Report

Reciprocal Exchange Patterned by Market Forces Helps Explain Cooperation in a Small-Scale Society

Highlights

- We analyzed cooperation in five commodities among Tsimane' horticulturalists

- Giving and receiving of each commodity varied according to supply and demand

- Reciprocal exchange, including trade of one commodity for another, was common

- Trade and divisions of labor emerged from optimal strategies in an informal economy

Authors

Adrian V. Jaeggi, Paul L. Hooper, Bret A. Beheim, Hillard Kaplan, Michael Gurven

Correspondence

adrian.jaeggi@emory.edu (A.V.J.), gurven@anth.ucsb.edu (M.G.)

In Brief

Jaeggi et al. analyze cooperation in different currencies among Tsimane' horticulturalists. They show that reciprocal exchange and trade of one commodity for another was common and varied according to supply and demand. These results suggest that trade and divisions of labor emerge from optimal strategies even in informal economies

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Reciprocal Exchange Patterned by Market Forces Helps Explain Cooperation in a Small-Scale Society

Adrian V. Jaeggi,[1,2,*] Paul L. Hooper,[1] Bret A. Beheim,[3] Hillard Kaplan,[3] and Michael Gurven[2,*]
[1]Department of Anthropology, Emory University, 1557 Dickey Drive, Atlanta, GA 30322, USA
[2]Department of Anthropology, University of California, Santa Barbara, Santa Barbara, CA 93106, USA
[3]Department of Anthropology, University of New Mexico, Albuquerque, NM 87131, USA
*Correspondence: adrian.jaeggi@emory.edu (A.V.J.), gurven@anth.ucsb.edu (M.G.)
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SUMMARY

Social organisms sometimes depend on help from reciprocating partners to solve adaptive problems [1], and individual cooperation strategies should aim to offer high supply commodities at low cost to the donor in exchange for high-demand commodities with large return benefits [2, 3]. Although such market dynamics have been documented in some animals [4–7], naturalistic studies of human cooperation are often limited by focusing on single commodities [8]. We analyzed cooperation in five domains (meat sharing, produce sharing, field labor, childcare, and sick care) among 2,161 household dyads of Tsimane' horticulturalists, using Bayesian multilevel models and information-theoretic model comparison. Across domains, the best-fit models included kinship and residential proximity, exchanges in kind and across domains, measures of supply and demand and their interactions with exchange, and household-specific exchange slopes. In these best models, giving, receiving, and reciprocating were to some extent shaped by market forces, and reciprocal exchange across domains had a strong partial effect on cooperation independent of more exogenous factors like kinship and proximity. Our results support the view that reciprocal exchange can provide a reliable solution to adaptive problems [8–11]. Although individual strategies patterned by market forces may generate gains from trade in any species [3], humans' slow life history and skill-intensive foraging niche favor specialization and create interdependence [12, 13], thus stabilizing cooperation and fostering divisions of labor even in informal economies [14, 15].

RESULTS AND DISCUSSION

The Economics of Cooperation

For some organisms, adaptive problems like producing food, competing for dominance, or staying healthy are best solved with the help of others, i.e., through cooperation. In many species, help is provided by genetic relatives [16] or through mutu-alism [17], but some conditions favor reciprocal exchange [1]. For instance, male chimpanzees depend on allies to compete for dominance but may lack suitable male kin partners, leading them to form long-term bonds with unrelated males [18, 19]. In a high-risk and high-variance foraging niche, as among vampire bats [20] and human foragers [21, 22], adults may find themselves with no food one day and surpluses the next, making reciprocal exchange better suited to buffer shortfalls than unidirectional investment by kin. Thus, the relative importance of reciprocity, as evidenced by long-term contingencies between giving and receiving, may equal or outweigh that of kinship [8, 11, 20, 23, 24].

Extensions of reciprocity within the framework of biological market theory [2, 25–27] further highlight how optimal cooperation strategies vary among individuals. For instance, differences in abilities or need can affect supply and demand of commodities, leading to comparative advantages that help promote the evolution of trade, i.e., exchanges of different commodities [2, 3]. Among primates, grooming may be exchanged in kind to meet hygienic needs but also may be traded for support, especially when rank differences are large [4, 5, 28]. Among human foragers, meat sharing buffers shortfalls but also broadcasts honest information about hunting prowess and generosity [2, 29, 30], which should increase partner value and result in trade for other benefits, though these have rarely been measured [8, 31]. Individual differences in cooperative traits like generosity and trustworthiness may also arise in part from supply and demand, with those able to provide commodities at low cost signaling their quality by being more generous; others signal trustworthiness by providing reliable returns to specific partners for benefits received [2, 32]. Biological market theory thus combines costly signaling and reciprocity [2, 27].

Here we analyze cooperation in five behavioral domains among Tsimane' horticulturalists of Bolivia (see the Experimental Procedures) and show that reciprocal exchange, including trade patterned by market forces, and individual differences in generosity and trustworthiness are dominant features of cooperation. This study fills an important empirical gap as naturalistic studies of human cooperation have often focused on exchanges in kind only [8, 33] and studies of trade in modern market economies typically assume enforceable contracts [3], both of which hamper comparison to the cooperation strategies pursued in biological markets by other species and our understanding of cooperation in pre-modern economies.

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Table 1. Information-Theory-Based Comparison of the Candidate Models for Each of the Five Commodities

Model	DIC (ΔDIC)[a]				
	Meat	Produce	Labor	Childcare	Sick Care
Null	3,123 (728)	2,338 (41)	998 (123)	509 (440)	560 (336)
Kinship and controls	2,600 (205)	2,345 (48)	986 (111)	217 (148)	263 (40)
In-kind reciprocity	2,598 (203)	2,349 (52)	986 (112)	195 (126)	263 (40)
In-kind reciprocity with varying slope for in-kind exchange	2,589 (194)	2,322 (25)	987 (112)	174 (105)	253 (30)
Full exchange	2,615 (220)	2,340 (43)	979 (104)	182 (113)	256 (33)
Full exchange with varying slope for in-kind exchange	2,581 (186)	2,319 (21)	980 (105)	152 (83)	248 (25)
Full exchange with varying slopes for all exchanges	2,563 (168)	2,305 (8.0)	890 (15)	NA[b]	NA[b]
In-kind market forces	2,563 (168)	2,340 (43)	974 (99)	146 (77)	251 (28)
In-kind market forces with varying slope for in-kind exchange	2,556 (161)	2,313 (16)	976 (101)	123.4 (54.5)	240 (17)
In-kind market forces with varying slopes for all exchanges	2,428 (33)	2,305.3 (8.3)	882.7 (8.1)	NA[b]	NA[b]
Full exchange market forces	2,538 (142)	2,334 (37)	958 (83)	<u>73.8 (4.9), weight = 0.08</u>	241 (17)
Full exchange market forces with varying slope for in-kind exchange	2,518 (123)	2,311 (14)	963 (88)	<u>69.0 (0), weight = 0.92</u>	<u>223 (0), weight = 1.00</u>
Full exchange market forces with varying slopes for all exchanges	<u>2,395 (0), weight = 1.00</u>	<u>2,297 (0), weight = 0.966</u>	<u>874.6 (0), weight = 0.98</u>	NA[b]	NA[b]

Models that contributed to a combined DIC weight of >0.95 are underlined; weights <0.05 are not shown. See also Tables S1 and S2.
[a]ΔDIC, difference in DIC to the best model of the respective set (same column).
[b]These models could not be fit.

Model Comparison

We used Bayesian multi-level modeling to predict meat transfers (calories/day), produce transfers (calories /day), field labor (days/year), childcare (yes/no), and sick care (yes/no) among 2,161 household dyads from nine communities, allowing us to account for zero-inflated, non-Gaussian response variables and to model individual and local differences in cooperation through household- and community-specific intercepts and slopes [34] (see the Experimental Procedures and Supplemental Experimental Procedures). We applied model comparison based on the deviance information criterion (DIC) to identify which of our candidate models most parsimoniously fit the data and make the most generalizable predictions [35]. This is better suited for assessing the relevance of multiple hypotheses than conventional null-hypothesis testing [36].

Across domains, we considered a set of candidate models of increasing complexity (Tables 1 and S1): "null" models included varying (i.e., random) intercepts for donor, recipient, and community, thus capturing individual and local differences in giving (i.e., generosity or a household's propensity to cooperate more or less than average) and receiving, but no fixed effects; "kinship and controls" models added mean inter-household relatedness and geographic distance (with community-specific slopes), overall need (estimated total household production minus con-

sumption), and mid-parent ages for donor and recipient, the interaction of recipient need and kinship, and number of sampling days for donor production; "in-kind reciprocity" models added receiving the same commodity from each other household; "full exchange" models added receiving other commodities; "in-kind market forces" models included household-specific measures of donor and recipient supply and demand for each commodity exchanged in kind (meat, mean daily production and variance in production; produce, mean daily production and total field size; labor, field size and family size; childcare, field size and family size; sick care, family size), as well as interactions between donor supply and receiving in-kind (e.g., receiving meat × meat production); and "full exchange market forces" models added supply and demand for all commodities and their interactions with receiving. Throughout, we considered household-level differences in recip-rocating, i.e., the propensity to return benefits more or less contingently than average, which can be interpreted as trustwor-thiness, or exchange rates. This was either not included or was modeled with varying slopes for in-kind exchanges only or with varying slopes for all commodities.

Despite the large number of fixed (30) and varying (nine) effects, the most complex "full exchange market forces" models with varying slopes for all commodities were strongly favored by

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the model comparison across the five domains of cooperation, receiving an average DIC weight of 0.97 (Table 1). Indeed, addition of covariates and varying slopes improved DIC throughout the candidate model set, despite the penalty for complexity inherent in information criteria. Thus, reciprocity and trade explain cooperation above and beyond kin investment and standard controls, and the market forces of supply and demand and individual differences in the propensity to give (i.e., generosity), receive, or reciprocate (i.e., trustworthiness or exchange rates) play important roles in patterning cooperation. These results highlight the need to model market effects and individual differences in cooperation as encompassed by biological market theory, wherein individual- and context-specific costs and benefits shape optimal strategies with specific partners [2, 3, 27]. The unexplained between-household variance captured by the varying intercepts and slopes might indicate incomplete measures of supply and demand and of individual differences in propensities for cooperation beyond that.

Results of the Best Models

To extract more specific results, we focused on the best models (underlined in Table 1), averaging coefficients if no single model received a DIC weight >0.95. Our focus on five commodities broadens the scope of cooperation, but it makes unique predictions more difficult as multiple equilibria may exist for how individuals strike bargains to exchange different commodities for mutual gain [37, 38]. In general, though, we expect (1) households to exchange items that they produce in high supply for those needed in high demand, (2) magnitude or slope of reciprocation (i.e., exchange rates) to be higher for commodities in greater demand, and (3) reciprocation to be strongest for the sum of multiple commodities.

In the best models, the fixed effects explained low to moderate amounts of variance in the data (marginal coefficient of determination R_m^2 [39, 40] = 0.24 for meat, 0.08 for produce, 0.09 for labor, 0.33 for childcare, and 0.42 for sick care), and the fixed and varying effects combined explained almost all variation (conditional coefficient of determination R_c^2 [39, 40] = 0.99 for meat, 0.94 for produce, 0.96 for labor, 0.99 for childcare, and 0.84 for sick care; see the Supplemental Experimental Procedures), indicating that household-level intercepts and slopes captured most between-individual variation and left little residual variance unexplained. To compare the effect size of covariates within and between models, we calculated standardized coefficients (β; see the Supplemental Experimental Procedures) [36], with the associated p values indicating the proportion of posterior samples beyond 0 [41] (see Table S2 for model summaries including 95% confidence intervals). These p values (and confidence intervals) thus provide measures of precision and help us focus on generalizable findings, but they should not be interpreted as null-hypothesis testing, which may not be mixed with information-theoretic model comparison [35].

Some cooperation needs can be met by genetic relatives; indeed, kinship was associated with greater giving for all commodities (meat: $\beta = 0.03$, p < 0.001; produce: $\beta = 0.05$, p < 0.001; labor: $\beta = 0.05$, p < 0.001; childcare: $\beta = 0.18$, p < 0.001; sick care: $\beta = 0.33$, p < 0.001; Table S2). Greater distance between households, indicating higher transaction costs, was associated with lower giving (meat: $\beta = -0.07$, p < 0.001; pro-

duce: $\beta = -0.13$, p < 0.001; labor: $\beta = -0.02$, p < 0.001; childcare: $\beta = -0.24$, p < 0.001; sick care: $\beta = -0.21$, p < 0.001). When plotted on the scale of the observed data, however, kinship (Figure 1A) had a large yet uncertain predicted effect on childcare but minimal impact on other commodities. Distance effects (Figure 1B) reflect the residence structure typical for Tsimane' [42] as giving most commodities was greatest within 10 m, suggesting that demands were met within household clusters, whereas meat transfers increased within 100 m, consistent with a larger risk-buffering network for this more variable resource. This is consistent with small-scale societies more generally, where residential structure is to some extent patterned by the demands of cooperative production, such as forager band size optimizing risk-buffering and overall return rates [21, 43–45]. Some commodities like labor were largely unaffected by kinship or distance (Figures 1A and 1B), suggesting more strategic uses of this highly valued commodity (see below).

Beyond kinship and proximity, cooperation was significantly associated with exchange; Figure 2 provides an overview of this Tsimane' exchange economy. Giving meat was associated with receiving meat ($\beta = 0.11$, p < 0.001), consistent with theoretical expectations [21, 22] and previous research highlighting the role of meat sharing in buffering variable hunting returns [8, 46–48]; however, receiving produce was another strong predictor of giving meat ($\beta = 0.23$, p < 0.001), indicating divisions of labor in food production between households [15] (Figure 1C). Labor ($\beta = 0.02$, p < 0.1) and childcare ($\beta = 0.19$, p < 0.01) were exchanged in kind, suggesting economies of scale to turn-taking. However, labor was also traded for childcare ($\beta = 0.02$, p < 0.1) and vice versa ($\beta = 0.05$, p < 0.1), and receiving child care was associated with giving sick care ($\beta = 0.06$, p < 0.05). The relatively weak labor exchange effects (together with the low R_m^2 of the best labor model) might indicate that reciprocating partners are hard to attract as in other informal labor markets [33] and that valuable partners can impose high prices, such as high-ranking primates receiving larger amounts of grooming for support in more hierarchical groups [28]. In some cases, cooperation was unidirectional; receiving produce was negatively associated with giving labor ($\beta = -0.29$, p < 0.001), and receiving sick care with childcare ($\beta = -0.05$, p < 0.05). These unidirectional flows could be due to intergenerational transfers [42], differences in bargaining power [49, 50], competitive altruism [51], or missing commodities like mating or political support. In sum, commodities that require risk-buffering (meat) or provide opportunities for economies of scale in turn-taking (labor and childcare) were exchanged in kind, whereas those with low need for buffering (produce) or imbalanced supply and demand (sick care) were not. Trade effects (meat for produce, labor for childcare, and sick care for childcare) could indicate divisions of labor according to ability or need, as further explored below.

The exchange economy depicted in Figure 2 was affected by supply and demand (Table S2). High meat producers ($\beta = 0.02$, p < 0.001; Figure 1D) shared more meat, indicating the ability to share at low marginal cost, while higher variance in meat production also slightly increased sharing ($\beta = 0.01$, p > 0.1, Figure 1D), consistent with a higher chance of overproduction and greater need for risk-buffering for more variable producers [21]. Larger families gave less childcare ($\beta = -0.22$, p < 0.1),
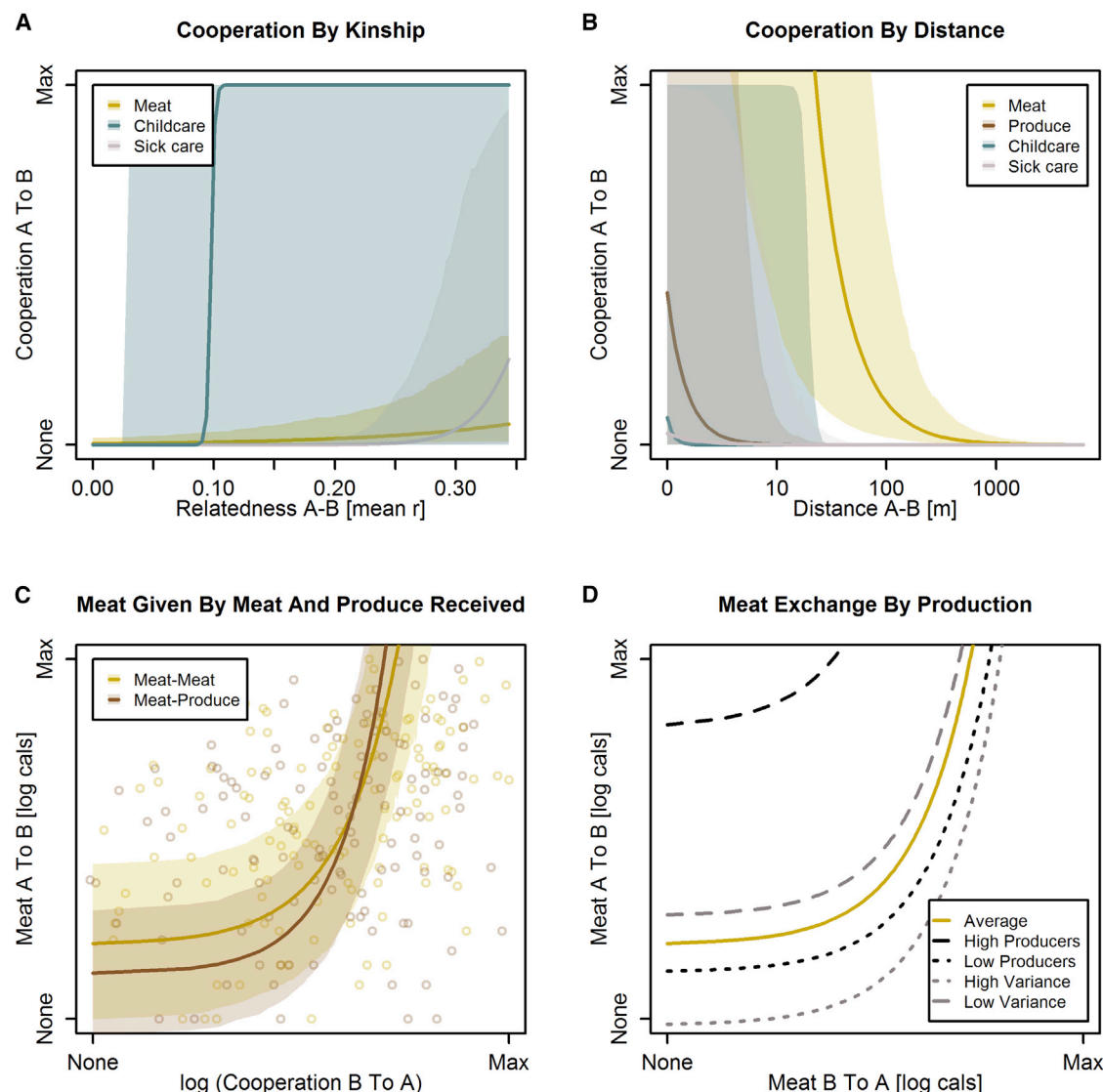
**Figure 1. Magnitude of Expected Cooperation among Households Described by the Best-Fit Models**

Cooperation in different domains (±95% confidence region) as a function of (A) average relatedness and (B) distance between households, (C) expected meat shared by meat received and produce received (dots are observed data), and (D) expected meat shared as a function of receiving meat for households that differ in their average or variability in meat production (minimum and maximum observed; see also Table S2). To plot cooperation in different currencies on the same scale, we standardized cooperation by dividing each observation by the maximum observed amount, producing a range from 0 (no cooperation given) to 1 (maximum amount of cooperation given). In each case, all other covariates were held at the population average. For (A) and (B), commodities that showed no perceptible increase over the range of the x axis were omitted.

suggesting greater demand and opportunity costs, but received less labor ($\beta = -0.02$, $p < 0.1$) and less sick care ($\beta = -0.16$, $p < 0.05$), suggesting the ability to meet demands within the household.

Contingencies between giving and receiving reflect exchange rates ("prices") for commodities, e.g., if households reciprocate less when receiving a commodity for which they have low demand. Thus, higher meat producers gave less produce, i.e., paid a lower price in return for meat compared to lower meat producers ($\beta = -0.10$, $p < 0.05$). Large families gave less produce in return for labor ($\beta = -0.05$, $p < 0.1$) and less labor ($\beta = -0.02$, $p < 0.05$) and childcare ($\beta = -0.12$, $p < 0.001$) in response to

receiving sick care than small families; this could mean that larger families were able to meet demands within the household (low demand) and paid less for outside services or that they could not afford to pay more (low supply) due to high demand within the household. Conversely, households reciprocated more when receiving commodities for which they had high demand; households with larger fields gave more produce in return for childcare than those with smaller fields ($\beta = 0.02$, $p < 0.05$). This result is consistent with higher producers having greater opportunity costs and therefore paying more for a service that helps free up their time for horticultural production with the very commodity that it allows them to produce. Finally, many
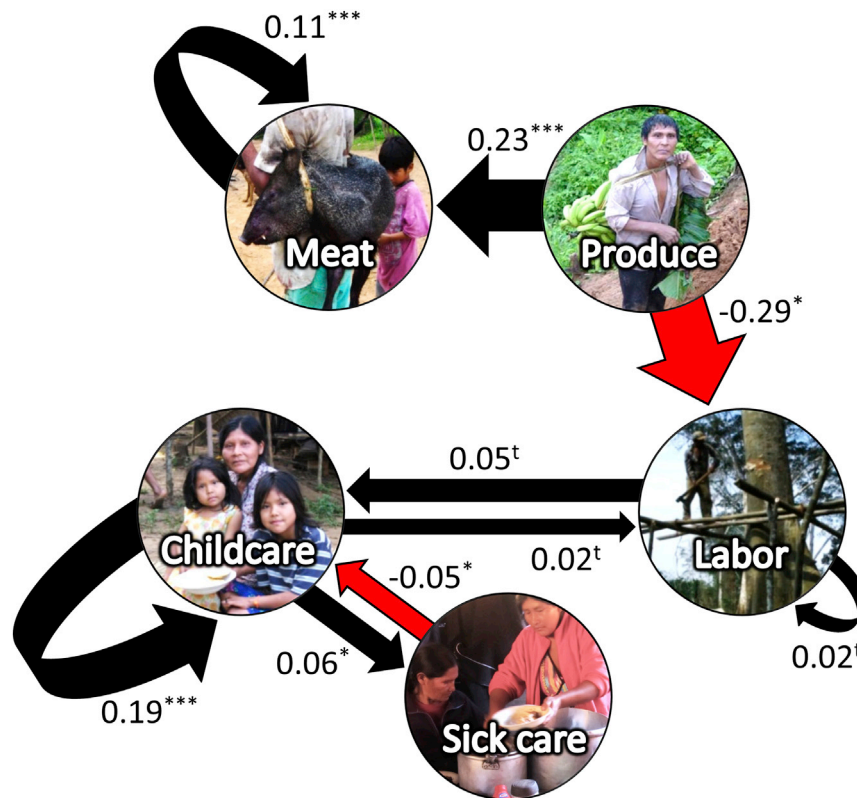
Figure 2. The Tsimane' Exchange Economy

Arrows are included for associations with at least a statistical trend (p < 0.1) and are proportional to the standardized coefficients (β; see Table S2). Black arrows indicate positive effects, and red arrows indicate negative ones. Numbers are standardized coefficients, and asterisks indicate p values (^{t}p < 0.1, *p < 0.05, **p < 0.01, ***p < 0.001). The direction of the arrow (from X to Y) should be read as "giving Y is associated with receiving X." Photo credits: meat, Benjamin Trumble; produce, Michael Gurven; childcare, Emily Miner; labor, Benjamin Trumble; sick care, Paul Hooper.

conceivable market effects were not found in our models, and some seemed contrary to expectation; more childcare was given in return for produce by households that should have little demand for produce as indicated by higher average production (β = 0.08, p < 0.05) and field size (β = 0.08, p < 0.05), and less childcare was given in return for meat by households experiencing high variance in meat production (β = −0.13, p < 0.001), which should indicate greater demand for meat transfers. These unexpected effects could reflect short-term shocks and other dynamics impacting families, leading to excess demand or supply of some commodities and therefore lack of equilibrium pricing and a failure of markets to clear. Overall, at least some household-specific cooperation strategies were consistent with market forces, i.e., the costs and benefits of giving and receiving given their own and others' supply and demand. While some studies have shown similar market effects on cooperation strategies in animals, e.g., baboons and chimpanzees adjusting grooming reciprocity and trade to rank differences and outside options [4, 6, 7], naturalistic studies of human cooperation have typically focused on food transfers and overall need only [8], thus likely underestimating the importance of exchange across diverse commodities and the extent to which households adjust their cooperation strategies to the market [33].

The possibility to exchange various commodities on a biological market and capitalize on comparative advantages provides individuals with diverse strategies for solving adaptive problems that could be more effective than more exogenous factors like kinship or residential proximity [8, 11, 23, 24]. To compare the combined partial effects of exchange across domains to these other factors, we converted each of the five commodities into an ordinal variable indicating no cooperation (0), A gave to B less than A gave to others on average (1), and A gave to B more than A gave to others on average (2); cooperation was thus standardized to each individual's ability and provides a measure of relative investment in the relationship (to calculate this variable, we used the total number of nominations for childcare and sick care). This ordinal scale allows the five types of cooperation to be summed to yield a total cooperation score (cf. [24]) ranging from 0–10. Total cooperation given was most strongly associated with total cooperation received (β = 0.14, p < 0.001), followed by kinship (β = 0.07, p < 0.001), distance (β = −0.04, p < 0.05), and donor age (β = −0.04, p < 0.05; Table S3; Figure 3; R_m^2 = 0.20). These results provide further evidence that cooperation was based on exchange above and beyond exogenous factors like kinship and proximity [8, 11, 23, 24, 52]. Nonetheless, kinship most likely provides a basis for the initial assortment of reciprocators [53]; indeed, related dyads (mean r > 0) were significantly more likely to be reciprocal than unrelated ones (χ^2 = 50.7, degrees of freedom [df] = 1, p < 0.001). Similarly, residential proximity could act as a filter for cooperative partnerships, initially resulting from assortment choices based on partner value, but then functioning to reduce transaction and monitoring costs.

In sum, our study highlights that reciprocal cooperation can provide a reliable solution to adaptive problems typical of human ecological niches [8, 23, 47, 48, 52, 54], as in some other species in which kin investment cannot sufficiently meet cooperation needs [9–11]. In a biological market for cooperation, individuals should be selected to adopt strategies that take the costs and benefits of cooperation based on supply and demand of commodities and reliable partners into account [2, 3, 27], resulting in diverse strategies that allow individuals to capitalize on comparative advantages in different domains of capital (embodied, relational, and material). Our study design, however, was cross-sectional and our analysis correlational; longitudinal studies with greater attention on outside options will be necessary to capture causal relations between giving and receiving, the dynamics of partner choice, the time frame of reciprocation, and fluctuations in commodity exchange rates [26, 55–57]. In

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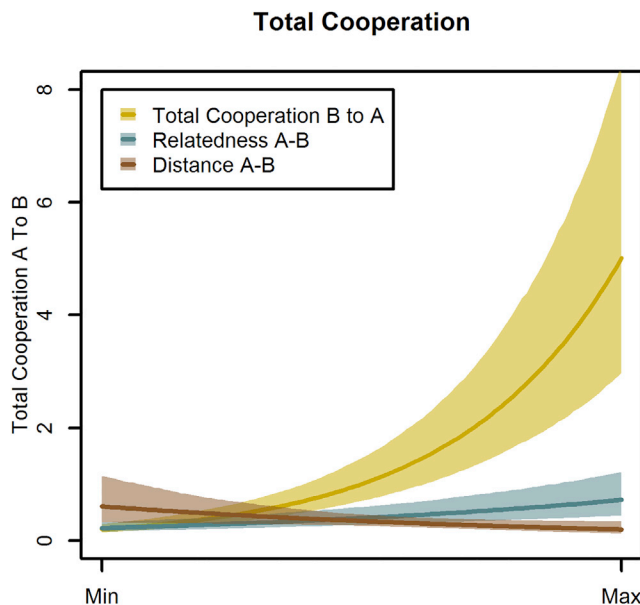
Total Cooperation

Figure 3. Predicted Total Cooperation Given as a Function of Total Cooperation Received, Average Relatedness, and Distance
Total cooperation refers to the sum of ordinal cooperation in each of five commodities, wherein 0 indicates no cooperation given, 1 indicates that A gives B less than A gives the average other household, and 2 indicates that A gives B more than A gives the average other household; total cooperation thus potentially ranges from 0–10. Aggregated minimum and maximum are calculated as in Figure 1. See also Table S3.

addition to variation in strategies stemming from differences in ability and need, household-specific proclivities for cooperation (generosity and trustworthiness) added significant fit to the models, highlighting a need to better understand individual differences in cooperation empirically and theoretically.

Lastly, although stable individual differences may generate comparative advantages leading to gains from trade in any species [3], humans' slow life history and skill-intensive foraging niche increase the payoffs to specialization and create interdependence within and among generations [12, 13, 42], thus stabilizing cooperation and fostering divisions of labor even in informal economies [14, 15]. In addition, increasing technological and social complexity during human history arguably posed new cooperation challenges, some of which were met through culturally evolved norms and institutions that reduced the cognitive demands and transaction costs of exchange and further stabilized cooperation [58, 59], which ultimately led to modern markets.

EXPERIMENTAL PROCEDURES

Study Population and Context of Cooperation
The Tsimane' are a population of ~15,000 Amerindians from the Beni region of lowland Bolivia. Their traditional economy is based on swidden horticulture (plantains, sweet manioc, rice, and corn), hunting, fishing, and gathering. Closely related families often co-reside in clusters of several households, within dispersed communities comprising multiple clusters. The Tsimane' had minimal contact with the Bolivian national economy until the 1970s but have since experienced increasing market integration [60]. Nonetheless, most of the Tsimane' diet comes from locally produced food, and monetized

transactions within communities are rare. Cooperation typically occurs among known partners, and there are few explicit norms of reciprocity.

The following forms of cooperation and other variables were included for analysis (see Table S4 for descriptive statistics and the Supplemental Experimental Procedures for more details on data collection).

Meat and Produce Sharing
Like other small-scale subsistence societies, the Tsimane' face a risk of food shortfalls due to variable returns, crop failure, illness or accidents, and other exogenous shocks [60, 61]. Such risks are greater for more perishable foods with more variance in production, i.e., game and fish (Table S4), whereas horticultural production is more predictable and shortfalls can be self-buffered through storage and overplanting.

Labor Sharing
Horticultural production is physically taxing and limited by labor input; hence, Tsimane' highly value receiving help in the field. Labor is sometimes given with explicit payment or expectation of reciprocity, but these instances were not included here.

Childcare
With large family sizes (total fertility rate = ~9) and extended absences due to foraging trips, town visits, or field or wage labor, there is great demand for alloparental childcare. In its extreme form, children are (temporarily) adopted, which is observed in ~15% of households.

Sick Care
Adult Tsimane' are incapacitated by illness or accidents on about 10% of days [61]. Health clinics are absent from most communities, and trips to the nearest hospital long and expensive. Receiving aid such as food, medicine, or money to buy medicine or pay for transportation can be crucial.

All data were collected by bilingual Tsimane' field assistants under the auspices of the Tsimane' Health and Life History Project (https://www.unm.edu/~tsimane/). All protocols were approved by the institutional review boards of the University of New Mexico and University of California, Santa Barbara, the Tsimane' government, community consensus, and all study participants. Data on all cooperative behaviors were available for 115 households from nine communities, with the risk set of exchange partners being all other households in the same community, resulting in 2,161 household dyads.

Data Analysis
Bayesian multilevel models were fit using the MCMCglmm package (Version 2.17) [41] in R 3.0.2 [62]. Binary variables (childcare and sick care) were modeled using a logit link function. Count data (meat, produce, and labor sharing) were modeled as Poisson distributed (with log link) with a zero-inflation intercept (with logit link) if necessary (see the Supplemental Experimental Procedures for full model equations and further details). DIC weights were calculated using the MuMIn package [63].

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and four tables and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2016.06.019.

AUTHOR CONTRIBUTIONS

Conceptualization, A.J. and M.G.; Data Curation, A.J. and P.H.; Formal Analysis and Visualization, A.J.; Validation, B.B.; Writing, A.J. and M.G.; Methodology, Resources, Supervision, Project Administration, and Funding Acquisition, M.G. and H.K.

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