

HADZA HUNTER-GATHERERS AND THE EVOLUTION OF HUMAN COOPERATION:
EVIDENCE AGAINST PARTNER CHOICE MODELS

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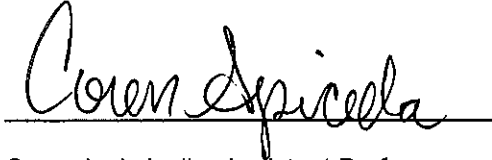
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ABSTRACT

HADZA HUNTER-GATHERERS AND THE EVOLUTION OF HUMAN COOPERATION: EVIDENCE AGAINST PARTNER CHOICE MODELS

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Human cooperation is exceptional in the animal kingdom, and explaining its evolution is a puzzle. One hypothesis is that the ability to track others' reputations and to choose our cooperative partners created biological markets, and competition within these markets selected for cooperators. Here, I test this hypothesis from the Hadza of Tanzania, one of the last remaining foraging populations. In Chapter 1, I use longitudinal data tracking cooperation in an economic game and residence patterns. In every year, contribution levels to the public good are similar within residence camps, fulfilling a necessary condition for the evolution of cooperation. However, cooperators in previous years were not more likely to live with cooperators in future years. Further, at the individual level, previous contributions did not predict future contributions. In Chapters 2 and 3, I use data from a ranking task in which Hadza ranked their campmates on character traits, hunting ability, and who they would like to live with in the future. In Chapter 2, I examine whether Hadza agree on perceptions of moral character. The Hadza disagree on which of their campmates exhibit moral character. The Hadza do agree though on what traits (e.g., generosity and hard work) contribute to overall moral character. These results indicate that the Hadza use similar criteria for evaluating moral character but do not agree on who exhibits these traits. The lack of agreement on perceptions of moral character may be due to the lack of stable moral dispositions among the Hadza. Finally, in Chapter 3, I examine

which traits the Hadza prefer when choosing potential campmates. I find that the Hadza have only weak preferences to live with campmates that exhibit character traits, and instead have stronger preferences to live with men who are better hunters. Further, there is no evidence that being a preferred campmate results in any benefits to one's reproductive success, further undermining partner choice theories. Together, these results indicate that partner choice and other reputation-based strategies do not maintain cooperation among the Hadza, and more broadly, suggests that such mechanisms were not responsible for the evolution of human cooperation.

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INTRODUCTION

Human cooperation differs from cooperation in other species in scope and scale. Whereas non-human animals cooperate almost exclusively with kin (Hamilton, 1964) or in dyads between known individuals (Trivers, 1971), humans regularly cooperate in groups with unrelated strangers. For example, people recycle, donate blood, tip servers, and vote. How humans evolved this propensity to cooperate is a puzzle to evolutionary biologists, and attempts to solve the puzzle have led to a dizzying array of proposed explanations (Rand & Nowak, 2013). What is needed then is not another explanation for the evolution of human cooperation, but data to test the already existing explanations.

One common and necessary element of the different explanations for human cooperation is positive phenotypic assortment. That is, cooperation must cluster, such that the benefits of cooperation preferentially flow to other cooperators (Apicella & Silk, 2019; Eshel & Cavalli-Sforza, 1982; Nowak, 2006; Wilson & Dugatkin, 1997). When cooperators cluster, they avoid costly exploitation from freeriders and the benefits of mutual cooperation offsets the cost of helping other. The variety of proposed explanations for human cooperation simply describe different mechanisms that lead to positive phenotypic assortment.

The different mechanisms proposed to generate assortment on cooperation can be categorized into two broad classes. The first class is *behavioral change* mechanisms, which generate assortment by changing the behavior of others. This includes mechanisms such as social and cultural learning (Boyd & Richerson, 1982, 2009), social contagion in networks (Fowler & Christakis, 2010; Rand, Nowak, Fowler, & Christakis, 2011), punishment (Boyd & Richerson, 1992; Gintis, 2000), or even a combination of

punishment and social learning (Chudek & Henrich, 2011; Henrich & Boyd, 2001). Through these mechanisms, cooperators can change the behavior defectors, allowing for cooperation to cluster. Many of these mechanisms though are costly for cooperators, and often creates a second-order cooperative dilemma. To solve this problem, theorists often—though not always—invoke group selection and gene-culture co-evolution as other necessary mechanisms to explain human cooperation (Henrich, 2004).

The second class of mechanisms proposed to generate assortment is *reputation-based* mechanisms. These are mechanisms in which people track the reputation of others and condition their own behavior on others' reputation. This can include whether to cooperate or defect on another person, such as indirect reciprocity (Alexander, 1987; Nowak & Sigmund, 2005), or whether to even interact with a person at all, such as partner choice models (Aktipis, 2011; Barclay, 2013; Baumard, André, & Sperber, 2013). Further, partner choice can create a biological market (Barclay, 2016a; Noë & Hammerstein, 1994), in which cooperative partners compete for access to other partners. This can lead to increased cooperation (Barclay & Willer, 2007; Hardy & Van Vugt, 2006) and further clustering of cooperators. These mechanisms are also generally assumed to be low-cost in a mobile organism, such as humans, and do not require group selection. As such, skeptics of group selection (Pinker, 2015), argue these mechanisms are more plausible than many of the proposed behavioral change mechanisms.

In this dissertation, I examine whether partner choice maintains cooperation in the Hadza of Tanzania, one of the last remaining groups of hunter-gatherers (Marlowe, 2010). I focus on partner choice for three reasons. First, partner choice has become increasingly popular among researchers, most notably in moral psychology. The problem

of evaluating and choosing potential partners is thought to be at the heart of many moral phenomena, including evaluations of moral character (Landy, Piazza, & Goodwin, 2016; Wojciszke, Bazinska, & Jaworski, 1998), the role of mental states in moral judgments (Young & Tsoi, 2013), moral licensing (Barclay, 2016a), deontological moral judgments (Everett, Faber, Savulescu, & Crockett, 2018), fairness (Baumard et al., 2013), among others. Second, and related to the previous point, partner choice is well supported in Western populations. Finally, partner choice seems particularly relevant to hunter-gatherers. Hunter-gatherers are nomadic with fluid residence patterns, such that they have regular opportunities to choose new partners. And because of their harsh environment, they depend on each other to cooperate in a number of domains, including food sharing, protection, and childcare (Apicella & Crittenden, 2016), so that the problem of deciding who to cooperate with has important consequences for hunter-gatherers.

Studying cooperation in hunter-gatherers, and especially Hadza, gives some insight into its evolution. For most of our evolutionary history, human ancestors lived as hunter-gatherer, and though contemporary hunter-gatherers are surely different from ancestral humans, their lifestyle and ecologies better approximate ancestral conditions than do university students. At minimum, we can start to understand the conditions under which partner choice may be a viable mechanism for maintaining cooperation.

One concern about studying contemporary hunter-gatherers is representativeness; contemporary foragers live in a variety of environments, from dry deserts in Africa, to lush rainforests in South America, and even to the extreme cold of the Arctic, and one group is not representative of all foragers. However, on a number of demographic and ecological variables, including caloric intake, number of children born, mortality rates,

and others, the Hadza are at or near the median value (Marlowe, 2010), so they are at least not outliers among foragers.

I look at three key prediction that follow from the partner choice theory of cooperation. First, people should prefer to live with more cooperative individuals. Chapters 1 and 3 examine this assumption using behavioral data from an economic game and directly eliciting preferences using a ranking task. Second, people must have stable cooperative or moral dispositions such that future cooperative behavior can be predicted from previous cooperative behavior – if not, then choosing a cooperative partner now does not guarantee that partner will be cooperative in the future. Chapter 1 uses longitudinal data from an economic game to examine this assumption, and Chapter 2 corroborates this result using independent observer rankings. Finally, for the trait to evolve, there must be a benefit to being a preferred partner that offsets the cost of cultivating a reputation as a cooperator. Chapter 3 examines the correlation between being a preferred campmate and reproductive success to test whether being a desirable social partner improves fitness.

CHAPTER 1: HUNTER-GATHERERS MAINTAIN ASSORTAVITY IN COOPERATION DESPITE HIGH-LEVELS OF RESIDENTIAL CHANGE AND MIXING

Widespread cooperation is a defining feature of human societies from hunter-gatherer bands to nation states. But explaining its evolution remains a challenge. While 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 hunter-gatherers, characterized by high mobility, residential mixing and low genetic relatedness, undermine assortment and add 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 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 important in generating the assortment necessary for cooperation to evolve.

Introduction

The scope and scale by which we help one another, including cooperative acts with those who bear no genetic relation to us, is considered a hallmark of being human. And yet, this emblematic feature of our humanity has challenged scientific thinking (Boyd & Richerson, 2006; Fehr & Fischbacher, 2003; Silk & Boyd, 2010). How can natural selection favor costly cooperation in the face of possible exploitation by defectors? Biologists have proposed multiple theoretical models to explain cooperation, but there is little evidence on what theories actually explain human behavior in evolutionarily-relevant settings. To understand this, we analyze data on cooperation and migration patterns in a hunter-gatherer population over a six-year period. Crucially, the data contain detailed information about how individual cooperative behavior persists, and how cooperators sort across time and space – vital elements that tease apart the most prominent theoretical models. And the presence of positive assortment of cooperators in space is a fundamental requirement of these models (Fletcher & Doebeli, 2009; Nowak, Tarnita, & Antal, 2010).

Current hunter-gatherers live in dynamic fission-fusion societies with substantial inter-group mixing and consequently, low within-group relatedness (Hill et al., 2011). This mobility poses a challenge to assortment. Common descent, where individuals preferentially interact with kin (Hamilton, 1964), and reciprocity, where individuals limit their cooperation to known reciprocators (Trivers, 1971) can generate assortment, but social mobility undermines it by decreasing relatedness among group members and

allowing cooperative groups to be invaded by free-riders or “rovers” (Dugatkin & Wilson, 1991; Enquist & Leimar, 1993). As such, these classic models fall short in explaining how cooperation evolved in early humans under these presumed social dynamics.

For this reason, three additional classes of theoretical models explaining cooperation and assortment have been emphasized. In models of biological markets involving partner choice, individuals compete for the most cooperative partners and the most cooperative choose each other (Barclay, 2016a). In models involving conditional strategies that respond to group-level behaviors, such as generalized reciprocity (Pfeiffer, Rutte, Killingback, Taborsky, & Bonhoeffer, 2005) and/or the switching of groups (Aktipis, 2011), cooperation can stabilize when the groups are small (Pfeiffer et al., 2005). In models of gene-culture co-evolution, culturally evolving social norms, supported by an underlying norm-psychology, can generate within-group similarity and between-group differences in cooperation (Chudek & Henrich, 2011).

While nearly all models involve some degree of behavioral flexibility such that an individual’s level of cooperation is contingent on the social environment, partner choice models assume that individuals have stable traits, often genetically determined, on which the choice of partners is based (Aktipis, 2011; Eshel & Cavalli-Sforza, 1982; J. M. McNamara, Barta, Fromhage, & Houston, 2008; Noë & Hammerstein, 1994). In these models, individuals can leave current partners or reject prospective partners based on their observations and past interactions. The real-world applications of these models hinge on the existence of trait-like differences in cooperativeness. Yet, few studies have examined longitudinal stability in cooperativeness in humans (Peysakhovich, Nowak, &

Rand, 2014; Volk, Thöni, & Ruigrok, 2012), and none have examined it in natural settings between members of existing social groups who know each other well.

To tease apart these existing theories, we study cooperation in an extant hunter-gatherer population – the Hadza of Tanzania – who 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 Western Educated Industrialized Rich and Democratic (WEIRD) societies (Henrich, Heine, & Norenzayan, 2010).

Method

Population

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 (Wood & Marlowe, 2013). Childcare is also shared (Crittenden & Marlowe, 2008).

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 (Hill, Wood, Baggio, Hurtado, & Boyd, 2014). Typical of most contemporary hunter-gatherers, residence patterns are fluid and are best described as fission-fusion grouping (Marlowe, 2010). 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 (Marlowe, 2010). 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 (Marlowe, 2010). 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 1.1). 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 (Apicella, 2018; Marlowe, 2010) but they do engage in a number of important rituals including a sacred epeme dance and meat-eating rituals (Marlowe, 2010). These rituals are thought to bond participants to one another (Hill et al., 2014).

Sample

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 1.1 presents the samples sizes for each and the number of participants in multiple years. 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; Table 1.2 presents further summary statistics of the demographic variables.

Table 1.1. Sample Sizes Within and Across Years

Year	2010	2013	2014	2016
2010	191	46	69	42
2013		99	57	31
2014			170	40
2016				127

Note. Total number of participants in each year on the diagonal. Other cells indicate number of participants in both years.

Table 1.2. Descriptive Statistics for Demographic Variables in Each Year

Measure	2010	2013	2014	2016
Males	$n = 94$	$n = 57$	$n = 86$	$n = 58$
Married	$n = 152$	$n = 76$	$n = 130$	$n = 90$
Age	37.1 (11.0)	40.0 (12.9)	39.6 (13.4)	37.6 (14.6)
Number of living children	3.1 (2.3)	3.3 (2.4)	3.5 (2.6)	3.2 (2.6)
Near market	$n = 106$	$n = 53$	$n = 63$	$n = 37$
Close relationships	0.12 (0.12)			0.14 (0.16)
Formal education		1.4 (2.7)		1.2 (2.5)
Household size		4.2 (2.2)		2.7 (2.0)
Food concern for the next month		$n = 56$		
Food concern for the next year		$n = 53$		
Trade		0.5 (0.8)		

Note. For descriptive statistics, values are counts or mean (standard deviation in parentheses) for that variable in each year.

Data collection

Data was 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 each year, camps were visited using 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 1.1).

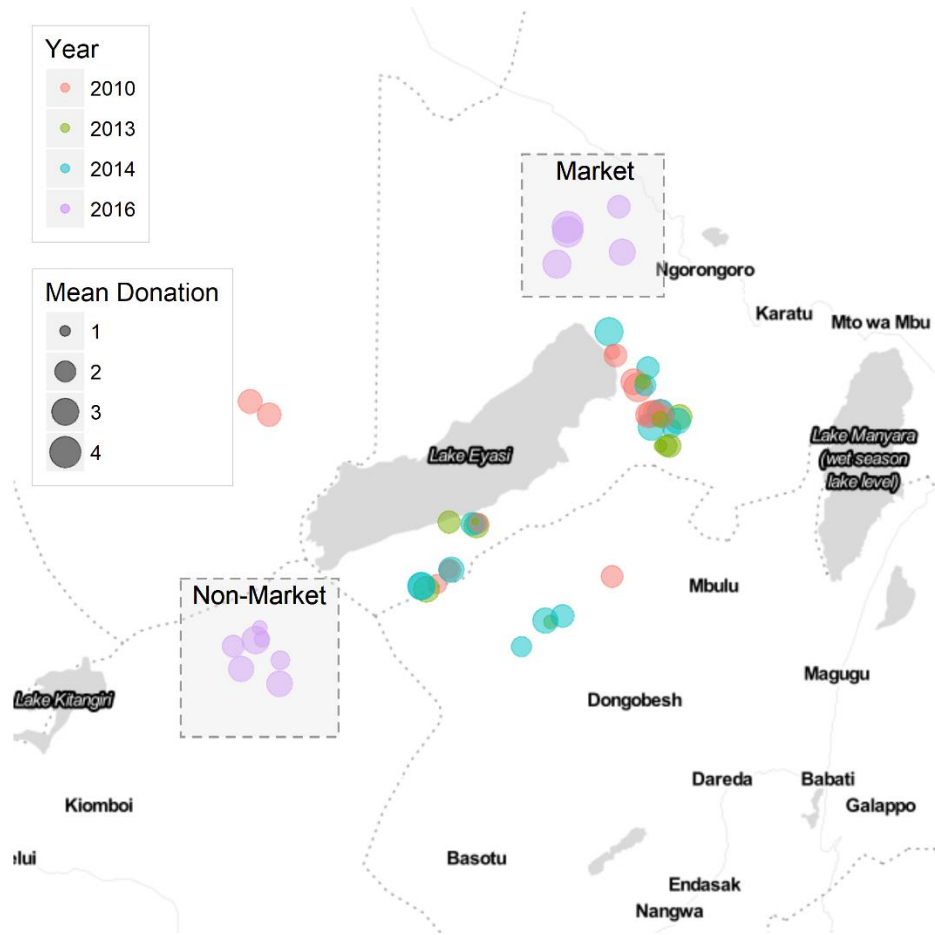


Figure 1.1. Map of camp locations and mean contributions. Circles represent the camps visited colored by year of data collection. The size of the point signifies the mean public goods contribution in the camp. GPS data are not available in 2016 due to missing equipment. The camps in 2016 are grouped by whether they were located in the market vs non-market region, but their placement is otherwise random.

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 (Jaeggi & van

Schaik, 2011; Kaplan & Gurven, 2005; Kaplan et al., 1985). The methods for the public goods game elicitation in the Hadza has been described previously (Apicella, Marlowe, Fowler, & Christakis, 2012).

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 sticks of 100% pure honey (2010, HoneyStix, GloryBee foods Inc. 2013, 2014, Honey Stix, Stakich Inc.), a prized food of the Hadza (Berbesque & Marlowe, 2009). 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. Participants 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 and that their decisions would be secret. Before participants 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 (Apicella, Azevedo, Christakis, & Fowler, 2014; Henrich, 2006; Henrich et al., 2001; Marlowe, 2004a).

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.

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.

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.

Risk. In 2013, 76 of the participants who played the public good game also completed a task measuring risk preferences. Participants were endowed with 4 honey sticks and then asked to bet any number of those sticks, with a 50/50 chance of doubling the bet or losing all gambled honey sticks.

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 (Wickham, 2017b), magrittr (Bache & Wickham, 2014), and dplyr (Wickham, 2011) packages. For regression analyses with robust standard errors, we used the lmtest (Zeileis & Hothorn, 2002), multiwayvcov (Graham, Arai, & Hagströmer, 2016) and sandwich

(Zeileis, 2004) packages. For visualizations, we used the ggplot2 (Wickham, 2009), scales (Wickham, 2017a), gridExtra (Baptiste, 2017), GGally (Schloerke et al., 2017), RColorBrewer (Neuwirth, 2014), ggmap (Kahle & Wickham, 2013), geosphere (Hijmans, 2017), network (Butts, 2008), sna (Butts, 2016), and igraph (Csardi & Nepusz, 2006) packages.

Variance in public good 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 tails 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.

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.

Results

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 contribution to different camps, but kept the population structure fixed (Apicella et al., 2012). 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 1.2). The 2010 results have been previously reported (Apicella et al., 2012). The long-term data indicate that assortment is a consistent feature of hunter-gatherer life, year after year.

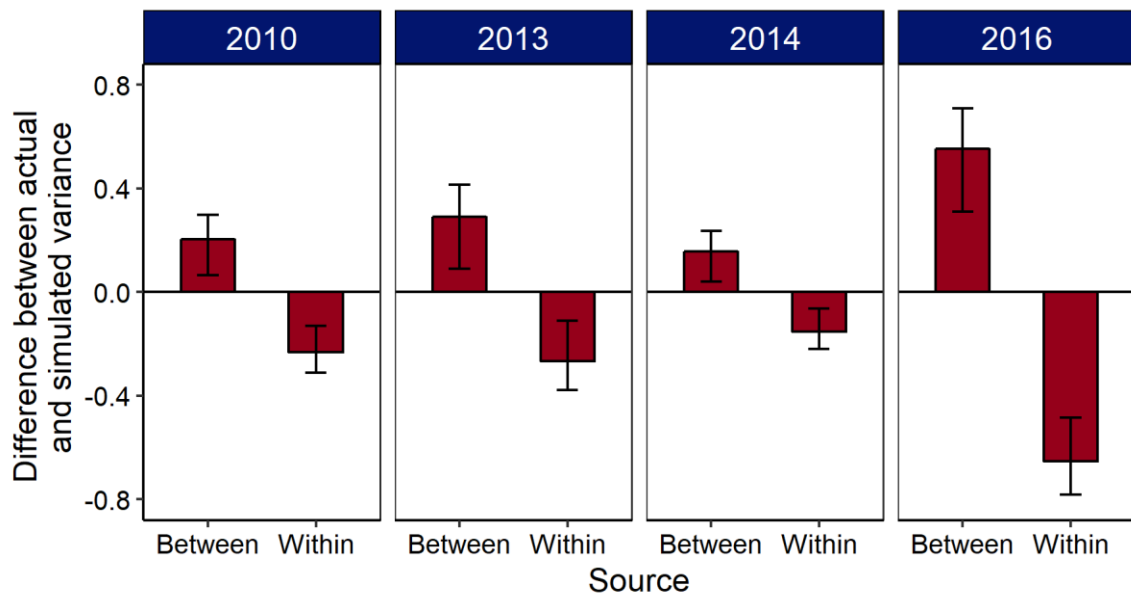


Figure 1.2. Difference between actual and simulated variance within and between residence camps in public goods contributions. Error bars are 95% confidence intervals.

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 (Bell, Richerson, & McElreath, 2009). F_{ST} is useful to consider here because if F_{ST} is large enough, then individually-deleterious but group-beneficial behaviors can evolve (Price, 1972). In 2010, 2013, 2014, and 2016, $F_{ST} = 0.26, 0.33, 0.24,$ and $0.39,$ respectively, and in every year was greater than expected in a random population, $p < 0.05$ (see Figure 1.3). These values are higher than observed genetic differentiation between nation-states, and are more similar to estimates of cultural differentiation between populations (Bell et al., 2009).

We examined whether this assortment was specific to cooperative decision-making or if other economic decision-making, specifically risk preferences, showed similar assortment. Using the risk preference data from 2013, we again simulated the between-camp and within-camp variance of risk preferences in a random population. The observed $F_{ST} = 0.35$ was greater than expected in a random population, 95% $F_{ST} = 0.26$. Moreover, contributions in the public good and honey sticks gambled were correlated, $r(74) = 0.28, p = 0.015$. We tested if cooperation remained clustered when controlling for risk preferences; again, the observed $F_{ST} = 0.28$ for contributions to the public good controlling for risk preference was greater than expected in a random population, 95% $F_{ST} = 0.26$. Finally, we also tested if risk preferences remained clustered within camps when controlling for contributions to the public good. They did; the observed $F_{ST} = 0.33$ for risk preferences controlling for contributions to the public good was greater than expected in a random population, 95% $F_{ST} = 0.27$. That is, cooperation and risk were both independently clustered within camps.

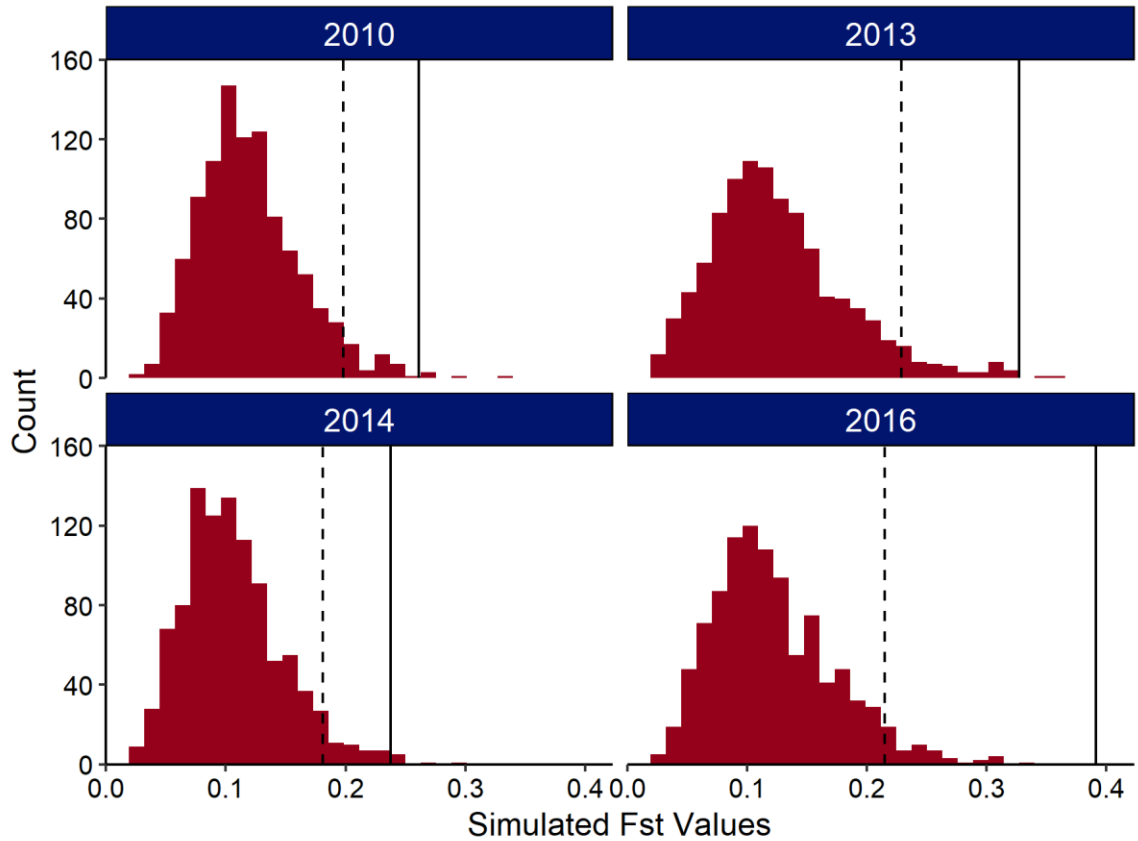


Figure 1.3. Simulated and observed F_{ST} values for public good contributions. We simulated and computed F_{ST} values of PG contributions for a random population for each year. The dashed line indicates where 95% of the simulated values fall below, and the solid line indicates the observed F_{ST} values.

The observed assortment on cooperation is remarkable because the Hadza, like other hunter-gatherers, have flexible living arrangements and high rates of migration (Hill et al., 2011, 2014). We too observe high rates of residential change. We calculated for each person the proportion of campmates at time t that lived in 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.

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 (Barclay, 2016a). 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 (Eshel & Cavalli-Sforza, 1982; J. M. McNamara et al., 2008; Noë & Hammerstein, 1994). 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 (Barclay, 2013, 2016a; Noë & Hammerstein, 1994), with cooperative individuals being sought after 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 1.4). 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. 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' contribution at time $t - 1$ and contributions relative to campmates' contributions at time t , $b = 0.01$, $SE = 0.10$, $t(132) = 0.06$, $p = 0.950$.

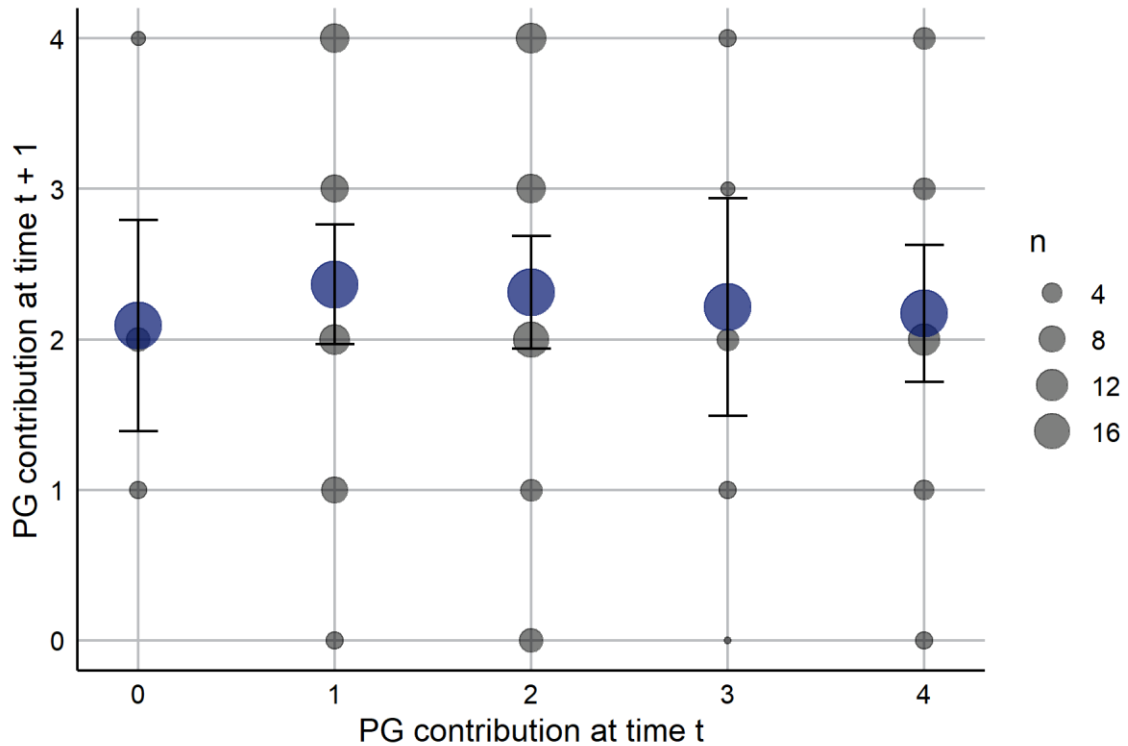


Figure 1.4. Contributions at time t by contributions at time $t - 1$. The unit of analysis is a participant year. Gray circles' size is proportional to the count of individuals. Blue circles represent the average of the contribution in the following year as a function of the contribution in the current year. Bars represent 95% CI.

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.

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 (see Table 1.3).

Table 1.3. Binary Logistic Regression on Dyads Living in the Same Camp

	<i>b (SE)</i>	<i>OR</i>	<i>Z</i>	<i>p</i>
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 previously	0.48 (0.10)	1.62	4.75	< 0.001

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 .

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. Further, in 2010 and 2016, the only years for which we have kinship data, 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 1.4).

Table 1.4. OLS Regressions of Public Goods Contribution on Mean Camp Contribution and Previous Contribution

	Model 1	Model 2	Model 3
Mean camp contribution	0.36*		0.36*
	(0.16)		(0.16)
Previous contribution		-0.01	-0.01
		(0.08)	(0.08)
2014	0.53*	0.76**	0.53*
	(0.22)	(0.25)	(0.23)
2016	0.76**	1.05***	0.76**
	(0.23)	(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 children	-0.03	-0.04	-0.03
	(0.03)	(0.03)	(0.03)
Exposure to market	-0.03	-0.04	-0.03
	(0.19)	(0.25)	(0.20)
Number of campmates at time t	-0.03*	-0.05***	-0.03*
	(0.01)	(0.01)	(0.01)

Note. Values are unstandardized OLS regression coefficients with standard errors in parentheses. All analyses are restricted to contributions in 2013, 2014, and 2016, and to individuals with a previous contribution in the sample year prior.

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

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 (Henrich et al., 2010).

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 (Aktipis, 2011; Eshel & Cavalli-Sforza, 1982; J. M. McNamara et al., 2008; Noë & Hammerstein, 1994). 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 (Barclay, 2016a). 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 (Barclay & Raihani, 2016). 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 (Apicella et al., 2012). 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 (Apicella, 2014). 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 (Gurven, 2014). Our findings, however, contrast with laboratory studies using Western samples illustrating small-to-medium-sized correlations in cooperative game play over time (Peysakhovich et al., 2014; Volk et al., 2012). 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 well-known, 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 (Peysakhovich & Rand, 2015; Stagnaro, Arechar, & Rand, 2017). 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 (Heine, 2001).

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 (Fowler & Christakis, 2010; Jordan, Rand, Arbesman, Fowler, & Christakis, 2013).

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 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. For example, research in WEIRD populations have found that incidental emotions resulting from weather (Hirshleifer & Shumway, 2003), sex (Gabbi & Zanotti, 2019), and sporting outcomes (Otto, Fleming, & Glimcher, 2016) influence economic decisions-making. It is possible that camps were similarly experiencing different fortunes on the days in which cooperation was measured

and this is the reason for clustering. This alternative is supported by the 2013 data in which risk preferences were similarly clustered; however, the fact that cooperation remained clustered after controlling for risk suggests this cannot entirely explain the observed clustering. 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 (Apicella et al., 2012; Hill et al., 2014). Examining the role of cooperation in Hadza camp formation and dissolution, as well as 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 (D. Smith et al., 2017), including norms of reciprocity. Recently, it has been documented that among Agta foragers, groups with more skilled storytellers are more cooperative (D. Smith et al., 2017). Moreover, there is a large literature demonstrating how ritual activities, which are thought to enable the expression of shared beliefs and norms, can impact cooperation and fairness (Sosis & Ruffle, 2003). 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 (Hill et al., 2014).

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 (Bowles & Gintis, 2004; Chudek & Henrich, 2011; Gurven, 2006) 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.

CHAPTER 2: HADZA HUNTER-GATHERERS DISAGREE ON PERCEPTIONS OF MORAL CHARACTER

To the extent that moral character is grounded in stable and observable truths, there should exist agreement between people in their judgements of others' character. In Western populations, this agreement is found. We examine whether this is universal in Hadza hunter-gatherers of Tanzania. Ninety-four judges ranked their campmates on global character and relevant character traits for a total of 824 observations. Judges disagreed on rankings of global character, generosity, and honesty, but agreed more on hard work and hunting ability. Individual rankings on specific traits predicted character evaluations. There was agreement between judges on the extent to which generosity and hard work related to character. These findings suggest that Hadza have shared beliefs about what traits constitute character, but disagree on which of their campmates exhibit these traits. We discuss these findings in light of other research suggesting that stable moral dispositions may not be universal.

Introduction

In Western societies, evaluation of moral character is an important component of person perception (Goodwin, 2015; Goodwin, Piazza, & Rozin, 2014). When learning about a new person, Italian undergraduates seek information about whether they are trustworthy (Brambilla, Rusconi, Sacchi, & Cherubini, 2011). When identifying features and traits most relevant to identity, online workers in the US consider morality to be an essential component (Strohmingner & Nichols, 2014). And when US undergraduates consider what attributes a partner should have in different types of relationships, morally relevant features, such as trustworthiness, are most important (Cottrell, Neuberg, & Li,

2007). This makes sense because a person's character is used to infer their intentions toward us and whether they would help or hinder our goals (Landy et al., 2016). Indeed, people use information about moral character to decide who to interact and cooperate with (Everett et al., 2018; Martin & Cushman, 2015; van der Lee, Ellemers, Scheepers, & Rutjens, 2017).

Despite the importance of moral character in person perception, some have argued that character does not exist and that people do not have stable moral dispositions (Doris, 2002; Harman, 2003). Social psychologists and philosophers have used classic findings from social psychology, such as the bystander effect (Darley & Latané, 1968; Latané & Darley, 1968) or the good Samaritan experiment (Darley & Batson, 1973), to argue against the existence of moral character and that moral behavior is determined wholly by the situation (Doris, 2002; Harman, 2003). One way to determine whether people behave similarly across situations is to examine agreement between independent observers. Because different observers are likely to interact with the target in different situations, if they agree in their evaluations, it then suggests there is a stable disposition that is being observed (Kenrick & Funder, 1988). So, if independent observers have similar perceptions of targets' moral character, then it provides some evidence for the existence of moral character.

People generally agree on who does, and does not, have moral character. In a US community sample, self-report and informant ratings of morally-relevant traits, such as honesty or guilt-proneness, moderately correlate (Cohen, Panter, Turan, Morse, & Kim, 2013). Independent observers in US community samples also agree on global evaluations of moral character, as well as specific moral traits and trait profiles. (Helzer et al., 2014).

And online workers in the US agree on morally relevant traits displayed by respected cultural figures, even across the US political divide (Frimer, Biesanz, Walker, & MacKinlay, 2013). Again, this agreement is used as evidence that moral character exists.

Like much of behavioral and social science research, samples in studies of moral psychology have largely been drawn from Western, Educated, Industrialized, Rich, and Democratic—or WEIRD—societies (Ellemers, van der Toorn, Paunov, & van Leeuwen, 2019; Henrich et al., 2010). Despite this, the importance of moral character in identity and person perception is theorized to be universal (Strohming, Knobe, & Newman, 2017). Most often, when moral psychology is examined in other cultures, the emphasis is on the content of moral norms and the shared or unique prescriptions and prohibitions across cultures (Curry, Mullins, & Whitehouse, 2019; Haidt, Koller, & Dias, 1993; Purzycki et al., 2018). Yet, when research has looked at processes in moral judgments, important differences have been found. For example, whether a wrong is done intentionally is an important distinction in moral judgments among Western populations, presumably because it reveals information about moral character (Landy & Uhlmann, 2018). However, unintentional violations are judged as wrong as intentional violations in some cultures, including the Hadza and South Pacific islanders (Barrett et al., 2016; R. A. McNamara, Willard, Norenzayan, & Henrich, 2019). To our knowledge, no research has been conducted on perceptions of moral character in small-scale societies.

There are reasons to suspect important differences in moral character and its perception in small-scale societies. First, there is some evidence for less personality variation in non-WEIRD societies. For example, personality traits in the Tsimané forager-horticulturalists of Bolivia do not cluster into five distinct factors, but rather two,

and there is less variation within those factors compared to Western samples (Gurven, von Rueden, Massenkoff, Kaplan, & Vie, 2013). And in fact, across 55 nations, populations with fewer economic opportunities to specialize have less variation in personality traits (Lukaszewski, Gurven, von Rueden, & Schmitt, 2017). To the extent that there is a relationship between personality traits and moral character (Thalmayer, Saucier, Srivastava, Flournoy, & Costello, 2019), we might then similarly expect less variation in morally-relevant character traits. Second, there is no evidence for generous dispositions in small-scale societies. In longitudinal data among the Hadza, contributions to a public good game were not predicted by previous contributions, but rather the contributions of an individual's campmates (K. M. Smith, Larroucau, Mabulla, & Apicella, 2018). Here, strong, local norms governing generosity may be reducing individual variation in morally-relevant behavior leading to a lack of agreement on perceptions of moral character.

In the current study, we examine perceptions of moral character among the Hadza of Tanzania, one of the last remaining hunter-gatherer groups in the world. The Hadza are an ideal population because they live in small groups of known individuals where behavior is observable, and because of their harsh environment, knowing who is moral would be seemingly important. We examine agreement on these perceptions in two ways. First, do Hadza agree on who has moral character? And second, do Hadza agree on what traits contribute to global moral character? To answer these questions, we ask the Hadza to rank their campmates on moral character, as well as specific traits of hard work, generosity, and honesty. We examine the consensus within each camp on rank orderings for each trait to answer the first question. We examine the relationship between the

specific traits and global character rankings and the variation between Hadza on the importance of the specific traits in determining global character to answer the second question.

Method

Population

The Hadza are a group of nomadic hunter-gatherers living in rural north Tanzania around Lake Eyasi. There are about 300 Hadza who still practice a foraging lifestyle (Marlowe, 2010). The Hadza have a sexual division of labor; men hunt for game, such as giraffe, impala, or zebra, and collect honey, while women gather plant items, such as tubers and berries. Food brought back to the camp that requires extended processing, such as meat and tubers, are distributed across the entire camp. Food and fresh water is scarce; about 80% of Hadza report concerns about whether there will be enough food in the next month (Apicella, 2018). Other threats to Hadza include high rates of disease and infection, and less commonly, attacks from predators, such as lions, hyenas, leopards, and snakes. Approximately 40% of children born will not live to reach the age of five (Blurton-Jones, 2016).

The Hadza live in temporary camps of about 30 adults and children, usually consisting of two to three unrelated nuclear families. The Hadza have multilocal residence pattern—men and women are equally likely to live with kin, though the average genetic relatedness for both sexes within camps is low (Blurton-Jones, 2016; Hill et al., 2011). Camps move location every 4 to 6 weeks as local resources are depleted, and people frequently join new camps as they please. Repeat interaction rates are low in

the Hadza (Hill et al., 2014), and from year-to-year, individuals are only living with about 20% of their previous campmates (K. M. Smith et al., 2018).

Though the Hadza have strong norms of food sharing, they do try to cheat these norms when possible. In economic games that measure rule-bending, Hadza will cheat to benefit themselves at the expense of their campmates (Apicella, 2018). Anecdotally, Hadza will sometimes try to bring in meat under the cover of darkness to avoid sharing with others and will sometimes even ask to hide carcasses under a researcher's vehicle (Marlowe, 2010). Hadza historically have little experience with centralized institutions involving punishment (e.g., police and courts). In economic games, the Hadza have low-rates of second- and third-party punishment (Henrich, 2006). And though most Hadza report believing in god (*Haine* or sometimes *Ishoko*), few attribute to *Haine* moralistic concerns or the power to detect and punish norm violations (Apicella, 2018). Thus, there are opportunities for the Hadza to show variation in moral behavior and for others to witness it, though observed deviations may not be punished.

Sample

The first author and research assistants visited 12 camps¹ during the dry-season in August-September 2016 using a snowball sampling procedure; after visiting one camp, members of that camp would direct us toward the nearest camp. We collected data until we could not identify any more camps. The number of adults in each camp ranged from three to twelve. We interviewed 94 judges who ranked 95 subjects (one participant left

¹ We collected data from a thirteenth camp that had 36 adults; judges found the task of ranking this many people arduous. We had judges in this camp rank the top twelve campmates on each trait instead. However, the analyses used here require people to be ranking the same set of participants, so we did not use these data. Data for this camp were never entered or analyzed.

camp after his photo was taken but before he was interviewed) for a total of $N = 824$ observations. Two judges ($n = 20$ observations) were removed because they refused to rank their campmates on honesty, stating that everyone in their camp is a liar. Another two observations were removed because of an error in recording the data. The final sample included 95 subjects ($n = 46$ men, mean age $M = 39.8$ years-old, $n = 68$ married) ranked by 92 judges for $n = 802$ observations.

Procedure

We asked judges to rank their campmates on generosity (“Who shares the most food?”), hard work or effort (“Who works the hardest to get food?”), honesty (“Who tells the fewest lies?”), and global moral character (“Who has the best heart?”). We asked about generosity, hard work, and honesty because in previous research when Hadza are asked to free list traits that make a good person these were some of the nominated traits (Purzycki et al., 2018). We used “good heart” as a global character judgment because this was the most common response in the free list task and the Hadza seem to equate good heart with being a good person. We also asked them to rank men on who is the best hunter (“Who is the best hunter?”), and which we include as a non-moral comparison. Finally, we asked them who they prefer as campmates, but do not include that data here.

To have judges rank their campmates, we took headshot photographs of all the consenting adults in a camp using a Fujifilm Instax Mini 90 Classic Instant Film Camera which printed 1.8×2.4 inch images. We then conducted private interviews in Swahili with each adult. A research assistant would shuffle the photographs and lay them in front of the judge. The assistant would then ask the judge, “Who shares the most food?” After the judge picked a photograph, the assistant would remove the photograph, shuffle the

remaining photographs, and repeat the question. This was repeated until all campmates were ranked on that trait. The entire process was then repeated for each trait. The Hadza have previously done this task multiple times to rank campmates on hunting ability (Apicella, 2014; K. M. Smith, Olkhov, Puts, & Apicella, 2017; Stibbard-Hawkes, Attenborough, & Marlowe, 2018).

Analysis

We used Bayesian regression models for inferential analyses. Bayesian analyses compute the probability the observed data are generated by a hypothesized parameter value, conditional on the model assumptions and prior probabilities (Kruschke & Liddell, 2018a; McElreath, 2016). This produces a distribution of probability values across a range of possible parameter values. This allows us to describe the estimated strength of the relationship and the uncertainty around the estimate, rather than focusing on point hypothesis testing (Kruschke & Liddell, 2018b). In our analyses we use weakly regularizing priors; these are conservative priors that are skeptical of large associations and that restrict the estimates to more plausible values (McElreath, 2016).

We analyzed the data in R (R, 2017) using the ‘rjags’ (Plummer, 2018) and ‘brms’ (Bürkner, 2017) packages. Both packages use Monte Carlo Markov Chains to draw samples from the posterior distributions, drawing more samples from regions with higher probabilities to estimate the posterior distribution; the packages use different algorithms to explore the distribution. We also used the ‘tidyverse’ (Wickham, 2017b), ‘tidybayes’ (Kay, 2018), ‘ggridges’ (Wilke, 2018), and ‘irr’ (Gamer, Lemon, & Fellows, 2012) packages.

Results

Do Hadza agree on who is moral?

We examined the extent to which Hadza agree on the ranking of each trait by computing a Kendall's W for each trait for each camp. Kendall's W is a coefficient of consensus for ranking data, and it has a range of zero to one, with zero indicating no agreement between raters and one indicating complete agreement (Zar, 1996). A suggested benchmark for Kendall's W is that 0.5 indicates moderate agreement and 0.3 indicates weak agreement. The observed values are presented in Figure 2.1. The median value for good heart was 0.19 and ranged from 0.04 to 0.31, the median value for effort was 0.25 and ranged from 0.07 to 0.60, the median value for generosity was 0.19 and ranged from 0.00 to 0.48, the median value for honesty was 0.19 and ranged from 0.10 to 0.44, and the median value for hunting ability was 0.40 and ranged from 0.16 to 0.63. The median values for effort, generosity, honesty, and good heart all fall below the suggested benchmark for weak agreement.

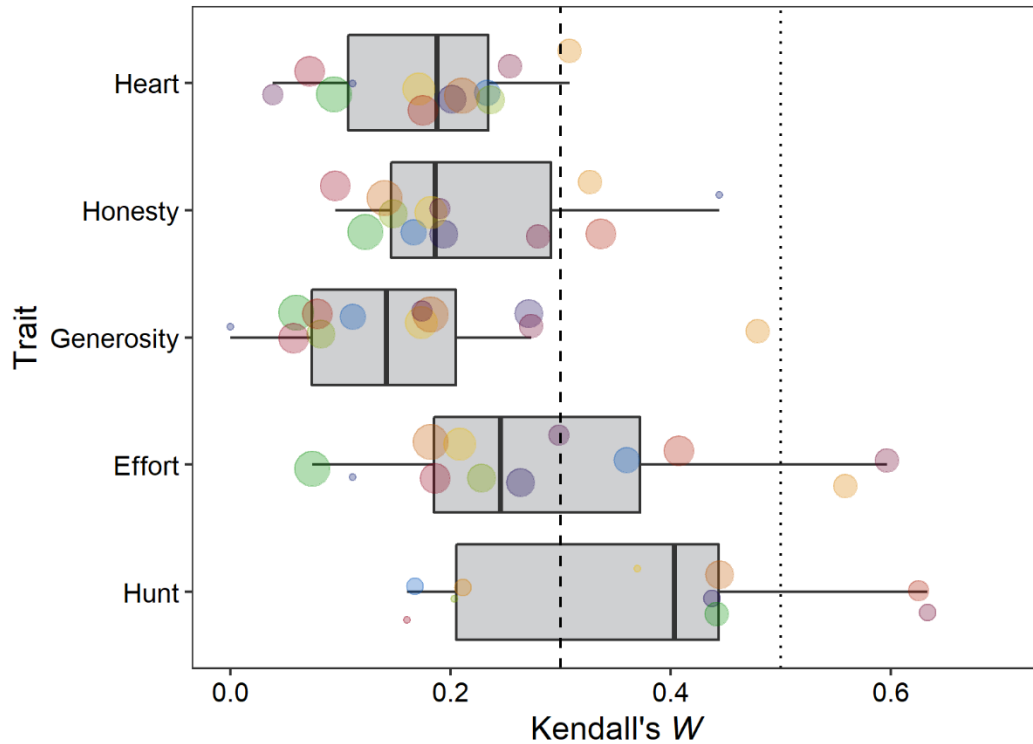


Figure 2.1. Kendall's W for each trait for each camp with boxplots. The points represent observed values, the size of the points represent the number of subjects ranked, and the color indicates camp. The light dashed line is at 0.5, which is suggested as moderate agreement, and the heavy dashed line is at 0.3, which is suggested as weak agreement. Two camps had only one man and were not included in the calculation for ranking on hunting ability.

For inferential analyses, we used a transformed value of Kendall's W . A transformed Kendall's W has a chi-square distribution such that $m(k - 1)W \sim X^2(k - 1, \lambda)$, where m is the number of judges, k is the number of items being ranked, and λ is the non-centrality parameter (Zar, 1996). This allows us to estimate a population-wide level of agreement within each camp; the estimated values were then be used to simulate statistics describing the level of agreement. We fit a linear regression model with a non-

central chi-square distribution likelihood estimating λ given the transformed W 's for each trait and camp and the number of subjects ranked. We included random intercepts for camps, and dummy-coded the traits relative to the good heart rankings. To fit the model, we used 'rjags' (Plummer, 2018) with four chains; the chains had 10,000 iterations burn-in and each chain sampled 5,000 iterations from the posterior distribution for a total of 20,000 samples.

Table 2.1. Estimated Non-centrality Parameter and Simulated Kendall's W for each Trait

Trait	λ	$W (m = 6)$	$W (m = 8)$	$W (m = 10)$
Heart	2.19 [0.94, 3.74]	0.24 [0.20, 0.29]	0.16 [0.14, 0.19]	0.12 [0.11, 0.14]
Honesty	1.70 [0.63, 4.12]	0.24 [0.19, 0.31]	0.16 [0.14, 0.20]	0.12 [0.11, 0.15]
Generosity	1.31 [0.41, 3.04]	0.21 [0.18, 0.27]	0.15 [0.13, 0.18]	0.12 [0.10, 0.13]
Effort	3.85 [1.62, 7.35]	0.30 [0.22, 0.41]	0.19 [0.15, 0.25]	0.14 [0.12, 0.18]
Hunt	5.07 [2.13, 8.83]	0.58 [0.36, 0.90]	0.33 [0.21, 0.48]	0.22 [0.15, 0.31]

Note. Values are modal values from the posterior with 90% HDI intervals in brackets. λ is the estimated non-centrality parameter. W values are simulated from the non-centrality parameter for a camp with m judges. For all traits but hunting, there are $k = m$ subjects; for hunting, $k = m/2$.

Table 2.1 presents the estimated non-centrality parameter for each trait. From these non-centrality parameters, we simulated Kendall's W 's for each trait; because W is dependent on the number of judges and people being ranked, we simulated W for a small ($m = 6$), medium ($m = 8$), and large ($m = 10$) camp. For all the good heart, generosity, and honesty, even in the small camp, the simulated values fell below the 0.30 value for weak agreement, whereas for effort the values in small camps were near this benchmark and

for hunting ability the values in the small camp were above the benchmark for moderate agreement (0.50). In larger camps, the estimated W for every trait falls below 0.30, except for hunting ability, which in medium camps still falls above that benchmark. We also directly compared the estimated non-centrality parameters between each trait (see Table 2.2) to compare agreement holding camp size constant; Hadza agreed more on rankings of hunting ability and effort than they did on rankings of good heart, generosity, and honesty.

Table 2.2. Comparisons of Estimated Non-centrality Parameters Between each Trait

	Heart	Honesty	Generosity	Effort	Hunt
Heart		0.52	0.80	0.05	0.01
Honesty	0.49		0.73	0.09	0.02
Generosity	0.20	0.27		0.02	0.00
Effort	0.95	0.92	0.98		0.25
Hunt	1.00	0.99	1.00	0.75	

Note. Values are proportions of posterior in which λ for the trait in the row is greater than the λ for the trait in the column.

We converted the simulated W values to r such that $r = \frac{mW-1}{m-1}$; r is the mean Spearman's ρ between each possible pair of judges (Zar, 1996), or the expected agreement between pairs of judges. In a medium sized ($m = 8$) camp, the modal simulated r value for good heart $r = 0.04$ [90% HDI: 0.02, 0.08], for honesty $r = 0.04$ [90% HDI: 0.02, 0.09], for generosity $r = 0.03$ [90% HDI: 0.01, 0.06], for effort $r = 0.08$ [90% HDI: 0.03, 0.15], and for hunting $r = 0.23$ [90% HDI: 0.10, 0.41]. Figure 2.2 presents the

distribution of simulated r values for each trait for each small, medium, and large camps. These values indicate that judges disagree on their rankings of campmates' character.

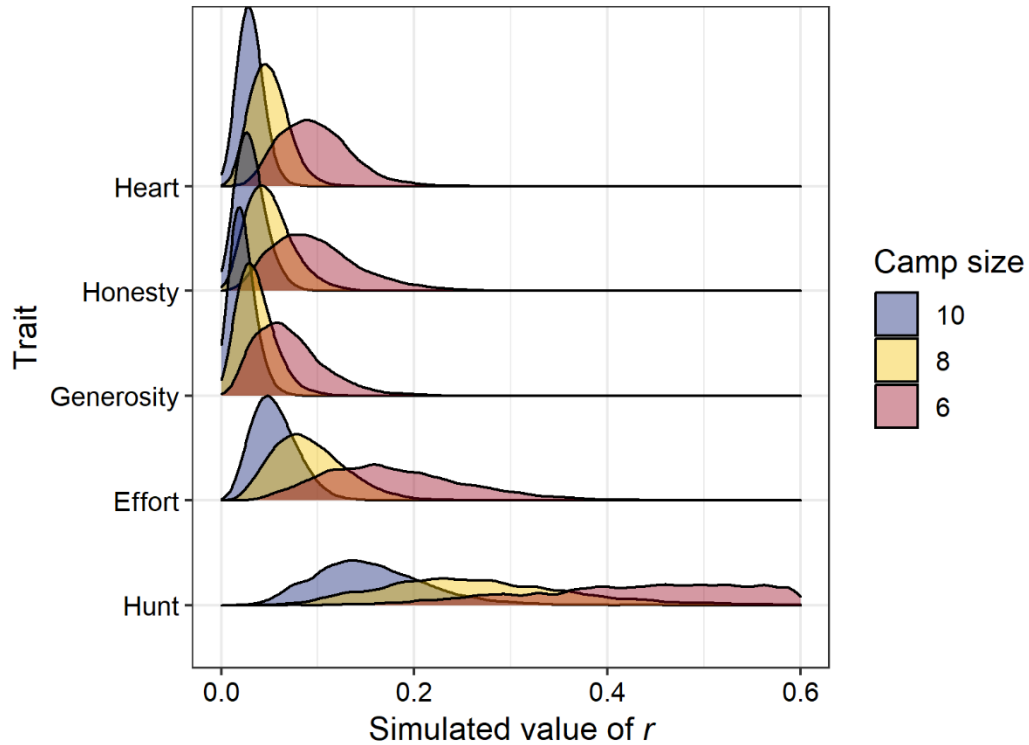


Figure 2.2. Simulated r values from the estimated non-centrality parameter for each trait. For heart, honesty, generosity, and effort, the number of judges and the number of subjects being ranked are equal to camp size; for hunting, the number of subjects being ranked is half the camp size.

Do Hadza agree on what makes someone moral?

To examine which traits Hadza consider important to moral character, we fit an ordered logistic model regressing rankings of good heart on rankings of effort, generosity, and honesty, as well as the subject's sex, age (z -scored), marital status, and the relationship between judge and subject (i.e., self, spouse, kin, or none). Character rankings were centered within each camp such that rank changes are relative to the camp

median. We include random intercepts for camp and subject, random slopes for camp and judge for every effect, and random slopes for subject for the effects of character rankings and the relationship between judge and subject. We fit the model using ‘brms’ (Bürkner, 2017), which implements Stan (Carpenter et al., 2017) to estimate the posterior. We used one chain with 20,000 iterations, the first 10,000 iterations were warm-up, with a step parameter of $\delta = 0.95$.

Population-level effects

We first examined the population-level effects. Table 2.3 presents the coefficients for all variables in the model. There was strong evidence that higher rankings on effort and generosity were related to higher rankings on good heart, while there was suggestive evidence that higher rankings on honesty were related to higher rankings on good heart. There was some evidence that older Hadza had higher rankings on good heart, otherwise demographic variables did not relate to rankings on good heart. We simulated rankings of good heart as a function of rankings on effort, generosity, and honesty in the largest camp ($n = 12$) and computed the expected difference in good heart ranking between the highest and lowest ranked person on each trait. The modal difference for effort was 3.2 (90% HDI: 1.9, 4.4) ranks, for generosity 1.7 (90% HDI: 0.2, 3.0) ranks, and for honesty 0.9 (90% HDI: -0.3, 2.6) ranks. Figure 2.3 presents the full range of simulated rankings.

Table 2.3. Model Regressing Good Heart Ranking on Character Rankings and Subject Demographics

Coefficient	<i>b</i>	90% HDI	% > 0
Effort	0.24	0.13 – 0.35	100
Generosity	0.13	0.02 – 0.24	97.2
Honesty	0.08	-0.04 – 0.20	88.1
Female	0.21	-1.37 – 1.62	54.3
Married	0.29	-0.31 – 0.73	76.5
Age	0.22	-0.13 – 0.54	85.4
Spouse	0.32	-0.38 – 1.22	79.1
Kin	0.34	-0.39 – 1.02	78.4
Self	0.00	-0.87 – 1.06	56.1

Note. The coefficient estimate is the mode of the posterior distribution. The 90% highest posterior density interval (HDI) is the narrowest interval containing 90% of the posterior, or the 90% most plausible coefficient estimates. The last column is the percent of the posterior greater than zero.

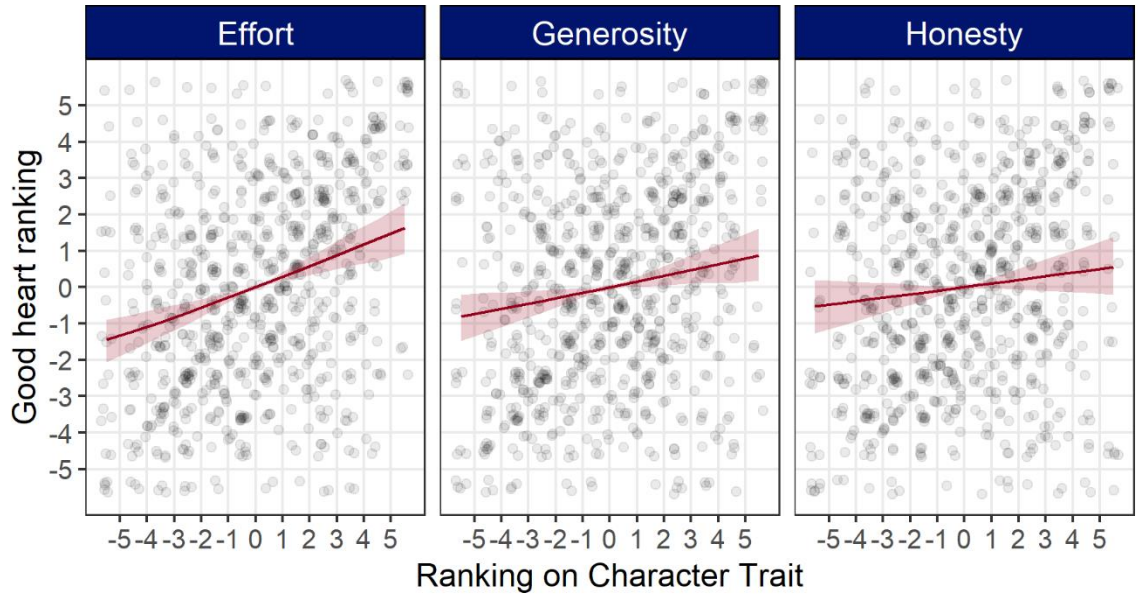


Figure 2.3. Ranking on good heart by ranking on each character trait, centered within camp. Predictions were simulated by generating 10,000 values from an ordered logistic distribution for each ranking and the mean of these generated values were predicted ranking. The line is the modal simulated value and the shaded region is the 90% credible interval.

Judge-level effects

To determine whether judges agreed on how much the specific traits contributed to an individual's global character, we examined variation between judges on the relationship between character rankings and good heart rankings. First, we fit a series of eight models including varying slopes for judges for none, one, two, or all of the character traits; the eight models were otherwise identical. This allowed us to examine whether including extra parameters to estimate varying slopes for judges was worth the improved fit. Table 2.4 presents fit statistics for these models, including the Akaike weight. The Akaike weight is the probability that a model would best predict a new

sample of data compared to all the other models under consideration (McElreath, 2016). The Akaike weight is distributed across most of the models. Models including random slopes for effort had 0.35 of the weight, models including random slopes for generosity had 0.54 of the weight, and random slopes for models including honesty had 0.95 of the weight; this indicates that the model most likely to best estimate the data is likely to include disagreement between judges on the contribution of honesty to good heart, and is less likely to include disagreement on the contribution of effort and generosity to good heart. there is good evidence for disagreement between judges on the contribution of honesty to good heart, and less evidence for disagreement on generosity and effort. Rather than selecting one model as the best fitting, we constructed a weighted-average posterior using the Akaike weights (McElreath, 2016) and examined the variation between judges using that posterior.

Table 2.4. Fit of Models Regressing Good Hearts Rankings on Character Rankings

Model	WAIC	SE_{WAIC}	p_{WAIC}	Akaike weight
Baseline	1760.77	29.80	100.90	0.02
Effort	1761.11	29.61	107.82	0.01
Generosity	1761.14	29.58	113.17	0.01
Honesty	1754.80	31.13	123.21	0.30
Effort + Generosity	1761.29	29.50	118.45	0.01
Effort + Honesty	1756.49	30.99	128.09	0.13
Generosity + Honesty	1754.68	30.99	139.14	0.32
Full	1755.60	31.03	142.67	0.20

Note. Model names refer to what character traits in the model had random slopes for judges. WAIC is the widely-applicable information criterion estimate; a lower number indicates a better fitting model. SE_{WAIC} is the standard error of the WAIC estimate, p_{WAIC} is the effective number of parameters in the model, and the Akaike weight is computed from WAIC and is the probability that the model will best predict a new set of data among the considered models.

In the weighted-average posterior, the modal σ_{Judge} of varying slopes for effort was 0.00 (90% HDI: 0, 0.13), for generosity 0.00 (90% HDI: 0.00, 0.26), and for honesty 0.24 (90% HDI: 0.09, 0.38). We also compared the σ_{Judge} to the population coefficient; the percent of the posterior for which the σ_{Judge} was greater than the population coefficient for effort was 2.0%, for generosity 40.2%, and for honesty 88.8%; there was good evidence that knowing a particular judge’s belief of the role of honesty in character provided more information than knowing the population’s belief, but this was not the case for effort and generosity. Finally, as another way to examine consensus, we computed the expected proportion of judges to have a negative slope between rankings

on each trait and rankings on good heart. The modal expected proportion of negative slopes for effort was 0.00 (90% HDI: 0.00, 0.04), for generosity 0.00 (90% HDI: 0.00, 0.38), and for honesty 0.38 (90% HDI: 0.00, 0.51). Again, for honesty, even though at the population level more honest Hadza were ranked higher on good heart, a number of judges ranked more honest Hadza *lower* on good heart. Figure 2.4 presents at the mean of the posterior the simulated variation between judges across rankings.

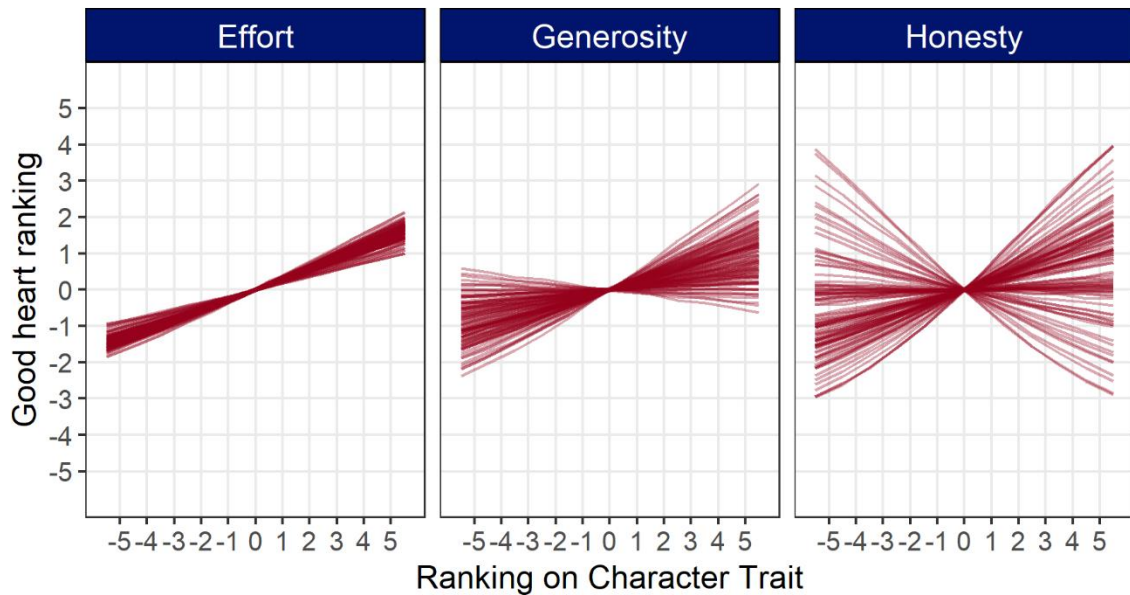


Figure 2.4. Ranking on good heart by ranking on each character trait, centered within camp. Predictions were simulated by generating 10,000 values from an ordered logistic distribution for each ranking and the mean of these generated values were predicted ranking. Each line is a simulated judge’s slope taken from the mean of weighted-average posterior.

Discussion

In WEIRD societies, people evaluate the moral character of others and use those perceptions to decide with whom to interact. Underscoring the importance of character in

these populations, independent observers agree on how moral others are (Helzer et al., 2014). But is this universal? To answer this, we asked if Hadza hunter-gatherers agree on who is moral and what traits make someone moral. The Hadza disagree on which of their campmates have a good heart, are generous, and are honest, and agree more on which campmates are hard working (effort) and produce the most food (hunting ability). At the level of the population, hard work, generosity, and honesty contribute to global character; however, there is variation between Hadza judges on how much honesty contributes to global character, though judges agree more on how much hard work and generosity contribute to character. Overall, these results suggest that Hadza use some of the same criteria—hard work and generosity—for evaluating moral character, but disagree on who displays those traits, leading to disagreement on global character perceptions.

Agreement between independent observers on ratings about a trait is taken as evidence for that trait existing because raters are likely observing the same behaviors despite being in different situations (Kenrick & Funder, 1988). The disagreement between Hadza judges on character traits suggests that Hadza may have little stable variation in moral dispositions.² However, disagreement does not definitively rule out the existence of moral character. For example, the Hadza may have been unwilling to make assessments about their campmates' character, though notably we do see agreement on hunting ability, which is highly valued in the Hadza. Or there could be disagreement because there are not many opportunities to display moral behavior; however, it should be easy to observe moral behavior because they live together in small groups and depend

² To be clear, the claim is *not* that the Hadza are not moral or that morality is not important to them. Rather, the claim is that individuals' moral behavior varies across time, changing to adapt to local circumstances.

on each other for survival. Finally, another alternative is that Hadza display consistent moral behavior to specific people; that is, a person could always be generous to one campmate and selfish to another campmate, leading to disagreement between campmates in evaluations of moral character. Future research exploring the stability of judge-subject rankings across time could address this alternative interpretation.

One alternative interpretation of the data is that the Hadza can agree on moral character, and in fact they do have moral dispositions, but that our measure is unreliable and cannot detect agreement. A good measure measuring a phenomenon that does not exist and a bad measure measuring a phenomenon that does exist will produce the same result: noise. However, we argue there are two reasons to suspect that our measure would be reliable enough to detect agreement on moral character if it existed. First, we were able to detect moderate relationships between the specific character traits and moral character, indicating reliability was not so low as to be unable to detect any effects. Second, we did find moderate agreement on hard work and hunting ability. And in fact, given what we know about the noisy relationship between hunting returns and hunting reputation (Stibbard-Hawkes et al., 2018), the fact that we were able to detect agreement suggests low reliability can not fully explain the disagreement in perceptions of moral character.

It may seem that hunting ability would be easily observable, but in the anthropological literature, this is notoriously difficult to measure, and because of this hunting reputation is criticized as a measure of hunting success (Hill & Kintigh, 2009). First, hunting ability is rarely directly observed, as most hunting happens alone. And second, there is high variance in hunting returns, in which men return to camp with

nothing on most days, but occasionally (about 3% of days) bring in large game (Hawkes, O'Connell, & Blurton-Jones, 1991). In fact, for anthropologists to reliably estimate hunting ability using hunting returns, they need 200 to 600 days of observations (Hill & Kintigh, 2009). Despite this, in our study and others (Stibbard-Hawkes et al., 2018), the Hadza are able to agree on who the best hunters are, and hunting reputation does relate to proxies of actual hunting ability, such as strength, accuracy, and ecological knowledge (Apicella, 2014; Stibbard-Hawkes et al., 2018). This suggests that if there are moral dispositions among the Hadza, the signal is much weaker than that of hunting ability, which is itself a noisy signal (Stibbard-Hawkes, 2019). If it is this hard to detect moral dispositions, it then raises the question of whether the Hadza can reliably determine character enough to provide useful social information.

Data measuring morally-relevant behavior, such as generosity, further suggest a stable variation in lack of moral dispositions in the Hadza and other non-WEIRD populations. In a longitudinal study, a Hadza's previous generosity in an economic game did not predict their subsequent contributions, and instead the only significant predictor was how much his or her campmates contribute (K. M. Smith et al., 2018). And in a small study ($n = 12$) of the Tsimané of Bolivia, generosity in a dictator game in one year did not predict generosity in a later year (Gurven, 2014).

These results further support recent research finding that character and moral reputation do not play a role in Hadza campmate preferences. When asked who they prefer to live with, Hadza do not choose the most generous people, whether generosity is measured using an economic game (Apicella et al., 2012) or via reputation (K. M. Smith & Apicella, 2019). Rather, Hadza prefer to live with better hunters (K. M. Smith &

Apicella, 2019; Wood, 2006). If moral behavior changes across time and situations as our results here suggest, then choosing campmates based on their current behavior is useless. Instead, traits related to productivity, such as being a hard worker or a good hunter, may become more important in campmate preferences (Barclay, 2016b); if everyone is expected to share because of strong norms, such as in the Hadza, then choosing productive campmates is more important. And in fact, a preference for productive partners may influence friendships in Western societies. US undergraduates and online workers prefer partners in economic games and are more generous to partners who are perceived to be more productive, even though it is irrelevant to the game (Eisenbruch, Grillot, Maestriperi, & Roney, 2016; Eisenbruch & Roney, 2017). The effect of a productivity preference in various relationships may be a fruitful area for future research.

Throughout the latter half of the 20th century, the situationist paradigm in social psychology casted doubt on the existence of moral character. However, more recent research in moral psychology has argued that moral character does in fact exist (Fleeson, Furr, Jayawickreme, Meindl, & Helzer, 2014). In Western societies, people agree on who is moral (Helzer et al., 2014), and perceptions of moral character play an important role in social cognition (Goodwin, 2015; Landy & Uhlmann, 2018). Our results here question the universality of moral character and its centrality in social life, and highlights the importance of cross-cultural research using underrepresented samples. By conducting research with populations in a variety of socio-ecologies, we can better understand the variation in our moral psychology.

CHAPTER 3: PARTNER CHOICE IN HUMAN EVOLUTION: THE ROLE OF CHARACTER, HUNTING ABILITY, AND RECIPROCITY IN HADZA CAMPMATE SELECTION

The ability to choose the partners we interact with is thought to have been an important driver in the evolution of human social behavior, and in particular, for our propensity to cooperate. But evidence for this claim comes largely from Western populations. Here, we investigate qualities associated with being a preferred partner (i.e. campmate) in Hadza hunter-gatherers of northern Tanzania. Ninety-two Hadza participants from 12 camps ranked their current campmates on character traits (i.e. hard work, generosity, and honesty), hunting ability in men, and their preference for them as future campmates. We found positive but weak associations between rankings on character traits and being a preferred campmate. However, there was suggestive evidence that being perceived as a better hunter was a more important criterion than any character traits for being a preferred campmate in men. And we found little evidence to suggest that partner preferences were reciprocated among campmates. Finally, we found little evidence to suggest that being a preferred campmate is associated with greater reproductive success, which suggests there is little benefit to being a valued partner. Together, these findings suggest that social selection for character traits was not a powerful driving force in the evolution of human cooperation.

Introduction

Living in groups can offer many benefits to animals. Group living offers protection from predators, access to mates, opportunities for collaborative foraging, and the potential exchange of resources, among other benefits. However, social living

introduces competition to gain access to partners that provide the most benefits. If the most valuable partners can choose who to share their benefits with, and they in turn want the most valuable partners they can access, then partners that offer the most benefits are a valuable resource to compete over. This is commonly observed in the context of mate choice, where the most prized males and females will pair (Buston & Emlen, 2003), often resulting in the sexual selection of traits that provide an advantage over same-sex competitors. However, sexual selection is a form of *social selection* (Lyon & Montgomerie, 2012; West-Eberhard, 1983), and social animals can compete for access to valuable partners in a number of domains, leading to the evolution of costly morphological and behavioral traits.

Social selection may have been especially important in human evolution, and in particular, the evolution of cooperation (Barclay, 2016a; Baumard et al., 2013; Tooby & Cosmides, 1996). While mutual cooperation can benefit both partners, cooperation risks costly exploitation. However, if people have the option to leave exploitative social partners for more cooperative ones, then cooperation can be a stable strategy (Aktipis, 2011; Rand, Arbesman, & Christakis, 2011). Because valuable cooperative partners have the option to leave and pick other valued partners, people must compete for access to the most cooperative people. And the best way to compete for a valuable partner is to also be a valuable partner.

Valuable social partners are those that can provide the most benefits to their partners. The benefit potential partners provide is the function of two values: their willingness and their ability to confer benefits (Barclay, 2013, 2016a). A skilled but stingy partner is able to generate benefits but does not share them, and a generous but

incompetent partner may share but fail to generate any benefits to be shared. As such, people are expected to independently track reputations in each domain. And in fact, Dominican laborers who depend on their neighbors for assistance in producing bay oil, do track willingness and ability separately (Macfarlan & Lyle, 2015). The value placed on generosity or competence also depends on the variation in available partners along these dimensions (Barclay, 2016b). For example, if potential partners are all similarly generous, then competence becomes more valued than generosity. Thus, willingness and ability to confer benefits, that is, character or competence, are expected to be important traits in partner selection.

There is considerable evidence across populations that people prefer to interact with people who are generous and cooperative. In the US, when considering the ideal partner for a variety of relationships, people identify cooperative traits, such as trustworthiness and fairness, as being important (Cottrell et al., 2007; Goodwin et al., 2014; Landy et al., 2016). When being observed, people will compete to be chosen as partners by being more cooperative, and cooperative people are in fact chosen more often as social partners (Barclay & Willer, 2007; Sylwester & Roberts, 2010). Among Dominican horticulturalists and Quechuan agropastoralists, people who have cooperative reputations have more social ties (Lyle & Smith, 2014; Macfarlan, Quinlan, & Remiker, 2013; Macfarlan, Remiker, & Quinlan, 2012). And when the Martu foragers of Australia select hunting partners, they prefer to hunt with people who share more food, regardless of their actual hunting ability (Bliege Bird & Power, 2015; Bliege Bird, Scelza, Bird, & Smith, 2012). Across a number of societies, people preferentially interact with and help people perceived to have high character.

Less attention has been paid to the role of ability and productivity in preference for social partners, though some evidence exists that people prefer productive partners. For example, US participants prefer to continue relationships with productive partners, especially when productivity is indicative of future ability to generate benefits (Eisenbruch & Roney, 2017). Even partners who are simply perceived to be more productive are preferred more as social partners (Eisenbruch et al., 2016). However, when choosing between generous or productive partners, people prioritize generosity partners (Eisenbruch & Roney, 2017; Raihani & Barclay, 2016). And in several non-Western societies, productive people receive a number of social benefits. For example, among Aché forager-horticulturalists, productive hunters receive more food transfers when sick than less productive hunters (Gurven, Allen-Arave, Hill, & Hurtado, 2000). In Dominican and Peruvian villages, people with reputations for being productive have more cooperative relationships (Macfarlan & Lyle, 2015). And in Hadza hunter-gatherers, both men and women prefer good gatherers and hunters, respectively, as mates (Marlowe, 2004b). These results suggest that selection for productivity may have also been important in the evolution of human partner choice.

The competition to gain access to valuable partners in some partner choice models can create a biological market, where there is agreement on who is most valued and the most valued partners can demand other valued partners (Noë & Hammerstein, 1994). One important assumption is that there are benefits to being a desired partner. This affords more social opportunities, which could lead to greater access to resources, including food, coalitionary support in conflicts, and assistance when ill or injured, all of which could ultimately result in greater reproductive success. For example, being a good hunter

can lead directly to greater reproductive success by attaining more food, but being a good hunter can also indirectly lead to greater reproductive success because of better social partners that provide other benefits. For example, in the Agta and BaYaka foragers (Chaudhary et al., 2016; Page et al., 2017), people with more social ties receive more help, more food transfers, and have greater reproductive success.

Alternatively, rather than competing to be valued by everyone, people may compete to be valued by a few select partners; specifically, those partners who value them above others. That is, people can form friendships (Hruschka, 2010; Tooby & Cosmides, 1996). Whereas the biological market strategy is to be popular and valued by many, the friendship strategy is to be selective and discriminating with whom one interacts. Here, you would expect partners to reciprocate friendships. Consistent with this, among US college and online samples, people reciprocate friendship rankings among their best friends (DeScioli & Kurzban, 2009; DeScioli, Kurzban, Koch, & Liben-Nowell, 2011). In the context of cooperation, cooperation can evolve when people seek out partners who cooperate specifically with them, even if they are uncooperative in general (Hruschka & Henrich, 2006). Thus, rather than preferring the most cooperative partners, friendship models predict that people should prefer partners who are specifically generous to them. In US samples, people more harshly judge a friend who is not generous to them but is generous to someone else compared to a friend who is not generous to anyone, including them (Barakzai & Shaw, 2018). And among Agta hunter-gatherers, people are more likely to share with people who share with them specifically rather than the most generous person (Daniel Smith et al., 2018). These studies suggest that

friendship pays off because it gives access to partners that value and invest in you specifically, rather than providing benefits promiscuously.

The reviewed literature suggests that social selection and our ability to choose who to interact may have played an important role in the evolution of human cooperation. To compete for access to valuable cooperative partners, people must themselves be valuable partners. Partners can be valuable because they are willing to share benefits, are able to generate benefits, or because they reciprocate benefits to their partners specifically. Previous research provides evidence for partner choice for each of these ways. However, this research has been largely conducted in Western populations (Henrich et al., 2010) and in contexts not ecologically relevant for the evolution of human cooperation. Moreover, past studies do not consider all three types of value within a single study.

In the current study, we examine the role of character, productivity, and reciprocity in partner choice among Hadza hunter-gatherers, whose way of life more closely approximates life before the advent of agriculture (Apicella & Barrett, 2016; Marlowe, 2005). In previous research using a behavioral measure of cooperation (i.e., one-shot public good game), cooperation did not seem to be an important criterion for choosing potential campmates among the Hadza. Hadza who contributed more in the public good game were not more likely to be nominated as potential campmates (Apicella et al., 2012). Moreover, Hadza who contributed more to the public good in a previous year did not live with more cooperative campmates in a future year (K. M. Smith et al., 2018). And there also does not seem to be a benefit to being a valued campmate; Hadza who were more often nominated as potential campmates did not have greater reproductive

success (Apicella et al., 2012). This set of findings are inconsistent with predictions from models of partner choice based on cooperation within a biological market. Instead, research suggests that Hadza prefer people with whom they have a ritual relationship (Hill et al., 2014). And preferences for future campmates are reciprocated within same-sex networks (Apicella et al., 2012). These latter findings lend some preliminary support to friendship models of cooperation (Hruschka, 2010; Tooby & Cosmides, 1996).

There are a number of possibilities why previous research on Hadza campmate preferences failed to find a preference for cooperators. A possibility is that the economic game used does not reliably capture *reputation* as a cooperator. One reason could be because the game measures one narrow domain of cooperation among many in Hadza life, such as food sharing, childcare, and protection (Apicella & Crittenden, 2016). Another reason is that nominations included cross-camp networks and Hadza may not have up-to-date information about potential campmates' cooperativeness, possibly because behavior changes faster than reputation spreads (Macfarlan et al., 2013). To address this concern, here we use informant rankings to measure perceptions of their campmates' character, hunting ability (in men), and their preference for them as future campmates. We use these data to answer the following questions:

1. Do Hadza prefer campmates who they rank higher on character traits?
2. Do Hadza prefer male campmates who they rank higher on character traits or hunting reputation?
3. Are Hadza campmate preferences reciprocated?
4. Is being a preferred campmate or reciprocating relationships associated with greater reproductive success?

Method

Population

The Hadza are a group of nomadic hunter-gatherers living along the Central Rift Valley in northern Tanzania. There are approximately 1000 people who identify as Hadza, but only about 200 to 300 Hadza still obtain most of their calories via foraged foods and maintain a hunter-gatherer lifestyle (Marlowe, 2010). The Hadza have high rates of morbidity and mortality, and approximately 40% of children born will die before reaching the age of five (Blurton-Jones, 2016). Fresh water is scarce and hunger is a concern. Over 80% of Hadza report being concerned with having enough food to eat (Apicella, 2018). Hadza life is built on high levels of cooperation – food, protection, and childcare is shared (Crittenden & Marlowe, 2008).

Hadza life is marked by a sexual division of labor where men spend time hunting and collecting honey and women spend time gathering food resources such as berries and tubers. Food, and in particular meat and items requiring extended processing (e.g., tubers), is widely shared among camp members (Marlowe, 2010), though producers may be able to direct some of the food to their kin (Wood & Marlowe, 2013). The Hadza have no formal status hierarchies, and Hadza are largely autonomous and able to make their own decisions.

The Hadza live in temporary camps of about 30 adults and children, typically consisting of a few unrelated nuclear families. Like most other hunter-gatherers, average relatedness within camps is low and Hadza live with only a few primary kin and have a multilocal resident pattern (Hill et al., 2011). Living arrangements are fluid. Entire camps shift locations every four to eight weeks in response to local resource availability.

Membership within camps also change regularly, with individuals or families freely relocating to other camps (Hill et al., 2014). In a longitudinal census across years, people on average were only living with about one in five of their campmates from previous years (K. M. Smith et al., 2018). This fluid social structure means the Hadza are regularly choosing new campmates to live with and can freely leave campmates they no longer want to live with.

The Hadza do not have formal sanctioning mechanisms for norm violations. Historically, the Hadza have had little to no interaction with authoritarian government institutions such as a police force, court system, or prisons. Though the Hadza do have beliefs in gods, they generally do not ascribe to them moralistic concerns or the ability to detect and punish transgressions (Apicella, 2018; Purzycki et al., 2016), though there is evidence this is changing. And in economic games, the Hadza have low rates of second- and third-party punishment (Henrich, 2006). These conditions—relying on campmates to cooperate, frequent movement and changing of campmates, and little threat of punishment—make the Hadza an ideal population to study the role of cooperative reputation in partner choice.

Sample

We visited 12 camps during the dry-season in August-September 2016 using a snowball sampling procedure; after visiting one camp, members of that camp would direct us toward the nearest camp. We collected data until we could not identify any more camps. The number of adults in each camp ranged from three to twelve. We had 95 subjects ranked by their campmates for $N = 730$ observations. However, we removed two subjects with missing demographic information, and we removed two judges because

they refused to rank their campmates on honesty, insisting everyone lies. Another judge refused to rank more than two campmates on preferred future campmates. Our final sample had 93 subjects ($n = 44$ men; estimated age $M = 39.9$, $SD = 14.5$ years-old; $n = 67$ married), ranked by 92 judges, for $n = 683$ observations. In analyses examining relationships with rankings of hunting ability, only men were ranked (see below). For those analyses, our sample had 42 male subjects (two men were the sole man in their respective camps and could not be ranked) being ranked by 84 subjects for $n = 324$ observations.

Procedures

Upon entering a camp, we took photographs of each participating adult using a Fujifilm Instax Mini 90 Classic Instant Film Camera which printed 1.8×2.4 inch images. Photographs were headshots taken approximately 2 meters away against a grey photo screen. In separate interviews, a research assistant would shuffle the photographs of a judge's campmates and randomly array the photographs in front of the judge. The interviewer then asked, "Who is the most generous?" After the judge chose a person in the array, the interviewer removed the person who was selected, picked up all the photographs, shuffled them, and arrayed them out again in front of the judge before repeating the question. This was repeated until all campmates were ranked. Judges also ranked themselves among their campmates on all dimensions except preferred campmate; however, because our research questions are about preferred campmates, we removed self-rankings and entered rankings as if the judges did not rank themselves. All interviews were conducted in Swahili by a Tanzanian research assistant and overseen by the first author. The Hadza have previous experience on this task and ranking their

campmates on hunting ability (Apicella, 2014; K. M. Smith et al., 2017; Stibbard-Hawkes et al., 2018).

We asked participants to rank campmates on five traits. These were generosity (“Who is the most generous?”), effort (“Who works the hardest to get food?”), honesty, (“Who is the most honest?”), hunting ability, (“Who is the best hunter?”), and who they prefer to live with (“Who would you most like to live with if you were to move camp tomorrow?”). We asked every participant these questions in the same order. We chose to ask about generosity, effort, and honesty because previous interviews suggest these to be important character traits to the Hadza (Purzycki et al., 2018). For hunting ability, we asked men and women to rank only men on this trait. After participants ranked campmates on who they would like to live with we asked the participants to explain their relationship with each campmate. We classified a pair as kin only if both participants named each other as primary genetic kin (siblings or parent-child).

We collected data on demographic information in separate interviews. We asked participants whether they were married and estimated their age based on appearance. We asked each participant to list the names of all children born to them and then list the names of those who had died. These data were used to calculate reproductive histories.

Data analysis and software

We analyzed the data using multilevel Bayesian regression models. Bayesian analyses produce posterior distributions for parameters describing the likelihood that a particular value of the parameter would generate the observed data, conditional on the prior probability and assumptions within the model (Kruschke & Liddell, 2018a; McElreath, 2016). Our goal in the study was to estimate the relationship between

rankings on the various traits and describe the uncertainty around those estimates; Bayesian analyses provide a framework for quantifying these values in the posterior distributions (Kruschke & Liddell, 2018b). As such, we emphasize describing the posterior distributions rather than explicit hypothesis testing. We use multilevel models to better pool information across clusters, such as camps, subjects, and judges, and to address imbalances in sample sizes across clusters (McElreath, 2016). We used weakly regularizing priors; these are priors that are centered at zero and function to avoid overfitting to the data and improve computation (McElreath, 2016).

We conducted the analyses in R (R, 2017) using the ‘brms’ (Bürkner, 2017), and ‘tidyverse’ (Wickham, 2017b) packages. The ‘brms’ package uses the programming language Stan (Carpenter et al., 2017) to implement Monte Carlo Markov Chains to sample estimates from the posterior distribution. For Stan parameters, all models used one chain of 20,000 iterations, and 10,000 of those iterations were warmup, with a step parameter of $\delta = 0.90$.

Results

Before inferential analyses, we first examined zero-order correlations between the rankings on character traits and preferred campmate. We computed correlations between each variable at the individual observation level, ignoring clustering within camps, subjects, and judges. All rankings were centered within camp. Table 3.1 presents the correlations. All variables were moderately correlated with each other at about the same range of values.

Table 3.1. Zero-Order Correlations Between Character and Preferred Campmate

Rankings

	Effort	Generosity	Honesty	Hunting	Preferred campmate
Effort	1	0.27	0.20	0.29	0.25
Generosity		1	0.27	0.17	0.23
Honesty			1	0.22	0.23
Hunting				1	0.29
Preferred campmate					1

Note. Values are Pearson's *rs*. Hunting reputation only includes men being ranked.

What character traits do Hadza prefer in campmates?

We estimate the extent to which a judge's perceptions of a campmate's relative effort, generosity, and honesty relate to the judge's preference for that person as a future campmate. To do this, we regressed ranking of preferred campmate on the rankings of the other traits using ordered logistic regressions. An ordered logistic regression assumes there is an unobserved parameter and a set of unobserved thresholds for each category or rank; as the parameter surpasses each threshold, the observed rank increases, such that the probability of having a higher rank increases as the parameter increases (McElreath, 2016). The analysis assumes the parameter is a linear function of the variables in the model.

Rankings on the character traits were centered within each camp so that a one-rank change in any camp is relative to its median. Analyses included varying intercept

and slopes for all effects at the camp level, varying intercept and varying slopes for the character rankings at the subject level, and varying slopes for subject's demographics and character rankings at the judge level. The priors for intercepts were normal distributions with $\mu = 0$, $\sigma = 2$, the priors for coefficients were normal distributions with $\mu = 0$, $\sigma = 0.5$, the priors for the standard deviations in varying effects were half-Cauchy distributions with $\mu = 0$, $\sigma = 0.5$, and the priors for correlations between varying effects were LKJ correlation distributions with $\eta = 4$.

We fit eight models predicting preferred campmate ranking from character reputation and demographics. The first model regressed preferred campmate ranking on subject demographics only; demographics were sex, age as a z -score, marital status, and whether the judge and participant were primary kin or spouse. The other models regressed preferred campmate ranking on one, two, or all of the character traits and demographics. Among the eight models, the full model with effort, generosity, honesty, and demographics was the best fitting model based on the widely-applicable information criterion (WAIC; see Table 3.2 for model comparisons). Using the WAIC, we calculated an Akaike weight for each model. The Akaike weight is the estimated probability that a model would best predict a new sample of data within the given set of models (McElreath, 2016). The full model had the entire Akaike weight and we consider only that model further.

Table 3.2. Fit of Models Regressing Preferred Campmate Rankings on Character Rankings and Subject Demographics

Model	WAIC	SE_{WAIC}	p_{WAIC}	Akaike weight
Demographics	2999.98	27.96	94.01	0.00
Effort	2964.81	32.10	129.57	0.00
Generosity	2984.81	29.77	119.74	0.00
Honesty	2972.37	29.97	126.95	0.00
Effort + Generosity	2939.85	34.12	168.02	0.00
Effort + Honesty	2937.57	33.32	170.30	0.00
Generosity + Honesty	2956.29	30.66	166.37	0.00
Full	2889.27	34.56	223.01	1.00

Note. WAIC is the widely-applicable information criterion estimate; a lower number indicates a better fitting model. SE_{WAIC} is the standard error of the WAIC estimate, p_{WAIC} is the effective number of parameters in the model, and the Akaike weight is computed from WAIC and is the probability that the model will best predict a new set of data among the considered models.

Table 3.3 presents the estimates for the coefficients in the full model. There was good evidence that judges preferred older Hadza and their kin as campmates. There was also good evidence that judges preferred to live with Hadza they consider harder working, more generous, and more honest, and the strength of these relationships were approximately similar for all three character traits. To better understand the strength of these relationships, we simulated rankings on preferred campmate in the largest camp (11 ranks) and computed the difference in preferred campmate ranking between being highest and lowest ranked on each character trait. The modal expected rank difference for effort

was 1.1 ranks (90% HPDI: 0.0, 2.5), for generosity was 1.2 ranks (90% HPDI: 0.1, 2.3), and for honesty was 1.6 ranks (90% HPDI: 0.5, 2.6). Figure 3.1 presents the rankings centered within camp as well as the regression line from the simulated predictions. We also simulated the probability that someone ranked highest on each character trait would be ranked at least one rank higher on preferred campmate than someone ranked lowest on that character trait. The modal probability for effort was 58.8% (90% HPDI: 43.3%, 78.8%), for generosity was 60.2% (90% HPDI: 43.9%, 76.3%), and for honesty was 68.0% (90% HPDI: 50.5%, 80.6%).

Table 3.3. Full Model Regressing Preferred Campmate Ranking on Character Rankings and Subject Demographics

Coefficient	<i>b</i>	90% HPDI	% $</> 0$
Effort	0.11	0.00 – 0.24	95.7
Generosity	0.11	0.01 – 0.22	95.4
Honesty	0.15	0.04 – 0.26	99.1
Female	-0.04	-0.52 – 0.36	60.2
Married	0.21	-0.21 – 0.60	79.1
Age	0.41	0.13 – 0.66	98.7
Spouse	0.10	-0.39 – 0.61	65.7
Kin	0.35	-0.10 – 0.80	90.3

Note. The coefficient estimate is the mode of the posterior distribution. The 90% highest posterior density interval (HPDI) is the narrowest interval containing 90% of the posterior, or the 90% most plausible coefficient estimates. The last column is the percent of the posterior greater than (or less than in the case of Female) zero.

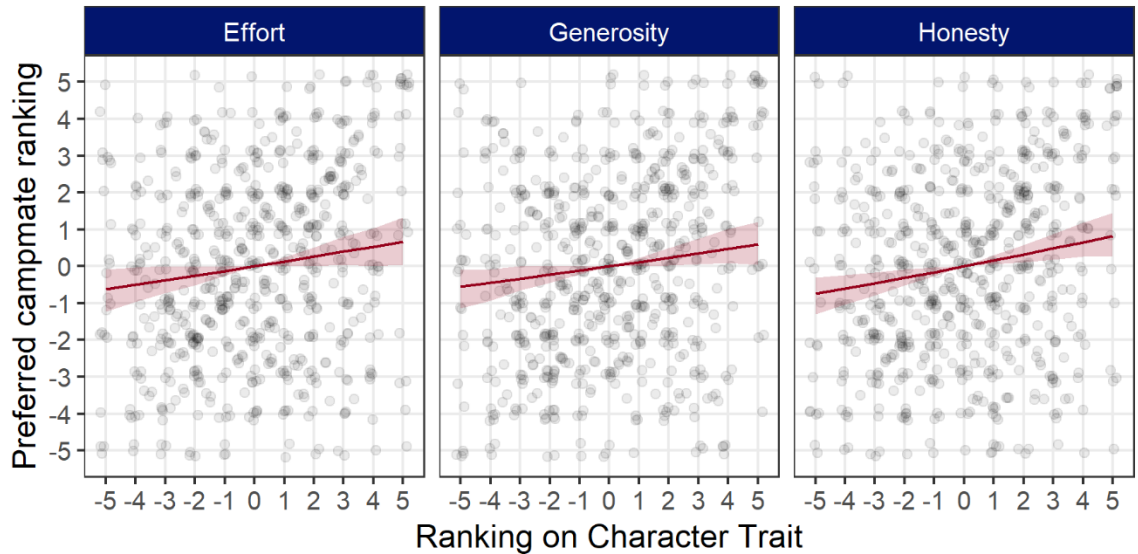


Figure 3.1. Ranking on preferred campmate by ranking on each character trait, centered within camp. Predictions were simulated by generating 10,000 values from an ordered logistic distribution for each ranking and the mean of these generated values were predicted ranking. The line is the mean simulated value and the shaded region is the 90% credible interval.

Do Hadza prefer male campmates with better character or hunting reputation?

We estimated the extent to which a judge's perception of a male campmate's character and his hunting ability relate to the judge's preference for that man as a future campmate, again using ordered logistic regressions. We used the same priors and varying effects as the ones used in the section above. We fit four models predicting preferred campmate ranking from character traits, hunting ability, and demographics. The first model regressed preferred campmate ranking on subject demographics only; demographics were age as a z-score, marital status, and whether the judge and participant were primary kin or spouse. The other models were rankings on character traits and

demographics, hunting ability and demographics, and the full model with character traits, hunting ability, and demographics. Among the four models, the full model with character traits, hunting ability, and demographics was the best fitting model (see Table 3.4). The full model again has the full Akaike weight.

Table 3.4. Fit of Models Regressing Preferred Campmate Rankings on Character Traits, Hunting Ability, and Subject Demographics for Men

Model	WAIC	SE_{WAIC}	p_{WAIC}	Akaike weight
Demographics	1451.63	20.29	51.41	0.00
Character traits	1424.09	25.34	109.35	0.00
Hunting ability	1433.04	22.43	82.92	0.00
Full	1381.94	27.47	153.84	1.00

Note. WAIC is the widely-applicable information criterion estimate; a lower number indicates a better fitting model. SE_{WAIC} is the standard error of the WAIC estimate, p_{WAIC} is the effective number of parameters in the model, and the Akaike weight is computed from WAIC and is the probability that the model will best predict a new set of data among the considered models.

Table 3.5 presents the estimates for the coefficients in the full model. There was good evidence that judges prefer men who are older and who are married more as campmates. There was also good evidence that judges preferred more generous men as campmates and little evidence that judges preferred hard working or honest men as campmates. We again simulated rankings on preferred campmate in the largest camp and computed the difference between being highest and lowest ranked on each character trait and hunting ability (we simulated eight ranks for hunting ability because the largest camp

had only eight hunters). The modal expected rank difference for effort was 0.8 ranks (90% HPDI: -1.0, 2.6), for generosity was 1.6 ranks (90% HPDI: -0.3, 3.0), for honesty was 0.8 ranks (90% HPDI: -1.1, 2.3), and for hunting was 2.4 ranks (90% HPDI: 0.4, 4.2). Figure 3.2 presents the rankings centered within camp as well as the regression line from the simulated predictions. We again simulated the probability that someone ranked highest on each character trait would be ranked at least one rank higher on preferred campmate than someone ranked lowest on that character trait. The modal probability for effort was 55.3% (90% HPDI: 28.7%, 82.9%), for generosity was 70.4% (90% HPDI: 42.8%, 88.3%), for honesty was 55.3% (90% HPDI: 27.5%, 78.3%), and for hunting was 83.3% (90% HPDI: 51.5%, 95.9%).

Table 3.5. Full Model Regressing Preferred Campmate Ranking on Character Traits, Hunting and Subject Demographics for Men

Coefficient	<i>b</i>	90% HPDI	% \leq / $>$ 0
Effort	0.09	-0.10 – 0.28	78.8
Generosity	0.15	-0.03 – 0.31	91.5
Honesty	0.06	-0.11 – 0.23	73.6
Hunting	0.34	0.04 – 0.63	96.7
Married	0.53	-0.04 – 1.15	92.7
Age	0.43	-0.08 – 0.81	90.9
Spouse	-0.06	-0.69 – 0.62	55.5
Kin	-0.02	-0.64 – 0.59	51.6

Note. The coefficient estimate is the mode of the posterior distribution. The 90% highest posterior density interval (HPDI) is the narrowest interval containing 90% of the posterior, or the 90% most plausible coefficient estimates. The last column is the percent of the posterior greater than (or less than for Spouse and Kin) zero.

We also compared the difference in coefficient estimates across the posterior between hunting ability and each character trait. The modal difference between hunting ability and effort was $\Delta b = 0.20$ (90% HPDI: -0.11, 0.61; 86.2% $\Delta b > 0$), t between generosity was $\Delta b = 0.18$ (90% HPDI: -0.17, 0.52; 82.1% $\Delta b > 0$), and honesty was $\Delta b = 0.29$ (90% HPDI: -0.08, 0.60; 89.9% $\Delta b > 0$). There was some evidence that judges had stronger preferences for hunting ability than character.

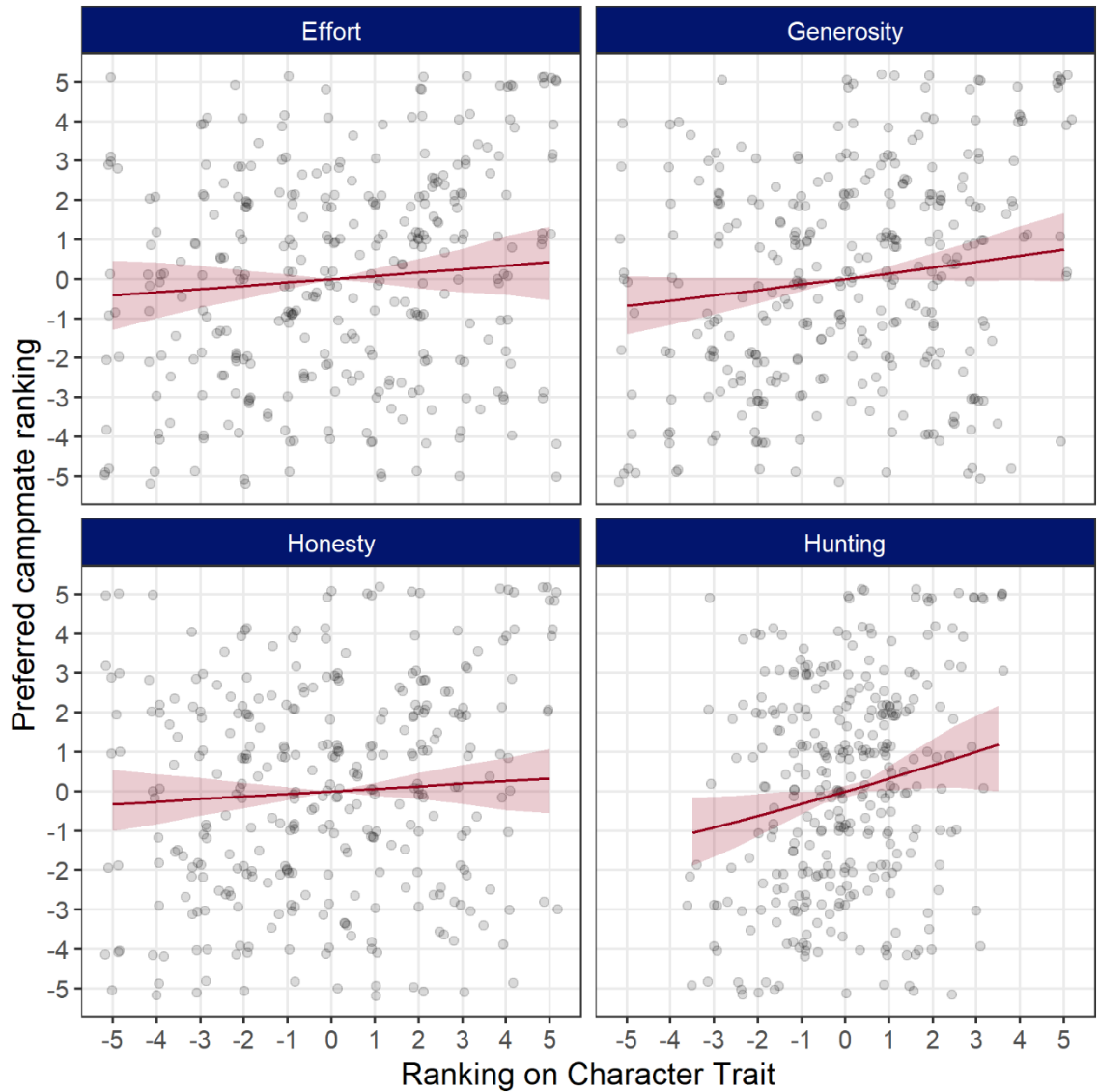


Figure 3.2. Ranking on preferred campmate by ranking on each character trait and hunting ability, centered within camp. Predictions were simulated by generating 10,000 values from an ordered logistic distribution for each ranking and the mean of these generated values were predicted ranking. The line is the mean simulated value and the shaded region is the 90% credible interval.

Do Hadza reciprocate campmate preferences?

We next estimate to what extent Hadza reciprocate campmate preferences. That is, do Hadza prefer to live with campmates who prefer to live with them? We use reciprocated campmate preferences as a proxy of friendship to test friendship models of partner choice. We computed for each judge-subject dyad whether their rankings were concordant (both ranked each other at or above median or both ranked each other at or below the median) or not. Of the all the dyads, only 58.9% mutually ranked each other above or below the median, suggesting there is not a lot of reciprocity in campmate preferences. Figure 3.3 plots ego's ranking of alter and alter's ranking of ego, with a line connecting each dyad. If there was reciprocity, the plot would have short lines clustering the diagonal; however, the long lines indicate little reciprocity. We also examined individual variation in the extent to which Hadza reciprocate campmate preferences. We computed for each person a Kendall's τ between ego's rankings and their alters' rankings. Figure 3.4 plots the histogram of these values. There was variation between Hadza in the extent to which they reciprocated campmate preferences; values ranged from -1 to 0.75. The median value was -0.05 and 50% of the values fell between -0.45 and 0.07. Only 40.9% of the values were positive, again indicating there was little overall reciprocation in the population.

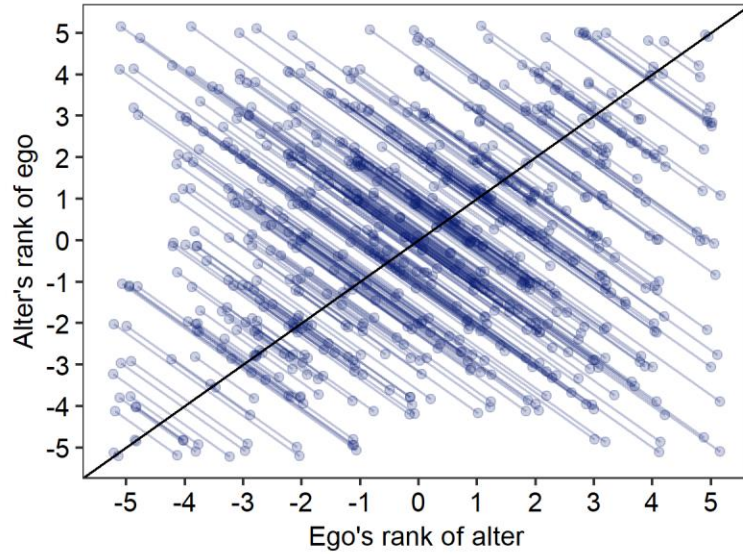


Figure 3.3. Plot of alter's rank of ego by ego's rank of alter. A line connects each dyad of ego and alter; reciprocity would be indicated by short lines near the diagonal.

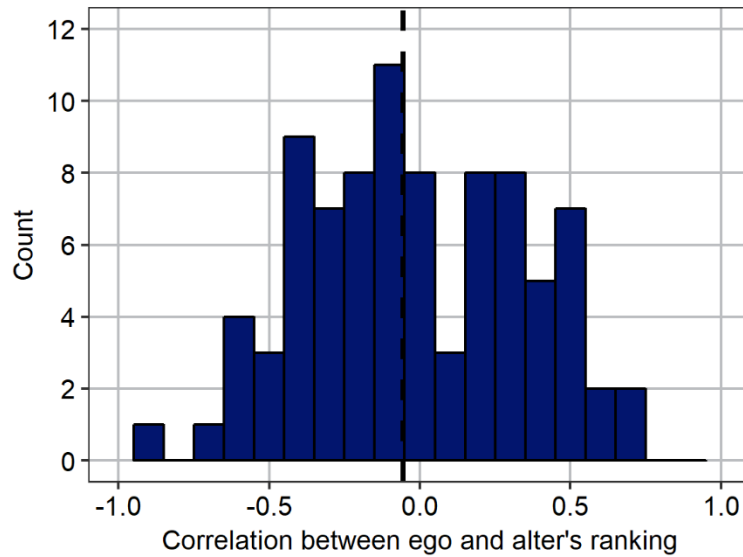


Figure 3.4. The distribution of each judge's correlation between their ranking of alter and alters' ranking of them using Kendall's τ . The dashed line indicates the median.

We estimated the extent to which campmate preferences are reciprocated by fitting two models using ordered logistic regressions. We regress rankings of campmate preferences and alter's ranking of ego on campmate preferences with demographic

variables, and a second model that also included rankings on effort, generosity, and honesty. Priors and model details were the same as the first section on campmate preferences. We compare the two models to the full model from that section with all three character traits and demographics (here referred to as the character model). The character model with the reciprocal rankings was the best fitting model of the three; however, the Akaike weight was split between that model and the full model including the reciprocal rankings (see Table 3.6). We constructed a weighted-average posterior of the two models (McElreath, 2016) and analyze that posterior further.

Table 3.6. Fit of Models Regressing Preferred Campmate Rankings on Character Traits, Reciprocal Rankings and Subject Demographics

Model	WAIC	SE_{WAIC}	p_{WAIC}	Akaike weight
Character	2889.27	34.56	223.01	0.20
Reciprocal rankings	2991.48	28.52	117.98	0.00
Full	2886.51	34.35	243.74	0.80

Note. WAIC is the widely-applicable information criterion estimate; a lower number indicates a better fitting model. SE_{WAIC} is the standard error of the WAIC estimate, p_{WAIC} is the effective

Table 3.7 presents the estimates from the weighted-average posterior. Again, there was good evidence that Hadza preferred older Hadza and their kin as campmates, and that Hadza prefer Hadza ranked higher on the character traits. However, there was little evidence that Hadza reciprocate campmate preferences. If there is a relationship between ego's and alter's rankings, it is likely smaller than the association between character rankings and campmate preferences. We compared the difference in coefficient

estimates across the posterior between each character ranking and the reciprocal ranking. The modal difference between effort and reciprocal ranking was $\Delta b = 0.14$ (90% HPDI: -0.04, 0.29; 87.6% $\Delta b > 0$), the modal difference between generosity and reciprocal ranking was $\Delta b = 0.10$ (90% HPDI: -0.05, 0.27; 87.2% $\Delta b > 0$), and the modal difference between honesty and reciprocal ranking was $\Delta b = 0.13$ (90% HPDI: -0.03, 0.29; 92.4% $\Delta b > 0$).

Table 3.7. Weighted-Average Posterior Regressing Preferred Campmate Ranking on Character Rankings, Reciprocal Rankings, and Subject Demographics

Coefficient	b	90% HPDI	% $</> 0$
Effort	0.12	0.00 – 0.25	95.8
Generosity	0.12	0.00 – 0.23	95.5
Honesty	0.15	0.04 – 0.25	98.6
Reciprocal ranking	0.00	-0.11 – 0.13	46.3
Female	-0.05	-0.50 – 0.37	59.9
Married	0.19	-0.19 – 0.62	79.9
Age	0.42	0.13 – 0.69	98.5
Spouse	0.13	-0.40 – 0.60	65.4
Kin	0.35	-0.11 – 0.81	89.9

Note. The coefficient estimate is the mode of the posterior distribution. The 90% highest posterior density interval (HPDI) is the narrowest interval containing 90% of the posterior, or the 90% most plausible coefficient estimates. The last column is the percent of the posterior greater than (or less than in the case of Female) zero. The distribution for Reciprocal ranking was bimodal, so a continuous HPDI was used.

Are there reproductive benefits to being a valued partner?

We estimate to what extent character reputation, being a preferred campmate, and reciprocating campmate preferences are associated with reproductive success. We computed a mean rank for each character trait and being a preferred campmate using the camp-centered ranks, and we used the Kendall's τ computed in the above section as a measure of reciprocated campmate preferences. We regressed subjects' number of living children on demographic variables (excluding age, see below), character reputation, desirability as a campmate, and tendency to reciprocate campmate preferences using a Poisson regression with a log link-function. A Poisson regression is a count regression that estimates the rate of an event or observation over time and space (McElreath, 2016). An important assumption is that the exposure time is constant across participants, and older Hadza have more reproductive opportunities. To address this, we add age as a constant offset, taking the logarithm of participant's age - 15, and for women, a max value of logarithm of 30 (max age 45) to reflect the reproductive window for Hadza (Blurton-Jones, 2016). Analyses included varying intercepts and slopes for each effect at the camp level. The priors for the intercepts were normal distributions with $\mu = 2$, $\sigma = 1$, the priors for coefficients were normal distributions with $\mu = 0$, $\sigma = 1.5$, the priors for the standard deviations in varying effects were half-Cauchy distributions with $\mu = 0$, $\sigma = 0.6$, and the priors for correlations between varying effects were LKJ correlation distributions with $\eta = 4$. The step parameter was increased to $\delta = 0.95$ to avoid divergent transitions during sampling (Carpenter et al., 2017).

We fit six models predicting number of living children from demographic variables, character reputation, desirability as a campmate, and tendency to reciprocate

campmate preferences. The demographics model included sex, marital status, and an interaction between sex and marital status. The character model included demographics and the mean rankings on effort, generosity, and honesty. The preferred campmate model included demographics and the mean ranking on being a preferred campmate. The reciprocated ranking model included tendency to reciprocate campmate preferences and demographics. The social selection model included mean ranking on being a preferred campmate, tendency to reciprocate campmate preferences, and demographics. Finally, the full model included mean rankings on effort, generosity, honesty, and being a preferred campmate, and tendency to reciprocate campmate preferences, and demographics. The demographics only model was the best fitting model (see Table 3.8). However, the Akaike weight is split between all the models, particularly those that do not include character rankings. We construct a weighted-average posterior from the other four models and examine that posterior further.

Table 3.8. Fit of Models Number of Living Children on Character, Preferred Campmate, and Reciprocated Rankings

Model	WAIC	SE_{WAIC}	p_{WAIC}	Akaike weight
Demographics	326.65	12.16	9.24	0.54
Character traits	332.77	11.92	13.71	0.03
Preferred campmate	329.32	12.08	10.45	0.14
Reciprocated rankings	328.28	12.13	10.32	0.24
Social selection	331.13	12.11	11.61	0.06
Full	336.83	12.02	15.92	0.00

Note. WAIC is the widely-applicable information criterion estimate; a lower number indicates a better fitting model. SE_{WAIC} is the standard error of the WAIC estimate, p_{WAIC} is the effective number of parameters in the model, and the Akaike weight is computed from WAIC and is the probability that the model will best predict a new set of data among the considered models; the weights do not add up to 1 because of rounding.

Table 3.9 presents the estimates for the coefficients in the average-weighted model. There was strong evidence that demographic variables relate to reproductive success; being a woman or married was associated with more living children, though the effect of marriage was much smaller for women than men. There was little evidence that being a more preferred campmate was associated with more living children (see Figure 3.5) or that have more reciprocated rankings was associated with more living children (see Figure 3.6).

Table 3.9. Weighted-Average Posterior Regressing Number of Living Children on Preferred Campmate Ranking, Reciprocated Rankings, and Demographics

Coefficient	b	90% HPDI	% $</> 0$
Intercept	-2.65	-3.05 – -2.17	100
Female	0.84	0.35 – 1.35	99.9
Married	0.72	0.30 – 1.20	99.9
Female \times Married	-0.76	-1.32 – -0.23	99.8
Preferred campmate	0.00	-0.05 – 0.04	8.8
Reciprocated rankings	0.00	-0.11 – 0.27	18.6

Note. The coefficient estimate is the mode of the posterior distribution. The 90% highest posterior density interval (HPDI) is the narrowest interval containing 90% of the posterior, or the 90% most plausible coefficient estimates. The last column is the percent of the posterior greater than (or less than for Intercept and Female \times Married) zero. The distributions for Preferred campmate and Reciprocated ranking were bimodal and a continuous HPDI was used.

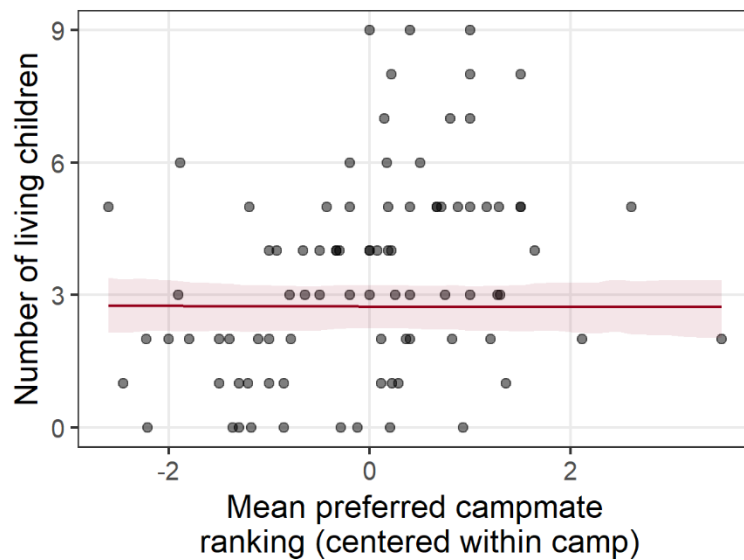


Figure 3.5. Number of living children by mean preferred campmate ranking. The line is the regression line from the median of the weighted-average posterior, and the shaded region is the 90% credible interval.

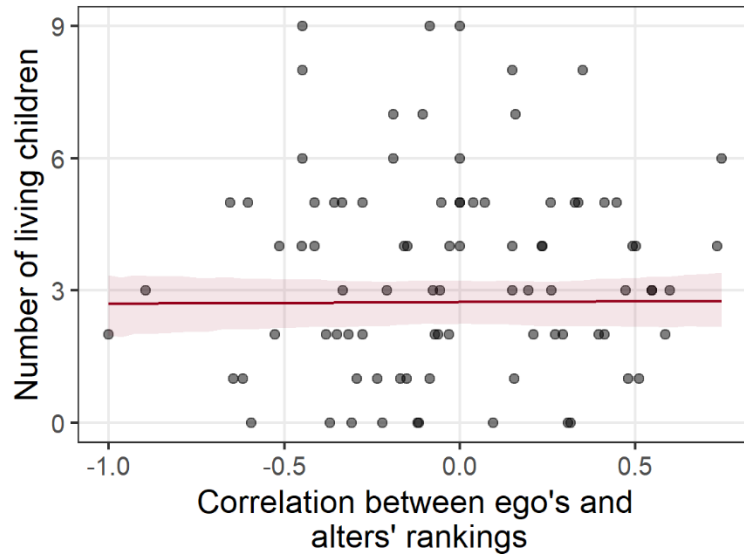


Figure 3.6. Number of living children by the correlation between ego’s and alters’ rankings. The line is the regression line from the median of the weighted-average posterior, and the shaded region is the 90% credible interval.

Discussion

Group living affords many advantages including the establishment of mutually beneficial exchange partners that can increase individual reproductive success. Yet, little work has examined the relative value of various traits in preferences for non-reproductive (i.e. social) partners in populations relevant for the setting of human evolution. Nor has work examined whether preferred partners gain reproductive benefits from being in high demand.

Here, we explored the determinants of partner choice among the Hadza, examining the role character, productivity, and reciprocity play in campmate preferences. We found positive, but arguably weak, associations between evaluations of effort, generosity, and honesty and being a preferred campmate. Instead, the evidence suggests

that hunting ability is more important than character when choosing male campmates, suggesting that productivity outweighs character when selecting social partners. Contrary to prior research, we also found little evidence to suggest that Hadza reciprocate campmate preferences. Finally, there was little evidence to suggest that being a desirable campmate or having stronger reciprocal relationships is associated with greater reproductive success. Together, these results suggest that preference for more cooperative partners do not play a role in maintaining cooperation among the Hadza.

The expected strength of the relationship between character traits and being a preferred campmate should be evaluated relative to the investment cost of improving one's relative reputation as a social partner and the benefits of being a preferred campmate. Our results provide little evidence that being a desired campmate is associated with greater reproductive success and suggests desirable partners receive few benefits. And though we do not have direct evidence of the costs of improving one's reputation, there is other evidence to suggest that it is often difficult—and thus costly—to reliably improve one's reputation. For example, hunting reputation only loosely tracks hunting ability and can only reliably distinguish the best hunters from the worst hunters (Stibbard-Hawkes et al., 2018). And among Dominican laborers, character reputation tends to be slow changing relative to changes in behavior (Macfarlan et al., 2013). That is, reputation is noisy relative to actual behavior, and changes in behavior do not guarantee changes in one's reputation. The high costs of increasing one's reputation and the low benefits of being a preferred campmate suggests that the associations observed here are too small for partner choice to be a viable mechanism for maintaining cooperation.

However, it is not the case that the Hadza have no preferences for campmates. There was evidence that perception of hunting ability was an important criterion for campmates. This finding is consistent with prior research showing that Hadza men prefer to live in hypothetical camps with better hunters (Wood, 2006). Moreover, individuals with traits associated with greater health, which may indicate better productivity, such as height, muscle mass, body fat were positively, were more likely to be nominated as future campmates (Apicella et al., 2012). However, the current results suggest there is little benefit to reproductive success by being a preferred campmate. This suggests there is no incentive for Hadza men to hunt to attain access to valuable social partners (Hawkes, 1993), and previous associations between hunting reputation and reproductive success in the Hadza (Apicella, 2014) may have been due to direct benefits provided to spouse and children (Wood & Marlowe, 2013), and/or access to higher quality mates (Hawkes, 1991).

There are three key limitations to the current study. First, we only examined three character traits: effort, generosity, and honesty. We chose these traits because they were previously identified by the Hadza as being morally relevant (Purzycki et al., 2018), and all involve putting someone else's welfare before one's own. However, there may be other character traits that Hadza believe are more important in campmates. Second, the rankings were within camp and there may be a limited range within the camp to estimate the association between perceptions of character and who is a preferred campmate or between who is a preferred campmate and reproductive success. However, given that these results are corroborated using between camp methods (Apicella et al., 2012; K. M. Smith et al., 2018), this may not be a problem in our data. Third, the analyses are

correlational, which may be particularly problematic for analyses of reproductive success. It could be that an unobserved variable is suppressing the relationships between being a preferred campmate and reproductive success.

A basic rule for the evolution of cooperation is that cooperation must “cluster,” with the benefits of cooperation preferentially flowing to other cooperators (Wilson & Dugatkin, 1997), and previous research among the Hadza has found that cooperation does indeed cluster within camps (K. M. Smith et al., 2018). Given the fluidity of hunter-gatherer groups and the flexibility of who hunter-gatherers can live with, one might expect partner choice for cooperation to be an important way to maintain clustering. However, a number of findings present difficulties to this hypothesis. First, for partner choice to be a viable strategy, current willingness to cooperate must reliably indicate future willingness to cooperate. However, among the Hadza, willingness to cooperate is not stable and instead changes to adopt to local norms (K. M. Smith et al., 2018). Second, people must prefer more cooperative partners. The results presented here suggest such preferences are weak, and other studies have failed to find an association between generosity in economic games and having more social ties in the Hadza (Apicella et al., 2012). And when actual living patterns are observed, cooperation in previous years does not predict more cooperative partners in future years (K. M. Smith et al., 2018). Third, being a preferred partner should be associated with greater reproductive success. The results here and previous results with the Hadza (Apicella et al., 2012) and the Batek foragers of Central Africa (Kraft, Venkataraman, Tacey, Dominy, & Endicott, 2018). These results are inconsistent with partner choice models of cooperation, and suggest that partner choice does not maintain cooperation in hunter-gatherer groups.

Why would the Hadza not have stronger preferences for more cooperative campmates? An important assumption in partner choice models is that there is meaningful variation along the dimensions of cooperativeness and productivity for which to choose partners based on. When there is reduced variability on one dimension, the other dimension becomes more important in partner choice decisions (Barclay, 2016b). And without variation, then people are interchangeable along that dimension and the threat of exiting the relationship provides no incentive for partners to cooperate.

One possibility is that strong norms of egalitarianism govern cooperative behavior in hunter-gatherers (Cashdan, 1980), which reduces variation in cooperative behavior as people conform to the local norms (K. M. Smith et al., 2018). Another possibility is that populations from small-scale societies have behavioral variation. For example, the Tsimané of Bolivia have fewer personality traits and vary less upon those dimension compared to university samples (Gurven et al., 2013). And across societies, populations with access to fewer economic niches have less behavioral variation than Western societies (Lukaszewski et al., 2017). One explanation is that more economic opportunities allows for more behavioral variation and encourages individuation to fill those niches (Gurven, 2018; Smaldino, Lukaszewski, von Rueden, & Gurven, 2018). In population likes the Hadza with no economic specialization, there is little room for behavioral variation, including variation on cooperative behavior. As a result, there is no compete on being cooperative partner.

Our results suggest that the Hadza do not choose partners based on cooperation. Rather, a campmates' ability to produce benefits in the first place play a more important role in how Hadza choose campmates. We argue that social selection for cooperative

partners is unlikely to have played a major role in the evolution of human cooperation and that social selection for productive partners may have played a larger role in shaping human partner choice decisions.

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