Demography and ecology drive variation in cooperation across human populations

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Recent studies argue that cross-cultural variation in human cooperation supports cultural group selection models of the evolution of large-scale cooperation. However, these studies confound cultural and environmental differences between populations by predominantly sampling one population per society. Here, we test the hypothesis that behavioral variation between populations is driven by environmental differences in demography and ecology. We use a public goods game played with money and a naturalistic measure of behavior involving the distribution of salt, an essential and locally valued resource, to demonstrate significant variation in levels of cooperation across 16 discrete populations of the same small-scale society, the Pahari Korwa of central India. Variation between these populations of the same cultural group is comparable to that found between different cultural groups in previous studies. Demographic factors partly explain this variation; age and a measure of social network size are associated with contributions in the public goods game, while population size and the number of adult sisters residing in the population are associated with decisions regarding salt. That behavioral variation is at least partly contingent on environmental differences between populations questions the existence of stable norms of cooperation. Hence, our findings call for reinterpretation of cross-cultural data on cooperation. Although cultural group selection could theoretically explain the evolution of large-scale cooperation, our results make clear that existing cross-cultural data cannot be taken as empirical support for this hypothesis.

evolution of cooperation | cultural norms | common-pool resource | real-world measure | economic game

Several recent cross-cultural studies in small-scale (1–3) and large-scale (4–6) societies demonstrate variation in patterns of cooperation across cultural groups. This behavioral variation is attributed to culturally inherited cooperative norms and taken as support for cultural group selection models of large-scale cooperation (1, 2, 7). However, these studies have mostly sampled from one population per culture. Thus, they confound cultural and environmental differences between populations and cannot determine whether the behavioral variation across populations is driven by conformism to cultural norms or by environmental (demographic and ecological) differences. Crucially, the evolution of large-scale cooperation via cultural group selection (7–13) depends on behavior being acquired via cultural transmission, such that behavioral variation between populations is maintained by conformism to group norms.

We examine whether there are differences in levels of cooperation across discrete populations of the same endogamous cultural group, and we find that environmental drivers (local ecology and demography) are responsible for behavioral variation across our study populations. Moreover, variation between these populations of the same cultural group is comparable to that found between different cultural groups in previous studies. Our finding that behavioral variation is at least partly contingent on environmental differences between populations questions the existence of stable cultural norms of cooperation. Hence, although cultural group selection could theoretically explain the evolution of large-scale cooperation, our results make clear that existing cross-cultural data cannot be taken as empirical support for this hypothesis.

Our study populations are 16 villages of a small-scale forager-horticulturist society called the Pahari Korwa of central India (14) (details are provided in *SI Text*, Fig. S1, and Tables S1 and S2). Heavily reliant on gathered forest products, which are a primary source of food and income, Pahari Korwas also practice agriculture on small tracts of land. These economic resources are supplemented by opportunistic hunting, fishing, and wage labor. The Pahari Korwa live in mostly uniethnic villages that vary considerably in size, migration rates, and access to markets. They predominantly commute by foot, and there is no a priori reason to believe that current migration rates are significantly higher than they were in the past. The settlements have well-defined boundaries; tracts of forest and hills separate neighboring villages. In this endogamous, patrilineal, and patrilocal society, exogamous marriages usually incur severe penalties entailing ostracism and expulsion from the tribe and village. Pahari Korwa populations thus present an excellent model system for this study: a set of real-world uniethnic metapopulations of the same endogamous cultural group, with distinct population boundaries and considerable demographic and ecological variation across them. Table 1 presents summary statistics for our study populations.

We used two measures of cooperative behavior. The first is an anonymous one-shot public goods game (PGG). Participants were divided into groups of six players. Each player received an endowment of 20 Indian rupees (henceforth rupees) and decided how much of it she wished to contribute to a group pot in divisions of five rupees. Once all six players made their decisions, the total amount in the pot was doubled and then split equally between all six players. Each player's earnings consisted of the money she retained from her endowment plus an equal share of the earnings from the group pot. In this game, the income-maximizing strategy entails that a player contribute nothing to the group pot.

Our second measure is a naturalistic evaluation of behavior that involves taking a useful commodity from a common pool. We used salt, which is valued among the Pahari Korwa because it is an essential commodity that they cannot obtain directly from the forest or manufacture themselves, and one that they are most likely to buy at market (14). On concluding the PGGs in a village, when a participant collected her earnings at a private location, she was informed that one of the authors (S.L.) had brought along x kg of salt to distribute among the y individuals who participated in the games and that $z = x/y$ kg of salt was thus available per person. The participant could then take as much of the total amount of available salt (x kg) as she desired without her decision becoming public knowledge. The stated amount was

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Table 1. Summary statistics of demographic variables and sample sizes for the study populations

Village number	Village name	Population size*	Percentage of migrants in sample†	Percentage of non-Korwas‡	Distance from major town, km§	PGG players (*n*)	Salt takers (*n*)
1	Chipni Paani	27	92 (12)	0	24	12	11
2	Mahua Bathaan	61	32 (22)	16	44	18	22
3	Jog Paani	64	53 (19)	25	47	7	13
4	Semar Kona	64	29 (17)	17	24	9	13
5	Bihidaand	73	48 (21)	21	33	15	15
6	Khunta Paani	97	52 (31)	27	36	22	27
7	Kaua Daahi	102	41 (32)	0	46	18	24
8	Pareva Aara	111	44 (36)	14	42	24	34
9	Musakhol	117	37 (30)	26	35	16	16
10	Kharranagar	125	42 (38)	0	50	24	37
11	Tedha Semar	141	40 (30)	3	45	19	12
12	Vesra Paani	157	25 (44)	25	27	22	20
13	Barghat	194	31 (42)	10	41	24	9
14	Aama Naara	207	33 (43)	6	69	30	9
15	Bakrataal	254	54 (39)	7	26	15	28
16	Ghatgaon	957	15 (47)	5	13	26	12

A total of 301 individuals participated in the PGG, and 302 made the salt decision across 16 villages; 190 individuals participated in both. Not all PGG players received salt; they were not offered any salt if it ran out before they collected their payments. Not all those who received salt participated in the PGG.
*Includes all adults and children residing in the focal village.
†Numbers in parentheses indicate the size of the sample used to estimate the proportion of migrants. Migrants are individuals (Pahari Korwas) currently residing in the focal village but born in another village. Migration often follows marriage, particularly for females.
‡Percentage of the focal village population that was not Pahari Korwa.
§Distance from Ambikapur, the largest town in the study region.

given to her, along with her earnings from the game. In each village, we started with a total quantity of salt (in kg) equal to the total number of participants, such that the initial amount available per person was 1 kg. We then recalculated and updated the total amount available (x), the number of people remaining (y), and the amount available per person ($z = x/y$) for each person based on how much salt remained after the preceding person had taken her desired quantity of salt. We stopped distributing salt either when the penultimate person had taken salt or when the amount available per person fell below 100 g per person. Participants encountered the salt for the first time when they individually collected their payments and had no prior information about it. The income-maximizing strategy entails that a player take all the available salt. For each player, we use the deviation of the salt taken from the amount available per person as a measure of cooperative propensity. The more negative a player's salt deviation, the more selfish is the player's behavior.

The salt decision involves anonymously sharing large quantities of a desirable commodity outside an experimental context with a large group of people from an individual's village; hence, it provides a measure of large-scale cooperation in a real-world context that is comparable to behavior in anonymous one-shot economic experiments. We use these salt decisions to measure behavioral variance across villages and to assess whether behavior captured by a formal economic game, such as the PGG, correlates with a naturalistic measure of cooperation in a real-world context.

We use multilevel multivariate response models (15) to analyze variation explicitly at the village and individual levels in our data (structured as individuals within villages). Traditional regression models used in previous cross- and intracultural studies (e.g. 1–4, 16–19) treat the units of analysis as independent, an assumption that is severely violated if group membership, whether at the culture or population level, affects individual behavior. Also, previous intracultural studies (16, 19) sampled an inadequate number of populations to make reliable inferences about the extent of within-culture variation. Multilevel models correct for the nonindependence of clustered data, reducing the likelihood of type I errors. Multivariate response models let us simultaneously examine the effect of explanatory variables on our two response variables, PGG contribution and salt deviation. We can also partition the correlation between the two response variables into village and individual level components.

Results and Discussion

Distributions of both PGG contributions (Fig. 1) and salt deviations (Fig. 2) vary considerably across villages, including the modes and means. A total of 4.1% [95% Bayesian credible interval (BCI) = 1, 11.6] of the variance in PGG contributions and 18.2% (95% BCI = 7.3, 35.5) of the variance in salt deviations occurs between villages [Table S3, null model (multilevel)]. The between-village variation in salt deviation is remarkable; in some villages, the salt ran out before less than half of the players had taken any salt, whereas almost everyone received some salt in other villages. Once village and individual descriptors are included in the model, the unexplained between-village variance is reduced to 1.4% (95% BCI = 0.3, 4.7) in PGG contributions and 11.8% (95% BCI = 3.8, 26.5) in salt deviations [Table S3, full model (multilevel)].

Variance in ultimatum game offers between 15 small-scale societies was estimated at about 12% (1). Behavioral variance between 16 populations of the same small-scale society is therefore comparable to that between 15 populations of 15 different small-scale societies. Seven percent of the variance in average contributions in repeated PGG experiments run in 16 populations of 15 different large-scale societies was estimated to be between populations (4); mean contributions in the first round of the PGG varied between about 8 and 14 units of the initial endowment (also 20 units). Mean PGG contributions across 16 populations of the same society in this study vary between 7.2 and 14.7 units (Fig. 1). Hence, the variance in contributions and range of mean contributions across 16 populations of the same society are comparable to those across 16 populations of 15 different societies. By demonstrating significant within-culture, between-population variation, our findings challenge the existence of stable culturally inherited cooperative norms.

We tested whether the variation between and within populations is explained by properties of populations and individuals

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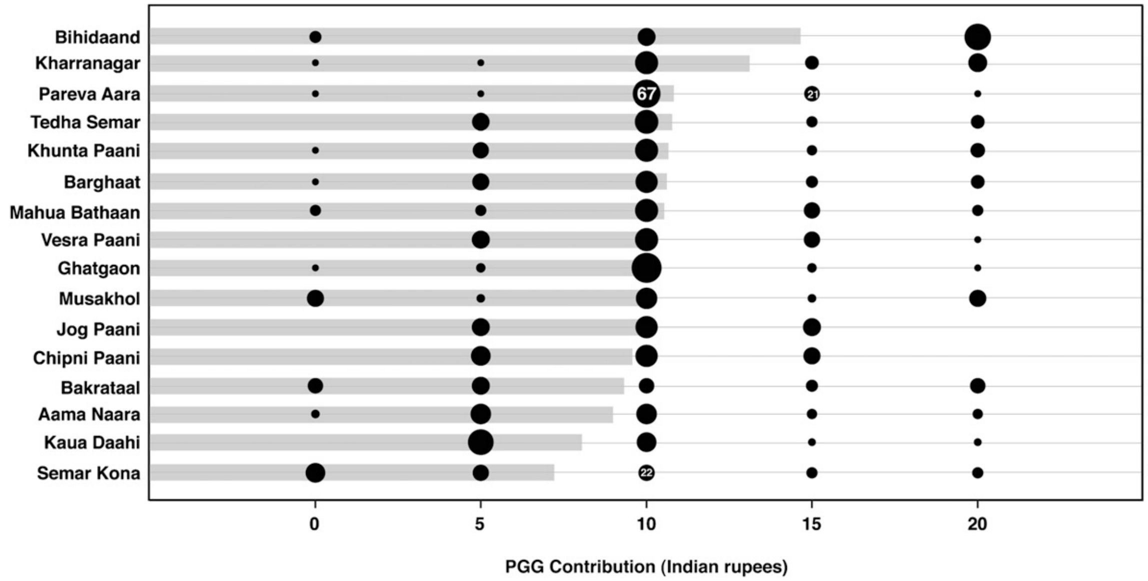

Fig. 1. Distributions of PGG contributions across 16 villages. For each village on the *y* axis, the areas of the black bubbles represent the proportion of individuals from the village that made a contribution of the value on the *x* axis. To indicate scale, the numbers in some bubbles are the percentage proportions represented by those bubbles. Gray horizontal bars indicate the mean contributions for villages. Villages are ordered by their mean contributions; the bottom village (Semar Kona) has the lowest mean. Counts on the right (*n*) represent the number of players from each village (total *n* = 301). The overall mode across villages is 10 rupees (mean ± SD = 10.40 ± 5.48).

(details are presented in Table S4, and a discussion of these results is provided in *SI Text*). The only explanatory variables that have a significant association with PGG contribution are age and number of individuals from other villages invited to the annual harvest festival by a player's household; both have small positive effects on PGG contribution. We interpret the number of invitees to the annual harvest festival as a measure of social network size along the lines of another study (20); this festival is one of the biggest in the calendar year, during which people visit others' homes and invite their friends and relatives to eat and drink at their homes. Only two variables are significantly associated with player salt deviation, namely, village population size and the number of adult sisters residing in the village, both of which have negative effects; people in larger villages or with

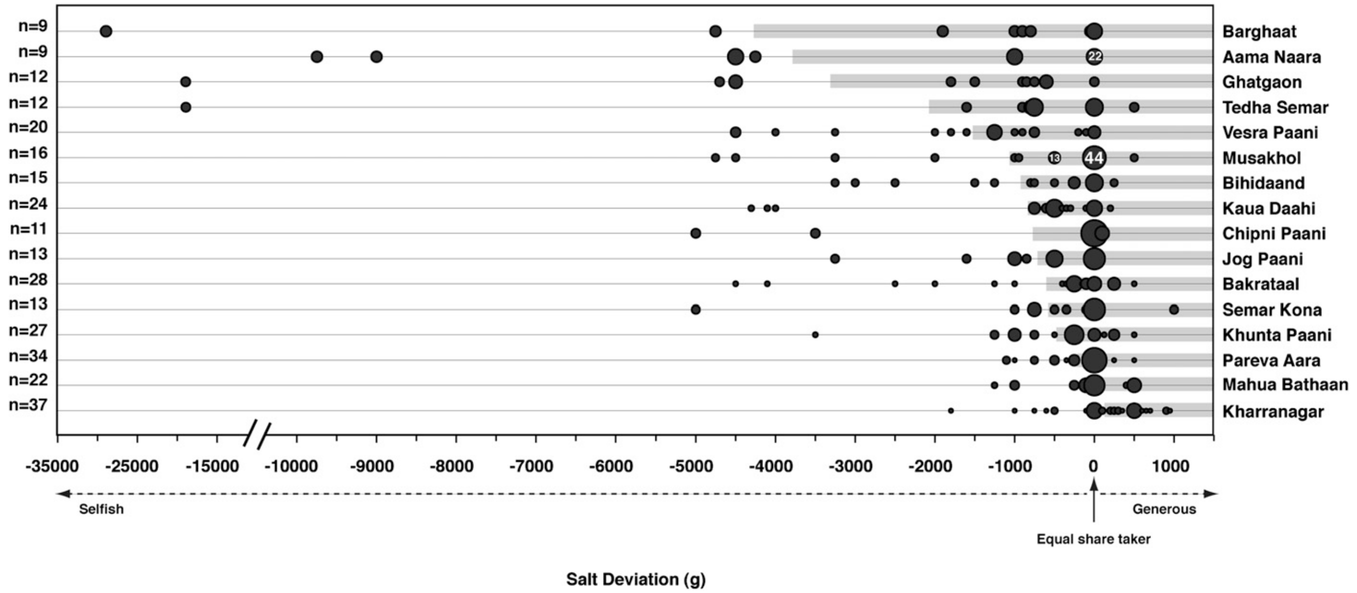

Fig. 2. Distributions of salt deviations (amount available per person − amount taken) across 16 villages. For each village on the *y* axis, the areas of the black bubbles represent the proportion of individuals from the village with salt deviation of the value on the *x* axis. Note the break in the *x* axis. To indicate scale, the numbers in some bubbles are the percentage proportions represented by those bubbles. Gray horizontal bars indicate the mean salt deviations for villages. Villages are ordered by their mean salt deviations; the bottom village (Kharranagar) has the highest mean. The dashed line below the *x* axis marks whether a value of salt deviation indicates an "equal share taker" (salt taken = amount available per person), a "selfish" individual (salt taken > amount available per person), or a "generous" individual (salt taken < amount available per person). Counts on the left (*n*) represent the number of salt takers from each village (total *n* = 302). The overall mode across villages is 0 g (mean ± SD = −913.33 ± 2,619.02).

more adult sisters residing in the village take more of the salt. Pseudo-R^2 values indicate that for PGG contribution, about 28% of variance between populations and 4% of variance within populations are explained by these explanatory variables. For salt deviation, about 32% of variance between populations and 9% of variance within populations are explained by these explanatory variables. Players' migration histories, frequency of market contact, and multiple measures of wealth have little effect on their PGG contributions or salt decisions.

The negative relationship between levels of cooperation and village population size is in the direction predicted by most evolutionary models. Two recent studies found that individuals from large populations are more willing to punish defectors (3, 17); they infer that the enforcement of norms promoting cooperation is stronger in large and more complex societies. Both of these studies sampled from one or a few populations per society and assumed that population size effects reflected the influence of societal complexity. Our results challenge this conclusion because we demonstrate an association between population size and cooperation that is independent of variation in structural features of populations, such as socio-political complexity and religion.

PGG contributions and salt deviations show a significant positive correlation across individuals (details are presented in Table S3); however, partitioning the correlation shows that most of the association is at the village level ($\rho = 0.397$), with only a weak correlation at the individual level ($\rho = 0.043$). Once explanatory variables are included in the model, residual correlation increases substantially at the village level ($\rho = 0.871$) and only marginally at the individual level ($\rho = 0.057$). This suggests that properties of the common village environment trigger similar cooperative propensities in the PGG and salt decisions but that individual variation in some aspect of personality does not determine behavior in these measures of cooperation.

In summary, we find significant variation in cooperative behavior across 16 populations of the same small-scale society, and this variation is partly explained by demographic differences between populations. Theory predicts that factors like population size and age structures affect the balance of cooperation and competition within a population (21, 22). It is possible that some of the behavioral variation between our study populations is driven by norms at the level of the population or village unit rather than at the level of the endogamous cultural unit; this hypothesis needs to be tested empirically. However, village-level norms can exist only if conformism to these norms is strong enough to counter any behavioral variation introduced within villages by the high levels of migration that we report (Table 1). Moreover, the fact that behavioral variation is at least partly contingent on environmental differences between populations questions the existence of stable norms of cooperation. Our findings call for reinterpretation of cross-cultural data on cooperation based on samples from one population (or a few populations) per culture (1–6); behavioral variation currently attributed to cultural norms may, in fact, be driven by ecological and demographic differences between populations. Thus, existing cross-cultural data do not provide support for cultural group selection models of the evolution of cooperation.

In cultural group selection models (7–10, 12), cultural transmission mechanisms, such as conformism, by definition, do not involve individuals computing the benefit of a behavior in a particular environment. Instead, individuals who conform simply copy the highest frequency behavior. Thus, conformism to group norms produces patterns of behavioral variation that are not solely contingent on the environment and maintains behavioral variation between populations despite genetic mixing and migration. The finding that behavior is correlated with the environment does not let us infer whether it is transmitted culturally or genetically; however, it also does not let us reject the hypothesis that behavior is solely contingent on the environment and not on group norms. Moreover, if cultural transmission produces environmentally contingent patterns of behavioral variation that are similar to those produced via the genetic transmission of behavior, it may simply be a proximate transmission mechanism and will not necessarily lead to cultural group selection as described in the models. Thus, our findings present an empirical challenge for cultural group selection as a general explanation for the evolution of large-scale cooperation and emphasize the central role of demography and ecology in shaping human social behavior.

Materials and Methods

This study has full approval from the Ethics Committee at University College London, and informed consent was obtained from all participants. The following is a summary of our methods and analyses. Further details are provided in *SI Text*.

PGGs. All games were played between February 2 and May 16, 2008. All games in most villages were administered on the third day after arrival in the village (the second day in four villages and the fourth day in one village) and completed in a single day. Mean age ± SD of participants was 34.59 ± 12.13 y, and 46% were female.

To summarize the key features of our standardized protocol:

i) Instructions were delivered from a standardized script (*SI Text* section 1.8) in Sargujia, and real money was used to demonstrate game rules and examples. Only individuals who correctly answered a set of questions played the game; the questions were designed to assess their understanding of the game and experimental set-up.

ii) Decisions were made individually at a private location, and no names were recorded; a player's only identification was a numbered token.

iii) Those who had played the games were prevented from interacting with those who had not yet played.

iv) All games in all villages were administered by one of the authors (S.L.), usually on the third day after arrival in the village (the second or fourth day in a few cases) and were completed in a single day. Before this study, the authors had no contact with any individual from any of the 16 villages included in this study.

Our study design therefore excludes the following confounding causes of variation across populations: (*i*) context and framing effects, (*ii*) experimenter variation, (*iii*) experimenter familiarity, (*iv*) differences in recruitment methods and time periods over which games were conducted in different populations, and (*v*) differences in protocols. Cross-cultural studies (1–4), mostly administered by multiple researchers, did not exclude and could not test for these confounding causes of variation between their study populations.

Participants collected their payments individually at a private location in exchange for their identification tokens, and the order in which they did so was randomized. All payments were made in real money in exact change.

Salt Decisions. Participants made their salt decisions on arriving to collect their payments at a private location. The salt decision was made before a player's earnings from the games were made known and given to her. The private location for the payments was chosen so that players could subsequently go home by a route unseen by the other waiting players. This ensured that each player could take away her desired salt quantity unseen by others and that waiting participants did not prematurely find out about the salt. Hence, participants encountered the salt for the first time when they individually collected their payments and possessed no prior information about it. They did not know how much salt was available to anyone else.

All information about the salt was delivered by one of the authors (S.L.) from a standardized script (*SI Text* section 1.8), and a research assistant weighed the desired quantity. The total amount available (x) and the amount available per person ($z = x/y$) were calculated to the nearest 100 g for each person.

Semiexperimental methods, as implemented with the salt decision, offer promise for modifying economic game methodology to obtain measures of human behavior outside an experimental context. Such measures are more likely to capture behavior in the real world. By definition, it is impracticable to obtain real-world observational data on individual behavior under one-shot anonymous conditions. Data on repeated and/or nonanonymous real-world behavior do not allow a fair evaluation of the real-world external validity of one-shot anonymous economic games because behavior under repeated

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nonanonymous conditions may be driven by different factors from that under one-shot anonymous conditions.

Demographic and Individual Data. Demographic and other data on individuals were collected via a standardized questionnaire administered by a research assistant. Once all games in a village had been completed, a population census was conducted and the geographic coordinates for every house in the village were recorded using a global positioning system (Garmin GPS 12XL). Geographic information systems (GIS) data were processed and analyzed in ArcGIS (version 9.2; Environmental Systems Research Institute). Table S5 lists all village and individual descriptors that were included in the analyses and provides a description of each variable.

Analyses. Multilevel multivariate response models (15, 23, 24) were used to analyze variation explicitly at the village and individual levels in our structured data (individuals within villages) and the relationship of population and individual descriptors with the measure of cooperation (response variable). Multivariate response models allow us to model multiple response variables, PGG contribution and salt deviation in this case, simultaneously. They therefore allow simultaneous estimation of effects of explanatory variables on each response variable. Models contained two response variables, PGG contribution and salt deviation, for individuals (level 1) nested within villages (level 2). We also obtained the residual correlation between the two response variables, both at the individual (level 1) and village (level 2) levels, through an analysis of the covariance structure. Multivariate response models accommodate missing data for the response variables; individuals who had a response value for only PGG contribution or salt deviation were included in the analyses. All multilevel analyses were conducted in MLwiN, version 2.14 (23, 24). We mainly use an information-theoretic model-fitting approach (25, 26) to analyze data and interpret results. Analyses proceeded in four stages (details provided in *SI Text* section 1.6 and Tables S6–S8) and included a series of domain-wise (sets of related variables, such as those measuring wealth and kin, as described in Table S5) models in view of the large number of variables analyzed and the potential correlations between them.

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