Social networks and cooperation in hunter–gatherers

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Social networks show striking structural regularities[1,2], and both theory and evidence suggest that networks may have facilitated the development of large-scale cooperation in humans[3–7]. Here, we characterize the social networks of the Hadza, a population of hunter-gatherers in Tanzania[8]. We show that Hadza networks have important properties also seen in modernized social networks, including a skewed degree distribution, degree assortativity, transitivity, reciprocity, geographic decay and homophily. We demonstrate that Hadza camps exhibit high between-group and low within-group variation in public goods game donations. Network ties are also more likely between people who give the same amount, and the similarity in cooperative behaviour extends up to two degrees of separation. Social distance appears to be as important as genetic relatedness and physical proximity in explaining assortativity in cooperation. Our results suggest that certain elements of social network structure may have been present at an early point in human history. Also, early humans may have formed ties with both kin and non-kin, based in part on their tendency to cooperate. Social networks may thus have contributed to the emergence of cooperation.

Humans are unusual as a species in the extent to which they form longstanding, non-reproductive unions with unrelated individuals—that is, we have friends. Cooperation is a defining feature of these friendships[9]. Humans also learn from and influence each other, evincing an exceptional reliance on cultural transmission[10]. These facts contribute to the propensity of humans to form social networks, which can range in size from dozens to millions of people[1].

Social networks display certain empirical regularities—in settings as diverse as villages, schools, and workplaces—in terms of variation in the degree distribution (number of social ties), transitivity (the likelihood that two of a person's friends are in turn friends), degree assortativity (the tendency of popular people to befriend other popular people), reciprocity (the increased likelihood of an outbound tie to be reciprocated with an inbound tie from the same person), and homophily (the tendency of similar people to form ties). Some properties (such as a fat-tailed degree distribution) may be seen in many contexts (such as neuronal, electronic and social networks). Other properties are more distinctively social, and may have adaptive significance. For instance, degree assortativity may constrain the spread of pathogens[11], high transitivity may help reinforce social norms (although it can also reduce the flow of new information), and homophily may facilitate collective action[12].

However, technological advances (such as in communication, transportation and agricultural systems), demographic changes (such as in population density, inter-group marriage and dispersal), and social innovations (such as in formal institutions) have all changed the social landscape of humans from that in which they evolved. This raises the question of whether features observed in modernized social networks are ancient or contemporary in origin. Yet the observed regularities in social networks, coupled with the fact that networks can affect diverse individual-level outcomes, suggests that natural selection may have played a part in the formation of human networks. Indeed, some egocentric network attributes, such as the number or kind of friends a person has, or a person's tendency to be central in a network, may have a partially genetic basis[13,14].

The evolutionary relevance of social networks is also suggested by their role in cooperation. Evolutionary theories of cooperation rely on explicit or implicit assumptions regarding social structure[3]. Direct reciprocity assumes that the same individuals will encounter each other repeatedly[4]. Similar conclusions have been reached regarding indirect reciprocity[15]. Other theoretical models of kin selection, generalized assortativity[5], group competition[6] and social networks[7] have also explicitly recognized the importance of population structure, showing that cooperation can evolve if individuals tend to interact with others of the same type (cooperators with cooperators and defectors with defectors). If real-world interactions do not exhibit such assortativity, then none of these theories can explain the widespread cooperation in humans that we observe today.

To discover the possibly adaptive origins of human social networks, and their relationship to cooperation, we wanted to examine network features in an evolutionarily relevant setting, that is, in a population whose way of life is thought to resemble that of our early ancestors[8]. Although cooperation is widespread in human societies, modern hunter-gatherers possibly exemplify this feature best—extensively sharing food, labour and childcare. It is likely that the high levels of cooperation observed in modern hunter-gatherers were also present in early humans[16]. Thus far, little work has focused on networks in hunter-gatherers. Related topics have included estimation of the total size of hierarchical social units[17], examination of the role of resource production in social organization and residence patterns[18], and evaluation of food sharing[19]. We know of no study that has attempted to map the complete social network of a foraging population to study its dyadic building blocks (ties between pairs of people) and macroscopic structure, as well as the role of cooperation.

Therefore, we performed a comprehensive, socio-centric network study of the Hadza hunter-gatherers of Tanzania. Connections between individuals were identified in two ways: subjects were asked with whom they would like to live in the next camp (the 'campmate network'), and to whom they would give an actual gift of honey (the 'gift network') (see Methods). We studied 205 individuals, and there were 1,263 campmate ties and 426 gift ties. By measuring a comprehensive set of statistics, we evaluated whether Hadza networks differ quantitatively from random networks in the same ways that modernized networks do.

Cumulative distributions of in-degree (the number of times an individual is nominated) are shown in Fig. 1a. As is typical of networks[2], the degree distributions have significantly fatter tails than a similarly sized group composed of individuals randomly forming the same number of social ties (Kolmogorov–Smirnov test, $P < 10^{-15}$ for all comparisons). Degree distributions for the male and female campmate networks did not differ (Kolmogorov–Smirnov test, $P = 0.86$ for in-degree and 0.59 for out-degree).

As in modernized societies[20], we find that the probability of a social tie decreases with increased geographic distance (see Supplementary Fig. 6a). Of significance to kin selection theory, we also find that the

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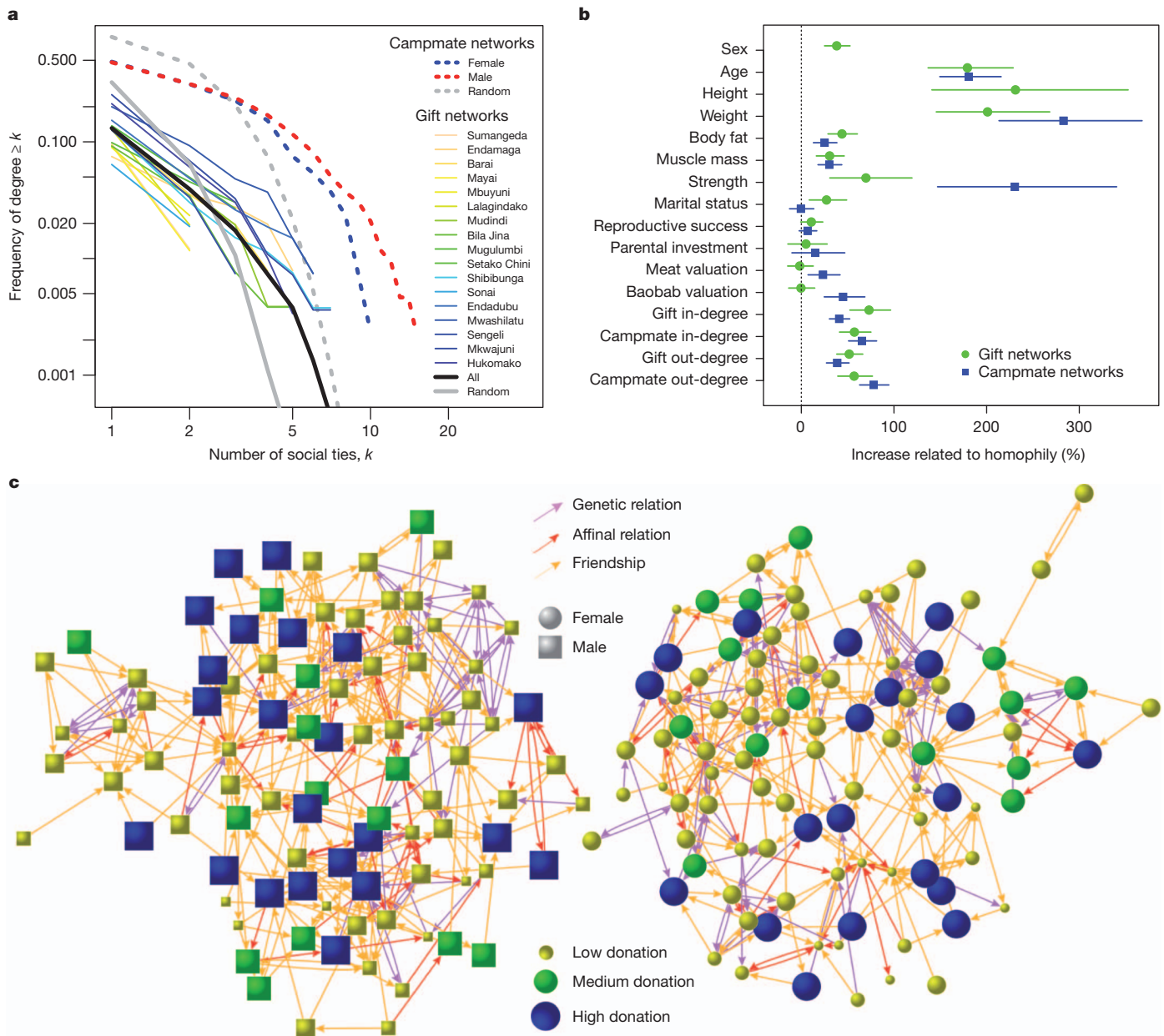
Figure 1 | Structural features of modern social networks also exist in Hadza networks. **a**, Cumulative in-degree distributions show the fraction of the population that has at least k social ties. The distributions for the campmate and gift networks are significantly different from random networks with the same number of nodes and edges (Kolmogorov–Smirnov test, $P < 10^{-15}$) and have fatter tails; the random distributions are shown separately for campmate and gift networks (in grey). The gift networks within each camp (ordered by size of camp from smallest, yellow, to largest, blue) show similar distributions of in-degree. **b**, Estimates based on dyadic models of social ties (see Supplementary Information) show that a 1-s.d. change in similarity in characteristics between two people significantly increases the likelihood of a social tie (homophily).

Horizontal lines indicate 95% confidence intervals. For the campmate networks, sex is not included because all ties are same-sex; homophily for height is not shown because it does not fit on the scale (the estimate is 801%, 95% confidence interval 549–1,148%), and homophily for cooperation is shown in Fig. 2c. **c**, Graphs of the campmate networks show that cooperators tend to be connected to cooperators and cluster together (see also Fig. 2b). Node colour and size indicates donation, shape indicates sex. Arrows point from an ego (the naming person) to an alter (the named person). Arrow colours indicate whether the ego and alter are related genetically, affinally (by marriage) or not at all (friendship).

probability that two individuals are connected increases as the genetic relatedness between the pair increases, in both the campmate and the gift networks (see Supplementary Fig. 6b).

We used regression analysis to evaluate the relationship between personal characteristics and degree (see Supplementary Information). In both the campmate and gift networks, age, height, weight and marital status are positively and significantly related to both out-degree and in-degree (see Supplementary Fig. 7a, b). For example, in the gift network, an 8.7-cm (one standard deviation, 1 s.d.) increase in height is associated with a 125% increase in out-degree and a 173% increase in

in-degree, suggesting that taller people are both more socially active and more socially attractive. The significance of these associations survives when we add numerous controls to the models, including camp-level fixed effects, geographic distance, genetic and affinal relationships, spouse relationships, age and sex (see Supplementary Information). Other characteristics associated with degree in at least one of the models include body fat, muscle mass, handgrip strength, the value placed on meat, and reproductive success, but none of these survive controls in both the campmate and gift networks, except body fat for in-degree and handgrip strength for out-degree (see Supplementary Information).

The selection of physically fit reproductive partners (in both traditional and modernized societies) makes sense from an evolutionary perspective, given the gains in resources and genetic benefits that can be passed on to offspring. But hunter-gatherers also prefer to form connections to non-reproductive partners who are physically fit, suggesting that this tendency might also be both common and ancient in origin. Food acquisition and processing in foragers is labour and time-intensive, requiring strength and stamina, as well as skill and knowledge[21]. Thus, forming connections with physically fit individuals probably translates into increased resources.

Hadza networks also resemble modernized human networks insofar as they too differ from random networks with respect to reciprocity[16,22]. An 'ego' (the naming person) is 44.2 times (95% confidence interval 37.6–51.4) more likely to name an 'alter' (the named person) in the campmate network, and 14.3 times (95% confidence interval 12.2–16.4) more likely to name an alter in the gift network, if the alter reciprocated the social tie by also naming the ego as a friend (indeed, this happens even though nominations are private). Reciprocity remains significant even when controlling for genetic and non-genetic family ties, suggesting that reciprocity also exists between unrelated individuals.

Hadza networks also evince degree assortativity. People with higher in-degree name more social contacts, and people with higher out-degree are more likely to be named (see Supplementary Fig. 7a, b), even in models with controls (including a control for reciprocity). In other words, individuals who nominate more friends are popular even among those they themselves did not nominate.

Yet another property Hadza networks have in common with modernized human networks is that they have higher transitivity than expected in random networks[23]. In the campmate networks, transitivity is 0.17 for females and 0.16 for males, while in the gift networks, the average transitivity is 0.41 (see Supplementary Fig. 7c). By comparison, in random networks with the same number of nodes and edges, transitivity is always less than 0.01.

Turning to homophily (Fig. 1b), in both the campmate and gift networks, social ties are significantly more likely when two people are similar in age, height, weight, body fat and handgrip strength. Thus, as in other human networks, hunter-gatherers who are socially connected tend to resemble one another. For example, a 7.5-kg (1 s.d.) increase in the similarity of weight is associated with a tripling of the probability (+201%) that two people are connected. There is also evidence of homophily on marital status, muscle mass, and the value placed on meat and baobab, but these relationships do not survive in the models with controls, except for the value of meat in the campmate network (see Supplementary Information).

Hunter-gatherer life is characterized by imbalances in productivity and consumption (for example, owing to differences in strength, which varies across an individual's lifetime), and this is reflected in divisions of labour[24]. Thus, one might expect that choices of campmates would reflect complementarity (heterophily) rather than homophily. On the other hand, homophily may facilitate collective action because similar individuals are more likely to share assumptions, experiences and goals[25], and also because similarity increases empathy, which in turn facilitates cooperation[12]. We find no significant heterophily on any attribute examined.

We also directly compared the measured Hadza parameters to values for 142 sociocentric networks of adolescent students in the USA and to two sociocentric networks of adult villagers in Honduras. The Hadza parameters fall within the observed ranges in these other networks, often near the centre of the distribution (see Supplementary Information). However, comparison of the precise values is limited by, among other things, variation in how ties were ascertained. Further research will be needed to clarify how details of human social network structure might vary across settings, if at all.

Graphs of the Hadza social networks (Fig. 1c) show that they tend to be structured in a way that is relevant for cooperative behaviour, as

elicited in public goods games. In particular, there is homophily on cooperation: cooperators tend to be connected to other cooperators, and non-cooperators to non-cooperators.

Although natural selection is said to favour defection in unstructured populations where all individuals have an equal chance of interacting with one another, cooperation can evolve if population structure permits clustering[5]. This feature allows cooperators to increase in the population because they benefit from the public goods provided by fellow cooperators with whom they interact. A key prediction of some evolutionary models is thus that there should be relatively more variance in cooperative behaviour between groups as compared to within groups[6]. But it was not known whether such assortment in cooperative behaviour actually exists in populations thought to resemble our early human ancestors.

In Fig. 2a, we show a comparison of the observed variance in donations to the public good to the variance obtained when we keep the population structure fixed and randomly reshuffle the observed distribution of donations across all individuals. Compared to chance, there is significantly more between-camp variation ($P = 0.01$) and significantly less within-camp variation ($P = 0.01$) in cooperative behaviour.
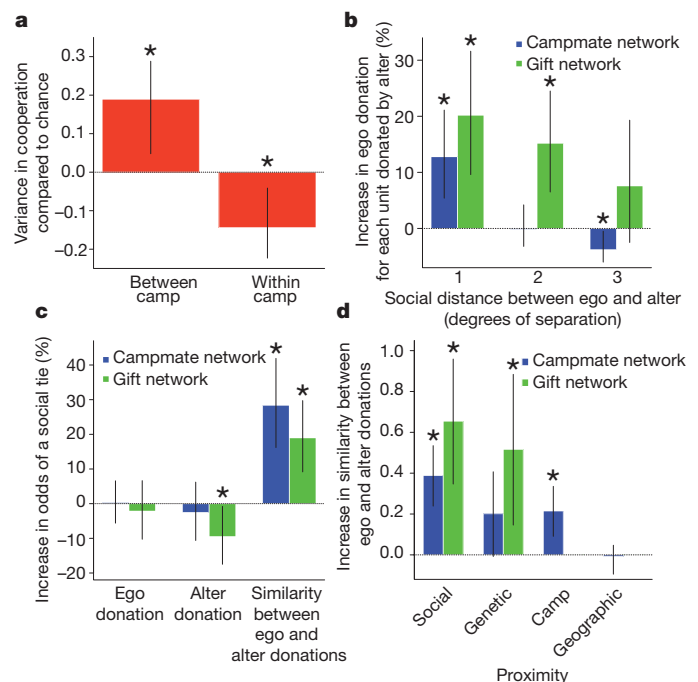

Figure 2 | Donations in the public goods game are associated with social network characteristics. a, A comparison of variance in observed donations with variance in 1,000 simulations in which donations were randomly shuffled between all individuals in the population shows that between-group variance in cooperation is significantly higher than expected, and within-group variance is significantly lower than expected, at the camp level. **b**, An analysis of cooperative behaviour across all camps shows that correlation in cooperation extends to one degree of separation in the campmate networks and two degrees (to one's friend's friends) in the gift networks. Moreover, there is anti-correlation at three degrees of separation in the campmate network, suggesting polarization between cooperators and non-cooperators. **c**, Correlation in behaviour cannot be explained by cooperators being more likely to form or attract social ties. Instead, subjects with similar levels of giving are significantly more likely to be connected at the dyadic level. **d**, Finally, several measures of proximity are independently associated with similarity in donations, but social proximity (the inverse of the degree of separation between two people in the network) appears to be just as important as genetic proximity (relatedness) and physical proximity (residence in the same camp) in a multivariate test. (Gift networks are defined only within camps and so are not presented for 'camp' and 'geographic' proximity in Fig. 2d.) Vertical lines indicate 95% confidence intervals and asterisks indicate estimates with $P < 0.05$. See the Supplementary Information for details of the models.

We investigated the role of network connections with respect to group-level variation in cooperation by studying the tendency of cooperative individuals to be connected to other cooperators. We regressed public-good donations on the donations of a person's friends (see Supplementary Information). Each extra stick of honey donated is associated with an extra 0.13 sticks (95% confidence interval 0.05–0.21) donated by each friend in the campmate networks and an extra 0.21 sticks (95% confidence interval 0.10–0.32) donated by each friend in the gift networks. Moreover, in the gift networks, the association extends to two degrees of separation; each friend's friend donates an extra 0.15 sticks (95% confidence interval 0.07–0.25) for every stick a person donates (Fig. 2b). And, interestingly, at three degrees of separation, there is significant anti-correlation in the campmate networks (–0.04 sticks, 95% confidence interval –0.00 to –0.06), suggesting that cooperative and non-cooperative clusters tend to be polarized (though this might also reflect a finite-size effect, given the small size of Hadza society).

Dyadic analyses of social ties show that people who donate more do not have higher out-degree or in-degree (Fig. 2c). In fact, in the gift networks, there is a weakly significant negative association between donations and in-degree, though this relationship does not survive in the models with controls (see Supplementary Information). This suggests that we can reject the hypothesis that hunter-gatherers unconditionally prefer to form ties with cooperators. However, there is significant homophily on cooperation in both the campmate and gift networks, and the relationship survives in the model with controls for the campmate network: cooperators are preferentially connected to other cooperators.

To determine whether social network structure may help to explain variation in cooperative behaviour, we considered three different kinds of proximity that could be generating the similarity: geographic, genetic and social. If the physical environment is an important source of variation, then geographic proximity should help to predict similarity in cooperative behaviour. Additionally, people who live in the same camp should be more similar than those who do not. If genes are an important source of variation, then genetic proximity (measured as relatedness) should help to predict similarity in cooperative behaviour. But if social networks are a source of variation, then social proximity (measured separately for the campmate networks and gift networks by the inverse of the degrees of separation between two people) should help to predict similarity in cooperation. In separate regression models, each kind of proximity is significantly related to similarity in cooperation (see Supplementary Information). In contrast, age and sex similarity are not significant predictors. However, when we include all the proximity measures in one model, geographic proximity ceases to matter (Fig. 2d). Moreover, social proximity, as measured in both the campmate networks and the gift networks, appears to be just as important as genetic proximity and camp co-residence, suggesting that cooperative behaviour may be best understood as a process influenced by a combination of not only genes and environment, but also social networks.

The Hadza represent possibly one of the most extreme departures from life in industrialized societies, and they remain relatively isolated from modern cultural influences. Yet all the examined properties of social networks seen in modernized societies also appear in the Hadza. Compared with random networks, Hadza networks, like modernized networks, exhibit a characteristic degree distribution, greater degree assortativity, transitivity, reciprocity and homophily than would be expected from chance, and a decay with geographic distance.

To the extent that the Hadza represent our late Pleistocene ancestors[8], the network properties and social preferences in the Hadza may indeed reflect elements of human sociality along with which high levels of human cooperation evolved. Whether certain aspects of human social network structure existed still further back in our hominid past is unclear. Evaluating the resemblances between non-human and human primate networks is difficult, in part because the qualitative nature of dyadic ties can vary considerably across species[26]. Nevertheless, some network properties may be quite old. For instance, age and sex predict both the quantity and quality of many primate interactions, and primate networks may demonstrate homophily[26]. Possibly, certain aspects of social network structure might appear in any vertebrate species that forms social networks[27], because particular structural features might facilitate the solution of problems common to such species (for example, those related to coordinated action, infection resistance and information transmission).

Humans' ability to trace descent bilaterally and form strong relationships with both sets of kin not only maximizes their kin ties but also increases their ability to move freely; once an organism is able to recognize paternal kin, potential inbreeding can be avoided without the need for evolution to favour a sex-biased dispersal pattern. Whereas chimpanzee females disperse and males typically spend their lives in their natal community, hunter-gatherers of both sexes can stay in or leave their natal group[18], with individuals changing camp membership throughout their lives. It is thus possible that relaxed constraints on social mobility patterns provided humans a greater opportunity to make friends, which in turn allowed cooperators more opportunities to form ties with other cooperators and break ties with defectors.

Although the Hadza have a preference for kin as both campmates and gift recipients (indicating a potential for kin selection), the Hadza also actively form many ties with non-kin. In fact, recent work examining co-residence patterns across hunter-gatherer societies suggests that first-order relatives make up less than 10% of residential camps[18], raising the question of how high levels of cooperation are maintained in groups of mostly unrelated individuals. The pervasive sharing of food that characterizes hunter-gatherer life is one plausible evolutionary mechanism[24], but theories of kin selection and reciprocal altruism, used to explain food sharing, have been criticized on the grounds that they require producer control over resource distribution[24]. On the other hand, regardless of whether foragers have producer rights, they do maintain flexibility in choosing their friends and campmates, thus providing some control over resource distribution.

In summary, Hadza networks are structured in a way that is consistent with the evolution of cooperative behaviour. Cooperators tend to be connected to cooperators at both the dyadic and network level, conditions necessary to sustain cooperation[28]. This phenomenon cannot be explained by camp-level differences in the contextual environment because it persists in a model that controls for camp-level fixed effects. However, it might be explained by two alternative hypotheses. One is that cooperators tend to form ties preferentially with other cooperators, leaving defectors no choice but to form ties to the remaining non-cooperators[29]. Another is that people may influence the cooperative behaviour of their networks, as demonstrated in experimental studies[30]. But regardless of the causal mechanism, homophily on cooperation and selective formation of network ties create conditions that would make it easier for cooperative behaviour to evolve[28]. This suggests that social networks may have co-evolved with the widespread cooperation in humans that we observe today.

METHODS SUMMARY

We surveyed 205 adults in 17 Hadza camps. Cooperation was elicited by examining subjects' contributions to a public good using sticks of honey. Both women and men donated slightly more than half of their endowment.

We collected network data at both the population level and the camp level. We discerned same-sex network ties across the entire Hadza population by asking each individual: "With whom would you like to live after this camp ends?" We call this the 'campmate network'. On average, women chose 6.0 ($\pm$1.9 s.d.) campmates and men chose 7.1 ($\pm$2.1 s.d.) campmates. To facilitate this, we used posters containing facial photographs of a census of 517 adult Hadza (see Supplementary Information).

We discerned network ties in an additional way. Every adult in each camp (100%) was given three sticks of honey, which they could anonymously distribute to other adults, of either sex, in their camp. Participants could give all the honey to one person or distribute it to up to three different people. We call this the 'gift network'. On average, both women and men chose to give to 2.2 ($\pm$0.8 s.d.) recipients.

Anthropometry measures were also collected, as well as marital status, reproductive histories, and many other measurements, and we computed the genetic relatedness of all pairs of people. The data were analysed with regression models and other methods (see Supplementary Information).

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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1. Onnela, J. P. *et al.* Structure and tie strengths in mobile communication networks. *Proc. Natl Acad. Sci. USA* **104,** 7332–7336 (2007).
2. Barabási, A. L. & Albert, R. Emergence of scaling in random networks. *Science* **286,** 509–512 (1999).
3. Nowak, M. A., Tarnita, C. & Wilson, E. O. The evolution of eusociality. *Nature* **466,** 1057–1062 (2010).
4. Boyd, R. & Richerson, P. J. The evolution of reciprocity in sizable groups. *J. Theor. Biol.* **132,** 337–356 (1988).
5. Eshel, I. & Cavalli-Sforza, L. L. Assortment of encounters and evolution of cooperativeness. *Proc. Natl Acad. Sci. USA* **79,** 1331–1335 (1982).
6. Bowles, S. Group competition, reproductive levelling, and the evolution of human altruism. *Science* **314,** 1569–1572 (2006).
7. Ohtsuki, H., Hauert, C., Lieberman, E. & Nowak, M. A. A simple rule for the evolution of cooperation on graphs and social networks. *Nature* **441,** 502–505 (2006).
8. Marlowe, F. W. *The Hadza: Hunter-gatherers of Tanzania* (University of California Press, 2010).
9. Hruschka, D. J. *Friendship: Development, Ecology, and Evolution of a Relationship* (University of California Press, 2010).
10. Boyd, R. & Richerson, P. J. Why culture is common but cultural evolution is rare. *Proc. Br. Acad.* **88,** 73–93 (1996).
11. Badham, J. & Stocker, R. The impact of network clustering and assortativity on epidemic behaviour. *Theor. Popul. Biol.* **77,** 71–75 (2010).
12. Krebs, D. Empathy and altruism. *J. Pers. Soc. Psychol.* **32,** 1134–1146 (1975).
13. Fowler, J. H., Dawes, C. T. & Christakis, N. A. Model of genetic variation in human social networks. *Proc. Natl Acad. Sci. USA* **106,** 1720–1724 (2009).
14. Fowler, J. H., Settle, J. E. & Christakis, N. A. Correlated genotypes in friendship networks. *Proc. Natl Acad. Sci. USA* **108,** 1993–1997 (2011).
15. Boyd, R. & Richerson, P. J. The evolution of indirect reciprocity. *Soc. Networks* **11,** 213–236 (1989).
16. Bowles, S. & Gintis, H. The evolution of strong reciprocity: cooperation in heterogeneous populations. *Theor. Popul. Biol.* **65,** 17–28 (2004).
17. Hamilton, M. J. *et al.* The complex structure of hunter–gatherer social networks. *Proc. R. Soc. Lond. B* **274,** 2195–2203 (2007).
18. Hill, K. R. *et al.* Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science* **331,** 1286–1289 (2011).
19. Gurven, M., Hill, K. & Kaplan, H. From forest to reservation: transitions in food sharing behavior among the Ache of Paraguay. *J. Anthropol. Res.* **58,** 93–120 (2002).
20. Onnela, J. P., Arbesman, S., Gonzalez, M. C., Barabasi, A. L. & Christakis, N. A. Geographic constraints on social network groups. *PLoS ONE* **6,** e16939 (2011).
21. Smith, E. A. *et al.* Wealth transmission and inequality among hunter-gatherers. *Curr. Anthropol.* **51,** 19–34 (2010).
22. Fehr, E. & Fischbacher, U. The nature of human altruism. *Nature* **425,** 785–791 (2003).
23. Davis, J. A. Clustering and hierarchy in inter-personal relations: testing two graph theoretical models in 742 sociomatrices. *Am. Sociol. Rev.* **35,** 843–851 (1970).
24. Kaplan, H. & Gurven, M. in *Moral Sentiments and Material Interests: The Foundations of Cooperation in Economic Life* (eds Gintis, H., Bowles, S., Boyd, R. & Fehr, E.) 75–113 (MIT Press, 2005).
25. Cole, T. & Teboul, B. J. C. Non-zero-sum collaboration. reciprocity, and the preference for similarity: developing an adaptive model of close relational functioning. *Personal Relationships* **11,** 135–160 (2004).
26. Brent, L. J. H., Lehmann, J. & Ramos-Fernández, G. Social network analysis in the study of nonhuman primates: a historical perspective. *Am. J. Primatol.* **73,** 720–730 (2011).
27. Whitehead, H. *Analyzing Animal Societies: Quantitative Methods for Vertebrate Social Analysis* (University of Chicago Press, 2008).
28. Nowak, M. A. Five rules for the evolution of cooperation. *Science* **314,** 1560–1563 (2006).
29. Rand, D., Arbesman, S. & Christakis, N. A. Dynamic social networks promote cooperation in experiments with humans. *Proc. Natl Acad. Sci. USA* **108,** http://dx.doi.org/10.1073/pnas.1108243108 (2011).
30. Fowler, J. H. & Christakis, N. A. Cooperative behavior cascades in human social networks. *Proc. Natl Acad. Sci. USA* **107,** 5334–5338 (2010).

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METHODS

Over a two-month period during the summer of 2010, we surveyed 205 adults (18–65 years old, 103 women and 102 men) by visiting 17 distinct Hadza camps within approximately 3,825 square kilometres (see map in Supplementary Information).

Cooperation was elicited by examining all subjects' voluntary contributions to a public good within each camp. Subjects were endowed with four sticks of honey, the favourite food of the Hadza[31], and they then faced the decision of how to divide their endowment into a private account and a public account where the goods would be distributed evenly with all other adult camp members who also played the game (with N substantially greater than 4). Subjects were instructed that they could give any amount to the public good or keep any amount for themselves, and their choices were secret (see Supplementary Information). They were told that the researcher would triple any amount contributed to the public good, and that, only after all adult camp members played the game, they would receive both the honey in their private account as well as their share of honey from the aggregate contributions to the public good. Both women (mean = 2.32, standard error = 0.12) and men (mean = 2.22; standard error = 0.12) donated slightly more than half of their endowment. This is the first public-good experiment conducted with the Hadza, and, similarly to other small-scale societies, we find that Hadza behaviour is not governed by pure self-interest[32].

We collected network data at both the population level and the camp level using a different 'name generator' for each[33]. The Hadza live in camps consisting of approximately 30 individuals (including both adults and children)[8]; we include only adults here (an average of 11.7 ($\pm$6.0 s.d.) adults live in each camp). Camps shift location every 4–6 weeks and individual membership in camps is fluid[8]. Because food that is brought into camp is widely shared[34], and because sharing of food is thought to be one of the main benefits of group living owing to the high variance in individual food returns[35], choosing with whom to live is consequential. Hence, we discerned same-sex network ties across the entire Hadza population by asking each individual: "With whom would you like to live after this camp ends?" We call this the 'campmate network'. The participants were instructed that they could choose up to a maximum of ten individuals, either currently living in their camp or outside their camp. On average, women chose 6.0 ($\pm$1.9 s.d.) campmates and men chose 7.1 ($\pm$2.1 s.d.) campmates (and 3% of women and 21% of men chose the maximum of 10). To facilitate this process and eliminate potential data

collection errors, we used posters containing full-frontal facial photographs of a census of 517 adult Hadza (see Supplementary Information).

At the camp level, we discerned network ties in an additional, novel way. Every adult in each camp (100%) was given three sticks of honey, which they could anonymously distribute to other adults, of either sex, currently living in their camp. Participants were told that they could give all the sticks of honey to one person or distribute them to up to three different people, but, unlike in the procedures used to elicit cooperation (which were administered separately), they could not keep the sticks for themselves. We call this the 'gift network'. The network discerned this way yields a maximum out-degree of 3, but it is also a weighted network, because people could choose to give more honey to certain alters. On average, both women and men chose to give to 2.2 ($\pm$0.8 s.d.) recipients. While, ordinarily, gifts among the Hadza are not anonymous and involve reputation effects, the Hadza do understand the importance and feasibility of a gift given anonymously. We elected to measure ties this way because it was objective and could characterize phenomena such as reciprocity with limited bias.

Finally, anthropometry measures (including height, weight, body fat percentage, muscle mass and hand-grip strength) were collected, as well as marital status, reproductive histories, and other measurements; we also computed the genetic relatedness of all pairs of people (see Supplementary Information). The data were analysed with GEE regression models[36,37], and confirmatory analyses were also done using other methods (see Supplementary Information).

31. Berbesque, J. C. & Marlowe, F. W. Sex differences in food preferences of Hadza hunter-gatherers. *Evol. Psychol.* **7,** 601–616 (2009).
32. Henrich, J. *et al.* In search of *Homo economicus*: behavioral experiments in 15 small-scale societies. *Am. Econ. Rev.* **91,** 73–78 (2001).
33. Campbell, K. E. & Lee, B. A. Name generators in surveys of personal networks. *Soc. Networks* **13,** 203–221 (1991).
34. Hawkes, K., O'Connell, J. F. & Blurton Jones, N. Hadza meat sharing. *Evol. Hum. Behav.* **22,** 113–142 (2001).
35. Smith, E. A. in *Hunter Gatherers* Vol. 1 *History, Evolution and Social Change* (eds Ingold, T., Riches, D. & Woodburn, J.) 222–251 (Berg, 1988).
36. Liang, K. Y. & Zeger, S. Longitudinal data analysis using generalized linear models. *Biometrika* **73,** 13–22 (1986).
37. Schildcrout, J. S. Regression analysis of longitudinal binary data with time-dependent environmental covariates: bias and efficiency. *Biostatistics* **6,** 633–652 (2005).