biol Sci 370(1683):20150005.
- 47. Glowacki L, von Rueden C (2015) Leadership solves collective action problems in small-scale societies. Philos Trans R Soc Lond B Biol Sci 370(1683):20150010.
- 48. King AJ, Johnson DDP, Van Vugt M (2009) The origins and evolution of leadership. Curr Biol 19(19):R911-R916.
- 49. Hooper PL, Kaplan HS, Boone JL (2010) A theory of leadership in human cooperative groups. J Theor Biol 265(4):633-646.
- 50. Viterna JS (2006) Pulled, pushed, and persuaded: Explaining women's mobilization into the Salvadoran guerrilla army. Am J Sociol 112:1-45.
- 51. Collins R (2008) Violence: A Micro-sociological Theory (Princeton Univ Press, Princeton). 52. Hruschka D (2010) Friendship: Development, Ecology, and Evolution of a Relationship (Univ of California Press, Los Angeles).
- 53. Girvan M, Newman MEJ (2002) Community structure in social and biological networks. Proc Natl Acad Sci USA 99(12):7821-7826.
- 54. Cameron CA, Gelbach J, Miller D (2011) Robust inference with multiway clustering. J Bus Econ Stat 29:238-249.