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Hunter-Gatherers Maintain Assortativity in Cooperation despite High Levels of Residential Change and Mixing

Highlights

- Assortment on cooperation is a characteristic feature of hunter-gatherer life
- Assortment persists despite substantial migration and residential mixing
- No evidence for stable social types or a preference to live with cooperators
- Individuals respond in kind to the cooperative behavior of their group members

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In Brief

For cooperation to evolve, cooperators must interact with other cooperators. Smith et al. use panel data from a population of extant hunter-gatherers to show how assortativity in cooperation is maintained.



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Hunter-Gatherers Maintain Assortativity in Cooperation despite High Levels of Residential Change and Mixing

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SUMMARY

Widespread cooperation is a defining feature of human societies from hunter-gatherer bands to nation states [1, 2], but explaining its evolution remains a challenge. Although positive assortment of cooperators is recognized as a basic requirement for the evolution of cooperation, the mechanisms governing assortment are debated. Moreover, the social structure of modern huntergatherers, characterized by high mobility, residential mixing, and low genetic relatedness [3], undermines assortment and adds to the puzzle of how cooperation evolved. Here, we analyze four years of data (2010, 2013, 2014, 2016) tracking residence and levels of cooperation elicited from a public goods game in Hadza hunter-gatherers of Tanzania. Data were collected from 56 camps, comprising 383 unique individuals, 137 of whom we have data for two or more years. Despite significant residential mixing, we observe a robust pattern of assortment that is necessary for cooperation to evolve; in every year, Hadza camps exhibit high between-camp and low within-camp variation in cooperation. We find little evidence that cooperative behavior within individuals is stable over time or that similarity in cooperation between dyads predicts their future cohabitation. Both sets of findings are inconsistent with models that assume stable cooperative and selfish types, including partner choice models. Consistent with social norms, culture, and reciprocity theories, the strongest predictor of an individual's level of cooperation is the mean cooperation of their current campmates. These findings underscore the adaptive nature of human cooperation-particularly its responsiveness to social contexts-as a feature that is important in generating the assortment necessary for cooperation to evolve.

RESULTS

Cooperation can only evolve if the benefits of cooperation preferentially flow between those who cooperate. Consequently, all mechanisms proposed for the evolution of cooperation necessarily generate positive phenotypic assortment on cooperation [1, 2]. We analyze data on cooperation using a public goods game and residence patterns in Hadza hunter-gatherers over a six-year period (2010, 2013, 2014, 2016; Table S1). Games were played using a favorite food item—sticks of honey. Participants could contribute 0–4 honey sticks to the public goods, and all subjects split the sum of contributions multiplied by 3. Games were played between all adults of the same residence groups, herein called "camps", and demographics were recorded (Table S2). Figure 1 shows the location and levels of cooperation of camps in each year.

Cooperators Cluster in Camps Each Year

We first tested if individuals with similar public goods contributions cluster within camps each year. We compared the observed variance in public goods contributions with variance from 1,000 simulations. The simulations randomized participants and their contributions to different camps but kept the population structure fixed [4]. For each simulation and the actual data, we measured the mean variance in public goods contributions between participants within each camp (within-camp variance) and the variance in mean camp public goods contributions across all camps (between-camp variance). In each year, less variance was observed within camps and more variance was observed between camps than expected in a random population (p < 0.05, Figure 2). The 2010 results have been previously reported [4]. The long-term data indicate that assortment is a consistent feature of hunter-gatherer life year after year.

We also analyzed between-group variation by computing an F_{ST} statistic for each year. F_{ST} typically quantifies the genetic differentiation between populations but can be used to quantify between-group variation in cultural traits [5]. F_{ST} is useful to consider here because if F_{ST} is large enough, then individually deleterious but group-beneficial behaviors can evolve [6]. In 2010, 2013, 2014, and 2016, F_{ST} = 0.26, 0.33, 0.24, and 0.39, respectively, and was greater than expected every year in a random population, p < 0.05 (see Figure S1). These values are



higher than observed genetic differentiation between nationstates and are more similar to estimates of cultural differentiation between populations [5].

The observed assortment on cooperation is remarkable because the Hadza, like other hunter-gatherers, have flexible living arrangements and high rates of migration [3, 7]. We too observe high rates of residential change. We first calculated for each person the proportion of campmates at time *t* that lived in the same camp with the individual at time t + 1. The mean proportion of repeated campmates was 21.9%. While camp residence changes yearly, we still see public goods contributions clustering within camps each year (Figure 3).

No Dispositional Types or Preference for Cooperators

Assortment provides an overall solution to the problem of cooperation, but the mechanisms responsible for it are debated. One mechanism we explore is partner choice, where cooperation is sustained because people choose to interact with cooperators and the most cooperative choose each other [8]. Partner choice models often assume that individuals have a stable—sometimes genetically determined—level of cooperation, and individuals choose and reject partners based on this [9–11]. Under these models then, we should expect Hadza individuals to exhibit stable cooperative behavior. We also expect that behavior in the public goods at time *t* to relate to camp residency at time *t*+1 with two possible patterns. If camp residency works like a market [8, 10, 12], with cooperative individuals being sought after

Figure 1. Map of the Hadza Camps Visited around Lake Eyasi in Northern Tanzania

Circles represent the camps visited colored by year of data collection. The size of the point signifies the mean public goods contribution in the camp. GPS data are not available in 2016 due to missing equipment. The camps in 2016 are grouped by whether they were located in the market versus non-market (see STAR Methods) region, but their placement is otherwise random.

and thus choosing each other, then we should observe individuals with similar cooperative levels at time t living with each other at time t+1. However, if camp residency does not work like a market but cooperators are still preferred, then we should observe cooperators retaining more campmates between years.

We examined whether individuals' public goods contributions were related across years (Figure 4). Specifically, we tested whether current and past contributions were correlated for individuals in contiguous samples (n = 143 observations) by regressing public goods contributions at time *t* on contributions at time *t*-1 controlling for year. In this and all subsequent regressions, we include robust standard errors clustered on repeated observations. There was no

relationship between individuals' current and previous contributions, b = 0.00, SE = 0.09, t (139) = 0.05, p = 0.959; this remains nonsignificant when controlling for demographic variables and exposure to markets (Table S4), and when analyzed using an ordered logit regression (Table S5). We considered the possibility that individuals prefer to give relative to the camp mean; that is, some people prefer to contribute less than, more than, or as much as their campmates across years. We computed the difference between a person's public goods contribution and the mean of the rest of their campmates and repeated the analysis again with these values. There was no relationship between contributions relative to campmates' contributions at time t-1 and contributions relative to campmates' contributions at time t, b = 0.01, SE = 0.10, t (132) = 0.06, p = 0.950.

Are individuals with higher public goods contributions more likely to continue living with their campmates in the future? To test this, for 2010, 2013, and 2014, we calculated for each individual who was in the sample at time *t* and time *t*+1 the proportion of campmates at time *t* that lived in the same camp with the individual at time *t*+1. We regressed public goods contributions at time *t* on the proportion of repeated campmates. There was a negative but nonsignificant relationship. Individuals who contributed more at time *t* had fewer repeated campmates at time *t*+1, b = -0.02, SE = 0.01, *t* (141) = -1.92, p = 0.057. Thus, there is no evidence that cooperators continue to live with more of their campmates or find more cooperative campmates in the future.



Figure 2. Difference between Actual and Simulated Variance within and between Residence Camps in Public Goods Contributions Error bars are 95% confidence intervals (CIs). See also Figure S1.

To further test if cooperative individuals were choosing to live with similarly cooperative individuals, we tested if the absolute difference in public goods contributions in a past year predicted whether Hadza will live together in a future year. We created a dataset for 2010, 2013, and 2014 of every possible dyad in each year, removing dyads if neither individual was present in the next sample. This resulted in 21,086 observations with 18,126 unique dyads across years. Of these observations, 789 (3.9%) of dyads were in the same camp. Using a binary logistic regression, we regressed whether the dyad lived in the same camp at time *t*+1 on the similarity of public goods contributions at time *t*. Individuals who contributed similar amounts were not more likely to live in the same camp in future years, *b* = 0.01, SE = 0.04, *OR* = 1.01, *Z* = 0.24, p = 0.814, which remained nonsignificant after controlling for demographics variables (Table S3).

Campmates Influence Cooperative Behavior

To explore the role of social context, we tested whether an ego's contribution can be predicted by the mean contribution of their current campmates. First, we calculated for each person a camp mean contribution excluding ego's own contribution. We regressed public goods contributions of ego on the mean contribution of other camp members controlling for year. We find that for each additional honey stick contributed by camp members, ego contributed, on average, another half-stick of honey, b = 0.55, SE = 0.15, t (138) = 3.60, p < 0.001. Note, we control for number of campmates since this affects the marginal per capita return. The result also remains significant when controlling for sex, age, marital status, reproductive success and market exposure (Table S4) and when analyzed using an ordered logit regression (Table S5). Further, in 2010 and 2016, the only years for which we have kinship data (see STAR Methods), we regressed public goods contributions on campmates' mean contributions controlling for number of close relationships (i.e., number of primary kin and spouse) in camp. Campmates' mean contributions remained significant in this regression, *b* = 0.79, SE = 0.06, *t* (314) = 12.53, p < 0.001.

For participants in which we have overlapping data across years, we also examine whether the mean contribution of an ego's current campmates is a better predictor of ego's current contribution than ego's past contribution. For each year, we regressed ego's current contribution at time *t* on the mean contribution of their campmates at time *t* and ego's contribution at time *t*-1. For each additional honey stick given by camp members, ego again contributed an additional half-stick of honey, b = 0.50, SE = 0.16, *t* (132) = 3.11, p = 0.002. There was still no effect of previous contribution on current contribution, b = -0.01, SE = 0.08, *t* (132) = -0.15, p = 0.879. The results did not change when controlling for demographic variables (Table S4) or when using an ordered logit (Table S5). We also find no evidence that having played the game in a prior year predicts subsequent contributions (Table S6).

DISCUSSION

While multiple theoretical models have been proposed to explain the evolution of cooperation, there is little evidence on what theories actually explain cooperation in evolutionarily relevant settings. The Hadza provide an important test case for evolutionary models of cooperation: Their daily life is marked by widespread sharing of food, labor, and childcare. And their lifeways more closely approximate pre-Neolithic populations compared to samples drawn from industrialized settings [13].

While nearly all models involve some behavioral flexibility such that an individual's level of cooperation is contingent on the social environment, most partner choice models assume that individuals have fixed, often heritable, dispositions on which the choice of partners is based [9–11, 14]. In these models, individuals can leave current partners or reject prospective partners based on their own personal interactions with that partner or their observations of them. We find no evidence that cooperative behavior persists over time—a condition that makes it difficult for observers to make informed decisions on who to choose as partners.

Natural selection should favor individuals who select partners based on the benefits their cooperative behavior generates, which is determined by both their partner's willingness and ability to cooperate [8]. Whether willingness or ability to cooperate is valued more as a criterion for partners will depend, in part, on which trait is more variable in the population [15]. In laboratory studies, participants display a preference for partners who are willing to cooperate, possibly because cooperative contributions are artificially constrained. Conversely, the Hadza have strong norms governing cooperation and sharing. If everyone shares because they are expected to, then one's ability to share may be valued more than their willingness to share. In fact, when given the choice, the Hadza do not choose the most cooperative individuals as campmates [4]. Instead, physical traits show small but positive correlations with how often individuals are chosen as campmates, possibly because these traits indicate one's ability to acquire resources [16]. Testing whether the Hadza trade-off willingness to cooperate for other qualities would be an interesting avenue for future study.

In a small sample of Tsimane' forager-horticulturalists (n = 12), generosity was not shown to correlate over time [17]. Our findings, however, contrast with laboratory studies using Western

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Figure 3. Camp Residence, Mixing, and Cooperative Clustering across Years

Points represent individuals grouped in space by their current camp. In 2010, individuals are colored based on current camp membership. In 2013, 2014, and 2016, individuals are colored based on camp membership in the prior wave of data collection; gray points indicate the individual was absent in the prior wave. Circles represent high cooperators (individuals who gave two or more honey sticks) and triangles represent low cooperators (individuals who gave less than two honey sticks). Camps are randomly placed in a grid. See also Table S3.

samples illustrating small- to medium-sized correlations in cooperative game play over time [18, 19]. The discrepant results may also be due to the longer intervals between testing in our study. Also, the Hadza are playing the game with different, but wellknown, individuals each year. In laboratory settings, individuals often play in the same anonymous or unfamiliar group setting each time. However, when these individuals are assigned to cooperative or non-cooperative environments, they adopt the dominant strategy and use the cooperator or defector strategy at later times [20, 21]. Finally, cultural differences in dispositional consistency may also explain the divergent results. Compared to individuals from collectivist societies, Westerners tend to describe themselves in terms of underlying traits and have a stronger preference for self-consistency [22].

While we cannot isolate the exact mechanism(s) generating the within-group homogeneity on cooperation, we find that cooperative behavior in any given year is best predicted by the cooperativeness of one's current residence group. The results are consistent with social learning of local norms and reciprocity theories of cooperation that assume people have reciprocal, conditional strategies. And the findings concur with laboratory experiments demonstrating that cooperative and selfish play in economic games influences others to behave similarly, leading to the spread of different cooperative behaviors in the population [23, 24].

By using an economic game as our measure of cooperation, as opposed to measuring naturally occurring levels of cooperation, we traded off some ecological validity for increased experimental control. We chose the public goods game due to its

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direct relevance to hunter-gatherer life, where collective action problems are a daily occurrence. We observe that across years, the Hadza, on average, contribute 56% of their endowment to the public goods, providing some reassurance that local institutions are mapping onto game play.

It is difficult to establish the same degree of control in field settings that are found in the laboratory. Thus, the problem of omitted variable bias is a concern, as there may be other influences on cooperation that were unobserved. Future work would benefit from more in-depth examinations into other factors that influence Hadza decisions to cooperate.

A third limitation of the study is that we collected data at discrete points far apart in time and are limited by how much we can say about the formation and breakdown of camps in relation to cooperation. Hunter-gatherer residence is determined by multiple and complex demographic, ecological, and personal factors [4, 7]. Examining the role of cooperation in Hadza camp formation and dissolution and also examining how initial variation in levels of cooperation between individuals converges on a stable equilibrium within a camp are important areas for future exploration.

Studying the conduits of norm establishment and reinforcement in hunter-gatherers hold particular promise. Storytelling, for instance, may be an effective way to teach and establish norms [25], including norms of reciprocity. Recently, it has been documented that among Agta foragers, groups with more skilled storytellers are more cooperative [25]. Moreover, there is a large literature demonstrating how ritual activities, which are thought to enable the expression of shared beliefs



Figure 4. Contributions at Time t by Contributions at Time t-1

The unit of analysis is a participant year. Size of gray circles is proportional to the count of individuals. Blue circles represent the average of the contribution in the following year as a function of the contribution in the current year. Bars represent 95% Cl. The 45-degree line represents the null hypothesis that people have cooperative types. See also Tables S4, S5, and S6.

and norms, can impact cooperation and fairness [26]. Hadza life is replete with public and private ritualistic activities – including song, dance, meat-eating, storytelling and puberty initiation practices – which are thought to play an important role in cementing relationships and promoting cooperation [7].

Our findings challenge all evolutionary models of cooperation that assume fixed social types. Consistent with models stressing the importance of contingent reciprocity, cultural learning, and social norms [27–29], we find that individuals' cooperative behavior is best predicted by the cooperativeness of their neighbors. The findings highlight the flexible nature of human cooperation and the remarkable capacity of humans to respond adaptively to their social environments.

STAR***METHODS**

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SUPPLEMENTAL INFORMATION

Supplemental Information includes one figure and six tables and can be found with this article online at https://doi.org/10.1016/j.cub.2018.07.064.

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AUTHOR CONTRIBUTIONS

C.L.A. and K.M.S. contributed to study design and writing. K.M.S., C.L.A., and T.L. analyzed the data. C.L.A., I.A.M., and K.M.S. collected data. All authors commented on drafts of the manuscript.

DECLARATION OF INTEREST

The authors declare no competing interests.

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STAR*METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Data and analysis scripts	Open Science Framework	https://osf.io/kc6ux/
Software and Algorithms		
R: A Language and Environment for Statistical Computing	Comprehensive R Archive Network	R version 3.4.1
Other		
Honeystix	GloryBee Foods	Cat#11685
Wildflower Honey stix	Stakich	N/A

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Coren Apicella (capicella@psych.upenn.edu)

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Study Site

The Hadza are nomadic foragers occupying the Lake Eyasi basin within the Great Rift Valley in Northern Tanzania. They sleep outside under the stars or in makeshift huts constructed of grass and trees. Approximately 1,000 individuals identify as Hadza, but only 200-300 individuals obtain the majority of their calories by hunting and gathering. It is this latter group that is the focus of this research.

Men hunt birds and mammals using bows and poison-tipped arrows and collect honey. Women gather plant foods including baobab fruit, berries, and tubers. Food is shared widely within camps, especially big game but producers of the food can channel the food in ways that benefit their kin [30]. Childcare is also shared [31].

The Hadza live in temporary camps that average about 30 individuals. Camps generally consist of several unrelated nuclear families. Relatedness within camps is low with primary kin comprising, on average, 1.43 and 1.93 of men and women's campmates respectively [7]. Typical of most contemporary hunter-gatherers, residence patterns are fluid and are best described as fission-fusion grouping [32]. Camps can merge or split. Individuals too, can freely relocate to new camps. Every 4-8 weeks entire camps shift location usually in response to resource availability. Because the Hadza have few capital goods and personal possessions, the physical costs associated with moving remain low.

While there is striking diversity among forager societies, it is thought that the social, economic, and political arrangements of the Hadza are similar to other hunter-gatherer societies. A study of hunter-gatherer social life using ethnographic data from 437 past and present foraging societies found that the vast majority of forager societies, including the Hadza, live in small groups, practice central place foraging and food sharing [32]. The Hadza also fall at or near the median value on a variety of key demographic traits such as the percentage of calories contributed to the diet by men and women, infant mortality rate, fertility rate, inter-birth intervals and so on [32]. Thus, apart from the fact the Hadza still maintain a subsistence lifestyle, there is good reason to believe that they are not outliers in other major respects.

Ethno-tourism, which largely began about 10-15 years ago has had the largest impact on Hadza life. And tourists visiting the Hadza continue to rise each year. While tourists can now be found in every region of Hadzaland, the vast majority of visits take place in camps on the north-eastern side of Lake Eyasi, close to the village Mangola, due to its proximity to paved roads that lead to Arusha and safari parks (Figure 1). Tours usually last a couple of hours and culminate with a cash payment to the camp which then the Hadza can spend in the village.

The Hadza have been described as having little belief in omniscient, moralizing gods [32, 33] but they do engage in a number of important rituals including a sacred epeme dance and meat-eating rituals [32]. These rituals are thought to bond participants to one another [7].

Sample Characteristics

Across years, we visited 56 Hadza camps collecting data from 383 unique individuals. For 137 participants, we have data from at least two years (Table S1). The mean age was similar across the years, ranging from 37 to 40 and women comprised 51%, 42%, 49% and 46% of the sample in 2010, 2013, 2014, and 2016, respectively. Further summary statistics can be found in the supplementary materials (Table S2).

Ethical Permissions

Institutional approvals were obtained prior to conducting this study from the Committee on the Use of Human Subjects at Harvard University, The University of Pennsylvania Institutional Review Board and the Tanzanian Commission for Science and Technology (COSTECH). Verbal informed consent was obtained from all participants due to low literacy rates.

METHOD DETAILS

Data Collection

Data were collected in four separate years – usually during the dry season – over a six-year period (2010, Aug/Sept; 2013, July; 2014, Oct/Nov; 2016, Aug/Sept). Data collection was supervised by different authors in different years: (CLA in 2010, 2013; IM in 2014 and KMS in 2016). In 2014 and 2016 Tanzanian researchers blind to the hypotheses collected the data. In each year, camps were visited using a technique not unlike snowball sampling. After establishing contact with the first camp, Hadza would direct the researchers to the next nearest camp. GPS coordinates were recorded for all camps in each year, with the exception of 2016 when the GPS receiver met an unfortunate end. Nevertheless, we were able to divide the camps in 2016 into market and nonmarket groups based on their general proximity to the village (Figure 1).

Public Goods Game

We used a public goods game as our measure of cooperation. This game is directly applicable to hunter-gatherer life where collective action problems are faced by groups on a daily basis. We used a food item instead of money since explanations for the evolution of cooperation have highlighted the importance of food sharing [34–36]. The methods for the public goods game elicitation in the Hadza has been described previously [4].

Cooperation was elicited by examining participants' voluntary contributions in a public goods game played with adult members of their camp. All games were conducted in Swahili and inside a vehicle for privacy. All adults in each camp were invited to participate with the exception of the very elderly and infirm. In 2010, 2013 and 2014 the game was played on the last day the researcher was in camp in order to limit possible discussion. Participants were also told that the game was secret. Since decisions were made in private, any assertions made by participants regarding their decision need not be truthful. In 2016, the game was played throughout the researcher's stay in the camp. Importantly, we find the same pattern of results.

Participants were endowed with four straws of 100% pure honey (2010, Honeystix, GloryBee foods 2013, 2014, Honey Stix, Stakich), a prized food of the Hadza [37]. Each honey stick contains roughly 15 calories. Participants then faced the decision of how to divide their honey sticks into a private account and a public account. Participants were told that the goods would be distributed evenly with all other adult camp members who also played the game. They were instructed that they could keep any amount from 0-4 sticks of the honey or donate them to the public goods by inserting them into an opaque cardboard box with an opening at the top. Subjects were told that for every stick of honey they donated, the researcher would donate an additional 3 sticks of honey to the public pot, and that, after all adult campmates played the game, the honey would be divided equally among them. Participants were also told that they would receive their undonated honey at the same time as the public honey was distributed to avoid confounding generosity with patience. Before subjects made their decision, the researcher simulated all their possible choices so that subjects were shown the additional amount of honey added to the box for each decision.

The Hadza have had experience playing various games to measure economic (e.g., endowment effect and risk) and social preferences (e.g., dictator, ultimatum, third-party punishment) with researchers over the last decade [38–41].

This is the basic script used each year in both English and Swahili.

English

We are playing a game with honey. This game is voluntary. You do not have to play this game. You will not be punished if you choose not to play. This study is a secret. I will not tell anyone the decision you make. Also, I will not tell you the decision that anyone else makes. All adults living in your camp will have the opportunity to play this game.

This game involves honey (show them 4 honey sticks). Inside these sticks is honey to eat. The decisions you make and the decisions other people make will affect how much honey you get and how much honey your other camp members get. You will only receive your share of honey after everyone has had a chance to the play the game. Any honey you receive will be given to you in secret, and nobody will see how much honey you get.

Here are 4 sticks of honey (hand it to them). You need to choose how many sticks to keep and how many sticks to put inside this box. You can choose to:

- keep all of the sticks of honey
- keep 3 of the sticks
- keep 2 of the sticks
- keep1 stick
- keep zero sticks.

No one will know how many sticks you choose to keep. Any honey that you do not keep will be put in this box and shared equally with all the people who played this game, including yourself. For every stick of honey you put in this box, I will add 3 sticks.

CellPress

- If you put in 1 stick, I will add 3 sticks.
- If you put in 2 sticks, I will add 6 sticks.
- If you put in 3 sticks, I will add 9 sticks.
- If you put in 4 sticks, I will add 12 sticks.
- If you keep all 4 honey sticks for yourself, I will not add any honey to the box.
- If everyone puts honey in the box, then the box will fill up and everyone will get a lot more honey. If no one or only a few people put honey in the box, then there will be very little honey to share.

Swahili

Tunaenda kucheza mchezo wa asali. Mchezo huu ni hiari. Unaweza kuamua usicheze mchezo huu. Hautaadhibiwa kama utaamua kutocheza. Somo hili ni siri. Sitamwambia mtu yeyote maamuzi utakayofanya. Pia, sitakwambia maamuzi ambayo mwingine amefanya. Watu wazima wote wanaoishi kwenye kambi yako watakuwa na nafasi ya kucheza mchezo huu. Mchezo huu unahusisha asali (waoneshe fimbo 4 za asali). Ndani ya fimbo hizi ni asali unaweza kuila. Maamuzi ambayo unafanya na maamuzi ambayo watu wengine wanafanya yanaathiri jinsi wewe unavyopata asali na watu wengine pia kambini. Utapata tu sehemu yako ya asali baada ya kila mtu kupata nafasi ya kucheza mchezo. Na asali utakayopata utapewa kwa siri na hakuna yeyote atakayeona umepata asali ngapi.

Hizi ni fimbo 4 za asali (mkabidhi). Unatakiwa uchague ni fimbo asali ngapi ubakiwe nazo na asali ngapi uweke ndani ya boksi hili. Unaweza kuchagua:

Kubakiwa na fimbo zote za asali

- Kubakiwa na fimbo 3
- Kubakiwa na fimbo 2
- Kubakiwa na fimbo 1
- Kutobakiwa na fimbo, sifuri
- Hakuna mtu ambaye atajua umeamua kubakiwa na fimbo ngapi
- Na asali yeyote ambayo hutobakiwa nayo itawekwa ndani ya boksi hili na zitagawanywa sawa kwa sawa na kila mtu ambaye amecheza mchezo huu, ukiwemo wewe
- Kwa kila fimbo ya asali utakayoweka ndani ya boksi hili, nitaongeza fimbo 3.
- Ukiweka fimbo 1, nitaongeza fimbo 3
- Ukiweka fimbo 2, nitaongeza fimbo 6
- Ukiweka fimbo 3, nitaongeza fimbo 9
- Ukiweka fimbo 4, nitaongeza fimbo 12
- Kama utabakiwa na fimbo zote 4 za asali kwa ajili yako, sitaongeza asali yeyote ndani ya boksi
- Kama kila mtu ataweka asali kwenye boksi, hivyo boksi litajaa na kila mtu atapata asali nyingi sana. Kama hakuna mtu au watu wachache wataweka asali kwenye boksi, kutakuwa na asali kidogo sana za kugawana/shirikiana

Additional Control Variables

Basic Demographics. Age, marital status, spouse's names and reproductive histories were recorded each year.

Education. Participants were asked the number of years that they attended school in 2013 and 2016. Public goods contributions were regressed on the number of years of formal education.

Household size. We asked participants the number of other individuals living in their household in 2013 and 2016. This typically includes children and spouse and occasionally other close family members. We regressed public goods contributions on household size.

Concerns about food. In 2013, participants were asked two forced choice questions about whether they were worried there would be enough food for their family in 1) over the next month or 2) over the year. Participants answered yes or no to both questions, such that a "yes" indicated participants were worried about having enough food.

Trade. In 2013, participants were asked to estimate how many days out of the past seven they personally went to a market or trade center to buy or sell something.

Close Relationships in Camp. In 2010 and 2016, we asked participants to provide the names of their biological parents, which allowed us to identify primary kin (full siblingships and parent-child relationships) living together. For each individual, we then calculated the proportion of their campmates that were primary kin or a spouse as a measure of "close relationships."

Time of Day. In 2010, 2013, and 2014, the public goods game was played after all other data were collected and in a short time period. Time was not recorded in these three sample years. In 2016, the public goods game was played throughout the study period so that the time the game was played varied within camps. Time of day was categorized into three periods: morning if the game was played between 8:00 and 12:00, afternoon if played between 12:00 and 16:00, and evening if played between 16:00 and 18:00.

QUANTIFICATION AND STATISTICAL ANALYSIS

Software

All analyses were conducted in R. For data manipulation, we used the tidyverse [42], magrittr [43], and dplyr [44] packages. For regression analyses with robust standard errors, we used the Imtest [45], multiwayvcov [46] and sandwich [47] packages. For visualizations, we used the ggplot2 [48], scales [49], gridExtra [50], GGally [51], RColorBrewer [52], ggmap [53], geosphere [54], network [55], sna [56], and igraph [57] packages.

Variance in public goods contributions

To test if public goods contributions clustered within camps, we measured variance between camps and variance within camps in public goods contributions. Variance between camps was the variance in camp mean contributions between camps, and variance within camps was the mean variance within each camp between individuals in public goods contributions. For each year, we then simulated the population distribution of these values. Public goods contributions were randomly re-assigned without replacement within the population structure. For each run, the variance between and within camps in public goods contributions was saved. The actual variances were compared to the distribution of simulated variances; if the actual variances fell within the extreme tales of the distribution (2.5% or 97.5%) the variances were determined to be significantly different from chance. We also computed F_{ST} values for each simulation run and the observed value by dividing between-camp variance by total variance in public goods contributions.

Regression analyses

For regression analyses that did not involve variables from previous years, all observations in 2010, 2013, 2014, and 2016 were used. All models had robust standard errors clustered on the individual. For models that include mean camp public goods contribution, we calculated for everyone the mean of other camp members' contribution such that an individual's mean camp public goods contribution did not include ego's own contribution. For these analyses, robust standard errors were also clustered on the camp. For regression analyses that involved variables from previous years, observations in 2013, 2014, and 2016 were included only if the individual was in the previous sample year. For these analyses, robust standard errors were clustered on the individual, and if the analysis include mean camp public goods contribution, they were clustered on the camp as well.

Given the limited range possible in public goods contributions, it could be argued that these data should be analyzed as if they were ordinal. We again conducted the key analysis regressing individual public goods contributions on mean camp contributions and previous contributions using an ordered logit to test the robustness of our results. Again, we limit the analysis to contributions in 2013, 2014, and 2016 including only participants who also had contributions in the previous year. Again, we clustered the robust standard errors on the individual and camps.

Analysis of Dyads Living Together in Future Years

We constructed a dataset of dyads to analyze who lives with whom in each year. To do this, we went through 2010, 2013, and 2014 and for each individual *i* in the sample at time *t* and time t + 1, we went through each individual *j* at time *t* and recorded whether *i* and *j* lived in the same camp at time *t*, at time t + 1, and their similarity in public goods contributions at time *t*, as well as their similarity on demographic variables at time *t*. Similarity scores were calculated by finding the absolute value of the difference between *i* and *j* on the variable and multiplying that value by -1 so that greater values indicate more similarity on the variable. We used a binary logistic regression and regressed whether *i* and *j* lived together at time t + 1 on the other variables with robust standard errors clustered on dyads.

DATA AND SOFTWARE AVAILABILITY

Scripts and de-identified data are available at https://osf.io/kc6ux/.

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Supplemental Information

Hunter-Gatherers Maintain Assortativity

in Cooperation despite High Levels

of Residential Change and Mixing

Kristopher M. Smith, Tomás Larroucau, Ibrahim A. Mabulla, and Coren L. Apicella



Figure S1. Simulated and Observed F_{ST} Values for Public Good Contributions, Related to Figure 2. Using the simulation method described in the STAR methods, we simulated and computed F_{ST} values of PG contributions for a random population for each year. The dashed line indicates where 95% of the simulated values fall below, and the solid line indicates the observed F_{ST} values. In each year, we observed a greater F_{ST} value in PG contributions than expected in a random population.

Table of Sample S	izes within and A	cross rears, herau	u io stat memo	us.	
Year	2010	2013	2014	2016	
2010	191	46	69	42	
2013		99	57	31	
2014			170	40	
2016				127	

Table S1 Sam	ple Sizes	Within a	and Across	Years.	Related to	STAR	methods.
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 \overline{Note} . Total number of participants in each year on the diagonal. Other cells indicate number of participants in both years.

Measure	2010	2013	2014	2016	Relation with PG
					contributions
PG	2.3 (1.2)	1.7 (1.2)	2.5 (1.1)	2.2 (1.4)	
contributions					
Males	<i>n</i> = 94	<i>n</i> = 57	<i>n</i> = 86	<i>n</i> = 58	0.10 (0.10)
Married	<i>n</i> = 152	<i>n</i> = 76	<i>n</i> = 130	<i>n</i> = 90	-0.06 (0.13)
Age	37.1 (11.0)	40.0 (12.9)	39.6 (13.4)	37.6 (14.6)	0.01 (0.004)
Number of	3.1 (2.3)	3.3 (2.4)	3.5 (2.6)	3.2 (2.6)	-0.02 (0.03)
living children					
Near market	<i>n</i> = 106	<i>n</i> = 53	<i>n</i> = 63	<i>n</i> = 37	0.39* (0.16)
Close	0.12 (0.12)			0.14 (0.16)	-1.11 (2.34)
relationships					
Formal		1.4 (2.7)		1.2 (2.5)	0.01 (0.06)
education					
Household size		4.2 (2.2)		2.7 (2.0)	0.00 (0.06)
Food concern		<i>n</i> = 56			-0.74 (0.44)
for the next					
month					
Food concern		<i>n</i> = 53			-0.51 (0.53)
for the next					
year					
Trade		0.5 (0.8)			0.15 (0.19)

Table S2 Demographic Variables and Their Relationship to Public Goods Contributions.Related to STAR Methods.

Note. For descriptive statistics, values are counts or mean (standard deviation in parentheses) for that variable in each year. See STAR method for more description of each variable. Values in the "Relationship with PG contributions" are unstandardized coefficients (standard error in parentheses) of contributions regressed on that variable only—that is, each variable was entered into a separate regression—controlling for year, with robust standard errors clustered on the individual and camp.

 $p^* > 0.05$

	<i>b</i> (<i>SE</i>)	OR	Ζ	р
Intercept	-3.51 (0.17)	0.03	-20.37	< 0.001
Lived together previously	0.37 (0.14)	1.44	2.56	0.010
Similarity in PG contributions	0.01 (0.04)	1.01	0.24	0.814
Both male	0.18 (0.11)	1.20	1.71	0.087
Both female	0.28 (0.10)	1.33	2.74	0.006
Both married	-0.01 (0.09)	0.99	-0.10	0.922
Both single	-0.67 (0.33)	0.51	-2.03	0.042
Similarity in age	0.01 (0.004)	1.01	1.65	0.099
Similarity in number of living children	0.05 (0.02)	1.05	2.47	0.014
Both lived in market region previously	0.13 (0.11)	1.13	1.10	0.273
Both lived in non-market region	0.48 (0.10)	1.62	4.75	< 0.001
previously				

Table S3. Binary Logistic Regr	ession on Dyads I	Living in the Same	Camp, Related to
Figure 3.			

Note. Whether the dyad lived in the same camp at time t + 1 was regressed on variables in the model. All variables in the model are taken from time t. See STAR method for more detail on the analysis.

	Model 1	Model 2	Model 3	Model 4	Model 5
Mean camp	0.55***	0.36*			0.36*
contribution	(0.15)	(0.16)			(0.16)
Previous			0.00	-0.01	-0.01
contribution			(0.09)	(0.08)	(0.08)
2014	0.44^{*}	0.53*	0.75^{**}	0.76^{**}	0.53*
	(0.19)	(0.22)	(0.24)	(0.25)	(0.23)
2016	0.50	0.76^{**}	0.76	1.05^{***}	0.76^{**}
	(0.26)	(0.23)	(0.39)	(0.23)	(0.23)
Male		0.17		0.18	0.17
		(0.19)		(0.19)	(0.19)
Age		0.00		0.00	0.00
		(0.01)		(0.01)	(0.01)
Married		0.25		0.33	0.25
		(0.31)		(0.29)	(0.31)
Number of living		-0.03		-0.04	-0.03
children		(0.03)		(0.03)	(0.03)
Exposure to market		-0.03		-0.04	-0.03
		(0.19)		(0.25)	(0.20)
Number of		-0.03*		-0.05***	-0.03*
campmates at time t		(0.01)		(0.01)	(0.01)

Table S4. OLS Regressions of Public Goods Contribution on Mean Camp Contribution and Previous Contribution, Related to Figure 4.

Note. Values are unstandardized OLS regression coefficients with standard errors in parentheses. The first two models test the effect of campmates' contributions on ego's contributions, with the second model adding demographic controls. The third and fourth model test to what extent current contributions are associated with previous contributions, with the fourth model adding demographic controls. Finally, the fifth model tests both effects together, with the demographic controls. All analyses are restricted to contributions in 2013, 2014, and 2016, and to individuals with a previous contribution in the sample year prior. p < 0.05, p < 0.01, p < 0.01

	Model 1	Model 2	Model 3	Model 4	Model 5
Mean camp	0.96***	0.69**			0.69**
contribution	(0.28)	(0.31)			(0.31)
Previous			0.00	-0.05	-0.06
contribution			(0.13)	(0.12)	(0.12)
2014	0.54^*	0.77^{*}	1.00^{**}	1.14^{**}	0.74^{*}
	(0.27)	(0.33)	(0.34)	(0.39)	(0.32)
2016	0.71	1.24^{***}	1.12	1.77^{***}	1.25***
	(0.38)	(0.34)	(0.62)	(0.37)	(0.33)
Male		0.20		0.31	0.23
		(0.33)		(0.32)	(0.33)
Age		0.00		0.01	0.00
		(0.02)		(0.02)	(0.02)
Married		0.32		0.55	0.34
		(0.53)		(0.49)	(0.54)
Number of living		-0.04		-0.07	-0.04
children		(0.05)		(0.05)	(0.05)
Exposure to market		-0.07		-0.15	-0.08
		(0.33)		(0.42)	(0.33)
Number of		-0.05*		-0.08**	-0.05^{*}
campmates at time t		(0.02)		(0.02)	(0.02)

Table S5 Ordered Logit Regressions of Public Goods Contribution on Mean CampContribution and Previous Contribution, Related to Figure 4.

Note. To establish robustness, we conducted the OLS regressions using an order logit regression. See STAR method for details. Values are unstandardized logit regression coefficients with standard errors in parentheses. All analyses are restricted to contributions in 2013, 2014, and 2016, and only to individuals with a previous contribution in the sample year prior. p < 0.05, p < 0.01, p < 0.01, p < 0.001

	b	SE	t	р
2014	0.27	0.09	3.12	0.002
2016	0.18	0.11	1.60	0.111
Cooperated	0.06	0.13	0.61	0.640
previously				
Defected	0.09	0.15	0.61	0.540
previously				
Camp mean	0.72	0.06	12.00	< 0.001

Table S6. OLS Regression of Current Public Goods Contribution on Previous Play,Related to Figure 4.

Note. Analysis regressed current PG contributions on participants' behavior in previous sample. Individuals who contributed as much or more than their previous campmates were coded as previous cooperators, whereas individuals who contributed less than their previous campmates were coded as previous defectors. Thus, the analysis compared previous behavior to individuals who did not participate in the previous sample. Robust standard errors were clustered on the individual and camp.