

**THE EVOLUTION OF
LARGE-SCALE COOPERATION
IN HUMAN POPULATIONS**

Shakti Lamba

Department of Anthropology

UCL

A thesis submitted for the degree of

Doctor of Philosophy

2010

DECLARATION

I, Shakti Lamba, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

ABSTRACT

Large-scale cooperation between unrelated humans is a major evolutionary puzzle. Natural selection should favour traits benefiting the self, whereas cooperation entails a cost to self to benefit another. The work presented in this thesis makes an empirical contribution towards understanding the evolution of large-scale cooperation in humans.

Theory posits that large-scale cooperation evolves via selection acting on populations amongst which variation is maintained by cultural transmission. While cross-cultural variation in cooperation is taken as evidence in support of this theory, most studies confound cultural and environmental differences between populations. I test and find support for the hypothesis that variation in levels of cooperation between populations is driven by differences in demography and ecology rather than culture.

I use economic games and a new ‘real-world’ measure of cooperation to demonstrate significant variation in levels of cooperation across 21 villages of the same small-scale, forager society, the Pahari Korwa of central India. Demographic factors explain part of this variation. Variation between populations of the *same* cultural group in this study is comparable in magnitude to that found between *different* cultural groups in previous studies.

Experiments conducted in 14 of the villages demonstrate that the majority of individuals do not employ social learning in the context of a cooperative dilemma. Frequency of social learning varies considerably across populations; I identify demographic factors associated with the learning strategy individuals employ.

My findings empirically challenge cultural group selection models of large-scale cooperation; behavioural variation driven by demographic and ecological factors is unlikely to maintain stable differences essential for selection at the population-level. This calls for re-interpretation of cross-cultural data sampled from few populations per society; behavioural variation attributed to ‘cultural norms’ may reflect environmental variation. The work presented in this thesis emphasises the central role of demography and ecology in shaping human social behaviour.

ACKNOWLEDGEMENTS

I thank the Pahari Korwa for welcoming me into their villages and homes and for their hospitality. I am indebted to Gangaram Paikra; this study would not have been possible without his extraordinary help and unfailing support in Chhattisgarh.

The work presented in this thesis has benefited from the input of Ruth Mace, Laura Fortunato, David Lawson, Heidi Colleran, Tom Currie, Kesson Magid and Fiona Jordan, in the form of discussion, comments and encouragement. I am grateful to Ruth Mace for acting as my primary supervisor and to Michael Stewart for acting as my secondary supervisor.

This research was funded via a Cogito Foundation PhD Studentship, a Cogito Foundation Research Grant, a Parkes Foundation Small Grant and a UCL Graduate School Research Grant.

I thank Kundal Singh, Anil Kumar, Laxman Shastri, Narendra Das, Shivcharan Das and Petrus Lakra for their assistance and company in the field. Many thanks to Tirki Ji and Chandrabhan Singh for their input on logistics, as well as to Lata Paikra and members of the organisation Chaupal for looking after me through my stay in Chhattisgarh. I also thank Karam Vir Lamba and Katharine Balolia for help with entering the data and checking it for errors, as well as Christian Hennig and Mai Stafford for advice on multilevel analyses, and Andrew Bevan for advice on GIS analyses.

I am very grateful to Laura Fortunato and David Lawson who provided detailed and thoughtful comments on a draft of the entire thesis. Many thanks to Gayatri Lamba for proof-reading the thesis and to Waleed Mohammed for help with formatting.

Above all, I am grateful to my family for their continuing and unfailing love and support and to Waleed Mohammed for looking after me through it all.

CONTENTS

Figures	11
Tables	13
Acronyms	18
Definitions	19
Chapter 1. Introduction	20
1.1 Preamble.....	20
1.2 The evolutionary dilemma of cooperation	20
1.3 Solving the dilemma of cooperation	22
1.3.1 Natural selection in a structured population.....	22
1.3.2 The function of population structure - variance between groups or relatedness within them	23
1.3.3 Defining relatedness.....	25
1.3.4 Generating phenotypic relatedness	26
1.4 Evolutionary models of cooperation	27
1.4.1 Kin selection (relatedness by common ancestry).....	27
1.4.2 Green beard and tag-based models (relatedness by assortment).....	28
1.4.3 Reciprocity (relatedness by prior interaction).....	30
1.5. The evolutionary dilemma of large-scale cooperation.....	31
1.6 Solving the dilemma of large-scale cooperation.....	32
1.6.1 Cultural group selection (relatedness by social learning)	32
1.6.2 The empirical evidence	33
1.7 Aims of the thesis.....	37
1.8 Structure of the thesis.....	39

Chapter 2. Study populations and methods.....	40
2.1 Features of a good model system for this study.....	40
2.2 The Pahari Korwa	41
2.2.1 Ethnographic description	41
2.2.2 Distribution	44
2.2.3 Climate, flora and fauna.....	45
2.3 Study site.....	46
2.3.1 Establishing the field-site.....	46
2.3.2 Study set-up.....	47
2.3.2.1 Sampling and logistics	47
2.3.2.2 Village details.....	49
2.4 Methods.....	55
2.4.1 Behavioural data.....	55
2.4.1.1 Anonymity	55
2.4.1.2 Game instructions and testing.....	56
2.4.1.3 Administration	56
2.4.1.4 Payments	57
2.4.2 Demographic and individual data	58
2.4.3 Qualitative data	64
2.5 Analyses	64
2.5.1 Data processing	64
2.5.2 Multilevel models	64
2.5.3 GIS analyses.....	67
 Section I. Variation in cooperation across populations	 68
 Chapter 3. Variation in cooperation across populations: evidence from the ultimatum game.....	 69
3.1 Introduction	69
3.1.1 Background and related research	69
3.1.2 Behavioural measures	71
3.2 Results	72

3.2.1 Proposers	73
3.2.1.1 Do proposer offers vary across populations?	73
3.2.1.2 Do properties of populations and/or individuals explain variation in proposer offers between and within populations?.....	75
3.2.2 Responders	77
3.2.2.1 Does responder behaviour vary across populations?	77
3.2.2.2 Do self-reported MAOs vary across populations?.....	79
3.2.2.3 Do properties of populations and/or individuals explain variation in self-reported MAOs between and within populations?.....	82
3.2.3 Is proposer behaviour contingent on responder behaviour?	86
3.3 Discussion	87
3.3.1 Variation in proposer behaviour	87
3.3.2 Correlates of proposer behaviour	87
3.3.3 Variation in responder behaviour.....	89
3.3.4 Self-reported behavioural strategies.....	91
3.3.5 Discrepancies in proposer and responder behaviour.....	92
3.3.6 Concluding remarks	93
3.4 Methods.....	94
3.4.1 Experimental set-up	94
3.4.2 Statistical analyses	95

Chapter 4. Variation in cooperation across populations: evidence from public goods games and a ‘real-world’ measure of behaviour **97**

4.1 Introduction	97
4.1.1 Background and related research	97
4.1.2 Behavioural measures	99
4.2 Results	101
4.2.1 Do PGG contributions and salt deviations vary across populations?	102
4.2.2 Do properties of populations and/or individuals explain variation in PGG contribution and salt deviation between and within populations?	105
4.2.3 Is there a correlation between individuals’ PGG contributions and salt deviations?.....	107

4.3 Discussion	107
4.3.1 Variation in cooperative behaviour	107
4.3.2 Correlates of cooperative behaviour	107
4.3.3 A new measure of cooperation	110
4.3.4 Concluding remarks	111
4.4 Methods	112
4.4.1 Public goods game set-up	112
4.4.2 Salt decisions set-up	113
4.4.3 Statistical analyses	114
Section II. Social learning in the cooperative domain	115
Chapter 5. Social learning in the cooperative domain: evidence from public goods game experiments	116
5.1 Introduction	116
5.1.1 Background and related research	116
5.1.2 Behavioural measures	120
5.2 Results	125
5.2.1 Is there evidence that individuals use information on the MC and HEC in making their PGG2 contributions?	126
5.2.2. Do the overall frequencies of learning strategies vary?	130
5.2.3. Does the distribution of learning strategies vary across populations?	132
5.2.4. Are properties of populations and/or individuals associated with the learning strategies employed by individuals?	139
5.2.5. Do different learning strategies result in the acquisition of different behavioural traits?	142
5.3 Discussion	146
5.3.1 Evidence for social learning in a cooperative dilemma	146
5.3.2 Correlates of learning strategies	147
5.3.3 The impact of learning on the distribution of trait variants	150
5.3.4 Unidentifiable strategies	151
5.3.5 Concluding remarks	152

5.4 Methods.....	153
5.4.1 Experimental set-up	153
5.4.2 Statistical analyses	154
 Section III. Conclusion	 156
 Chapter 6. Conclusion	 157
6.1 Implications for an understanding of the evolution of large-scale cooperation in humans	157
6.2 Implications for an understanding of the structure of cultural inheritance systems	163
 References	 166
 Appendix A. Game Scripts	 195
A.1 Ultimatum game (UG)	195
A.2 Public goods game round 1 (PGG1)	203
A.3 Salt decision	212
A.4 Public goods game round 2 (PGG2)	213
 Appendix B. Data Sheets	 218
B.1 Individual data sheet.....	218
B.2 Village data sheet	222
B.3 Housing data sheet.....	225
B.4 Qualitative data sheet	226
 Appendix C. Statistical Analyses	 229
C.1 UG Proposer offer (Chapter 3, Section 3.2.1).....	230
C.1.1 Univariate Models	230
C.1.2 Domain-wise models.....	232
C.1.3 Full model fitting summary.....	234
C.2 UG Responder MAO (Chapter 3, Section 3.2.2).....	235
C.2.1 Univariate Models	235

C.2.1.1 Normal linear models	235
C.2.1.2 Ordinal multinomial models	237
C.2.2 Domain-wise models	239
C.2.2.1 Normal linear models	239
C.2.2.2 Ordinal multinomial models	241
C.2.3 Full model fitting summary	243
C.2.3.1 Normal linear models	243
C.2.3.2 Ordinal multinomial models	244
C.3 Salt decision and PGG1 contribution (Chapter 4, Section 4.2)	245
C.3.1 Univariate Models	245
C.3.2 Domain-wise models	247
C.3.3 Full model fitting summary	249
C.4 PGG2 contribution (Chapter 5, Section 5.2.1)	250
C.4.1 Univariate Models	250
C.4.2 Domain-wise models	252
C.4.3 Full model fitting summary	254
C.5 PGG2 learning strategies (Chapter 5, Sections 5.2.3 and 5.2.4)	255
C.5.1 Univariate Models	255
C.5.1.1 Four category classification of learning strategies (payoff copier, conformist, individualist and unidentifiable)	255
C.5.1.2 Three category classification of learning strategies (social learner, individualist and unidentifiable)	258
C.5.2 Domain-wise models	260
C.5.2.1 Four category classification of learning strategies (payoff copier, conformist, individualist and unidentifiable)	260
C.5.2.2 Three category classification of learning strategies (social learner, individualist and unidentifiable)	262
C.5.3 Full model fitting summary	264
C.5.3.1 Four category classification of learning strategies (payoff copier, conformist, individualist and unidentifiable)	264
C.5.3.2 Three category classification of learning strategies (social learner, individualist and unidentifiable)	267

FIGURES

2.1 Map of Chhattisgarh.....	44
2.2 Maps of (A) the distribution of the 21 study villages and the town Ambikapur, and (B) the elevation of the 21 study villages and Ambikapur.....	51
3.1 Distributions of UG proposer offers across 21 villages.....	74
3.2 Distributions of UG responder responses across 21 villages.....	78
3.3 Distributions of UG responder MAOs across 16 villages.....	81
4.1 Distributions of PGG contributions across 16 villages.....	103
4.2 Distributions of salt deviations across 16 villages.....	104
5.1 Classification of a player's learning strategy.....	124
5.2 Distributions of (A) PGG2 contributions, and (B) PGG1 contributions, across 14 villages.....	128
5.3 Frequencies of player learning strategies for individuals from 14 villages pooled together.....	131
5.4 Distributions of player learning strategies across 14 villages. Figures compare frequencies of, (A) payoff copiers, conformists, individualists and unidentifiable individuals, and (B) social learners, individualists and unidentifiable individuals. ...	134

5.5 Frequencies of player learning strategies within each village. Figures compare frequencies of (A) payoff copiers, conformists, individualists and unidentifiable individuals, and (B) social learners, individualists and unidentifiable individuals..... 141

5.6 Mean contributions to the group pot in the PGG1 and PGG2 pooled across 14 villages for players with different learning strategies for (A) payoff copiers, conformists, individualists and unidentifiable individuals respectively, and (B) social learners, individualists and unidentifiable individuals respectively 144

TABLES

2.1 Summary statistics of demographic variables for the study populations and the behavioural measures of cooperation implemented in each village.....	50
2.2 Village means for basic individual descriptors and residence and migration variables for participants from each study population..	52
2.3 Village means for measures of wealth, market contact and social networks for participants from each study population..	53
2.4 Summary of amenities in each village.	54
2.5 List of village and individual descriptors included in all analyses.	60
3.1 Numbers (n) of proposers and responders from each of 21 study villages.....	72
3.2 (A) Associations of each predictor term (fixed effect) with proposer offers in the null (intercept only) and full models. (B) Village and individual level variance components for proposer offer in the null and full models	76
3.3 Numbers (n) of UG responder responses for each of 21 study villages.....	77
3.4 (A) Associations of each predictor term (fixed effect) with responder MAO in the null (intercept only) and full models. (B) Village and individual level variance components for responder MAO in the null and full models	84
3.5 (A) Associations of each predictor term (fixed effect) with the probability of responder MAO \leq 10 Indian rupees in the null (intercept only) and full models. (B) Village level variance and the VPC for the logit (probability of responder MAO \leq 10 Indian rupees) in the null and full models.....	85

3.6 Income-maximising offers (IMO) and mean proposer offers for villages where at least one offer was rejected. 86

4.1 Numbers (n) of PGG players and salt takers from each of 16 study villages 101

4.2 (A) Associations of each predictor term (fixed effect) with salt deviation and PGG contribution respectively in the null (intercept only) and full models. (B) Village and individual level variance components for salt deviation and PGG contributions respectively in the null and full models 106

5.1 Number of players (n) who played both PGG1 and PGG2 from each of 14 study villages 125

5.2 Null model (intercept only) variance components for PGG1 and PGG2 contributions 127

5.3 (A) Associations of each predictor term (fixed effect) with PGG2 contribution in the null (intercept only) and full models. (B) Village and individual level variance components for PGG2 contribution in the null and full models 129

5.4 Results of chi-squared tests comparing frequencies of player learning strategies for individuals from 14 villages pooled together..... 132

5.5A Associations of each predictor term (fixed effect) with the odds of being a payoff copier, conformist or unidentifiable relative to an individualist respectively, in the null (intercept only) and full models 135

5.5B Variance components for the log odds of being a payoff copier, conformist or unidentifiable relative to an individualist respectively in the null and full models.... 135

5.6A Associations of each predictor term (fixed effect) with the odds of being a social learner or unidentifiable relative to an individualist respectively, in the null (intercept only) and full models	137
5.6B Variance components for the log odds of being a social learner or unidentifiable relative to an individualist respectively in the null and full models.....	137
5.7 Results of Kruskal-Wallis and Mann-Whitney tests comparing the PGG1 and PGG2 contributions of players with different learning strategies from 14 villages pooled together.....	145
C.1 Univariate associations between each predictor term (fixed effect) and UG offer.....	230
C.2 Multivariate associations between domains of predictor terms (fixed effects) and UG offer	232
C.3 Summary of model-fitting process in the fourth stage of analyses for UG offers....	234
C.4 Univariate associations between each predictor term and UG MAO.....	235
C.5 Univariate associations between each predictor term (fixed effect) and logit (probability of UG MAO Indian Rupees 10+ or below).....	237
C.6 Multivariate associations between domains of predictor terms (fixed effects) and UG MAO	239
C.7 Multivariate associations between domains of predictor terms (fixed effects) and logit (probability of UG MAO Indian Rupees 10+ or below).....	241
C.8 Summary of model-fitting process in the fourth stage of analyses for UG MAO modelled as a continuous variable	243

C.9 Summary of model-fitting process in the fourth stage of analyses for UG MAO modelled as an ordinal variable..... 244

C.10 Univariate associations between each predictor term (fixed effect) and Salt deviation and PGG1 contribution respectively 245

C.11 Multivariate associations between domains of predictor terms (fixed effects) and Salt deviation and PGG1 contribution respectively 247

C.12 Summary of model-fitting process in the fourth stage of analyses for Salt deviation and PGG1 contributions..... 249

C.13 Univariate associations between each predictor term (fixed effect) and PGG2 contribution.. 250

C.14 Multivariate associations between domains of predictor terms (fixed effects) and PGG2 contribution 252

C.15 Summary of model-fitting process in the fourth stage of analyses for PGG2 contribution. 254

C.16 Univariate associations between each predictor term (fixed effect) and the log-odds of being a payoff copier, conformist or unidentifiable relative to an individualist respectively 255

C.17 Univariate associations between each predictor term (fixed effect) and the log-odds of being a social learner or unidentifiable relative to an individualist respectively 258

C.18 Multivariate associations between domains of predictor terms (fixed effects) and the log-odds of being a payoff copier, conformist or unidentifiable relative to an individualist respectively. 260

C.19 Multivariate associations between domains of predictor terms (fixed effects) and the log-odds of being a social learner or unidentifiable relative to an individualist respectively 262

C.20 Summary of model-fitting process in the fourth stage of analyses for payoff copiers, conformists and unidentifiable individuals, relative to individualists respectively .. 264

C.21 Alternative Block 1 analyses for model-fit summary presented in Table C3.20. .. 266

C.22 Summary of model-fitting process in the fourth stage of analyses for social learners, and unidentifiable individuals, relative to individualists respectively 267

ACRONYMS

UG	Ultimatum game
PGG	Public goods game
SD	Salt decision
PGG1	Public goods game round 1
PGG2	Public goods game round 2
MAO	Minimum acceptable offer
IMO	Income maximising offer
HEC	Highest earner's contribution
MC	Modal contribution
DIC	Deviance information criterion
BCI	Bayesian confidence interval
VPC	Variance partition coefficient

DEFINITIONS

The definitions in this list apply throughout this thesis.

Culture

Information capable of affecting individuals' phenotypes which they acquire from other conspecifics by teaching or imitation (Boyd & Richerson 1985).

Social learning / Cultural transmission

The non-genetic transfer of information from one individual to another via mechanisms such as teaching, imitation and language (Boyd & Richerson 1985; Mesoudi 2009). The above two terms are used interchangeably.

Cultural group/ ethnic group/society

A group of individuals whose members identify with each other and are recognised as a group by others on the basis of shared ancestry, language, religion, institutions or other ethnic traits. The above three terms are used interchangeably. This definition emphasises that other than when groups are defined on the basis of shared ancestry, the defining traits of a group are culturally transmitted.

Environment

The ecological and demographic features of an organism's habitat.

CHAPTER 1

INTRODUCTION

1.1 Preamble

At the height of Nazi persecution of the Jews during the Second World War, all 117 inhabitants of a small Dutch village called Nieuwlande resolved that each household would hide and shelter at least one Jewish person during the German occupation of The Netherlands. The 117 residents of Nieuwlande are among the 23,226 individuals (as of January 1st, 2010) on whom the State of Israel has conferred the title of ‘The Righteous among the Nations’, an honour bestowed on non-Jews who risked their lives to save Jews from extermination during the Holocaust (Yad Vashem 2010). The honourees include people from 44 countries.

1.2 The evolutionary dilemma of cooperation

Humans are not always selfish. Helping behaviour is commonplace in most human societies and, one may argue, it is the very premise of social organisation. The degree and scale of helping may vary across human populations, but its ubiquity is unequivocal. What makes widespread and frequent helping behaviour so remarkable? More often than not, extending help to another individual imposes an immediate cost on the helper, be this in terms of material resources, time or energy. The term cooperation refers to such instances of costly helping. The preamble in Section 1.1 demonstrates the magnitude of the costs that individuals are willing to bear for the sake of others, as well as the scale and universality of cooperation in humans. Inhabitants of an entire village extended help to individuals who were not even members of their families; this large-scale cooperation entailed a high risk of

1.2 THE EVOLUTIONARY DILEMMA OF COOPERATION

death, arguably the greatest cost an individual can incur. Moreover, the behaviour of the residents of Nieuwlande was not unique; thousands of individuals from across 44 nations took the same risk.

Natural selection should favour traits that increase the fitness of an organism (Li 1967; Price 1970; Robertson 1966), where fitness represents the lifetime number of offspring an organism produces. Assuming that costs and benefits from behaviour translate into fitness losses and gains respectively, cooperation by definition entails an apparent reduction in the immediate fitness of an organism. The evolution of cooperation thus presents an inherent dilemma – how does natural selection favour the cooperative trait that decreases the immediate fitness of an organism?

This thesis contributes towards an understanding of the evolution of large-scale cooperation in human populations. I begin, in Section 1.3, by outlining a unifying theoretical framework that can be used to study the evolution of cooperation across species. Within this framework, in Section 1.4 I review the principal theoretical models of the evolution of cooperation (excluding large-scale cooperation) and the empirical evidence in support of these models in humans. In Section 1.5 I provide a definition of large-scale cooperation as regarded in this thesis, and explain why the theoretical models described in Section 1.4 do not provide a satisfactory explanation for its evolution in humans. In Section 1.6 I review the theoretical models proposed to explain the evolution of large-scale cooperation in humans, and identify the empirical questions that must be addressed for these models to find support in nature. In Section 1.7 I define the aims of this thesis in light of the empirical questions identified in Section 1.6. Finally, Section 1.8 provides an outline of the structure of the thesis.

1.3 Solving the dilemma of cooperation

In this section I outline a unifying theoretical framework that can be used to study the evolution of cooperation across species.

1.3.1 Natural selection in a structured population

Evolution by natural selection is characterised by a change in trait frequency from one generation to the next (Darwin 1859) when the trait under selection affects the survival or reproduction of its bearers. A solution to the evolutionary dilemma of cooperation must therefore explain how an individually costly cooperative trait increases in frequency in a population when competing with an individually advantageous selfish trait. An appropriate point of departure is the Price equation (*Equation 1*: Price 1970, 1972). For a population divided into several sub-populations indexed by s , Price's equation is an expression for the expected change in frequency of a trait under selection.

$\bar{w}\Delta\bar{q} = \text{Covariance}(w_s, q_s) + \text{Expectation}(w_s \Delta q_s)$	<i>Equation 1</i> Adapted from Price (1970, 1972)
<p>\bar{w} = Mean fitness of the trait in the whole population</p> <p>w_s = Mean fitness of the trait in a sub-population</p> <p>q_s = Trait frequency in one sub-population</p> <p>$\Delta\bar{q}$ = Change in trait frequency over one generation in the whole population</p> <p>Δq_s = Change in trait frequency over one generation in a sub-population</p>	

Price's equation demonstrates that the frequency of a trait will increase if the sum of the two terms on the right-hand side of the equation is positive. These two terms may be interpreted as the partitioned effects of natural selection acting at different levels of a structured population, i.e. a population comprising sub-populations; the levels represent the unit of grouping (e.g. for a population with two levels, sub-populations and individuals may be the two levels). The expectation term is recursive and can be expanded to include the effects of more levels (Hamilton 1975; Price 1970). The equation thus provides a powerful way of analysing selection in populations with structure (Grafen 1985, 2006).

1.3 SOLVING THE DILEMMA OF COOPERATION

The Price equation contains within it a schema for the evolution of cooperation: an individually costly cooperative trait may increase in frequency if its positive payoff at a higher level of selection in a structured population exceeds its cost at a lower level. Natural selection acting at multiple levels of a structured population may therefore be key to the evolution of cooperation.

1.3.2 The function of population structure - variance between groups or relatedness within them

A rearrangement of the Price equation demonstrates that selection at any level depends on the presence of variation at that level in the trait under selection (*Equation 2*: Hamilton 1975; Wade 1985). Higher variance in a trait at a given level corresponds to a greater effect of selection at that level.

$\bar{w}\Delta\bar{q} = \beta_{w_s, q_s} \text{Variance}(q_s) + \text{Expectation}(w_s\Delta q_s)$	<i>Equation 2</i> Adapted from Hamilton (1975)												
<table style="width: 100%; border: none;"> <tr> <td style="padding-right: 10px;">\bar{w}</td> <td>= Mean fitness of the trait in the whole population</td> </tr> <tr> <td style="padding-right: 10px;">w_s</td> <td>= Mean fitness of the trait in a sub-population</td> </tr> <tr> <td style="padding-right: 10px;">q_s</td> <td>= Trait frequency in a sub-population</td> </tr> <tr> <td style="padding-right: 10px;">$\Delta\bar{q}$</td> <td>= Change in trait frequency over one generation in the whole population</td> </tr> <tr> <td style="padding-right: 10px;">Δq_s</td> <td>= Change in trait frequency over one generation in a sub-population</td> </tr> <tr> <td style="padding-right: 10px;">β_{w_s, q_s}</td> <td>= Regression coefficient of w_s on q_s</td> </tr> </table>		\bar{w}	= Mean fitness of the trait in the whole population	w_s	= Mean fitness of the trait in a sub-population	q_s	= Trait frequency in a sub-population	$\Delta\bar{q}$	= Change in trait frequency over one generation in the whole population	Δq_s	= Change in trait frequency over one generation in a sub-population	β_{w_s, q_s}	= Regression coefficient of w_s on q_s
\bar{w}	= Mean fitness of the trait in the whole population												
w_s	= Mean fitness of the trait in a sub-population												
q_s	= Trait frequency in a sub-population												
$\Delta\bar{q}$	= Change in trait frequency over one generation in the whole population												
Δq_s	= Change in trait frequency over one generation in a sub-population												
β_{w_s, q_s}	= Regression coefficient of w_s on q_s												

This implies that the positive effect of inter-group selection will result in a net positive change in the population frequency of a cooperative trait, either if a certain level of variance is maintained between groups, or if the variance within groups is lowered, or both.

William Hamilton expressed this same condition for the positive selection of a cooperative trait in terms of the trait's fitness effects on the individual performing the helping behaviour

1.3 SOLVING THE DILEMMA OF COOPERATION

(Hamilton 1964a, 1975), henceforth referred to as the focal individual. Hamilton's rule tells us that a cooperative behaviour that costs the focal individual c units of fitness and benefits the recipient of cooperation by b units will evolve if $rb - c > 0$, where r represents the genetic relatedness of the focal individual to the recipient. Individuals act to maximise 'inclusive fitness', comprising a 'direct fitness' component attributed to an individual's own offspring and an 'indirect fitness' component attributed to the offspring of other genetically related individuals (Grafen 1984, 2009; Hamilton 1964a, 1964b). Helping behaviour that reduces direct fitness by an amount c can still evolve if it increases inclusive fitness via a positive effect on indirect fitness represented by rb . Hence, natural selection will favour cooperative behaviour preferentially directed towards related individuals. Relatedness (r) between preferentially interacting groups of individuals is equivalent to the 'variance ratio', the ratio of between-group to total variance in the cooperative trait in a population (Equation 3: Breden 1990; Fletcher and Zwick 2007; Queller 1985, 1992; Wade 1985).

$r = \frac{\text{Variance } (q_s)}{\text{Variance } (q)}$	<i>Equation 3</i>
	Adapted from Breden (1990)
q_s = Trait frequency in a sub-population q = Trait frequency in whole population	

Thus an increase in the value of between-group variance relative to total variance, the condition favouring cooperation via inter-group selection according to the Price equation, corresponds to an increase in relatedness (r) within groups of preferentially interacting individuals, the condition favouring cooperation according to Hamilton's rule (Wade 1978, 1980). Population structures that can maintain variation between groups and relatedness within them will promote the evolution of cooperation.

1.3.3 Defining relatedness

Hamilton’s rule can be reformulated and expressed wholly in terms of the direct fitness effect that a cooperative behaviour has on the focal individual (*Equation 4*: Fletcher and Doebeli 2009; Fletcher and Zwick 2006; Queller 1985, 1992).

$-c + b \frac{\text{Covariance}(q_i, p')}{\text{Covariance}(q_i, p)} > 0$	<p><i>Equation 4</i></p> <p>Adapted from Queller (1985, 1992)</p>
<p><i>c</i> = Fitness cost if the focal individual is cooperative <i>b</i> = Fitness benefit if the focal individual’s partner is cooperative <i>q_i</i> = A diploid individual’s frequency of the cooperation allele (0, ½ or 1) <i>p</i> = An individual’s phenotypic value (1 = cooperative, 0 = not cooperative) <i>p'</i> = An individual’s partner’s phenotypic value (1 = cooperative, 0 = not cooperative)</p>	

This reformulation of Hamilton’s rule expresses the cost (*c*) of a behaviour (phenotype) as the effect of that behaviour on the focal individual’s fitness, and the benefit (*b*) as the effect of the group average phenotype on the focal individual’s fitness (Breden 1990; Fletcher and Zwick 2006, 2007). By generalising Hamilton’s rule, the reformulation provides a unifying framework to study the evolution of cooperation. It is formulated in terms of the direct fitness of the cooperative genotype of the focal individual, augmented by the benefits received from others with a cooperative phenotype. For cooperation to evolve, a fundamental, most general condition must be met (Fletcher and Doebeli 2009; Fletcher and Zwick 2006): the cost born by a cooperative individual must be offset by the direct fitness benefit she receives from others with a cooperative phenotype.

It thus becomes apparent that relatedness (*r*), the covariance ratio term in Queller’s equation (*Equation 4*: Queller 1985, 1992), is really a measure of ‘phenotypic relatedness’ or, in other words, the likelihood that a cooperative individual is in a group with other cooperators (Fletcher and Doebeli 2009; Fletcher and Zwick 2007; Queller 1985). It is a measure of statistical association between like types (Hamilton 1975; Michod and Hamilton 1980; Orlove and Wood 1978; Seger 1981 and reviewed in Frank 1998). High phenotypic

1.3 SOLVING THE DILEMMA OF COOPERATION

relatedness between preferentially interacting group members ensures that the cost born by a cooperative individual can be offset by the benefit she receives from the cooperation of other group members. The conventional formulation of Hamilton's rule specifies relatedness (r) as the degree of genetic similarity between the focal individual and the recipient of cooperation. This is valid for phenotypic traits that are completely specified by their genotype (Fletcher and Zwick 2007), since the degree of genetic similarity corresponds to the phenotypic similarity between individuals. However, when genotype does not completely specify phenotype, genetic relatedness no longer coincides with phenotypic similarity and must be replaced with a measure of phenotypic relatedness. So long as there is covariance between phenotype and fitness, Price's equation can be used to estimate the change in the trait's frequency under selection.

1.3.4 Generating phenotypic relatedness

A cooperative trait will increase in frequency as the likelihood that a cooperator will interact with another cooperator increases. Mechanisms that increase this likelihood should promote the evolution of cooperation by allowing cooperators to preferentially associate. Associations between individuals may arise in space, time or via other mechanisms such as genetic or cultural similarity (see Sections 1.4.1 to 1.4.3 and Section 1.6.1). Solving the evolutionary dilemma presented by cooperation thus entails identifying mechanisms that create population structures allowing individuals with similar trait values to be associated within groups, and the maintenance of variance in trait values between groups. Since most population processes are likely to affect inter- and intra-group variation simultaneously (Fletcher and Zwick 2007), the distinction between the independent effects of the inter- and intra-group components of selection may be superfluous, except for serving as an analytical tool.

1.4 Evolutionary models of cooperation

I now review the existing principal theoretical models of the evolution of cooperation. While the theoretical framework outlined above (Section 1.3) applies to the evolution of cooperation in any species, I focus on the extent to which this framework explains cooperation in humans. I therefore do not review the vast literature on cooperation in other species (for reviews of this literature see Dugatkin 2002; Dugatkin 1999). For each model presented, I identify the mechanism that facilitates within-group relatedness between individuals for the cooperative phenotype. Since most of these models can be (and usually are) constructed such that the cooperative phenotype corresponds perfectly with the cooperative genotype, the benefits of cooperation to the focal individual can either be formulated wholly in terms of direct fitness (Fletcher and Doebeli 2009; Queller 1985, 1992) or in terms of indirect fitness (Hamilton 1964a; Queller 1985). Some authors make a distinction between the terms ‘cooperation’ and ‘altruism’ (Hamilton 1964a, 1964b; Lehmann and Keller 2006; West et al. 2007) or ‘weak altruism’ and ‘strong altruism’ (Wilson 1979, 1990) based on whether a helping behaviour provides any direct fitness benefits to the focal individual or only indirect fitness benefits respectively (Kerr et al. 2004). This distinction is no longer useful if we work within David Queller and Jeffrey Fletcher and colleagues’ framework for the evolution of cooperation as the inclusive fitness approach is simply an alternative accounting system that is applicable to a subset of the mechanisms facilitating the phenotypic association of cooperators (Fletcher and Doebeli 2009).

1.4.1 Kin selection (relatedness by common ancestry)

Cooperation can evolve when help is preferentially directed towards genetic relatives of the focal individual (Hamilton 1964a, 1964b, 1975). Kin selection (Maynard Smith 1964) describes the specific circumstance where cooperation evolves due to within-group relatedness arising via common ancestry. Common ancestry is a reliable indicator that the recipient of cooperation shares genes, including the cooperation allele, with the focal

1.4 EVOLUTIONARY MODELS OF COOPERATION

individual (Grafen 2007, 2009) and is therefore also likely to exhibit the cooperative phenotype. Limited dispersal in multi-generational populations or the collective dispersal of relatives in groups promotes the association of relatives and the action of kin selection (Gardner and West 2006; Hamilton 1964a; Irwin and Taylor 2001; Kümmerli et al. 2009; Mitteldorf and Wilson 2000; Nowak et al. 1994; Nowak and May 1992; Taylor and Irwin 2000; West et al. 2002).

At a proximate level, kin selection is contingent on the availability of information about common ancestry. This information may most commonly be obtained from spatial cues such as a shared nest, colony or household or phenotype-matching when interacting individuals can estimate genotypic similarity based on phenotypic resemblance (Hamilton 1964b; Holmes and Sherman 1982; Lacy and Sherman 1983; Lehmann and Perrin 2002; Reeve 1989; Sherman et al. 1997).

There is substantial empirical evidence that humans favour kin across domains such as food sharing (Gurven et al. 2002; Gurven et al. 2000b; Marlowe 2010), cooperative hunting (Alvard 2003; Morgan 1979), providing financial aid (Bowles and Posel 2005), child care (Anderson et al. 1999; Flinn 1988; Marlowe 1999), mitigation of conflict (Chagnon and Bugos 1979; Daly and Wilson 1988a; Daly and Wilson 1988b) and even in their willingness to suffer physical pain to benefit someone in an experimental context (Madsen et al. 2007).

1.4.2 Green beard and tag-based models (relatedness by assortment)

Cooperation can evolve when help is preferentially directed towards individuals specifically sharing the cooperative allele with the focal individual (Grafen 2009; Hamilton 1964a; Lehmann and Keller 2006; Wilson and Dugatkin 1997). Theoretical models vary based on the mechanism by which such assortment is achieved. For instance, linkage disequilibrium between the allele responsible for cooperation and another allele encoding some phenotypic trait (a green beard for example) allows individuals to identify others possessing the cooperation allele (Haig 1997; Jansen and van Baalen 2006). An alternative

1.4 EVOLUTIONARY MODELS OF COOPERATION

and earlier formulation of the ‘green beard effect’ specifies a single complex gene coding for both cooperative behaviour as well as the phenotypic trait indicating its presence in an individual (Dawkins 1976; Hamilton 1964a, 1964b). In other models, individuals assort based only on whether they are similar with reference to an arbitrary characteristic or tag (Axelrod et al. 2004; Riolo et al. 2001). Within-group relatedness arises because individuals’ phenotypes for the ‘green beard’ gene or tags act as reliable indicators of whether they are likely to exhibit the cooperative phenotype. The maintenance of linkage between ‘green beard’ and cooperative genes is essential for cooperation to evolve via this mechanism. Since mutation and recombination are likely to break down such linkage, ‘green beard’ effects are generally considered unstable (Blaustein 1983; Dawkins 1976; Lehmann and Keller 2006).

‘Green beard’ genes have been reported in some species (Keller and Ross 1998; Queller et al. 2003; Summers and Crespi 2005 and reviewed in West and Gardner 2010). The evidence pertaining to tag-based recognition of cooperators in humans is mixed. While some experimental studies suggest that people can use facial and other cues to identify likely cooperators (Fetchenhauer et al. 2009; Pradel et al. 2009; Verplaetse et al. 2007), there is considerable evidence demonstrating that most humans, including trained policemen, can detect likely cheaters no better than chance (Aamodt and Custer 2006; DePaulo 1994; DePaulo et al. 1985; Ekman and O’Sullivan 1991; Zuckerman and Driver 1985). It has been suggested that culturally inherited traits like accents, rituals and practices or adornments, as well as arbitrary behavioural signals such as secret handshakes, may serve as tags (Riolo et al. 2001).

Cooperation can also evolve as a costly signal indicating the underlying quality of an individual as a potential mate, friend or ally (Gintis et al. 2001; McAndrew 2002; Roberts 1998; Zahavi and Zahavi 1997). In this case, the cooperative allele itself acts as a tag and a reliable indicator that the focal individual possesses some other fitness enhancing trait which makes her a desirable mate or interaction partner (Miller 2007). There is empirical evidence that in humans cooperative behaviour enhances individuals’ status and standing, affording them social advantages in the long run (Alvard and Gillespie 2004; Birkás et al.

2006; Gurven et al. 2000a; Hawkes and Bird 2002; Sosis 2000 and reviewed in Miller 2007).

1.4.3 Reciprocity (relatedness by prior interaction)

Cooperation can evolve when help is preferentially directed towards individuals who are known cooperators (Alexander 1987; Aoki 1983; Axelrod 1984; Brown et al. 1982; Trivers 1971). Knowledge of the recipient's prior cooperative history may come from the focal individual's own previous interaction with them (Axelrod and Hamilton 1981; Trivers 1971) or from knowledge of others' prior interactions with them (Leimar and Hammerstein 2001; Lotem et al. 1999; Milinski et al. 2002b; Mohtashemi and Mui 2003; Nowak and Sigmund 1998a, 1998b; Panchanathan and Boyd 2003, 2004). Within-group relatedness arises because an individual's prior behaviour acts as a reliable indicator of the likelihood that she will exhibit the cooperative phenotype in the future. Reciprocal cooperation (also known as reciprocal altruism) is called 'direct' (Trivers 1971) if individuals interact repeatedly with the same partner, and 'indirect' (Alexander 1987) if they interact on repeated occasions but with different partners. The two conditions necessary for reciprocal cooperation to evolve are (i) repeated interactions between the same (direct reciprocity) or different (indirect reciprocity) individuals, and (ii) information or memory of the outcome of the previous interaction (direct reciprocity) or cooperative reputation of the partner (indirect reciprocity). The availability of information or memory of a partner's prior behaviour is thus essential for reciprocity to evolve. It is unclear whether reciprocal cooperation can lead to stable cooperation in a population, especially in the face of individuals making errors, possessing imperfect memory or information and participating in limited interactions (reviewed in Lehmann and Keller 2006). Reciprocal cooperation is also unlikely to evolve when reciprocating groups are large (Boyd and Richerson 1988a).

There is strong, accumulating empirical evidence from laboratory experiments and field studies that humans demonstrate both direct reciprocity (Clark and Sefton 2001; Fehr and Gächter 1998; Gächter and Falk 2002; Gurven 2004b, 2004c; Gurven et al. 2002; Gurven et

1.5 THE EVOLUTIONARY DILEMMA OF LARGE-SCALE COOPERATION

al. 2000b; Kaplan and Hill 1985 and reviewed in Fehr and Fischbacher 2003 and Gächter and Herrmann 2009) as well as indirect reciprocity (Alpizar et al. 2008; Milinski et al. 2001; Milinski et al. 2002a, 2002b; Seinen and Schram 2006; Wedekind and Braithwaite 2002; Wedekind and Milinski 2000 and reviewed in Fehr and Fischbacher 2003 and Gächter and Herrmann 2009). However, studies of food sharing in small-scale societies have reported the high frequency of reciprocity amongst kin (Allen-Arave et al. 2008; Gurven et al. 2000b). Kin selection and reciprocity may therefore augment and stabilise each other in establishing cooperation in these populations.

1.5 The evolutionary dilemma of large-scale cooperation

Humans cooperate with non-kin, anonymously, in non-repeated interactions. Harvey Hornstein and colleagues demonstrated such cooperation in a remarkable social experiment (Hornstein et al. 1968). They planted several wallets in different public locations in New York City. The wallets contained money and some form of identification of the owner. About 50% of these wallets were returned, money intact, by strangers who happened upon them in one of the busiest metropolises in the world. The ‘wallet experiment’ has been replicated many times since, in locations across the world. Although the rate of return decreases as the amount of money in the wallets increases and there is geographical variation in the frequency of return, experimenters usually recover a significant proportion of wallets (reviewed in Etzioni 1986; Knack 2001).

There are two broad reasons why kin-selection, tag based models, and reciprocity do not provide satisfactory explanations for the evolution of the form of cooperation described above:

- i. Individuals do not preferentially direct cooperation towards kin, cannot use a phenotypic cue to identify fellow cooperators under anonymous conditions, and do not have access to reputational information on the recipient or expect any opportunities for future interactions. The mechanisms (common ancestry, assortment and prior

1.6 SOLVING THE DILEMMA OF LARGE-SCALE COOPERATION

information) of attaining within-group relatedness essential for the evolution of cooperation are thus unavailable.

- ii. These models are based on the maintenance of within-group phenotypic relatedness via genetic relatedness between preferentially interacting individuals. In other words, the models entail that genetic variance be maintained between groups of preferentially interacting individuals, albeit via different mechanisms. Within-group genetic relatedness or between-group genetic variance decays in large populations with high rates of migration due to genetic mixing between populations (reviewed in Grafen 1984 and Henrich 2004). The models thus provide an inadequate account of cooperation in large populations with significant levels of migration.

The current challenge is to explain how cooperation evolves, (i) when it is directed toward non-kin, in anonymous, non-repeated interactions, and/or (ii) in large populations with high levels of migration. Henceforth, I refer to cooperation under either of these conditions as large-scale cooperation.

1.6 Solving the dilemma of large-scale cooperation

1.6.1 Cultural group selection (relatedness by social learning)

Explaining the evolution of large-scale cooperation requires the identification of a mechanism that can maintain significant between-group variance and within-group relatedness for the cooperative trait under selection, in the face of migration. If the trait (phenotype) is completely determined by genotype, then maintaining between-group variation in the trait corresponds to maintaining between-group genetic variation in the trait. Genetic variance is difficult to maintain in large populations with significant levels of migration (reviewed in Grafen 1984 and Henrich 2004). A solution to the evolutionary dilemma of large-scale cooperation therefore requires a mechanism that interrupts the correspondence between genotype and phenotype so that phenotypic or trait variation may be maintained between groups of interacting individuals despite genetic mixing. Since

1.6 SOLVING THE DILEMMA OF LARGE-SCALE COOPERATION

natural selection acts on the phenotype (Fletcher and Zwick 2007; Mayr 1997), so long as there is covariance between the phenotype and fitness, the phenotypic trait with a positive fitness benefit should be selected for.

One mechanism that allows phenotype to diverge from genotype is social learning. If individuals can acquire behaviour by learning from or copying the behaviour of other individuals in their environment, then phenotypic variance may be maintained between groups despite genetic mixing (Boyd and Richerson 1985; Henrich 2004; Henrich and Boyd 1998). Random behavioural variance introduced between groups by stochastic processes like drift may be stabilised by social learning strategies such as conformity (a tendency to copy high frequency behaviour) and payoff biased learning (a tendency to acquire behaviour that has produced the highest payoff or greatest success for another individual), thus maintaining multiple stable equilibria and phenotypic variance across groups; selection acting on these alternative stable equilibria among competing groups can lead to the evolution of cooperation if group-level cooperation positively affects group survival or proliferation (Boyd et al. 2003; Boyd and Richerson 1982; Boyd and Richerson 1985; Gintis 2003; Guzmán et al. 2007; Henrich 2004; Henrich and Boyd 1998; Henrich and Boyd 2001; Richerson and Boyd 2005). In the absence of social learning, phenotypic variation corresponding to genetic variation between groups would be depleted by migration between them. Hence, within-group relatedness arises in cultural group selection models because individuals in a preferentially interacting group are likely to have the same behavioural strategy due to social learning (cultural transmission). The cost of cooperation is offset by the direct fitness benefit that a focal individual receives from being part of a group of cooperators. It may therefore be possible to use Queller's formulation of Hamilton's Rule to analyse the evolution of cooperation via cultural group selection (Fletcher and Zwick 2006, 2007).

1.6.2 The empirical evidence

Although we have a theoretical framework that potentially explains the evolution of large-scale cooperation in humans, much of this theory remains empirically untested in real-

1.6 SOLVING THE DILEMMA OF LARGE-SCALE COOPERATION

world populations. In order to establish whether cultural group selection models of the evolution of cooperation find support in nature, there are two major empirical questions that need to be answered:

A. Is there stable, heritable variation in levels of cooperation across human populations?

If cultural transmission maintains behavioural variance between groups, then we should expect to find stable, heritable differences in levels of cooperation across groups. Note that it is not adequate to simply establish that there is variation across groups. Selection at the group level requires that the variation between groups be heritable. Hence, in order to ascertain whether stable between-group variation in cooperation exists in the real world, it is important to establish whether (a) there is between-group variation in cooperation, and (b) the drivers of any existing variation are likely to maintain stable, heritable differences between groups across generations.

Experimental cross-cultural studies in small-scale (Henrich et al. 2004; Henrich et al. 2001; Henrich et al. 2005; Henrich et al. 2010; Henrich et al. 2006) and large-scale (Cardenas and Carpenter 2005; Herrmann et al. 2008; Roth et al. 1991) societies demonstrate variation in patterns of cooperation across cultural groups. The findings of these studies are taken as support for the existence of stable variation in levels of cooperation across human populations (Henrich et al. 2005; Henrich et al. 2006). However, these studies have mostly sampled from one population (city/village/settlement) per culture and confound cultural and environmental differences between populations. We cannot differentiate whether the behavioural variation across populations is driven by cultural transmission or environmental (demographic or ecological) differences between populations. While variation driven by cultural transmission is heritable, variation driven by demographic or ecological factors is not necessarily stable or heritable; environmental drivers of behavioural variation are less likely to maintain stable differences essential for selection at the population level.

1.6 SOLVING THE DILEMMA OF LARGE-SCALE COOPERATION

If cultural transmission occurs such that individuals are equally likely to sample behaviour from different populations of the same cultural group, and the benefit of cooperation is at the level of the cultural group (increased survival or proliferation), then selection between cultural groups can lead to the evolution of cooperation. In this case, support for cultural group selection models entails (a) behavioural variation across cultural groups, and (b) significantly lower variation across populations of the same cultural group than between different cultural groups. If the latter condition is not met, i.e. we find that variation across populations of the same cultural group is equal to or greater than variation between cultural groups, then the strength of selection between cultural groups would have to be very much higher than the strength of selection within groups for individually costly cooperation to be favoured by selection at the level of the cultural group; however, this constraint is generally considered too stringent to be satisfied often in nature (Henrich 2004), although it remains a theoretical possibility. The first focus of this thesis is to test the predictions outlined above (Section 1.7).

Alternatively, if cultural transmission occurs such that individuals selectively sample behaviour only from their population, rather than from other populations of the same cultural group, and the benefit of cooperation is at the level of the population, then selection between populations of the same cultural group can lead to the evolution of cooperation. In this case, support for cultural group selection models entails (a) behavioural variation across populations of the same cultural group, and (b) significantly lower variation across individuals of the same population than between different populations (assuming that the strength of selection between populations is not very much higher than the strength of selection within populations). It is less likely that populations of the same endogamous cultural group are the units of selection at the group level. Migration rates between these inter-marrying populations are likely to be very high. Forces maintaining within-population similarity (such as conformity and punishment of norm violation) need to be strong enough to counteract the variation introduced by migration. It is also unlikely that individuals sample and acquire behaviour only from members of the same population when migration between populations is high; sampling behaviour across populations will decrease between-population variance.

1.6 SOLVING THE DILEMMA OF LARGE-SCALE COOPERATION

To demonstrate support for cultural group selection models when the unit of selection is the cultural group, we need to establish that there is behavioural variation across cultural groups and that the variation between different endogamous cultural groups is greater than that between populations of the same endogamous cultural group; this assumes that the strength of selection between cultural groups is not much higher than the strength of selection within groups. Current empirical data do not answer the first empirical question.

B. Do people use social learning to acquire cooperative strategies?

Cultural group selection models of cooperation assume that individuals acquire cooperative strategies via social learning. We therefore need to establish whether humans have any proclivity to acquire cooperative behavioural strategies via social learning. Note that it is not adequate to simply establish that individuals have a tendency to acquire behaviour in general via social learning. Social learning is expected to be employed selectively in different task domains (Eriksson and Coultas 2009; Eriksson et al. 2007; Rowthorn et al. 2009). Hence, we need to determine whether humans tend to specifically acquire behavioural strategies in the cooperative domain via social learning; the second focus of this thesis is to test this assumption made by cultural group selection models of large-scale cooperation (Section 1.7).

The empirical literature demonstrating that humans use social learning to acquire behaviour and make judgements and decisions is vast (Bandura 1977; Festinger 1954 and reviewed in Laland 2004 and Mesoudi 2009). While a small number of studies have investigated the role of conformist learning in determining behaviour in a public goods dilemma (Bardsley and Sausgruber 2005; Carpenter 2004; Samuelson and Messick 1986; Schroeder et al. 1983; Smith and Bell 1994; Velez et al. 2009), these studies do not unequivocally measure conformist learning as defined and implemented in cultural group selection models, i.e. the disproportionate tendency to copy the majority (Boyd and Richerson 1985; Efferson et al. 2008; Mesoudi 2009); it is only such a disproportionate individual proclivity to acquire majority behaviour that has demonstrable homogenising effects within populations and

1.6 SOLVING THE DILEMMA OF LARGE-SCALE COOPERATION

creates heterogeneity between them (Boyd and Richerson 1985; Efferson et al. 2008). Thus, the present literature (reviewed in Section 5.1.1) does not adequately address the question of whether humans acquire behavioural strategies via social learning specifically in the cooperative domain. Current empirical data do not answer the second empirical question.

1.7 Aims of the thesis

In this thesis I contribute toward answering the two aforementioned empirical questions. I investigate (i) whether there is variation in levels of cooperation across populations of the same endogamous, small-scale, forager-horticulturist society, the Pahari Korwa of central India, and (ii) whether people demonstrate any proclivity to acquire cooperative behavioural strategies via social learning. The thesis is divided into three sections:

1. Variation in cooperation across populations

In this section I examine whether there is variation in levels of cooperation within and between multiple populations of the *same* endogamous small-scale society, the Pahari Korwa, and whether demographic or ecological factors explain any part of this variation. This helps clarify whether behavioural variation between populations of the same endogamous cultural group is less than the behavioural variation found between different endogamous cultural groups in previous studies (Henrich et al. 2001; Henrich et al. 2005; Henrich et al. 2006; Herrmann et al. 2008); support for cultural group selection models, when the unit of selection is the cultural group, requires establishing that there is behavioural variation across cultural groups and that it is greater than the variation between populations of the same endogamous cultural group, assuming that the strength of selection between cultural groups is not much higher than the strength of selection within groups (Section 1.6.2). I control for cultural differences between populations to tease apart the effects on behavioural variation of environment (ecology and demography) versus culture. There are several reasons that advocate controlling for culture rather than environment in the first instance. First, finding variation between cultural groups living in the same

environment would not allow us to exclude the hypothesis that this variation is driven by demographic processes, unless we also ascertain the level of variation across populations of the same cultural group. Second, cultural identity is more clearly defined than consistency in environment, especially for endogamous small-scale societies, where there are clear rules regarding individuals' inclusion in and exclusion from the cultural group. Third, the null hypothesis derived from assuming systematic or mechanistic continuity with species that are acultural (although see Hoppitt et al. 2008, Laland 2008 and Laland and Janik 2006 for reviews of evidence for social learning in non-human animals) is that any within-species, between-population behavioural variation is driven by ecological and demographic processes.

I use three measures of cooperation: two different economic games (Camerer 2003; Kagel and Roth 1995) and one 'real-world' measure of cooperative behaviour in up to 21 distinct Pahari Korwa populations. I examine whether any existing variation in game behaviour within and between populations is explained by properties of populations and/or individuals. Economic games derived from behavioural game theory are the best available tools that we can currently employ to quantitatively measure one-shot, anonymous, cooperative behaviour in humans. They allow us the flexibility to control experimental parameters of interest or sources of error. Over past decades, they have provided great insights into human economic and social behaviour, both in the laboratory and in the field (Roth 1995b).

II. Social learning in the cooperative domain

In this section I use an economic game experiment to investigate whether individuals facing a public goods dilemma use information about others' behavioural strategies to make their decisions; the experiments were conducted in 14 Pahari Korwa populations. I further examine whether there is variation in the distribution of different learning strategies across populations and whether properties of populations and/or individuals are associated with the type of learning strategy employed by individuals. Finally, I consider whether the learning strategies employed by individuals influence the distribution of trait variants within populations.

III. Conclusion

In this section I summarise the findings from the previous two sections and discuss their collective implications for an understanding of the evolution of large-scale cooperation in humans, as well as the structure of cultural inheritance systems.

1.8 Structure of the thesis

In Chapter 2 I describe the study populations and provide an overview of the methods and analyses employed.

The remainder of the thesis is in three sections. Section I comprises Chapters 3 and 4. In Chapter 3 I present findings from the ultimatum game (UG), my first measure of cooperative behaviour, implemented in 21 Pahari Korwa villages. In Chapter 4 I present findings from two further measures of cooperative behaviour, a public goods game (PGG) and a new ‘real-world’ measure of behaviour, both implemented in 16 Pahari Korwa villages. Section II of the thesis consists of Chapter 5, where I present findings from public goods game experiments implemented in 14 Pahari Korwa populations, examining whether people employ social learning in the context of a cooperative dilemma. Each chapter opens with the relevant background to the sub-study and a review of related research, as well as a description of the behavioural measures employed and of the study design; this is followed by the findings of the sub-study and a discussion of these findings. Methodological details specific to each sub-study are provided at the end of each chapter; I have adopted this format rather than conventionally including the methods at the start of the chapter as these details are not crucial to the interpretation of results and may otherwise interrupt the narrative.

In Section III, consisting of Chapter 6, I conclude by discussing the implications of my findings for theory on the evolution of large-scale cooperation in humans and the structure of cultural inheritance systems.

CHAPTER 2

STUDY POPULATIONS AND METHODS

In this chapter I describe my study populations and provide an overview of the methods and analyses employed in the work presented in this thesis. Section 2.1 outlines the features of a good model system for this study and Section 2.2 provides an ethnographic account of the Pahari Korwa, as well as a description of the geographical region in which they live. Section 2.3 describes the study site and the study set-up, as well as provides details of the 21 villages included in this study. Sections 2.4 and 2.5 provide an overview of the methods and analyses employed respectively.

2.1 Features of a good model system for this study

The aim of this thesis is to identify whether there is significant variation in levels of cooperation across human populations, and whether social learning or environmental variability is the likely driver of any existing variation. The foremost requirement of a good model system for this study is therefore a set of real-world populations. Since I wish to control for cultural differences between the study populations, I require multiple populations of the same endogamous cultural group living as predominantly uni-ethnic communities. Furthermore, populations with distinct boundaries are essential in order to compare naturally defined populations and measure the population level correlates of cooperation. This will ensure that the analyses are not affected by the arbitrary assignment of population boundaries. To facilitate detection of any effects of demography and ecology on levels of cooperation across populations, the sample populations should capture sufficient variation in these variables. A final feature of a good model system is therefore populations that vary in size, migration rates, distances to towns and markets and so on. In summary, a good model system for this study comprises multiple, uni-ethnic meta-

populations of the same endogamous cultural group, with distinct population boundaries and demographic and ecological variation across populations; Pahari Korwa populations have all these features of a good model system.

2.2 The Pahari Korwa

2.2.1 Ethnographic description

The Pahari Korwa ('Hill Korwa') are a small-scale forager-horticulturist society, classified as a 'primitive tribal group' by the Government of India (UN FAO report 1998), and living largely in the central Indian state of Chhattisgarh. They belong to the Kolarian group of tribes, an ethno-linguistic grouping, with a close affinity to the Austro-Asiatic Munda language family (Rizvi 1989; Sharma 2007; Srivastava 2007). The introduction of forest protection laws by the Government of India in 1952 precipitated a shift from their traditional nomadic lifestyle completely reliant on hunting, gathering and swidden agriculture to settled communities based around individually owned land (Rizvi 1989). They remain heavily reliant on gathered forest products which are a primary source of food and income, but they also practice agriculture on small tracts of land, usually adjoining forested areas. These economic resources are supplemented by opportunistic hunting and fishing and wage labour. Men hunt in groups with bows and arrows and with the exception of the shooter who usually gets a larger share, the meat is shared equally. Typically hunted animals are wild boar, small deer species, and species of birds such as the kotri also known as the Rufous Treepie (*Dendrocitta vagabunda*). Fishing may be conducted solitarily, in pairs (often a conjugal pair), or in small groups, and the catch is shared equally. Fields are always tended by family units, but families with larger fields may enlist the help of other village residents in exchange for a meal and liquor. The staple is rice, but maize, millet, pulses, potatoes and small quantities of vegetables are also grown. Small numbers of goats, chickens and pigs are reared by families, mostly for personal consumption.

Individuals in all populations visited during this study speak Sargujia, a regional dialect of Hindi; the Korwa language is infrequently used on an everyday basis. Villages differ in

their access to markets. Most individuals attend a local weekly market with varying frequency where they buy, sell and barter goods. The weekly market usually assembles in one of the larger multi-ethnic villages in the plains, and is visited by people of various ethnicities from surrounding villages. Korwas often have to walk several kilometres downhill to their nearest market site. Settlements have well-defined boundaries; neighbouring villages are generally separated by large tracts of forest and hills. Both uni-ethnic as well as multi-ethnic villages of varying sizes exist, although uni-ethnic settlements predominate.

The Pahari Korwa typically live in nuclear households. Lineally extended households where a married couple live with their married children are also seen. An endogamous, patrilineal and patrilocal society, exogamous marriages usually incur severe penalties, typically entailing ostracism and excommunication from the tribe and village. The excommunication can sometimes be reversed by what amounts to a substantial fine imposed on the offenders; they sponsor a large ritual feast. The majority of Korwas marry monogamously, but polygyny is practiced by some, usually more affluent, men (Rizvi 1989; Srivastava 2007; personal observation). The Korwas practice bride-price. Although, following the marriage the woman usually moves to the home of the man, couples often cohabit at either's parents' home, and may even bear a first child before the formalities of the marriage are completed. There is no caste system.

Korwas live in either temporary huts made of Sal (*Shorea robusta*) tree branches with thatched roofs, or more permanent mud houses with a roof constructed from baked mud tiles (Rizvi 1989; Srivastava 2007; personal observation). Mud houses usually comprise one central room surrounded by a corridor on three sides. A verandah may be constructed on one side of the house and families who rear goats also build an enclosure for them in a section of the corridor within the main house. Korwa settlements are dispersed, with large distances between houses, often spanning a kilometre or more. Clustered settlements are rare. This may be largely because people build their homes adjoining their cultivated plots of land. In my qualitative interviews, subjects often cited proximity to their land as a criterion used to choose the location of their homes. Other criteria cited were proximity to

the forest and a generally good ambience and surroundings, including the availability of open space, as well as the presence of holy or ancestral spirits.

Across villages, sources of water include small streams and rivers, natural springs and wells and hand pumps constructed by the Indian government. People sometimes walk up to a kilometre to their primary source of water. Electricity has not reached most villages. Of the 21 villages that I worked in, only one village was partially electrified; here too power lines had been laid within the last five years and only a handful of houses were receiving a limited quota of electricity. Sal tree wood is the primary source of fuel, used essentially for cooking and to provide warmth in the winter.

The Korwas practice ancestor worship (Srivastava 2007; personal observation). They also worship indigenous gods and goddesses, often associated with the forest, hunting, or a prominent local geographical site such as a big hill or cave in the region. They have recently started adopting Hindu practices and deities in some villages, although these still tend to coexist with their indigenous divinities. Korwa festivals are usually centred around the sowing or harvest of certain crops, the harvest of seasonal forest products, or protection and prosperity during particular seasons like the monsoon (Rizvi 1989; personal observation). One of the biggest festivals in the calendar year is the harvest festival called 'Cherta', usually celebrated in the month of January. The festival is celebrated with gusto and involves the slaughter and consumption of chickens and goats, as well as the consumption of special foods and vast quantities of 'hadiya' (rice beer) and 'mahua' (potent alcohol manufactured from a flowering tree of the same name). People visit others' homes and invite their friends and relatives, both from the village and from other villages, to wine and dine at their homes. There is much merriment, music and dance and the celebration engulfs the village for two or three days.

2.2.2 Distribution

A hill tribe, the Pahari Korwa are mostly found in four northern districts of the central Indian state of Chhattisgarh (17.46 ° to 24.5 ° N, 80.15 ° E to 84.20 ° E) in India (Figure 2.1), namely, Surguja, Jashpur, Raigarh and Korba (Indian Census report 1991; Rizvi 1989; Sharma 2007). The region contains the eastern edge of the Satpura Range and the western edge of the Chotanagpur Plateau. Defined by table-land interspersed with hills and plains, the area is partly drained by the Mahanadi river basin. The district of Surguja contains the largest numbers of Korwas; here they are dispersed in about 260 villages and number at around 20,000 individuals (Hill Korwa Development Agency Report 2003). Villages show considerable variation in population size, ranging from about ten to several hundred individuals and are located at a range of distances from the region's main town, Ambikapur, which has a population of approximately 66,000.



Figure 2.1 Map of Chhattisgarh with inset displaying its relative location (shaded black) in India.

2.2.3 Climate, flora and fauna

Chhattisgarh has a hot and humid tropical climate. The Tropic of Cancer passes through the state. The northern hilly region where the Korwas reside is cooler than the rest of the state; summer temperatures range between 25 and 39 °C (Rizvi 1989). Average annual rainfall in the region is about 140 cm. The state falls in the Sal (*Shorea robusta*) forest belt and has 44% of its geographical area under forest cover. Other common species of trees are Teak (*Tectona grandis*), Mahua (*Madhuca indica*), Tendu (*Diospyros melanoxylon*), Amla (*Embilica officinalis*), Karra (*Cleistanthus collinus*) and Bamboo (*Dendrocalamus strictus*). The region has been home to the tiger, leopard and elephant, populations of which are either endangered or locally extinct. Sloth Bears, wild boar, sambhar deer, nilgai, chinkara, striped hyenas, porcupines and chital are more common. Chhattisgarh is also home to several species of birds including the wood pecker, peacock, jungle fowl, quail, gray-partridge and parrot.

2.3 Study site

2.3.1 Establishing the field-site

I first visited Chhattisgarh in May 2007 in order to set-up a field-site and conduct a pilot study. Prior to my visit, I had made contact with a local non-government organisation called Chaupal, based in the town of Ambikapur (District Sarguja), Chhattisgarh. Chaupal was established about eight years ago under the leadership of Mr. Gangaram Paikra, and comprises individuals from several tribal groups from within Chhattisgarh. The primary aim of this grass-roots organisation is to disseminate information on and facilitate access to national rural livelihood and employment schemes run by the Indian government. The organisation works in several hundred villages mainly across three districts of northern Chhattisgarh. Gangaram Paikra generously agreed to assist me in establishing my study. In May 2007, I made my way from Delhi to Ambikapur, rucksack on my back. An overnight train journey and a day-long bus ride later, I met Gangaram Paikra for the first time in Ambikapur. I had originally planned to conduct my research on a different tribal group, the Gond. However, upon spending several weeks in Chhattisgarh, I realised that the Gond are sub-divided into several endogamous communities and very rarely live in uni-ethnic villages. Further enquiries and research led me to the Pahari Korwa, who met my established criteria for a model population system.

With extraordinary and indispensable assistance from Gangaram Paikra and the other members of Chaupal, I spent the month of May recruiting and training research assistants, translating game scripts into Sargujia, standardising questionnaires used to collect demographic and individual data, working out the practical details of running the games in a village, identifying villages to work in and making logistical arrangements such as transportation to villages. My research assistants were members of Chaupal who are from villages in the region and combine their work at Chaupal with small-scale agriculture to maintain a livelihood. They are literate and have at least completed middle school. I ran the first set of games in the village of Gotidoomar in the last week of May 2007.

2.3.2 Study set-up

2.3.2.1 Sampling and logistics

I obtained a list of Pahari Korwa villages with their population sizes as estimated in the most recent Indian population census conducted in the year 2001 from the Hill Korwa Development Agency, a department of the Chhattisgarh state government. I also obtained more recent census data for a subset of these villages, collected by Chaupal in 2004 and 2005. Information from the lists was combined with that obtained from members of Chaupal to identify a set of villages incorporating reasonable variation in population size and distances from Ambikapur and each other. My sample of villages is therefore not random. Demographic variation in the village sample is a crucial feature of my study design (Section 2.1). To be certain of obtaining a dataset with reasonable demographic variation using a fully randomised sampling strategy, a large number of villages need to be sampled. Constraints on resources and time necessitated adoption of the sampling strategy for villages described above; this allowed me to obtain the minimum recommended sample size (about fifteen villages according to a rule of thumb) suitable for the application of multilevel models (Section 2.5.2).

The research team consisted of two research assistants and myself. Upon our arrival in a village, we would make contact with the village head or other senior person in the village and describe the purpose of our visit. We informed him that we were a group of researchers from a university (a big school) and were conducting a study with the Pahari Korwa. We stated that we would stay in the village for about a week, the first three days of which we would conduct a programme in which we sought the participation of village residents, both adult men and women. We further informed him that all participants in our study would receive 30 Indian rupees (henceforth rupees) and a meal for each day they attended, and would have the opportunity to earn more money based on their performance in certain games we would play with them. We assured him that participation was completely voluntary and that the games were thought-based and did not involve physical exertion. Once the village head was convinced of our credentials, we enlisted his help and that of any other assembled individuals to advertise the study in the village via door to door visits.

Individuals who willingly gathered on the day of the games participated in this study. Note that any non-Korwa residents in the village did not participate in the study.

23 villages were visited during the study period. The games were successfully conducted in 21 of these villages. We failed to conduct the games in two villages; although we advertised the study and stayed in these villages for two days, the residents did not gather to participate in the games. In these two villages, while most residents did not refuse to participate, they simply did not assemble on the day we were scheduled to conduct the games. These villages were located in a different district (District Jashpur) to the 21 villages successfully included in this study (District Sarguja) and were situated between 10 and 20 km apart. Possible reasons for their failure to participate may include mistrust of outsiders; residents of one village were mildly hostile to us. Pre-occupation with preparing their fields for the new crop and mending the roofs of their homes in readiness for the incoming monsoon may have been another reason.

As noted above in Section 2.2.1, Korwas usually live atop hills amidst forest with no road infrastructure, electricity or running water; access to most villages is therefore by foot. We provided a meal to every participant on the day of the games, and so transported rations catering two meals for about 50 people to each village along with our own supplies for a week. We thus carried about 45 kg of rice, 10 kg of lentils, 10 kg of potatoes, 10 kg of other vegetables and various other supplies and equipment to each village. We also took 50 kg of salt to each village in order to implement a ‘real-world’ measure of cooperation (see Sections 2.4.1, 4.1.2 and 4.4.2 for details). All supplies and equipment were transported in a four-wheel-drive vehicle up to the closest motorable point from where we trekked by foot, sometimes for several hours, up to the Korwa village. We often enlisted the help of residents of a nearby village accessible by car to help us carry the heavy rations from the vehicle to our destination village. Alternatively, two of us would trek to the Korwa village under investigation and bring back residents from there to help us carry the rations to their village. During our stay in each village, we resided in the home of one of the village residents who generously provided us space inside their house or in the verandah that is attached to most houses. We cooked our meals separately on a wood fire (our hosts provided us the firewood), and our hosts typically invited us to at least one meal at their

hearth. We presented our hosts a gift in the form of food rations and some money when we departed.

2.3.2.2 Village details

The study was conducted in a total of 21 Pahari Korwa villages. Table 2.1 summarises important demographic features of these villages and the behavioural measures of cooperation implemented in each village. Five villages were visited between May 23rd and June 21st, 2007 and the remaining 16 villages were visited between February 2nd and May 16th, 2008. Figure 2.2 displays the geographical distribution of study villages and the town of Ambikapur. Village means for participants from each study population are presented for basic individual descriptors, residence, and migration variables in Table 2.2 and for measures of wealth, market contact and social networks in Table 2.3 (see Table 2.5 for descriptions of these variables). Table 2.4 summarises the availability of amenities, such as a primary school and health care centre, in each village.

2.3 STUDY SITE

Table 2.1 Summary statistics of demographic variables for the study populations and the behavioural measures of cooperation implemented in each village.

Village number	Village name	Population size ¹	Percentage of migrants in sample ²	Percentage of non-Korwas ³	Distance from Ambikapur (km)	Measures of cooperation ⁴	Location of games
1	Chipni Paani	27	92 (12)	0	24	UG, PGG1, PGG2, SD	Village resident's hut
2	Mahua Bathaan	61	32 (22)	16	44	UG, PGG1, PGG2, SD	Village resident's hut
3	Jog Paani	64	53 (19)	25	47	UG, PGG1, SD	Village resident's hut
4	Semar Kona	64	29 (17)	17	24	UG, PGG1, SD	Outdoors under a tree
5	Bihidaand	73	48 (21)	21	33	UG, PGG1, PGG2, SD	School building
6	Khunta Paani	97	52 (31)	27	36	UG, PGG1, PGG2, SD	Outdoors under a tree
7	Kaua Daahi	102	41 (32)	0	46	UG, PGG1, PGG2, SD	School building
8	Pareva Aara	111	44 (36)	14	42	UG, PGG1, PGG2, SD	Village resident's hut
9	Musakhhol	117	37 (30)	26	35	UG, PGG1, PGG2, SD	Communal building
10	Kharranagar	125	42 (38)	0	50	UG, PGG1, PGG2, SD	Abandoned hut
11	Tedha Semar	141	40 (30)	3	45	UG, PGG1, PGG2, SD	Abandoned hut
12	Jaamjhor	144	37 (30)	44	25	UG	School building
13	Vesra Paani	157	25 (44)	25	27	UG, PGG1, PGG2, SD	Outdoors under a tree
14	Mirgandaand	163	56 (32)	35	5	UG	Village resident's hut
15	Barghaat	194	31 (42)	10	41	UG, PGG1, PGG2, SD	Village resident's hut
16	Gotidoomar	195	36 (50)	0	31	UG	Abandoned hut
17	Cheur Paani	197	40 (30)	1	33	UG	School building
18	Aama Naara	207	33 (43)	6	69	UG, PGG1, PGG2, SD	School building
19	Bakrataal	254	54 (39)	7	26	UG, PGG1, PGG2, SD	School building
20	Kheera Aama	290	29 (42)	18	31	UG	School building
21	Ghatgaon	957	15 (47)	5	13	UG, PGG1, PGG2, SD	Village resident's hut

¹ Includes all adults and children residing in the focal village.

² Numbers in parentheses indicate size of 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.

³ Percentage of the focal village population who were not Pahari Korwas.

⁴ Ultimatum game (UG); Public goods game: round one (PGG1), round two (PGG2); Salt decision (SD). The measures of cooperation are explained in Section 2.4.1

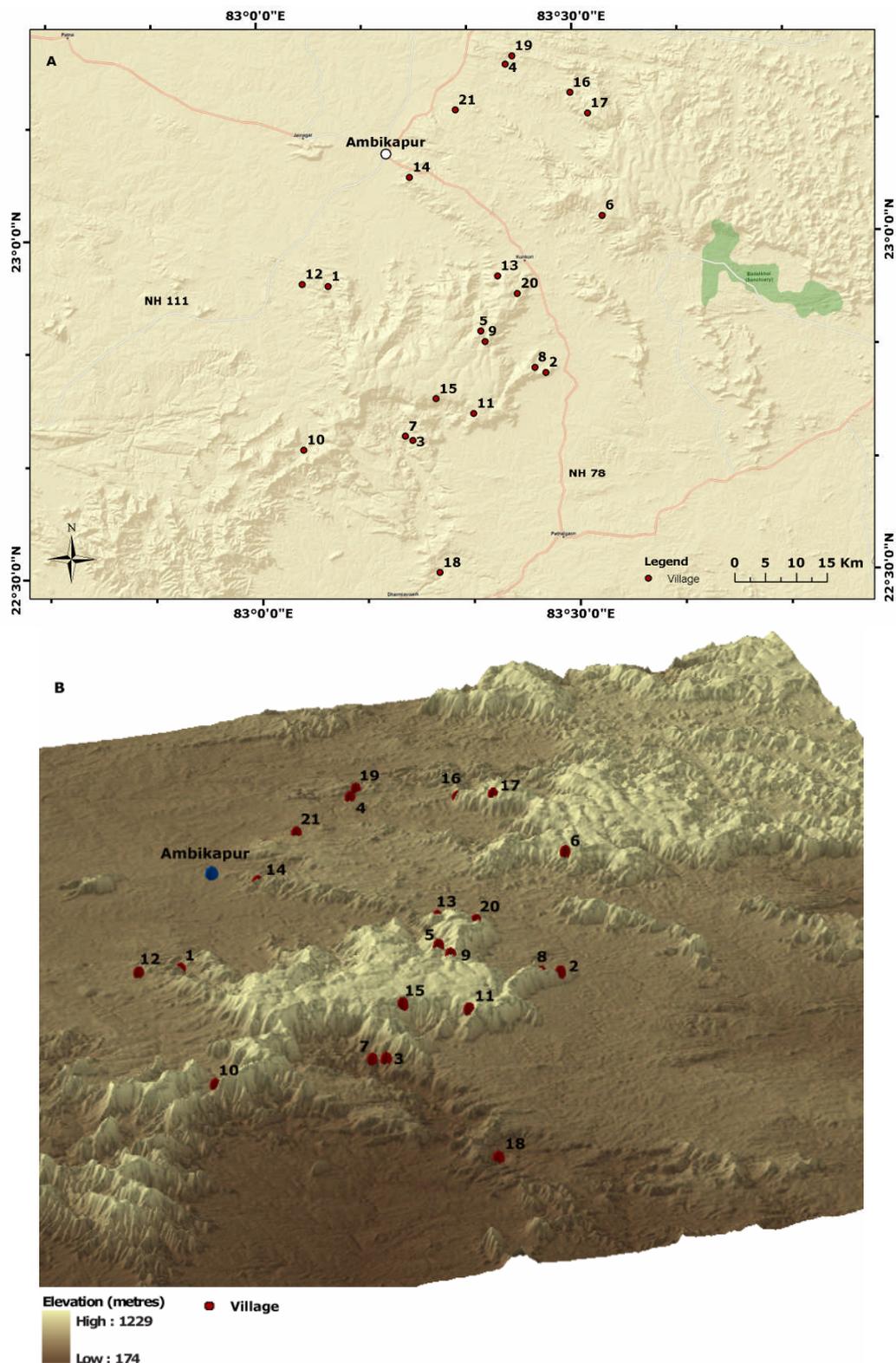


Figure 2.2 Maps displaying (A) the distribution of the 21 study villages and the town Ambikapur. Displayed numbers indicate relative population size (1 = lowest) and correspond to the ‘Village number’ column in Table 2.1. Two national highways intersect the region (NH 78 and NH 111), and (B) the elevation of the 21 study villages and Ambikapur.

2.3 STUDY SITE

Table 2.2 Village means for basic individual descriptors and residence and migration variables for participants from each study population. Values in parentheses are standard deviations.

Village number	Village name	Age ¹	Proportion female	Household size ²	Proportion ever married	Number of living children	Proportion 1=Illiterate 2=Literate ³	Proportion born in village	Time lived in village ¹	Number of migrations since birth ⁴	Sample size
1	Chipni Paani	31.75 (14.49)	0.42	4.17 (1.40)	0.92	1.92 (2.11)	1=0.83; 2=0.17	0.08	17.46 (12.73)	1.17 (0.39)	12
2	Mahua Bathaan	33.07 (7.77)	0.50	5.14 (2.12)	0.95	2.45 (2.02)	1=0.73; 2=0.18	0.68	25.09 (12.18)	0.68 (0.78)	22
3	Jog Paani	31.47 (13.80)	0.47	6.26 (2.88)	0.79	2.32 (2.14)	1=0.44; 2=0.22	0.47	21.68 (13.07)	0.53 (0.51)	19
4	Semar Kona	37.12 (16.58)	0.35	4.35 (1.97)	0.94	2.00 (1.50)	1=0.75; 2=0.13	0.71	31.65 (21.48)	0.53 (0.80)	17
5	Bihidaand	32.24 (10.89)	0.57	6.38 (2.36)	0.86	2.33 (1.93)	1=0.50; 2=0.20	0.52	24.81 (14.27)	0.57 (0.68)	21
6	Khunta Paani	33.79 (10.51)	0.58	6.45 (3.63)	1.00	1.68 (2.24)	1=0.67; 2=0.27	0.48	23.97 (15.46)	0.65 (0.71)	31
7	Kaua Daahi	35.98 (13.68)	0.38	4.91 (1.87)	0.97	2.47 (2.30)	1=0.38; 2=0.25	0.59	27.73 (17.06)	0.56 (0.67)	32
8	Pareva Aara	40.24 (15.15)	0.42	5.44 (2.53)	0.89	1.92 (2.02)	1=0.72; 2=0.11	0.56	32.32 (17.73)	0.50 (0.56)	36
9	Musakhhol	33.70 (8.84)	0.63	5.30 (2.29)	1.00	2.77 (2.40)	1=0.67; 2=0.13	0.63	27.19 (12.04)	0.40 (0.56)	30
10	Kharranagar	29.51 (7.84)	0.42	7.05 (2.25)	0.79	2.61 (2.60)	1=0.32; 2=0.21	0.58	22.47 (11.17)	0.74 (1.06)	38
11	Tedha Semar	35.80 (12.35)	0.43	5.43 (1.65)	0.87	2.27 (1.66)	1=0.73; 2=0.13	0.60	29.47 (13.96)	0.53 (0.82)	30
12	Jaamjhor	36.53 (13.87)	0.53	4.57 (1.59)	0.97	2.53 (1.91)	1=0.87; 2=0.13	0.63	31.03 (17.01)	0.37 (0.49)	30
13	Vesra Paani	35.44 (14.52)	0.43	5.80 (2.08)	0.91	2.09 (1.65)	1=0.73; 2=0.14	0.75	30.86 (14.47)	0.36 (0.65)	44
14	Mirgadaand	36.28 (15.32)	0.38	6.31 (2.13)	0.94	3.19 (1.69)	1=0.69; 2=0.06	0.45	26.81 (17.80)	0.72 (0.77)	32
15	Barghaat	41.14 (12.23)	0.48	6.36 (2.82)	1.00	3.33 (2.16)	1=0.52; 2=0.10	0.69	34.63 (17.17)	0.55 (0.77)	42
16	Gotidoomar	38.50 (12.35)	0.44	4.90 (2.12)	0.98	2.44 (1.90)	1=0.88; 2=0.08	0.64	32.80 (13.39)	0.38 (0.53)	50
17	Cheur Paani	38.43 (14.01)	0.27	4.17 (2.05)	1.00	1.77 (1.81)	1=0.73; 2=0.13	0.60	30.27 (17.11)	0.50 (0.82)	30
18	Aama Naara	35.59 (13.37)	0.33	6.63 (2.20)	0.93	2.58 (1.85)	1=0.59; 2=0.14	0.67	30.16 (15.01)	0.47 (0.74)	43
19	Bakrataal	32.53 (11.05)	0.54	5.16 (1.95)	0.97	2.16 (1.86)	1=0.56; 2=0.11	0.46	22.80 (13.22)	0.62 (0.72)	37
20	Kheera Aama	35.73 (10.13)	0.37	7.10 (3.21)	1.00	3.61 (2.30)	1=0.81; 2=0.10	0.71	30.74 (13.51)	0.32 (0.52)	41
21	Ghatgaon	34.87 (9.02)	0.40	6.21 (3.15)	0.98	3.26 (2.19)	1=0.48; 2=0.26	0.85	32.32 (10.59)	0.30 (0.62)	47

¹ In years.

² Number of people residing in the house and eating at a common hearth.

³ Illiterate individuals did not read, write or go to school. Literate individuals could read and write but did not go to school. The remaining proportion of individuals had some schooling.

⁴ Migration is defined as a change of residence to another village.

2.3 STUDY SITE

Table 2.3 Village means for measures of wealth, market contact and social networks for participants from each study population. Values in parentheses are standard deviations.

Village number	Village name	Proportion of earners in household	Rice months ¹	Outstanding loans in Indian rupees	Bazaar visits ²	Town visits ³	Festival invitees from own village ⁴	Festival invitees from other villages ⁵
1	Chipni Paani	0.55 (0.24)	2.04 (0.89)	362.50 (351.70)	1.67 (0.78)	6.03 (7.22)	4.25 (3.33)	1.42 (1.83)
2	Mahua Bathaan	0.53 (0.21)	1.99 (3.07)	109.09 (365.03)	2.82 (0.96)	11.36 (5.37)	5.68 (3.51)	0.91 (3.24)
3	Jog Paani	0.68 (0.28)	3.17 (3.29)	1563.16 (1708.54)	1.47 (0.61)	0.49 (0.56)	4.84 (2.97)	1.79 (1.75)
4	Semar Kona	0.64 (0.20)	3.32 (3.14)	58.82 (166.05)	1.65 (0.79)	1.84 (1.31)	5.12 (4.00)	0.41 (1.18)
5	Bihidaand	0.50 (0.25)	1.83 (1.27)	247.62 (1089.44)	2.14 (0.65)	1.06 (0.62)	14.29 (8.48)	9.67 (6.89)
6	Khunta Paani	0.62 (0.24)	1.52 (0.83)	1080.65 (3507.37)	1.03 (0.67)	0.50 (0.49)	6.32 (3.60)	1.48 (1.77)
7	Kaua Daahi	0.63 (0.25)	2.30 (2.09)	1912.50 (1828.58)	1.68 (0.82)	0.99 (0.60)	4.97 (2.87)	3.63 (3.31)
8	Pareva Aara	0.60 (0.21)	1.87 (1.82)	3333.33 (4472.14)	2.11 (0.88)	2.51 (1.23)	5.42 (4.54)	1.19 (1.80)
9	Musakhhol	0.56 (0.23)	2.93 (2.28)	815.00 (2511.46)	1.50 (0.51)	1.25 (0.98)	51.87 (20.50)	7.33 (13.38)
10	Kharranagar	0.50 (0.21)	2.89 (1.22)	3900.00 (3354.68)	1.92 (0.71)	0.21 (0.46)	7.87 (5.59)	6.87 (7.96)
11	Tedha Semar	0.57 (0.24)	1.58 (1.16)	56.67 (175.55)	1.47 (0.72)	0.77 (0.38)	6.03 (3.03)	1.60 (1.98)
12	Jaamjhor	0.52 (0.23)	2.85 (2.22)	1126.83 (2125.14)	1.90 (1.16)	11.20 (4.80)	16.53 (11.78)	2.93 (2.94)
13	Vesra Paani	0.59 (0.21)	2.22 (2.41)	90.91 (603.02)	2.15 (0.97)	7.33 (4.39)	12.41 (7.26)	1.32 (2.19)
14	Mirgandaand	0.49 (0.20)	3.13 (1.78)	1220.47 (2401.40)	2.66 (1.31)	10.38 (8.35)	16.22 (6.26)	5.84 (2.34)
15	Barghaat	0.45 (0.19)	3.46 (1.35)	2045.24 (2211.74)	1.58 (0.73)	1.68 (1.69)	5.21 (2.97)	1.12 (1.90)
16	Gotidoomar	0.61 (0.26)	2.76 (1.39)	328.50 (779.26)	1.87 (0.91)	0.00 (0.00)	2.66 (2.44)	0.36 (1.14)
17	Cheur Paani	0.68 (0.30)	3.95 (3.29)	131.33 (336.57)	2.43 (1.07)	0.00 (0.00)	6.24 (8.29)	0.59 (1.27)
18	Aama Naara	0.54 (0.22)	2.80 (1.94)	330.23 (634.16)	1.97 (0.82)	4.49 (3.74)	7.60 (4.72)	0.58 (1.33)
19	Bakrataal	0.60 (0.26)	2.53 (2.09)	0.00 (0.00)	1.58 (0.70)	1.19 (0.99)	6.32 (4.32)	0.38 (1.11)
20	Kheera Aama	0.44 (0.20)	4.88 (3.21)	2466.67 (6926.81)	2.68 (1.08)	0.33 (0.56)	8.78 (9.52)	2.00 (2.77)
21	Ghatgaon	0.45 (0.23)	2.07 (3.28)	10304.35 (51955.57)	1.55 (0.72)	2.47 (4.24)	3.11 (2.38)	0.72 (1.80)

¹ Number of months per year the household eats self-grown rice.

² Number of monthly visits to the local bazaar.

³ Number of monthly visits to the nearest town.

⁴ Number of people invited to harvest festival from own village; a measure of social network size.

⁵ Number of people invited to harvest festival from other villages; a measure of social network size.

2.3 STUDY SITE

Table 2.4 Summary of amenities in each village. (+) denotes presence; (-) denotes absence.

Village number	Village	Primary school	Health care centre	Post office	Intra-state bus ¹	Inter-state bus ²	Railway station	Weekly market ³	Panchayat office ⁴	NGO ⁵
1	Chipni Paani	-	-	-	-	-	-	-	-	+
2	Mahua Bathaan	+	-	-	-	-	-	-	-	-
3	Jog Paani	-	-	-	-	-	-	-	-	+
4	Semar Kona	-	-	-	-	-	-	-	-	+
5	Bihidaand	+	-	-	-	-	-	-	-	+
6	Khunta Paani	+	-	-	-	-	-	-	-	+
7	Kaua Daahi	+	-	-	-	-	-	-	-	+
8	Pareva Aara	+	-	-	-	-	-	-	-	+
9	Musakhol	+	-	-	-	-	-	-	-	+
10	Kharranagar	+	-	-	-	-	-	-	-	+
11	Tedha Semar	+	-	-	-	-	-	-	-	+
12	Jaamjhor	+	-	-	-	-	-	-	-	+
13	Vesra Paani	+	-	-	-	-	-	-	-	+
14	Mirgadaand	+	-	-	+	+	-	-	-	+
15	Barghaat	+	-	-	-	-	-	-	-	+
16	Gotidoomar	+	-	-	+	-	-	-	-	+
17	Chaur Paani	+	-	-	-	-	-	-	-	+
18	Aama Naara	+	-	-	-	-	-	-	-	-
19	Bakrataal	+	-	-	-	-	-	-	-	+
20	Kheera Aama	+	-	-	-	-	-	-	-	+
21	Ghatgaon	+	-	-	-	-	-	-	-	+

¹ Buses connecting districts within the state of Chhattisgarh stopping within a couple of kilometres from the focal village.

² Buses connecting Chhattisgarh to other states in India stopping within a couple of kilometres from the focal village.

³ Local weekly market located in the focal village.

⁴ Local village-level government office located in the focal village.

⁵ Non-government organisations undertaking developmental activities in the focal village.

2.4 Methods

2.4.1 Behavioural data

Three measures of cooperation were used in this study. Of these, two are economic games, namely, the ultimatum game (UG) and the public goods game (PGG) (Camerer 2003; Kagel and Roth 1995), while one is a ‘real-world’ measure of cooperation which I term the ‘salt decision’. The UG and the PGG are experimental tools developed by economists; they have previously been implemented extensively both in the laboratory as well as in field studies (see Section 3.1.1 and Section 4.1.1 for reviews of literature on the UG and PGG respectively). The ‘salt decision’ is a new measure of cooperation developed and implemented for the first time in this study (see Sections 4.1.2 and 4.4.2). Table 2.1 summarises the measures implemented in each village. The details of each game including specific game protocols are described in subsequent chapters. Here I illustrate the broad features common to all game protocols used.

The study design 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.

2.4.1.1 Anonymity

Participants made all game decisions once and anonymously, and were made explicitly aware of the one-shot, anonymous set-up of each game. A player made her decisions individually at a private location, and apart from the player and myself, no other individual was present while she made her decisions. Player names were not recorded; a player’s only identification in the study was a numbered token. Each player retained the same token throughout the study in order to facilitate the comparison of individuals’ decisions across all three measures of cooperative behaviour. Players were unaware of the identity of the individuals they played with and remained so even after the study was completed. No

village resident could therefore know the decision of a player or what s/he earned in the game, either during or after the study.

2.4.1.2 Game instructions and testing

Instructions were delivered from standardised scripts in Sargujia. I first translated game scripts from English to Hindi. The scripts were then translated from Hindi to Sargujia by research assistants. The back translation method was used to ensure accuracy of translation. Real money was used to demonstrate game rules and examples, and the instructions explicitly demonstrated the complete anonymity of decisions. Only players who individually answered a set of test questions correctly played any game. The questions were designed to assess their understanding of the game and features of the experimental set-up such as anonymity.

2.4.1.3 Administration

All games in all villages were administered by me within the first four days following our arrival in a village. Prior to this study, I had no contact with any individual from any of the 21 villages included in this study. This protocol minimised experimenter familiarity with the players. On each day of the games, all participants collected at a common location in the village that was usually outdoors. We then designated three sites; the first for players who were waiting to play the game, the second for those who had played, and the third as a private location where the players made their game decisions. The locations were at least 10-20 m apart from each other, typically further, and always out of earshot. The private location was often in the village school building or a village resident's hut, and on occasion an isolated outdoor site (Table 2.1).

The UG was played first, and was usually run for the first two days subsequent to our arrival in a village. This was followed by the PGG, generally played on the third day after our arrival in a village. All PGGs were completed in one day. Note that only those individuals who had successfully understood and played the UG were recruited to play the PGG on the third day. All games were played for real money with substantial stakes

ranging from one to two days' local wages. Stake size was determined as an approximate multiple of mean local wages estimated by sampling several villages in the study region. Individuals across all villages participate in similar economic activities and visit the same markets. Moreover, previous studies suggest that stake size does not significantly affect behaviour in the PGG and UG (Cameron 1999; Kocher et al. 2008). For all of the above reasons, the stakes were kept constant across villages.

Participants made all their game decisions by physically manipulating real money. Play order was randomised for all games. Individuals who had played a game were prevented from interacting with those who had not yet played that game; participants who had played the game were seated at a separate location to those who had yet to play and research assistants monitored the two groups to ensure there was no discussion about the game. Participants were forbidden from discussing the game during the study period and warned that the games would be discontinued if they did. We provided rations, which were cooked and consumed on the day of the games, for a full meal for each player. The meal was cooked by the waiting participants themselves; this kept them occupied for a few hours. They prepared a full meal for 25 to 30 people and manufactured plates and bowls from Sal tree leaves for everyone to eat off.

2.4.1.4 Payments

All participants received a show-up fee of 30 rupees, which is just under one day's local wages. From demographic data collected on 784 adults I estimated mean local wages in the region at 38.68 ± 12.05 rupees per day. The show-up fee was handed to players on the day that they participated in a game. Each player's earnings from the different games were summed and paid together on the final day of game play in each village, once all games had been completed. This was done because (a) it eliminated outcome-based feedback to UG players who played on the first day, and who could otherwise have communicated these outcomes to village residents scheduled to play on day two, thus influencing their decisions, (b) it allowed me to collect data on individuals' salt decisions (see Sections 4.1.2 and 4.4.2 for details) that could be compared to their PGG behaviour, and (c) it made it easier for me to pay individuals their exact earnings without doubling the amount of small currency that I

needed to carry to each village. Players collected their payments individually at a private location in exchange for their identification tokens, and the order in which they did so was randomised. All payments were made in real money in exact change. Players made their salt decisions (see Sections 4.1.2 and 4.4.2 for details) upon arriving to collect their payments at the private location. The salt decision was made before a player's earnings from the games were made known and given to her.

2.4.2 Demographic and individual data

Demographic and other data on individuals were collected via a standardised questionnaire (see Appendix B, Section B.1 for the individual data sheet). The questionnaire used to collect individual data was administered by a research assistant once a participant had played the UG. 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 (see Appendix B, Section B.3 for the housing data sheet) using a Global Positioning System (GPS; Garmin GPS 12XL). I also recorded whether a village had access to basic facilities such as a primary school, a hospital or health care centre, a post office, bus services, local government office or any non-government organisations working in the area, and the location of these facilities (see Appendix B, Section B.2 for the village data sheet).

Table 2.5 lists all village and individual descriptors that were included in all analyses and provides a description of each variable. Five village descriptors were included in this study. The village descriptors 'population size' and 'proportion of migrants' (a measure of migration rates between populations) are of interest because they are directly linked to the evolutionary stability of cooperation in a population; the theoretical literature demonstrates that large populations and high rates of migration work against the evolution of cooperation (reviewed in Grafen 1984 and Henrich 2004). The village descriptor 'proportion of non-Korwas' is used to examine whether any variation between villages is explained by the co-residence of other ethnic groups; theoretical and empirical studies demonstrate that inter-group competition can promote within-group cooperation (e.g. Bernhard et al. 2006; Burton-Chellew et al. 2010; Choi and Bowles 2007; de Cremer and van Vugt 1999; Puurtinen and Mappes 2009). The variables 'household dispersion' and 'distance from

major town' allow investigation of whether residence patterns show an association with levels of cooperation.

Individual descriptors included in this study were chosen in five domains; two of these domains, namely, 'basic individual descriptors' and 'wealth, markets and social networks', provide essential information on socio-economic characteristics of individuals, such as age, sex, household size, education, marital status and wealth, that may affect their behaviour. These domains also include measures of individual market contact since recent studies propose that market integration has a major impact on levels of cooperation (Henrich et al. 2005; Henrich et al. 2010). Variables in the domain 'residence and migration' capture the migratory history of each individual and thus allow analyses of whether or not, and to what extent, migrating to another population affects the behaviour of an individual. The domain 'children and grandchildren' measures the numbers of living offspring individuals have. Finally, the domain 'kin' measures the numbers of living relatives that an individual has and also records how many of these relatives reside in the same village as the individual. Variables in the latter two domains are used to investigate whether there is any support for kin selection models of cooperation (Section 1.4.1) in these populations. Note that data on the number of kin residing in the same village as the individual were not collected in the first five villages visited, namely, Gotidoomar, Cheur Paani, Kheera Aama, Mirgadaand and Jaamjhor (Table 2.1).

Table 2.5 List of village and individual descriptors included in all analyses.

Level	Domain	Variable name	Variable description
Village	Village descriptors	Population size	Total number of individuals residing in the focal village, including all adults and children.
		Proportion of migrants	Proportion of migrants in the sample of study participants from the focal village. Migrants are individuals currently residing in the focal village but born in another village.
		Proportion of non-Korwas	Proportion of the focal village population who were not Pahari Korwas.
		Household dispersion	Nearest neighbour index, calculated for households in each village using ArcGIS (see Section 2.5.3 for details). Values <1 represent a clustered distribution pattern, values >1 a dispersed distribution pattern.
		Distance from major town (km)	Distance in kilometers from Ambikapur, the largest town in the study region (Section 2.2.2).
Individual	Basic individual descriptors	Age (years)	Individual's age in years.
		Sex: female, male	Individual's sex.
		Education: illiterate, literate, some schooling	Individual's level of education. 'Illiterate' individuals could not read and write and did not go to school. 'Literate' individuals could read and write but did not go to school. Individuals with 'some schooling' had completed at least one grade in primary school (grades 1-5).
		Household size (individuals)	Number of people residing in the individual's house and eating at a common hearth.
		Marriage: ever married, never married	Individual's marital status, i.e. whether she has ever been married. Individuals who were divorced or separated at the time of the interview were recorded as 'ever married'.
Individual	Residence and migration	Birthplace: this village, other village	Individual's place of birth; this was recorded either as the focal village or other village.
		Time resident in this village (years)	Number of years the individual has been resident in the focal village.
		Number of times migrated	Total number of times the individual has migrated (changed residence to another village).
		Post-marital residence: natal village, other village	A married individual's place of residence post-marriage; this was recorded either as her natal village or other village.

Table 2.5 continued...

Level	Domain	Variable name	Variable description
Individual	Wealth, markets and social networks	Proportion of earners in household	Proportion of people in the individual's household (see variable Household size) who make a major contribution to the household income by gathering forest products sold in the market, practicing agriculture, undertaking waged labour or other employment such as in the local school.
		Months per year household eats self-grown rice	Number of months per year the individual's household eats rice grown on land owned by the individual's household.
		Outstanding loans (Indian rupees): yes, no	Whether the individual had any outstanding loans at the time of the interview.
		Number of monthly visits to local bazaar	Number of times a month that the individual visits the weekly local market held in a neighboring village. Individuals were asked to recall the number of visits they had made in the month preceding the month of the interview.
		Number of monthly visits to nearest town	Number of times a month that the individual visits the nearest town in the region to buy or sell goods. Individuals were asked to recall the number of visits they had made in the month preceding the month of the interview.
		People invited to harvest festival from own village	Number of people from the focal village that the individual invited to wine and dine at her home for the harvest festival (Cherta; see Section 2.2.1) held in the year of the interview. In all study villages Cherta had been celebrated within 1-4 months prior to the time of the interview.
		People invited to harvest festival from other villages	Number of people from other villages that the individual had invited to wine and dine at her home for the harvest festival (Cherta; see Section 2.2.1) held in the year of the interview. In all study villages Cherta had been celebrated within 1-4 months prior to the time of the interview.
Individual	Children and grandchildren	Children living	Number of living children the individual has.
		Children living together	Number of the individual's children who are living in the individual's household.
		Grandchildren living	Number of living grandchildren the individual has.
		Grandchildren living in village	Number of the individual's grandchildren who are living in the focal village.

Table 2.5 continued...

Level	Domain	Variable name	Variable description
Individual	Kin	Mother living: yes, no	Whether the individual's mother is living.
		Mother living in village: yes, no	Whether the individual's mother lives in the focal village.
		Mother participated in UG/PGG: yes, no	Whether the individual's mother participated in the UG/PGG on the same day as the individual.
		Father living: yes, no	Whether the individual's father is living.
		Father living in village: yes, no	Whether the individual's father lives in the focal village.
		Father participated in UG/PGG: yes, no	Whether the individual's father participated in the UG/PGG on the same day as the individual.
		Full siblings living	Number of living siblings the individual has who are born of the same mother and father as the individual, i.e. full siblings.
		Full brothers living	Number of living brothers the individual has who are born of the same mother and father as the individual, i.e. full brothers.
		Full brothers living in village	Number of full brothers the individual has co-residing in the focal village.
		Full brothers aged < 15 years living in village	Number of full brothers the individual has aged under 15 years and co-residing in the focal village.
		Full brothers aged \geq 15 years living in village	Number of full brothers the individual has aged 15 years or more and co-residing in the focal village.
		Full brothers living in other villages	Number of full brothers the individual has residing in a village other than the focal village.
		Full brothers aged < 15 years living in other villages	Number of full brothers the individual has aged under 15 years and residing in a village other than the focal village.
		Full brothers aged \geq 15 years living in other villages	Number of full brothers the individual has aged 15 years or more and residing in a village other than the focal village.
		Full brothers participated in UG/PGG	Number of the individual's full brothers who participated in the UG/PGG on the same day as the individual.

Table 2.5 continued...

Level	Domain	Variable name	Variable description
Individual	Kin	Full sisters living	Number of living sisters the individual has who are born of the same mother and father as the individual, i.e. full sisters.
		Full sisters living in village	Number of full sisters the individual has co-residing in the focal village.
		Full sisters aged < 15 years living in village	Number of full sisters the individual has aged under 15 years and co-residing in the focal village.
		Full sisters aged \geq 15 years living in village	Number of full sisters the individual has aged 15 years or more and co-residing in the focal village.
		Full sisters living in other villages	Number of full sisters the individual has residing in a village other than the focal village.
		Full sisters aged < 15 years living in other villages	Number of full sisters the individual has aged under 15 years and residing in a village other than the focal village.
		Full sisters aged \geq 15 years living in other villages	Number of full sisters the individual has aged 15 years or more and residing in a village other than the focal village.
		Full sisters participated in UG/PGG	Number of the individual's full sisters who participated in the UG/PGG on the same day as the individual.

2.4.3 Qualitative data

In every village visited, I made observational notes and, in addition conducted informal interviews with a few individuals to obtain historical information on the village as well as qualitative information on kin relations, sharing norms, religious and communal activities and day to day living patterns (see Appendix B, Section B.4 for the qualitative data sheet).

2.5 Analyses

2.5.1 Data processing

All data were manually entered into spreadsheets in Microsoft Office Excel 2003 version 11 (Microsoft Corporation 2003). A separate spreadsheet was created for each village. Error checks were performed by two people (including myself) by checking every entry for errors. The data were then collated to construct the full dataset and imported into the relevant statistical packages for analyses.

2.5.2 Multilevel models

I have used multilevel statistical models (Gelman and Hill 2007; Snijders and Roel 1999) to explicitly analyse variation at the village and individual levels in my structured data (individuals within villages), and the relationship of population and individual descriptors with the measure of cooperation (outcome variable). Multilevel models are used to analyse hierarchically clustered units of analysis, for instance individuals within villages within cultural groups. These models account for the possibility that units within a cluster, such as individuals from a village, may be more alike than units across clusters, such as individuals across villages. Ignoring the potential correlation of units within a cluster, i.e. the multilevel structure of data, can result in an underestimation of standard errors. Multilevel models correct for such non-independence of clustered data, reducing the likelihood of type I errors. They also allow us to accurately estimate the effects of groups along with group-level predictors. Traditional regression models used in previous cross- and intra-cultural studies (e.g. Gurven et al. 2008; Henrich et al. 2005) 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 behaviour. Rather than traditional significance testing, in this thesis I mainly use an information theoretic model fitting approach to analyse data and interpret results (see Burnham and Anderson 1998, Burnham and Anderson 2002 and Efferson and Richerson 2007 for comparative discussions of these approaches). All multilevel analyses were conducted in MLwiN version 2.14 (Browne 2009; Rasbash et al. 2009), while other statistical analyses were conducted in SPSS version 16.0.2 (SPSS Inc. 2008).

All multilevel models were run with two levels: individuals (level 1) nested within villages (level 2). Analyses proceeded in four stages. In the first stage, null models (with intercept terms only) were constructed with and without a multilevel structure and these were compared to establish whether the multilevel model provided a significantly better fit to the data. The Deviance Information Criterion (DIC) was used to compare models (Spiegelhalter et al. 2002). The DIC is a Bayesian measure of model fit and complexity; it accounts for the change in degrees of freedom between nested models. Models with a lower DIC value provide a better fit to the data and a difference in DIC values of 5-10 units or more is considered substantial (Burnham and Anderson 1998; Spiegelhalter et al. 2002). In the second stage, a series of multilevel univariate models were constructed to explore the relationship between each explanatory variable in the dataset and the outcome variable. A Wald test (Rasbash et al. 2009) was used to establish the statistical significance level of an explanatory variable. In the third stage, a series of domain-wise (sets of related variables such as those measuring wealth, kin etc. described in Table 2.5) models were produced to identify the important explanatory variables within each domain. Once again, the Wald test was used to establish the statistical significance of variables.

The full model was constructed in the fourth stage, implementing a step-wise procedure with three serially entered blocks of variables. The first block entered contained all those variables from the domains of village descriptors, basic individual descriptors, residence and migration, wealth, markets and social networks that reached significance at $p < 0.10$ within their domains (in the third stage domain-wise analyses); the block additionally contained age and sex even if they did not reach significance. The model obtained was then reduced by a backwards procedure eliminating predictor terms that did not reach

significance in a Wald test at the $p < 0.05$ level. However, reduced and non-reduced models were compared for fit using their DIC values and the model with the lower DIC value was always retained, whether or not the variables in it reached significance at $p < 0.05$. All variables that were not discarded at this stage were carried forward and the next block of variables was added into this model. The second block added contained all those variables from the domain of children and grandchildren that reached significance at $p < 0.10$ within this domain. The backward stepwise procedure was repeated with the new block of variables. The third block added contained all those variables from the domain of kin that reached significance at $p < 0.10$ within this domain. The variables age and sex were carried forward to the last block even if they did not reach significance at $p < 0.05$. They were only eliminated at the very end if they did not reach significance at the $p < 0.05$ level. Hence, the three blocks of variables were always added in the same order in a forward step-wise procedure, but within each block variables were eliminated in a backward step-wise procedure to obtain the full model. Appendix C presents the univariate and domain-wise models, and a step-wise summary of the full model fitting process implemented in the fourth stage, for all analyses presented in this thesis.

Iterative Generalised Least Squares (IGLS) estimation or Restricted Iterative Generalised Least Squares (RIGLS) estimation with a 2nd order predictive (or penalised) quasi-likelihood (PQL) approximation was used to fit all univariate (second stage) and domain-wise models (third stage). The null (first stage) and full models (fourth stage) were fitted using Markov Chain Monte Carlo (MCMC) estimation (Browne 2009) run for 10,000 iterations and a burn-in period of 500 iterations.

The small sample sizes in some villages are a reflection of the small populations in these villages (e.g. Chipni Paani had only 12 adults, all of whom participated in this study). Multilevel models account for sample size differences between populations when computing the variance components and parameter estimates. 70-100% of households had at least one household member participate in the games in all villages except Ghatgaon, Bakrataal and Tedha Semar, where this proportion was 17%, 55% and 55% respectively. The latter three villages are among those with the largest populations in my dataset (Table 2.1). Although I estimated how many households were represented by at least one

individual once all games had been completed, I did not collect data on which household each individual belonged to in order to avoid compromising players' anonymity. Hence, I cannot include households as an additional level in my models.

2.5.3 GIS analyses

Geographic Information Systems (GIS) data were processed and analysed in ArcGIS version 9.2 (ArcGIS 2006). All maps (Figure 2.2) were created and analysed using the WGS 1984 Geographic Coordinate System with a Transverse Mercator Projection. A 30m Digital Elevation Model (ASTER Global Digital Elevation Model V001) was used for the relevant map area; this was obtained from the NASA Land Processes Distributed Active Archive Center (<https://wist.echo.nasa.gov>). The base map [ESRI Street Map World 2D (old) © 2009 ESRI, and, TANA, ESRI Japan, UNEP-WCMC] used in Figure 2.2A was obtained from the ARCGIS Online Resource Centre (<http://resources.esri.com/gateway/index.cfm>). The nearest neighbour index (Clark and Evans 1954), calculated for households in each village, is used as the measure of household dispersion for each village (see village descriptors in Table 2.5).

SECTION I

VARIATION IN COOPERATION ACROSS POPULATIONS

CHAPTER 3

VARIATION IN COOPERATION ACROSS POPULATIONS: EVIDENCE FROM THE ULTIMATUM GAME

3.1 Introduction

3.1.1 Background and related research

The first question addressed in this thesis is: is there stable, heritable variation in levels of cooperation across human populations? In this chapter I present findings from the ultimatum game (UG), my first measure of cooperative behaviour, implemented in 21 Pahari Korwa villages.

Several studies have demonstrated variation in cooperative behaviour across human populations (Cardenas and Carpenter 2005; Henrich et al. 2004; Henrich et al. 2005; Henrich et al. 2010; Henrich et al. 2006; Herrmann et al. 2008; Marlowe et al. 2008; Oosterbeek et al. 2004; Roth et al. 1991); this variation has been attributed to cultural differences between populations. However, since these studies sampled from one (or very few) populations per culture, they confound cultural and ecological differences between populations (Section 1.6.2). We cannot differentiate whether cultural transmission or environmental (demographic and ecological) differences drive the observed behavioural variation across populations. Controlling for cultural differences between populations, I examine whether there is variation in levels of cooperation within and between multiple populations of the *same* endogamous small-scale society, the Pahari Korwa. I compare variance across populations of the same small-scale society to that found previously across

15 different small-scale societies (Henrich et al. 2005); if cultural transmission at the cultural group level drives variation across populations, then we should expect greater variation between cultural groups than across populations of the same cultural group. I further investigate whether environmental (demographic and ecological) factors explain any part of the variation across populations in my study. While variation driven by cultural transmission is heritable, variation driven by demographic or ecological factors is not necessarily stable or heritable; environmental drivers of behavioural variation are less likely to maintain stable differences essential for selection at the population-level.

The few studies that have examined intra-cultural variation in cooperative behaviour (Gurven 2004a; Gurven et al. 2008; Marlowe 2004) obtained inadequate sample sizes to enable reliable, explicit analyses of relative variation at the population and individual levels. Moreover, traditional regression models employed in these studies 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 behaviour (Section 2.5.2). While the above-cited studies do report behavioural variation across populations/camps of the same cultural group, small sample sizes (five to nine villages), unsuitable model populations with ill-defined population boundaries (e.g. Marlowe 2004), and the use of inappropriate statistical tools, make their estimates of population level variance unreliable.

The UG (Güth et al. 1982) is a two-player game where one of a pair of individuals, the ‘proposer’, must divide a sum of money (the stake, S) between herself and an unknown ‘responder’. If the responder accepts the proposer’s offer (x), the responder earns x , and the proposer earns $S-x$. If the responder rejects the offer, neither player earns anything. In this game the income-maximising strategy entails that a responder accept any offer made by the proposer. Assuming that the responder will play the income-maximising strategy, the income-maximising strategy for a proposer is to make the smallest possible offer. The UG is one of the most extensively employed experimental economic games. It has been played both in populations of small-scale societies (Henrich et al. 2005; Henrich et al. 2010; Henrich et al. 2006; Marlowe et al. 2008) and large-scale, industrialized societies, although mostly amongst university students in the latter (reviewed in Camerer 2003, Oosterbeek et al. 2004 and Roth 1995a). Behaviour in the UG varies considerably across populations of

small-scale societies (e.g. Henrich et al. 2005). There is less variation across populations of large-scale societies; individuals typically make offers between 40% and 50% of the stake and reject offers below about 30% of the stake (reviewed in Camerer 2003).

3.1.2 Behavioural measures

In this study, the UG was played with the rules described above (see Section 2.4 for details of study set-up and Section 3.4.1 for details of the games). The size of the stake (S) for each game was 100 rupees, equivalent to a little over two days' wages in the region. Offer values were restricted to multiples of five. Each individual played the game once and in one role, as a proposer or a responder, under anonymous conditions. Pairs of players were constituted by randomly matching token numbers. In 16 of the 21 populations where the UG was played, once a responder had made her decision regarding whether she wished to accept or reject the offered amount, I additionally asked her what minimum offer from a proposer she was willing to accept; this was recorded as the minimum acceptable offer (MAO) for that individual. The game outcome and payoffs were determined on the basis of the accept/reject response and players were fully aware of this. Hence, the MAO is a self-reported figure and players knew that its value did not affect their actual payoffs in the game. I use MAO values to examine whether players' self-reported behavioural strategies agree with their game behaviour. I also examine whether properties of the village and/or individual are associated with such self-reported MAOs.

I employ multilevel normal linear models (Browne 2009; Rasbash et al. 2009; Snijders and Bosker 1999) to explicitly analyse variation in UG behaviour at the village and individual levels.

3.2 Results

344 individuals participated as proposers and 340 as responders in UGs played across 21 villages. Table 3.1 presents sample sizes of UG proposers and responders for the 21 villages. The total number of proposers differs from the total number of responders since in eight villages an odd number of individuals participated in the games. In these villages, one individual was paired randomly with two other players from the village in order to determine the payoff to all participating players.

Table 3.1 Number (n) of proposers (total n = 344) and responders (total n = 340) from each of 21 study villages.

Village number	Village	Proposers (n)	Responders (n)
1	Chipni Paani	6	6
2	Mahua Bathaan	11	11
3	Jog Paani	10	9
4	Semar Kona	9	8
5	Bihidaand	11	10
6	Khunta Paani	16	15
7	Kaua Daahi	16	16
8	Pareva Aara	18	18
9	Musakhhol	15	15
10	Kharranagar	19	19
11	Tedha Semar	15	15
12	Jamjhor	15	15
13	Vesra Paani	22	22
14	Mirgadaand	16	16
15	Barghaat	21	21
16	Gotidoomar	25	25
17	Cheur Paani	15	15
18	Aama Naara	21	22
19	Bakrataal	19	18
20	Kheera Aama	20	21
21	Ghatgaon	24	23

In Section 3.2.1 I present findings on proposer offers; Section 3.2.1.1 examines whether proposer offers vary across populations and Section 3.2.1.2 investigates whether properties of villages and/or individuals explain any variation in proposer offers. In Section 3.2.2 I present findings on responder behaviour; Sections 3.2.2.1 and 3.2.2.2 examine whether responders' game responses and self-reported MAOs vary across populations respectively, and Section 3.2.2.3 investigates whether properties of villages and/or individuals explain

any variation in responders' self-reported MAOs. Finally, in Section 3.2.3 I investigate whether proposer and responder behaviour co-vary in the study populations.

3.2.1 Proposers

3.2.1.1 Do proposer offers vary across populations?

Distributions of proposer offers (Figure 3.1) vary considerably across villages. The modal offer across all villages is 50 rupees (50% of the stake). While the primary mode (the most frequently made offer) varies little across villages, the secondary mode (the second most frequently made offer) varies between 30 and 70 rupees across villages. Mean offers vary between about 31 and 52 rupees. 14.4% of the variance in offers occurs between villages [Table 3.2B; null model (multilevel)]. The DIC value for the null model with village level intercepts (multilevel) is about 44 units lower than for the null model without village level intercepts (single level), indicating that the multilevel model accounting for village effects provides a substantially better fit to the data (Table 3.2A; null models). Once village and individual descriptors are included in the full model, the unexplained between-village variance reduces to 11.2% [Table 3.2B; full model (multilevel)]. Variance in UG proposer offers between 15 small-scale societies was estimated at about 12% (Henrich et al. 2004; Henrich et al. 2005). Behavioural variance between 21 populations of the same small-scale society is therefore comparable to that between 15 populations of 15 different societies.

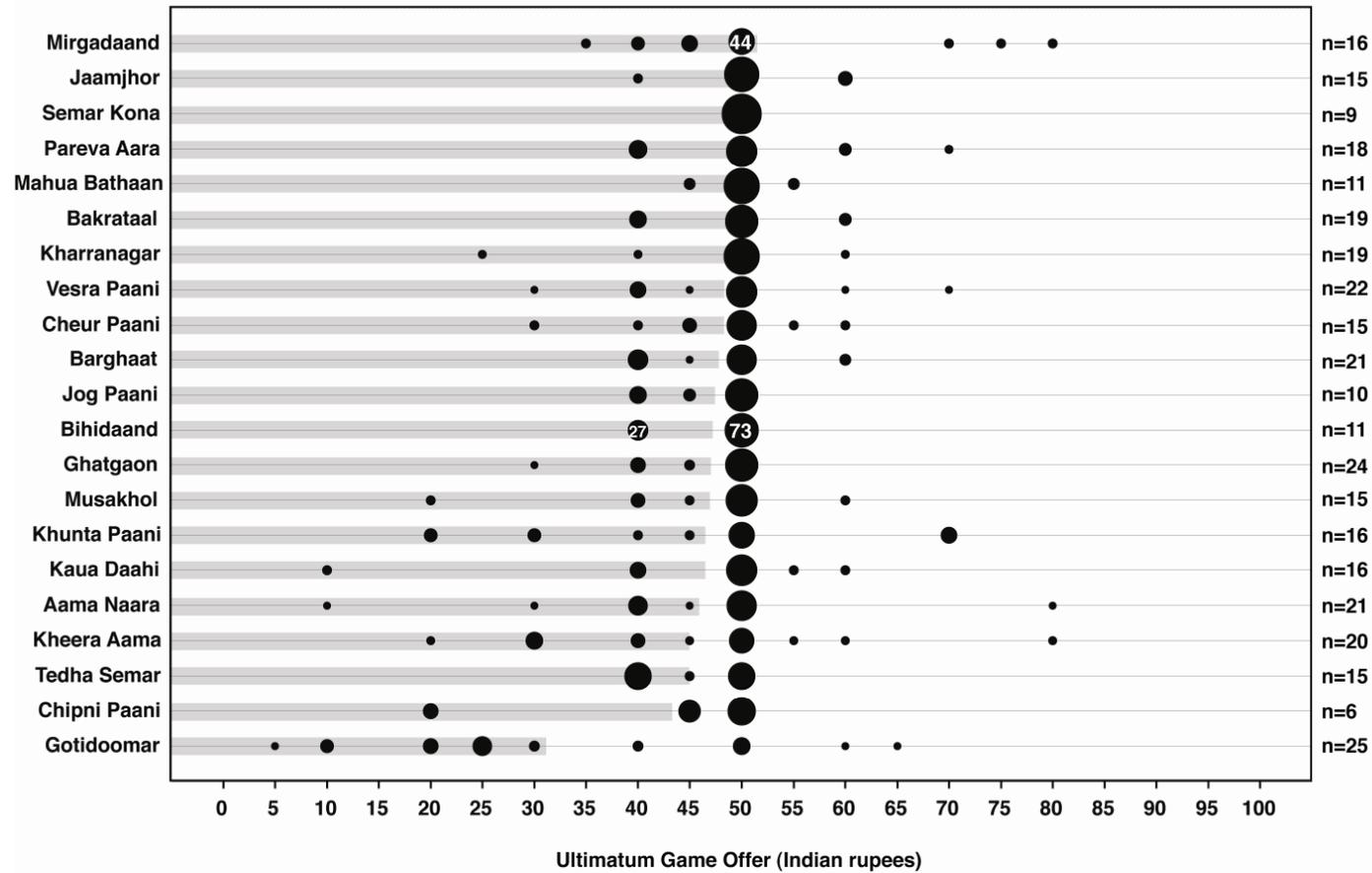


Figure 3.1 Distributions of UG proposer offers across 21 villages. For each village on the y-axis, the areas of the black bubbles represent the proportion of individuals from the village who made an offer of the value on the x-axis. To indicate scale, the numbers in some bubbles are the percentage proportions represented by those bubbles. Grey horizontal bars indicate the mean offers for villages. Villages are ordered by their mean offers; the bottom village (Gotidoomar) has the lowest mean. Counts on the right (n) represent the number of proposers from each village (total n = 344). The overall mode across villages is 50 rupees (mean \pm SD = 46.61 \pm 10.40).

3.2.1.2 Do properties of populations and/or individuals explain variation in proposer offers between and within populations?

One population descriptor and two individual descriptors are retained in the full model and explain a significant amount of variation in proposer offers between and within populations [Table 3.2A; full model (multilevel)]. Pseudo R^2 values¹ indicate that about 22% of variance between populations and 9% of variance within populations is explained by the three descriptor variables retained in the full model. The proportion of non-Korwas (village residents who are not Pahari Korwas) has a strong positive effect on proposer offers. Each additional non-Korwa living in the village is associated with offer values that are about 14 rupees (14% of the stake) higher on average. Note that non-Korwas did not participate in the games in any village. A player's household size has a small negative effect on her offer. People with an additional person in their household make offers that are about half a rupee lower on average. Finally, people who played on the second or third day of the games in any village made offers that were about five rupees higher on average. While I report p values for all variables, and although the effect of the proportion of non-Korwas ($p = 0.057$) and household size ($p = 0.060$) is marginally significant by conventional standards, I rely mainly on model fit criteria in interpreting these results (Section 2.5.2).

¹Pseudo R^2 values were computed according to Snijders and Bosker (1999).

Table 3.2 (A) Associations of each predictor term (fixed effect) with proposer offers in the null (intercept only) and full models. **(B)** Village and individual level variance components for proposer offer in the null and full models.¹ The variance partition coefficient [VPC = village level variance / (village level variance + individual level variance)] is 0.144 ± 0.054 (95% BCI² = 0.063, 0.273) in the null model, and 0.112 ± 0.049 (95% BCI² = 0.040, 0.228) in the full model. ***p<0.01, **p<0.05, *p<0.10

A				
Fixed effect	Proposer offer (Indian rupees)		DIC ³	
	$\beta \pm SE$	95% BCI ²		
Null models				
Intercept (single level)	46.624 ± 0.562***	45.506, 47.717	2590.199	
Intercept (multilevel)	46.928 ± 1.031***	44.903, 49.037	2546.072	
Full model (multilevel)				
Intercept	45.888 ± 1.853***	42.304, 49.607	2528.601	
Proportion of non-Korwas	13.821 ± 7.256*	-1.045, 27.509		
Household size (individuals)	-0.400 ± 0.213*	-0.819, 0.024		
Day on which game was played: day 2+ (ref: day 1)	4.940 ± 1.162***	2.658, 7.189		
B				
	Village level		Individual level	
	Variance ± SE	95% BCI ²	Variance ± SE	95% BCI ²
Null model (multilevel)	15.720 ± 7.090	6.314, 33.725	91.781 ± 7.310	78.660, 107.180
Full model (multilevel)	11.234 ± 5.674	3.705, 25.155	87.018 ± 6.873	74.694, 101.473

¹ For the two multilevel models (null and full), fixed effect parameters in each model are specified in Table 3.2A, while Table 3.2B presents the village and individual level variances in proposer offers for each model respectively. For instance, in Table 3.2A, the full model (multilevel) has four fixed effects including the intercept; for each fixed effect (column 1), the associated β value (column 2) and its 95% BCI² (column 3) can be read in the corresponding row. The DIC³ value (see Section 2.5.2 for details) for the model is presented in column 4 of Table 3.2A. The variance components for the full model (multilevel) can be read in the last row of Table 3.2B; column 2 represents the village level variance in proposer offers with its 95% BCI² (column 3), and column 4 represents the individual level variance in proposer offers with its 95% BCI² (column 5). The fixed effect parameters for the single level null model are presented in Table 3.2A; this model does not have variance components.

² Bayesian Credible Interval. Calculated from the posterior distribution, a k% interval contains k% of possible values of a parameter (Ellison 1996).

³ Deviance Information Criterion.

3.2.2 Responders

3.2.2.1 Does responder behaviour vary across populations?

Of the 340 offers that responders were presented with across 21 villages, only five offers of any value were rejected (Table 3.3; Figure 3.2); three of these five rejected offers had a value of 50 rupees (50% of the stake) and the remaining two rejected offers had values of 25 and 35 rupees respectively. Individuals virtually never reject offers in these populations, despite the fact that offers vary from 5% to 80% of the stake. There is no variation in responder behaviour across villages. Given the small number of rejections, no further analyses are conducted on responders' game responses.

Table 3.3 Numbers (n) of UG responder responses (total n = 340) for each of 21 study villages.

Village number	Village	Responses		
		Total (n)	Accept (n)	Reject (n) ¹
1	Chipni Paani	6	6	0
2	Mahua Bathaan	11	11	0
3	Jog Paani	9	9	0
4	Semar Kona	8	8	0
5	Bihidaand	10	10	0
6	Khunta Paani	15	15	0
7	Kaua Daahi	16	16	0
8	Pareva Aara	18	18	0
9	Musakhhol	15	15	0
10	Kharranagar	19	19	0
11	Tedha Semar	15	15	0
12	Jamjhor	15	15	0
13	Vesra Paani	22	22	0
14	Mirgadaand	16	15	1: 35
15	Barghaat	21	21	0
16	Gotidoomar	25	23	2: 25, 50
17	Cheur Paani	15	14	1: 50
18	Aama Naara	22	22	0
19	Bakrataal	18	18	0
20	Kheera Aama	21	20	1: 50
21	Ghatgaon	23	23	0

¹ Values listed after the colon are the values of the offers (in rupees) rejected.

3.2 RESULTS

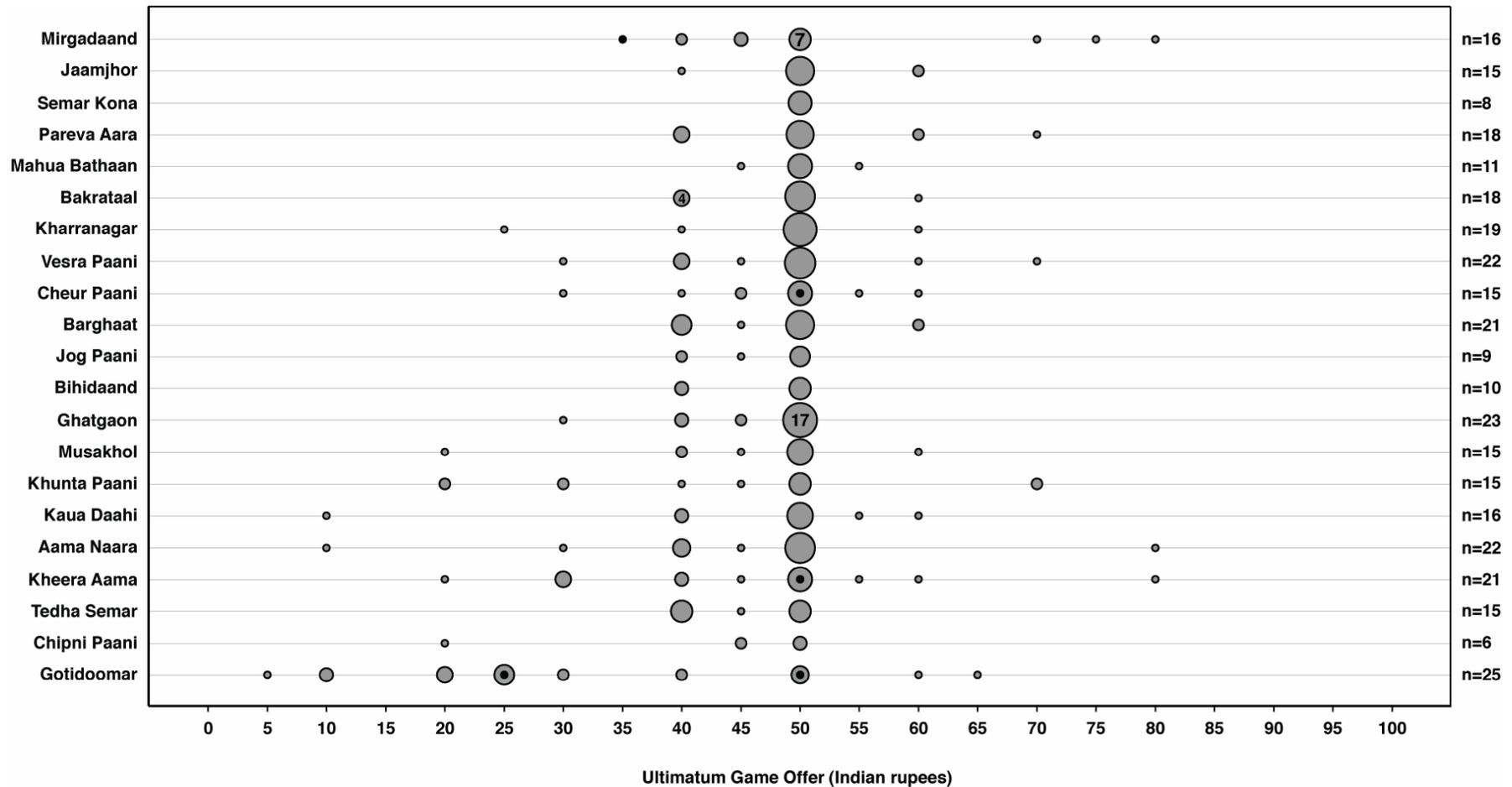


Figure 3.2 Distributions of UG responder responses across 21 villages. For each village on the y-axis, the areas of the grey bubbles represent the total number of proposer offers of the value on the x-axis, made in that village. The areas of the black bubbles represent the total number of proposer offers of the value on the x-axis rejected by responders from that village. To indicate scale, the numbers in some bubbles are the number of individuals represented by those bubbles. Counts on the right (n) represent the number of responders from each village (total n = 340). As per Figure 3.1, villages are ordered by their mean proposer offers; the bottom village (Gotidoomar) has the lowest mean.

3.2.2.2 Do self-reported MAOs vary across populations?

Distributions of responder MAOs (Figure 3.3) vary across villages. The modal MAO across all villages is zero. 80% of individuals across the 16 populations stated that they were willing to accept either nothing or the minimum non-zero division of the stake, i.e. five rupees. 4.9% of the variance in MAOs occurs between villages [Table 3.4B; null model (multilevel)]. The DIC value for the null model with village level intercepts (multilevel) is about 3.5 units lower than for the null model without village level intercepts (single level), indicating that the multilevel model accounting for village effects provides a slightly better fit to the data (Table 3.4A; null models). Once individual descriptors are included in the full model, the unexplained between-village variance reduces to 2.7% [Table 3.4B; full model (multilevel)].

Since the distribution of MAOs is skewed (80% of individuals have an MAO of zero or five and very few individuals have an MAO greater than 10), analyses were also conducted with the MAO modelled as an ordinal response variable with three categories (MAO = 0, MAO = 5, MAO => 10) (Table 3.5). In the ordinal multinomial model 3.3% of the variance in MAOs occurs between villages [Table 3.5B; null model (multilevel)]. The DIC value for the ordinal multinomial null model with village level intercepts (multilevel) is only about one unit lower than for the ordinal multinomial null model without village level intercepts (single level), indicating that the multilevel model accounting for village effects does not provide a considerably better fit to the ordinal data (Table 3.5A; null models); village level variance in MAOs is less important in these models. Once individual descriptors are included in the full ordinal multinomial model, the unexplained between-village variance reduces to 2% [Table 3.5B; full model (multilevel)].

Hence, although the percentage of between-village variance in MAOs is the same whether the MAO is modelled as a normal or ordinal response variable, differences between villages are more important in the normal linear models than in the ordinal multinomial response models. The ordinal response variable was constructed such that MAO values greater than or equal to 10 were pooled together with the result that between-village differences became unimportant in these models; this may indicate that between-village variance in MAOs

(captured by the linear models) may mostly be in the range and frequency of values greater than 10. In other words, villages may be similar in their distributions of MAO values of zero and five (see Figure 3.3).

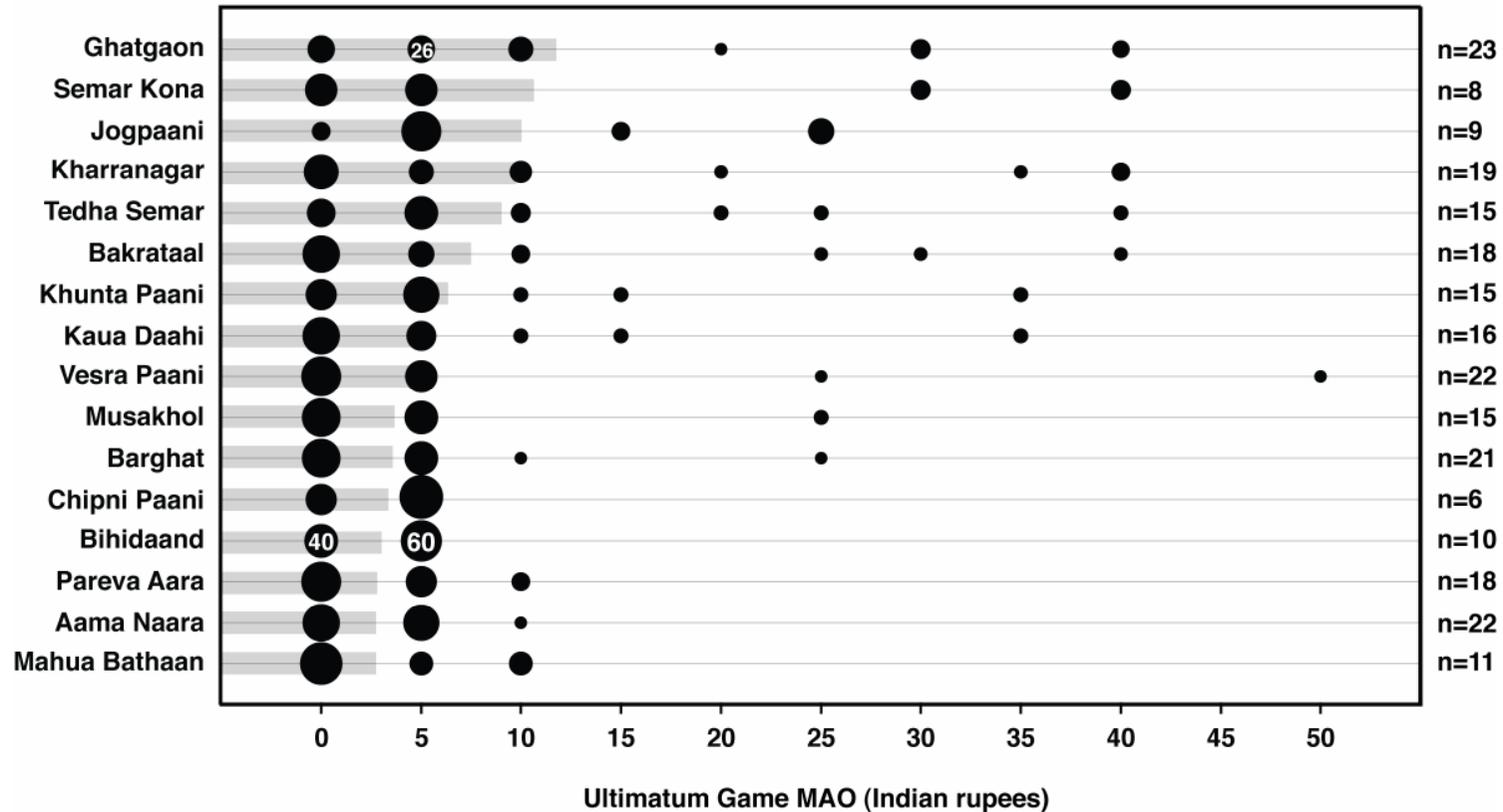


Figure 3.3 Distributions of UG responder MAOs across 16 villages. For each village on the y-axis, the areas of the black bubbles represent the proportion of individuals from the village who have an MAO of the value on the x-axis. To indicate scale, the numbers in some bubbles are the percentage proportions represented by those bubbles. Grey horizontal bars indicate the mean MAO for villages. Villages are ordered by their mean MAOs; the bottom village (Mahua Bathaan) has the lowest mean. Counts on the right (n) represent the number of responders from each village (total n = 248). The overall mode across villages is 0 rupees (mean \pm SD = 6.11 \pm 9.67).

3.2.2.3 Do properties of populations and/or individuals explain variation in self-reported MAOs between and within populations?

Five variables, all individual descriptors, explain significant variation in stated MAOs and are retained in the full normal linear model [Table 3.4A; full model (multilevel)]. Pseudo R^2 values indicate that about 25% of variance between populations and 9% of variance within populations is explained by the five descriptor variables retained in the full normal linear model. Women stated MAOs that are lower on average than men's MAOs by three rupees. Individuals born in the focal village stated MAOs that were about five rupees higher on average than those born elsewhere. However, those who remained resident in their natal village post-marriage stated MAOs that are lower on average by about five rupees than those who migrated elsewhere post-marriage. Players whose mothers were residing in the same village stated MAOs that were about three rupees higher on average than those whose mothers lived in another village. The number of full brothers aged 15 years or more that a player has living in other villages is positively associated with her stated MAO; each additional adult brother living in another village corresponds to a three rupee increase in a player's MAO value on average. Including interaction terms for sex and age respectively with each of the variables, birthplace, post-marital residence, mother in village and full brothers aged 15 years or more that a player has living in other villages respectively, does not substantially improve model fit; the interaction terms do not have a statistically significant association with responder MAOs. Hence, men, individuals residing in their natal villages, individuals residing in a non-natal village post-marriage, those whose mothers live in the village and those whose adult brothers do not, all seem to drive a harder bargain. The offer a proposer made to a responder is not a significant predictor of a responder's MAO (see Appendix C, Table C.4).

Two individual descriptors are significant predictors of MAO in the full ordinal multinomial model [Table 3.5A; full model (multilevel)], namely, a player's level of education and the frequency of her visits to town. Illiterate individuals are about three times more likely than those with some schooling to state an MAO less than or equal to ten

rupees. Individuals who make an additional trip to town each month are about 10% more likely to state an MAO less than ten rupees.

Table 3.4 (A) Associations of each predictor term (fixed effect) with responder MAO in the null (intercept only) and full models. **(B)** Village and individual level variance components for responder MAO in the null and full models.¹ The variance partition coefficient [VPC = village level variance/ (village level variance + individual level variance)] is 0.049 ± 0.049 (95% BCI² = 0.000, 0.170) in the null model, and 0.027 ± 0.037 (95% BCI² = 0.000, 0.129) in the full model. ***p<0.01; **p<0.05; *p<0.10

A				
Fixed effect	UG MAO (Indian rupees)		DIC ³	
	$\beta \pm SE$	95% BCI ²		
Null models				
Intercept (single level)	6.071 ± 0.648***	4.782, 7.335	1712.225	
Intercept (multilevel)	6.097 ± 0.850***	4.404, 7.834	1708.769	
Full model (multilevel)				
Intercept	5.220 ± 1.700***	1.939, 8.562	1695.834	
Sex: female (ref: male)	-3.216 ± 1.433**	-6.047, -0.425		
Birthplace: this village (ref: other village)	5.404 ± 2.449**	0.641, 10.254		
Post-marital residence: natal village (ref: other village)	-5.103 ± 2.480**	-10.086, -0.261		
Mother in village: yes (ref: no)	3.273 ± 1.431**	0.447, 6.068		
Full brothers aged ≥ 15 years living in other villages	3.362 ± 1.054***	1.297, 5.444		
B				
	Village level		Individual level	
	Variance ± SE	95% BCI ²	Variance ± SE	95% BCI ²
Null model (multilevel)	4.866 ± 5.275	0.004, 18.163	92.652 ± 9.225	76.393, 112.205
Full model (multilevel)	2.463 ± 3.591	0.002, 12.116	86.538 ± 8.500	71.599, 104.905

¹ For the two multilevel models (null and full), fixed effect parameters in each model are specified in Table 3.4A, while Table 3.4B presents the village and individual level variances in responder MAOs for each model respectively. For instance, in Table 3.4A, the full model (multilevel) has six fixed effects including the intercept; for each fixed effect (column 1), the associated β value (column 2) and its 95% BCI² (column 3) can be read in the corresponding row. The DIC³ value (see Section 2.5.2 for details) for the model is presented in column 4 of Table 3.4A. The variance components for the full model (multilevel) can be read in the last row of Table 3.4B; column 2 represents the village level variance in responder MAOs with its 95% BCI² (column 3), and column 4 represents the individual level variance in responder MAOs with its 95% BCI² (column 5). The fixed effect parameters for the single level null model are presented in Table 3.4A; this model does not have variance components.

² Bayesian Credible Interval. Calculated from the posterior distribution, a k% interval contains k% of possible values of a parameter (Ellison 1996).

³ Deviance Information Criterion.

Table 3.5 (A) Associations of each predictor term (fixed effect) with the probability of responder MAO \leq 10 Indian rupees in the null (intercept only) and full models. **(B)** Village level variance and the VPC¹ for the logit (probability of responder MAO \leq 10 Indian rupees) in the null and full models.² ***p<0.01, **p<0.05, *p<0.10

A				
Fixed effect	UG MAO \leq 10 Indian rupees		DIC ⁴	
	Antilogit (β) \pm SE	95% BCI ³		
Null model				
<i>single level</i>				
Intercept (MAO \leq 0)	0.440 \pm 0.031*	0.378, 0.500	524.486	
Intercept (MAO \leq 5)	0.804 \pm 0.025***	0.753, 0.849		
<i>multilevel</i>				
Intercept (MAO \leq 0)	0.437 \pm 0.039	0.362, 0.511	523.271	
Intercept (MAO \leq 5)	0.806 \pm 0.029***	0.746, 0.861		
Full model (multilevel)				
Intercept (MAO \leq 0)	0.217 \pm 0.051***	0.130, 0.325	506.081	
Intercept (MAO \leq 5)	0.623 \pm 0.068*	0.488, 0.747		
Education: illiterate (ref: some schooling)	0.768 \pm 0.054***	0.653, 0.861		
literate (ref: some schooling)	0.596 \pm 0.089	0.417, 0.759		
Number of monthly visits to town	0.525 \pm 0.011**	0.504, 0.548		
B				
	Village level variance		Variance partition coefficient (VPC) ¹	
	Variance \pm SE	95% BCI ³	VPC \pm SE	95% BCI ³
Null model (multilevel)	0.117 \pm 0.155	0.001, 0.546	0.033 \pm 0.039	0.000, 0.142
Full model (multilevel)	0.072 \pm 0.110	0.001, 0.393	0.020 \pm 0.029	0.000, 0.107

¹ VPC = village level variance / (village level variance + 3.29). Level 1 (multinomial response variable) has a standard logistic distribution with variance $\pi^2/3 = 3.29$ (Hedeker 2003).

² For the two multilevel models (null and full), fixed effect parameters in each model are specified in Table 3.5A, while Table 3.5B presents the village level variance in the logit (probability of responder MAO \leq 10 Indian rupees) and the VPC¹ for each model respectively. For instance, in Table 3.5A, the full model (multilevel) has four fixed effects including two intercept terms; for each fixed effect (column 1), the associated Antilogit (β) value (column 2) and its 95% BCI³ (column 3) can be read in the corresponding row. The DIC⁴ value (see Section 2.5.2 for details) for the model is presented in column 4 of Table 3.5A. The variance components for the full model (multilevel) can be read in the last row of Table 3.5B; column 2 represents the village level variance in the logit (probability of responder MAO \leq 10 Indian rupees) with its 95% BCI³ (column 3), and column 4 represents the VPC¹ for the logit (probability of responder MAO \leq 10 Indian rupees) with its 95% BCI³ (column 5). The fixed effect parameters for the single level null model are presented in Table 3.5A; this model does not have variance components.

³ Bayesian Credible Interval. Calculated from the posterior distribution, a k% interval contains k% of possible values of a parameter (Ellison 1996).

⁴ Deviance Information Criterion.

3.2.3 Is proposer behaviour contingent on responder behaviour?

The income-maximising offer (IMO), the offer that provides the highest expected payoff to a proposer given the distribution of rejections across offer values (see Section 3.4.2 for details of how this was calculated), is zero rupees as estimated from the distribution of rejections pooled across all 21 villages. Hence, the mean proposer offer for every village (Figure 3.1) was much higher than the IMO. In fact, all 344 offers made across 21 villages were higher than the IMO. I estimated the village specific IMO for the four villages where at least one offer was rejected (Table 3.6). The mean proposer offer was much greater than the IMO for all four villages. However, Mirgadaand, the only village with an IMO substantially greater than zero, is also the village with the highest mean proposer offer across all 21 villages. Only one offer of 35 rupees was rejected in Mirgadaand. Overall, proposers make offers substantially greater than the IMO and do not demonstrate behaviour consistent with income maximisation. Mean proposer offers are also considerably higher than mean self-reported MAOs in all villages.

Table 3.6 Income-maximising offers (IMO) and mean proposer offers for villages where at least one offer was rejected.

Serial Number	Village	IMO (Indian rupees)	Mean proposer offer
1	Gotidoomar	0	31.200
2	Kheera Aama	0	45.000
3	Cheur Paani	0	48.333
4	Mirgadaand	40	51.563

3.3 Discussion

3.3.1 Variation in proposer behaviour

Variation in UG proposer behaviour across 21 populations of the same small-scale society is comparable to that found previously across 15 different small-scale societies (Henrich et al. 2004; Henrich et al. 2005). There is significant behavioural heterogeneity across populations of the same endogamous cultural group. These findings challenge the conclusions of studies attributing behavioural variation across populations to cultural differences between them based on samples from one (or very few) populations per culture (e.g. Henrich et al. 2001; Henrich et al. 2005; Henrich et al. 2010; Henrich et al. 2006; Herrmann et al. 2008; Roth et al. 1991). Population level replicates within each society are crucial to determine whether there is behavioural variation between cultural groups in addition to the variation between populations. Behavioural variation currently ascribed to the cultural transmission of cooperative norms may, in fact, be driven by environmental (demographic and ecological) differences between populations.

It has been suggested that cultural transmission may occur at the level of the village unit, rather than at the level of the endogamous cultural unit (Gurven 2004a; Henrich et al. 2005). If between-village variation is maintained by cultural transmission within villages, cultural group selection could occur, the village being the unit of selection instead of the cultural group. I discuss this potential explanation for my results at some length in the final chapter of this thesis (Section 6.1).

3.3.2 Correlates of proposer behaviour

Proposer offers have a strong positive association with the proportion of non-Korwas residing in the village. Participants in this study always played with other Pahari Korwas and the non-Korwa residents of the village did not participate in the games. These results

may therefore be interpreted in two ways. First, the positive association of offers with the frequency of non-Korwas may indicate that Korwas tend to increase levels of cooperation towards Korwas when people of other ethnicities co-reside with them. Second, higher levels of cooperation may prevail in villages where individuals from multiple ethnicities co-reside, irrespective of whether the beneficiary of cooperation shares the ethnic identity of the cooperator. Data from this study cannot distinguish between these two interpretations. However, if the first interpretation is correct, then my results support the findings of previous work (e.g. Bernhard et al. 2006; de Cremer and van Vugt 1999; Tajfel et al. 1971 and reviewed in Brewer and Schneider 1990) that people tend to be more cooperative towards those they identify as the in-group (even if the criteria for grouping are arbitrary). Inter-group competition promotes within-group cooperation (Burton-Chellew et al. 2010; Choi and Bowles 2007; Puurtinen and Mappes 2009).

Alternatively, if the second interpretation is correct, then my results raise the possibility that in-group favouritism is not universal and that ethnic diversity may even promote cooperation under certain conditions, although it is unclear at this stage what the underlying mechanism for this may be. However, Yamagishi and colleagues have suggested that in-group favouritism observed in laboratory studies may reflect the operation of a 'group heuristic' (e.g. Karp et al. 1993; Yamagishi and Kiyonari 2000; Yamagishi and Mifune 2008; Yamagishi et al. 2008); people contribute more to their groups in expectation of indirect future payoffs from group members, i.e. via indirect reciprocity. Hence, one possibility is that people only increase cooperation toward the in-group when a grouping context is explicitly created; future work should investigate whether group biases continue to emerge when explicit references to the grouping context are eliminated.

Proposer offers are negatively associated with household size, i.e. the number of individuals residing in the same house and eating at a common hearth. Individuals with larger households may be provisioning more people, leaving them with lower resource surpluses; in my dataset, household size is positively correlated with the number of living children an individual has. Hence, cooperation may be more costly for individuals with large households. The analyses investigated associations between proposer offers and other demographic variables potentially correlated with household size, such as age and measures

of wealth; these variables were not retained in the full model and therefore do not explain the association between household size and proposer offers.

Finally, people who played on the second or third day of the games in any village made offers that were slightly but significantly higher than those who played on the first day. Individuals who played on the second or third day were not present at the venue of the games on preceding days. Since all players were informed of the outcome of their game decisions and received their game payments only once all games in a village had been concluded, later players could not have known the outcomes of games played on previous days. Individuals who played on day two or three may have learnt the game rules from those who played before them. They may also have asked people who had already played about the offers they made, accepted or rejected. Hence, although the association between day of play and proposer offer may be interpreted as an effect of learning, it is puzzling that those who played later increased rather than decreased their offers, given that Pahari Korwas never seem to reject offers of any value. It is unlikely that familiarity with the research team is responsible for an increase in offers as we had little interaction with village residents until the day they played the games. Since we ran the study for about 8-9 hours each day, there was little time for interaction outside the context of the study while we were still running the games in a village. The finding that day of play is associated with individuals' behaviour emphasises that researchers working in small populations need to take account of the length of time over which their data are collected.

3.3.3 Variation in responder behaviour

Only 1.5% of responders across 21 Pahari Korwa villages rejected offers of any value. Hence, individuals virtually never rejected offers of any size even though offers varied from 5% to 80% of the stake. Taken together, UG responders in these populations played the income-maximising strategy. The rejected offers were not the lowest made and in fact three of the total five offers rejected were for 50% of the stake. The rejection of offers of 50% of the stake is not unique to Pahari Korwa populations; it has been reported in

Sursurunga populations in Papua New Guinea and in Hadza populations in Tanzania (Barr et al. 2009; Henrich et al. 2006).

There is almost no variation in response distributions across villages. Variation in responder behaviour across 21 populations of the same small-scale society is lower than that found across 15 different small-scale societies (Henrich et al. 2004; Henrich et al. 2005; Henrich et al. 2006). Hence, since I find little variation in responder behaviour across populations of the same cultural group, I cannot reject the hypothesis that variation in responder behaviour observed across 15 different cultural groups in previous studies (Henrich et al. 2004; Henrich et al. 2005; Henrich et al. 2006) may in fact be driven by cultural differences between the study populations.

The low frequency of rejections observed in Pahari Korwa populations is comparable to that found in several other populations including populations of the Ache (0%), Tsimane (0%), Kazakh (0%), Quichua (0%), Isanga (3%), Orma (3.5%), Sanquianga (4%), Machiguenga (4.7%), Sangu herders (5%) and Samburu (5%) (Barr et al. 2009; Henrich et al. 2005). In about half of the 15 populations sampled by Henrich et al. (2005), responder behaviour was comparable to that observed in my study populations.

A meta-analysis of 75 UG studies (Oosterbeek et al. 2004) conducted across 26 countries, largely sampling university students, reveals that the average rejection rate across studies is 16%. However, rejection rates vary significantly by region (group of neighbouring countries), and reported rejection rates are less than 5% in populations from several countries including Bolivia (0%), Paraguay (0%), Kenya (4%), Peru (4.8%) and Mongolia (5%). The meta-analysis also demonstrates that, across studies, rejection rates are far more sensitive to changes in the relative proportion of the stake offered than the absolute value of the offered share. This suggests that “responders care (a lot) about the relative amount they receive” (Oosterbeek et al. 2004).

In summary, while responders in some parts of the world are willing to accept any offer made to them, those in other places care considerably about relative payoffs. Barr et al. (2009) find some support for their hypothesis that variation in inequality aversion explains

variation in UG behaviour across 15 small-scale societies. These patterns may reflect underlying differences in individuals' concern with absolute versus relative payoffs in different environments. For instance, selection may favour strategies that ensure near-equal splits of resources in stochastically more stable environments, where relative payoffs may matter more in terms of improving long-term fitness than maximizing absolute payoffs in the short-term. Individuals living in unpredictable environments, such as when there is a high prevalence of disease or reliance on seasonal resource bases to meet livelihood needs, may be less concerned with relative payoffs and more focussed on maximising immediate absolute payoffs. Hence, differences in levels of environmental uncertainty across populations may explain the observed patterns of variation in responder behaviour; 'fairness norms' may simply be behavioural heuristics reflecting the importance of relative versus absolute payoffs in particular environments.

3.3.4 Self-reported behavioural strategies

80% of responders reported that they were willing to accept either nothing or the smallest possible division of the stake, i.e. five rupees. Considering the low rate of actual rejections in these populations (even of small offers), these results suggest that the Pahari Korwa do as they say. The modal self-reported MAO across populations (zero) is equal to the IMO (calculated from the distribution of actual rejections). Moreover, even though the village level variation in MAO values is higher than the variation in actual responses, this does not necessarily imply divergence between real and self-reported behaviour. The modal MAO in all villages is either zero or five rupees and very few individuals stated MAOs greater than ten. Since only one proposer made an offer less than ten rupees, variation in real responses may have been comparable to variation in MAOs if more offers of zero and five rupees had been made. If people were simply justifying their accept/reject decisions, then we should expect a closer resemblance between the distributions of proposer offers and responder MAOs; I find no relationship between the two.

Variation in self-reported MAOs measured across 16 populations of the same small-scale society in this study is 4.9%; this is much lower than the variation in MAOs found

previously across 15 different societies (34.4%, Henrich et al. 2006). However, the two results are not really comparable because the MAO in this study is a self-reported value with no real payoff implications; in Henrich et al.'s (2006) study individuals' MAOs affected their payoffs. While the MAOs are unreliable measures of real bargaining preferences, they are a measure of what individuals would like others, or at least a visiting researcher, to believe. It is notable that most people in these populations project themselves as an easy bargain, at least in the game as it is presently framed. However, men, individuals residing in their natal villages, individuals residing in a non-natal village post-marriage, those whose mothers live in the village and those whose adult brothers do not, all emerge as harder bargainers in the full linear model. Taken together these results suggest that whether individuals reside in their natal village or not may be an important determinant of their projected or real (if self-reported MAOs reflect real bargaining preferences) behavioural strategies. Those who are illiterate and visit town more often are more likely to state a lower MAO in the full ordinal multinomial model. That different variables emerge as significant predictors of MAO in the linear (continuous data) and ordinal logistic (ranked data) models may indicate that individuals' MAOs are influenced by different variables above and below a certain threshold value.

3.3.5 Discrepancies in proposer and responder behaviour

In this study, proposers often offered substantial proportions of the stake, even though responders appear willing to accept any offer. The income-maximising offer - the offer that maximises proposers' expected payoffs given the observed probabilities of rejection across offer values - is much lower than the average offer made in all villages; this suggests that proposers were not acting strategically to maximise their income by making such high offers. My findings agree with those of previous studies demonstrating that mean offers in most populations of small-scale societies are much higher than income-maximising offers (Henrich et al. 2004; Henrich et al. 2005) and mean minimum acceptable offers (Henrich et al. 2010; Henrich et al. 2006). Moreover, while responders in my study collectively played the income-maximising strategy, proposers did not.

These data add to growing evidence that proposer and responder behaviour in the UG does not always co-vary. In populations of large-scale societies, there is much greater variation in rejection rates than in offers (Oosterbeek et al. 2004); I find the reverse pattern in my study populations. A recent study demonstrates that while proposers respond to reputation concerns by increasing their offers in a public context, responders do not do so (Lamba and Mace 2010). All these findings contradict models predicting that proposer behaviour should be a best response to responder behaviour in the UG (e.g. Bolton and Ockenfels 2000; Fehr and Schmidt 1999). Patterns of empirical data from the UG provide support for the hypothesis that proposer and responder strategies in a bargaining situation are influenced by different considerations and selection pressures.

3.3.6 Concluding remarks

I find significant variation in cooperative behaviour, measured via proposer's offers in the UG, across 21 populations of the same small-scale society. This variation is comparable to that found previously between 15 different small-scale societies. My results suggest that behavioural variation in proposer's offers that has previously been attributed to cultural differences between populations may in fact be driven by environmental differences between them. Environmental drivers of behavioural variation are unlikely to maintain stable, heritable differences essential for selection at the population-level. On the other hand, responders' behaviour varies little across 21 populations of the same small-scale society; variation in responder behaviour observed previously across populations from 15 different small-scale societies may be driven by cultural differences between them. Drivers of behavioural variation may differ for proposers and responders in a bargaining situation.

3.4 Methods

3.4.1 *Experimental set-up*

The games were played in two phases; five villages were visited between May 23rd and June 21st, 2007, and the remaining 16 villages were visited between February 2nd and May 16th, 2008. The games were played over two consecutive days in each village except one village (Vesra Paani) where they were played over four consecutive days. Games were played within two (18 villages), three (two villages), or four (one village) days following our arrival in a village. Mean age \pm SD of participants was 35.57 ± 12.49 years and 44% were female.

All participants collected at a common location in the village on the day of the games; only individuals who were playing on a particular day were present at the study venue on that day. They were collectively given general instructions about the day's programme. These instructions excluded a description of the rules of the game but explained that a set of one-shot, anonymous economic games would be played in pairs for real money (see Appendix A, Section A.1.1 for script). Players were tested collectively for their understanding of these general instructions. Upon arriving at the private location, players were individually instructed about the game rules and examples (see Appendix A, Sections A.1.2 and A.1.3 for game scripts). They were then tested for their understanding of the game rules and of the anonymity of their decisions. Only a player who individually answered all test questions correctly played the game. Players were randomly designated as proposers or responders. A proposer made her offer by manipulating real five rupee coins into two piles and placing them on two sides of a string, one pile for herself and one for the responder. A responder was presented with two piles of five rupee coins in accordance with the division made by the proposer, and asked whether she wished to accept or reject the pile offered to her. She was then asked what minimum offer from the proposer she would be willing to accept. In order to facilitate comprehension of this question, I started with a pile of five rupee coins summing to the amount the responder had accepted, deducted five rupees from the pile and asked if the amount was still acceptable to the player. This process was repeated until the player said she would not accept an offer value and the next greater

acceptable offer value was recorded as the MAO. The MAO was recorded as zero for players who were willing to accept an offer of value zero. The only five players who rejected the offers made to them came from the five populations where MAOs were not recorded.

Pairs of players were constituted by randomly matching token numbers. In eight villages, an odd number of individuals participated in the games. In these villages, one individual was paired randomly with two other players from the village, in order to determine the payoff to all participating players. This does not confound the analyses, which are conducted on the offers and responses of individuals, not their payoffs. Players were unaware of the total number of people who had successfully played the game and the number of individuals who did not play due to a failure to answer all test questions correctly.

3.4.2 Statistical analyses

Multilevel normal linear models (Browne 2009; Rasbash et al. 2009; Snijders and Bosker 1999) were used to analyse variation in proposer offers and responder self-reported MAOs across villages, and the association of population and individual descriptors with individuals' offers or self-reported minimum acceptable offers respectively. Responder MAOs were also modelled as an ordinal response variable with three categories (MAO = 0, MAO = 5, MAO \geq 10) using multilevel ordinal multinomial models with a logit link function (Browne 2009; Rasbash et al. 2009). The analyses for each outcome variable (proposer offer, responder MAO as continuous variable, responder MAO as ordinal variable) proceeded in four stages as described in Section 2.5.2.

The IMO was calculated as follows (Henrich et al. 2004). A binary logistic regression was run with responder response (accept/reject) as the dependent variable and proposer offer as the only explanatory variable. This regression estimates the relationship between the probability of acceptance and proposer offer, from the distribution of offers accepted and rejected. The parameter values derived from the regression equation (β and c) were used to

estimate the probability of acceptance (p_i) for each offer value (i) from 0 to 100 [$p_i = \exp(\beta i + c) / \{1 + \exp(\beta i + c)\}$], with i increasing in increments of five. The estimated probability of acceptance (p_i) for each offer value (i) was multiplied with the payoff received if that offer value was accepted; this is the expected payoff ($payoff_i$) from an offer [$payoff_i = p_i (S - i) = p_i (100 - i)$] given its probability of acceptance. The IMO is then the offer value with the highest expected payoff.

CHAPTER 4

VARIATION IN COOPERATION ACROSS POPULATIONS: EVIDENCE FROM PUBLIC GOODS GAMES AND A ‘REAL- WORLD’ MEASURE OF BEHAVIOUR

4.1 Introduction

4.1.1 Background and related research

Different measures of behaviour may not always yield consistent results. Therefore, in this chapter I continue to address the question of whether there is stable, heritable variation in levels of cooperation across human populations, using two further measures of cooperative behaviour. I present findings from a public goods game (PGG) and a new ‘real-world’ measure of behaviour, both employed in 16 Pahari Korwa villages.

A broad range of experimental games have the structure of a public goods dilemma (Ledyard 1995). Garrett Hardin’s ‘tragedy of the commons’ (Hardin 1968) typifies a public goods dilemma; this is a scenario in which although every individual increases her payoff by maximally harvesting a finite resource replenished at a constant rate that she shares with other consumers (e.g. grazing cattle on the village commons), if all consumers do the same, the consequent over-harvesting and depletion of the resource would result in a reduced payoff for all consumers. A PGG framed thus employs what is termed the “common-pool resource mechanism”. In an alternative formulation, the “voluntary contributions mechanism”, individuals must decide how much of a personal endowment they each wish

to contribute to a public good; the return from the public good is shared equally by all participating individuals, irrespective of how much they each contribute to it. The return from the public good is a positive function of the collective investment in it; the total amount contributed to the public good is multiplied by some factor and the product is divided equally among all participating individuals. The income-maximising strategy in a PGG implementing the voluntary contributions mechanism is to contribute nothing, but players profit more if everyone contributes something as opposed to if no one makes any contribution.

PGGs have been implemented extensively in the laboratory amongst samples of university students (reviewed in Davis and Holt 1993, Gächter and Herrmann 2009, Kollock 2003, Ledyard 1995, Sally 1995 and Zelmer 2003). Laboratory studies have provided substantial insights about individuals' behaviour in cooperative dilemmas. Studies have investigated how group size (e.g. Carpenter 2007; Isaac and Walker 1988; Isaac et al. 1994; Marwell and Ames 1979), payoff structures (e.g. Brandts and Schram 2001; Goeree et al. 2002; Isaac and Walker 1988), repeated interactions between players (e.g. Andreoni 1988; Andreoni and Croson 2008; Croson 1996; Ostrom et al. 1992), and opportunities for punishing defection (e.g. Fehr and Gächter 2000, 2002; Gächter et al. 2008; Gurerk et al. 2006; Ostrom et al. 1992; Rockenbach and Milinski 2006) affect levels of cooperation in a PGG. As expected, individuals cooperate more when the costs of cooperation are lower, there are opportunities for repeated interactions, and defection may be punished. However, substantial contributions are observed in PGGs even when players interact under one-shot, anonymous conditions (e.g. Gächter and Herrmann 2006; Gächter et al. 2004; Walker and Halloran 2004).

Few studies have examined variation in PGG behaviour across populations (Barr 2001; Henrich et al. 2005; Herrmann et al. 2008). Herrmann et al. (2008) implemented an anonymous, repeated PGG, with and without punishment, across 16 populations from 15 countries (large-scale societies); all participants in the study were university students. Henrich et al. (2005) employed an anonymous, one-shot PGG in six populations from six small-scale societies. Barr (2001) played anonymous and non-anonymous, repeated PGGs in 18 ethnically mixed villages in Zimbabwe. All three studies find significant variation in

players' contributions to the public good across populations. Herrmann et al. (2008) also find significant variation in the frequency and degree of punishment across countries. Henrich et al. (2005) and Herrmann et al. (2008) infer that cultural differences drive this behavioural variation between their sample populations. However, all three studies confound cultural and environmental differences between populations and thus cannot differentiate whether cultural transmission, or environmental variation, is the likely driver of the observed variation.

4.1.2 Behavioural measures

In this study, a PGG implementing the voluntary contributions mechanism was played under one-shot, anonymous conditions (see Section 2.4 for details of study set-up and Section 4.4.1 for details of the games). Participants were divided into groups of six players. Each player received an endowment of 20 rupees and decided how much of it she wished to contribute to a group pot in divisions of five rupees. Once all six players had 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-maximising strategy entails that a player contribute nothing to the group pot.

A new 'real-world' measure of behaviour was implemented that involves taking a useful commodity from a common pool (see Section 4.4.2 for details). I used salt, which is valued among the Pahari Korwa and a commodity that they are most likely to buy at market (Srivastava 2007). On concluding the PGG in a village, when a participant collected her earnings at a private location, she was informed that I had brought along x kg of salt to distribute amongst the y individuals who participated in the games and therefore $z = x/y$ kg of salt was 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 given to her along with her earnings from the game. In each village I started with a total quantity of salt (in kg) equal to the total number of participants so that the initial amount available per person was 1 kg. I then recalculated and

updated the total amount available (x), the number of people remaining (y), and the amount available per person ($z = x/y$) to the nearest 100 g for each person based on how much salt remained after the preceding person had taken their desired salt quantity. I stopped distributing salt when either the penultimate player 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 possessed no prior information about it. Moreover, they did not know how much salt was available to anyone else. The income-maximising strategy entails that a player take the maximum amount of available salt. For each player, I 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 is, the more selfish the player's behaviour. I use these salt decisions to measure behavioural variance across villages and to assess whether behaviour captured by a formal economic game, such as the PGG, correlates with a 'real-world' measure of cooperation.

I employ multilevel, multivariate response models (Rasbash et al. 2009; Snijders and Bosker 1999) to explicitly analyse variation at the village and individual levels. Multivariate response models let us simultaneously examine the effect of explanatory variables on multiple response variables, in this case PGG contribution and salt deviation. They also allow us to partition the correlation between the two response variables into village and individual level components.

4.2 Results

The PGG was played in a total of 16 villages. 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 if the salt ran out before they collected their payments. Not all those who received salt participated in the PGG if they had failed to understand the game rules. Table 4.1 presents sample sizes of PGG players and salt takers for the 16 villages.

Table 4.1 Number (n) of PGG players (total n = 301) and salt takers (total n = 302) from each of 16 study villages.

Village number	Village	PGG players (n)	Salt takers (n)
1	Chipni Paani	12	11
2	Mahua Bathaan	18	22
3	Jog Paani	7	13
4	Semar Kona	9	13
5	Bihidaand	15	15
6	Khunta Paani	22	27
7	Kaua Daahi	18	24
8	Pareva Aara	24	34
9	Musakhol	16	16
10	Kharranagar	24	37
11	Tedha Semar	19	12
12	Vesra Paani	22	20
13	Barghaat	24	9
14	Aama Naara	30	9
15	Bakrataal	15	28
16	Ghatgaon	26	12

In Section 4.2.1 I examine whether PGG contributions and salt deviations vary across populations. In Section 4.2.2 I investigate whether properties of villages and/or individuals explain any variation in PGG contributions and salt deviations. Finally, in Section 4.2.3 I examine whether there is a correlation between PGG contributions and salt deviations at the individual and village levels.

4.2.1 Do PGG contributions and salt deviations vary across populations?

Distributions of both PGG contributions (Figure 4.1) and salt deviations (Figure 4.2) vary considerably across villages, including the modes and means. 4.1% of the variance in PGG contributions and 18.2% of the variance in salt deviations occurs between villages [Table 4.2B; null model (multilevel)]. The between-village variation in salt deviation is remarkable; in some villages the salt ran out before less than half the players had taken any salt, while in others almost everyone received some salt. The DIC value for the null model with village level intercepts (multilevel) is about 58 units lower than for the null model without village level intercepts (single level), indicating that the multilevel model accounting for village effects provides a substantially better fit to the data (Table 4.2A; null models). Once village and individual descriptors are included in the full model, the unexplained between-village variance reduces to 1.4% in PGG contributions and 11.8% in salt deviations [Table 4.2B; full model (multilevel)]. Variance in UG behaviour between 15 small-scale societies was estimated at about 12% (Henrich et al. 2005). Once again, behavioural variance between 16 populations of the same small-scale society is comparable to that between 15 populations of 15 different small-scale societies.

Dummy variables encoding 16 populations from 15 different large-scale societies account for 7% of the variance in group average contributions in repeated PGG experiments (without punishment) run by Herrmann et al. (2008). In their study, mean contributions in the first round of the PGG vary between about 8 and 14 units of the initial endowment (also 20 units), and mean contributions averaged across all 10 rounds of the PGG vary between 4.9 and 11.5 units. Mean PGG contributions across 16 populations of the same society in this study vary between 7.2 and 14.7 units (Figure 4.1). Hence, the variance in contributions and range of mean contributions across 16 populations of the same society is comparable to that across 16 populations of 15 different societies.

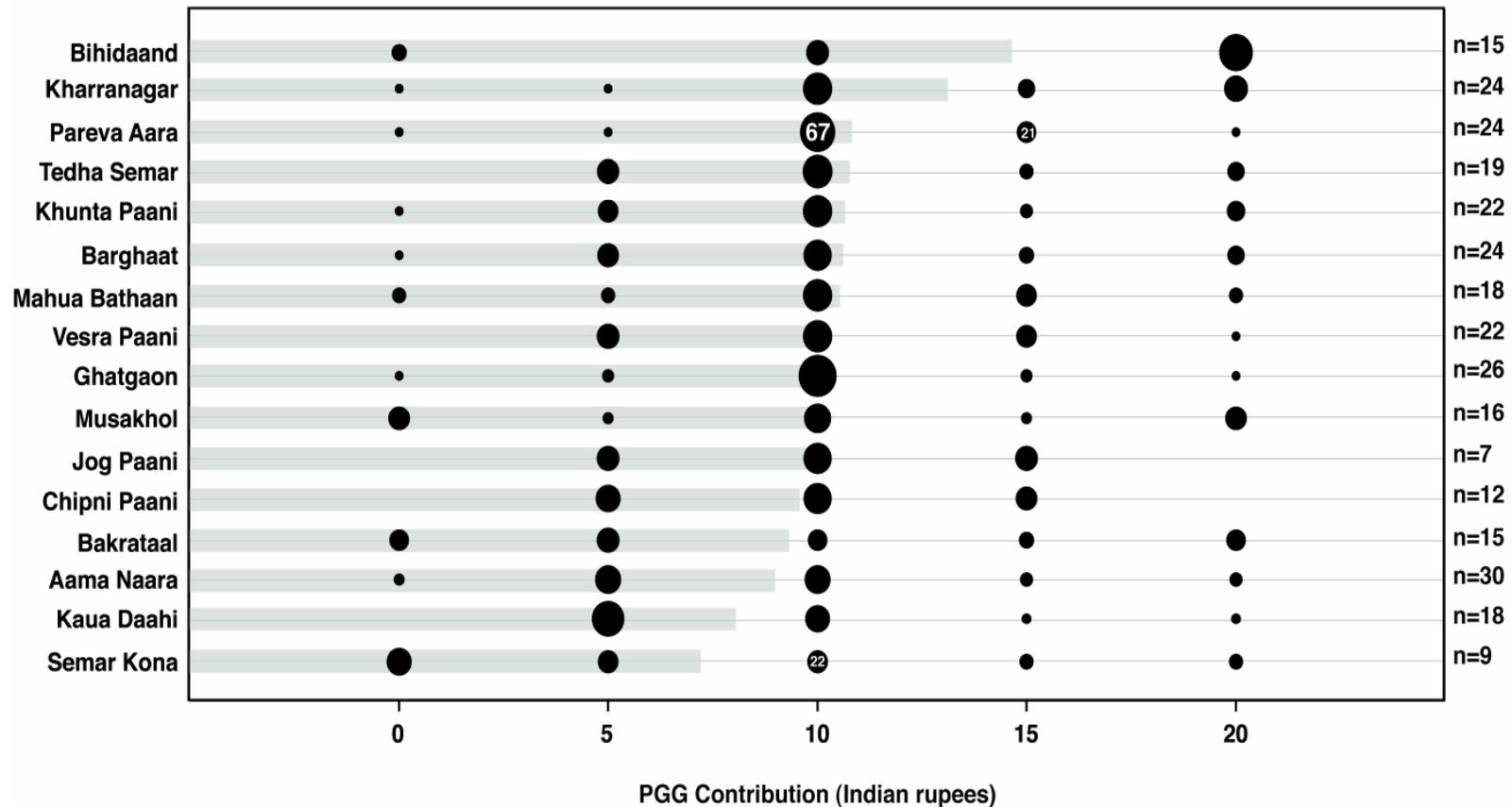


Figure 4.1 Distributions of PGG contributions across 16 villages. For each village on the y-axis, the areas of the black bubbles represent the proportion of individuals from the village who made a contribution of the value on the x-axis. To indicate scale, the numbers in some bubbles are the percentage proportions represented by those bubbles. Grey 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 \pm SD = 10.40 \pm 5.48).

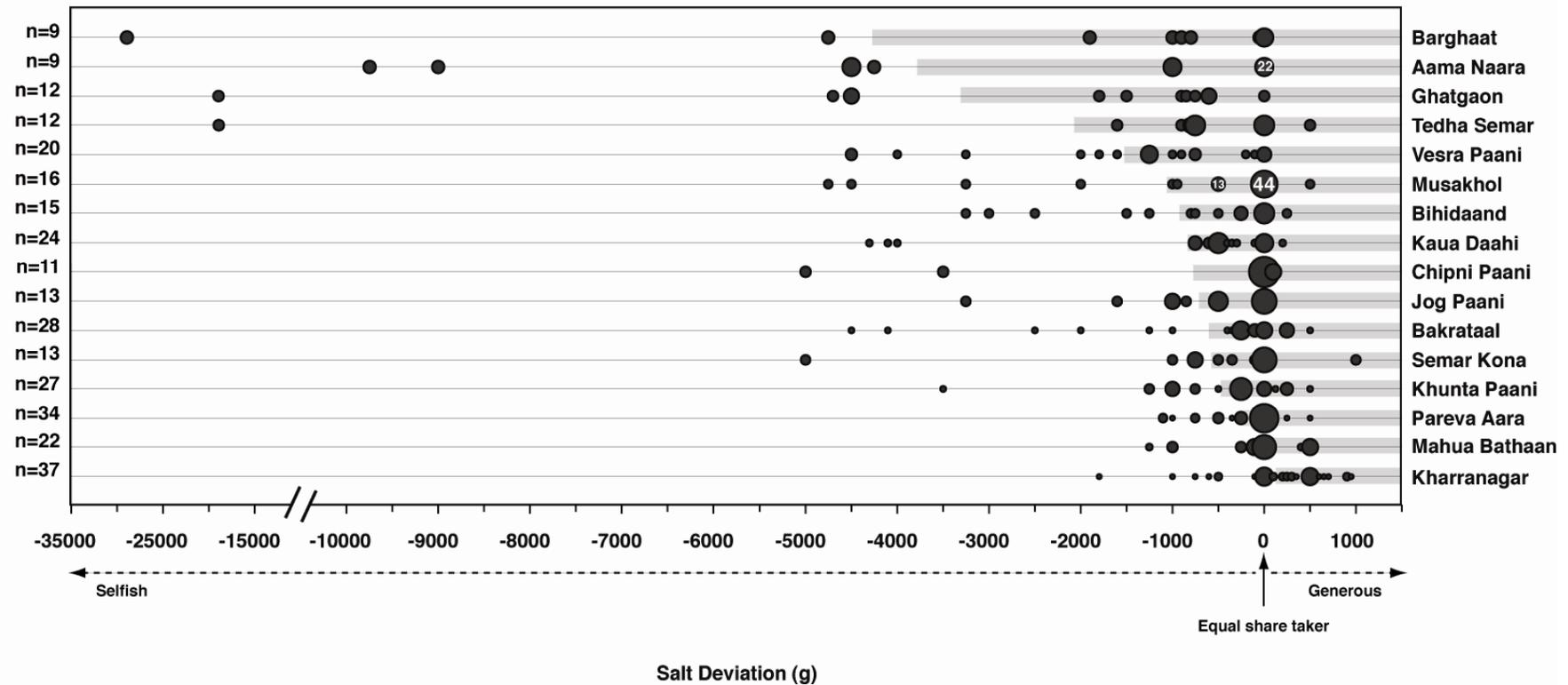


Figure 4.2 Distributions of salt deviations (amount available per person – amount taken) across 16 villages. For each village on the y-axis, the areas of the black bubbles represent the proportion of individuals from the village with salt deviation of the value on the x-axis. Note the break in the x-axis. To indicate scale, the numbers in some bubbles are the percentage proportions represented by those bubbles. Grey 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 \pm SD = -913.33 ± 2619.02).

4.2.2 Do properties of populations and/or individuals explain variation in PGG contribution and salt deviation between and within populations?

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 (representing a measure of social network size); both have small positive effects on PGG contribution [Table 4.2A; full model (multilevel)]. An increment of ten years in an individual's age corresponds to an increase in her PGG contribution by 3.7% of the initial endowment of 20 rupees. Ten additional people in a player's social network correspond to contributions that are higher by 5.8% of the initial endowment.

Only two variables are significantly associated with player salt deviation, namely, village population size and the number of full sisters over the age of 15 years (adult sisters) residing in the village, both of which have negative effects [Table 4.2A; full model (multilevel)]. 10 additional individuals in the village population are associated with salt deviations that are 29 g lower on average; players were more selfish in larger villages. The number of adult sisters residing in the village has a large effect on salt deviation; each additional adult sister living in the village corresponds to salt deviations that are lower by 624 g on average.

Pseudo R^2 values indicate that for PGG contribution about 28% of variance between populations and 4% of variance within populations is explained by the descriptor variables retained in the full model. For salt deviation about 32% of variance between populations and 9% of variance within populations is explained by the descriptor variables retained in the full model.

Players' migration histories, frequency of market contact and multiple measures of wealth have little effect on their PGG contributions or salt decisions. The total amount of salt available (pie size) has a small negative effect on salt deviation; people took more salt when more was available (see Appendix C, Table C.10). However, the association of behaviour with population and individual descriptors is independent of this pie-size effect.

Table 4.2 (A) Associations of each predictor term (fixed effect) with salt deviation and PGG contribution respectively in the null (intercept only) and full models. **(B)** Village and individual level variance components for salt deviation and PGG contributions respectively in the null and full models.¹ The variance partition coefficient [VPC = village level variance/ (village level variance + individual level variance)] is 0.182 ± 0.074 (95% BCI² = 0.073, 0.355) for salt deviation and 0.041 ± 0.029 (95% BCI² = 0.010, 0.116) for PGG contributions in the null model, and 0.118 ± 0.060 (95% BCI² = 0.038, 0.265) for salt deviation and 0.014 ± 0.012 (95% BCI² = 0.003, 0.047) for PGG contributions in the full model. The overall Spearman rank correlation between salt deviation and PGG contributions across all individuals is $\rho = 0.196$, $p = 0.007$, $n = 190$. *** $p < 0.01$, ** $p < 0.05$, * $p < 0.10$

A					
Fixed effect	Salt deviation (g)		PGG contribution (Indian rupees)		DIC ³
	$\beta \pm SE$	95% BCI ²	$\beta \pm SE$	95% BCI ²	
Null models					
Intercept (single level)	-913.646 ± 152.037***	-1209.508, -618.018	10.394 ± 0.321***	9.767, 11.021	12890.544
Intercept (multilevel)	-1210.605 ± 345.050***	-1887.124, -534.183	10.413 ± 0.436***	9.553, 11.285	12832.153
Full model (multilevel)					
Intercept	-513.409 ± 585.370	-1683.305, 616.786	7.618 ± 1.085***	5.484, 9.764	12821.456
Population size	-2.866 ± 1.390**	-5.587, -0.133	0.000 ± 0.002	-0.003, 0.003	
Age (years)	-9.363 ± 12.108	-32.871, 14.418	0.073 ± 0.027***	0.020, 0.126	
Sex: female (ref: male)	516.599 ± 288.477	-56.843, 1078.635	0.383 ± 0.647	-0.882, 1.655	
People invited to harvest festival from other villages	21.103 ± 25.984	-29.257, 71.955	0.116 ± 0.055**	0.008, 0.226	
Full sisters aged ≥ 15 years living in village	-623.783 ± 261.295**	-1138.715, -107.139	-0.139 ± 0.534	-1.172, 0.908	
B					
	Village level		Individual level		
	Variance ± SE	95% BCI ²	Variance ± SE	95% BCI ²	
Null model (multilevel)					
Salt deviation	1409354.625 ± 764246.813	491858.500, 3282888.500	6099303.5 ± 506483.656	5179439.000, 7151700.500	
PGG contribution	1.284 ± 0.97	0.290, 3.815	29.487 ± 2.464	25.023, 34.597	
Residual covariance ⁴	512.024 ± 551.762	-374.911, 1808.605	580.97 ± 829.541	-1027.803, 2207.266	
Residual correlation ⁴	0.397 ± 0.314	-0.310, 0.863	0.043 ± 0.061	-0.077, 0.161	
Full model (multilevel)					
Salt deviation	830317.813 ± 513355.531	241699.516, 2154373.500	6010546.000 ± 510689.003	5088691.000, 7072213.500	
PGG contribution	0.427 ± 0.380	0.092, 1.425	29.196 ± 2.439	24.825, 34.352	
Residual covariance ⁴	495.605 ± 334.386	90.628, 1349.136	749.763 ± 838.424	-889.288, 2399.088	
Residual correlation ⁴	0.871 ± 0.188	0.271, 0.991	0.057 ± 0.063	-0.067, 0.177	

¹For the two multilevel models (null and full), fixed effect parameters in each model are specified in Table 4.2A, while Table 4.2B presents the village and individual level variances in salt deviations and PGG contributions for each model respectively. For instance, in Table 4.2A, the full model (multilevel) has six fixed effects including the intercept; for each fixed effect (column 1), the associated β value for salt deviation (column 2) and its 95% BCI² (column 3), and the β value for PGG contribution (column 4) and its 95% BCI² (column 5) can be read in the corresponding row. The DIC³ value (see Section 2.5.2 for details) for the model is presented in column 6 of Table 4.2A. The variance components for salt deviation and PGG contribution in the full model (multilevel) can be read in the 9th and 10th rows of Table 4.2B respectively; column 2 represents the village level variance with its 95% BCI² (column 3), and column 4 represents the individual level variance with its 95% BCI² (column 5) for the corresponding rows. The last two rows of Table 4.2B present the residual covariance and residual correlation between salt deviation and PGG contribution in the full (multilevel) model respectively; the associated values at the village level (column 2) and their 95% BCI² (column 3), and at the individual level (column 4) and their 95% BCI² (column 5) can be read in the corresponding rows. The fixed effect parameters for the single level null model are presented in Table 4.2A; this model does not have variance components.

²Bayesian Credible Interval. Calculated from the posterior distribution, a k% interval contains k% of possible values of a parameter (Ellison 1996).

³Deviance Information Criterion.

⁴Between salt deviation and PGG contribution.

4.2.3 Is there a correlation between individuals' PGG contributions and salt deviations?

PGG contributions and salt deviations show a significant positive correlation across all individuals (Table 4.2); players who made higher contributions took away less salt. 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 full model, residual correlation increases substantially at the village level ($\rho = 0.871$), and 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 individual variation in some aspect of personality does not determine behaviour in these measures of cooperation.

4.3 Discussion

4.3.1 Variation in cooperative behaviour

Variation in PGG contributions and salt decisions between 16 villages of the same small-scale society is comparable to the variation previously found between 16 different large-scale societies (Herrmann et al. 2008) and 15 different small-scale societies (Henrich et al. 2005). This variation is partly explained by demographic differences between populations, such as population size and age structures. These results suggest that individuals' cooperative propensities are affected by local evolutionary dynamics that produce behavioural variation across populations which may not be stable.

4.3.2 Correlates of cooperative behaviour

Age and a measure of social network size have a positive effect on PGG contributions (Table 4.2). With the exceptions of Gächter and Herrmann (in press) and List (2004), age effects have seldom been observed in the PGG, perhaps since most experimental work is

conducted with undergraduate students of similar age. Egas and Riedl (2008) conducted a study implementing a PGG amongst a wider cross-section of individuals from The Netherlands and found that age was not a robust predictor of PGG contribution but was positively associated with the allocation of punishment in a PGG. Age had a small positive association with UG offers amongst the Sangu, a population of agro-pastoralists in southwest Tanzania (McElreath 2004a); UG offers in this study have a negative association with age, although this association is not statistically significant (Appendix C, Table C.1) and age was not retained in the full model.

It is notable that, specifically, the number of individuals invited to the harvest festival from other villages, as opposed to the player's village, is associated with PGG contributions. This finding raises the possibility that particular features of an individual's social network, such as its width or composition, influence levels of cooperation. Indeed, many authors suggest that the structure of the social network should impact levels of cooperation between members of the network, largely by increasing communication and/or allowing cooperators to selectively interact (Granovetter 2005; Jaramillo 2004; Lieberman et al. 2005; Ohtsuki et al. 2006; Santos and Pacheco 2005; Santos et al. 2006; Taylor et al. 2007). Among the Pahari Korwa, festival invitees from other villages often comprise affinal kin between whom the maintenance of reciprocal relationships may be important. A recent study demonstrates that more connected individuals in a network of interacting players make higher contributions to an anonymous PGG (Cardenas and Jaramillo 2007). Specific structural parameters of an individual's social network may indicate characteristics of other individuals in the network and whether they are likely cooperators.

The negative relationship between levels of cooperation and village population size identified in this study (Table 4.2) is in the direction predicted by evolutionary models (Boyd et al. 2003; Traulsen and Nowak 2006). Previous studies based on considerably smaller samples have either found no effect (Gurven et al. 2008), or a positive effect of population size (Henrich et al. 2005; Marlowe 2004). Population size is negatively correlated with the proportion of migrants in my populations and larger populations were often associated with degraded forest (personal observation). Hence, one possibility is that

ecological and resource constraints drive both these relationships, making cooperation more costly in larger populations and also making larger populations less attractive to migrants.

Two recent studies found that individuals from large populations are more willing to punish defectors (Henrich et al. 2010; Marlowe et al. 2008); they infer that the enforcement of norms promoting cooperation is stronger in large, more complex societies. Both these studies sampled from one or a few populations per society, therefore, their inference assumes that population size effects reflect the influence of societal complexity. My results challenge this conclusion since I demonstrate an association between population size and cooperation that is independent of variation in structural features of populations, such as socio-political complexity or religion.

The negative effect on salt deviation of sisters over the age of 15 residing in the village (Table 4.2), as opposed to other siblings, may also be related to the cost of cooperation. The average age of marriage for women is about 15 (Sharma 2007), so most of these adult sisters are probably women who married within their natal villages in a predominantly patrilocal society. 66.5% of all women (n = 388) in my survey sample moved to a village other than their natal village after marriage, as opposed to 15.6% of all men (n = 392). The additional pressure of competing for material or other resources (e.g. grandmaternal care) with kin who usually move out of the local group may make cooperation more costly, tipping the balance from kin-biased cooperation to competition (West et al. 2002). Frequencies of particular kin may cue individuals' likely average genetic relatedness to others in the local group, and indicate the intensity of competition experienced within the group at large, not just from direct kin. A similar and symmetrical effect was found in a matrifocal community, where men are the predominantly migrating sex; women made lower offers in a UG when they had more brothers in the village (Macfarlan and Quinlan 2008).

Players' migration histories, frequency of market contact and multiple measures of wealth have little effect on their PGG contributions or salt decisions. These variables are also not associated with players' UG offers. Henrich et al. (2005) constructed the variable "market integration" by ranking the 15 small-scale societies in their study based on ethnographic

observations of how frequently individuals from each society engage in market exchange; this variable accounted for a substantial amount of variation in UG offers across societies. In this study, individuals' frequency of market contact does not show an association with game behaviour.

There may be several reasons why salt decisions and PGG contributions are affected by different explanatory variables, including differences in the decision-structure, the use of a commodity as opposed to money, or the less game-like, more 'real-world' context of the salt decision. Different explanatory variables are associated with the three measures of cooperation implemented in this study; this is not surprising as the three measures have different decision and payoff structures which may be sensitive to different factors. However, further work is required to ascertain whether or not and why cooperation in different contexts may be sensitive to different explanatory variables. A large number of predictor variables were included in this study. Although there are theoretical grounds for why we might expect associations between these variables and cooperative behaviour (Section 2.4.2), replications of this study will establish whether the associations I find are stable and consistent across varied ecologies.

4.3.3 A new measure of cooperation

Semi-experimental methods, as implemented with the salt decision, offer promise for modifying economic game methodology to obtain measures of human behaviour outside the laboratory. Such measures are more likely to capture behaviour in the real world, i.e., they have greater external validity (Loewenstein 1999). To my knowledge, this is the first study that examines whether cooperative behaviour as captured by one-shot, anonymous economic games reflects real-world behaviour under comparable conditions. Polly Wiessner compared one-shot, anonymous game behaviour to non-anonymous, probably repeated, real-life interactions and, unsurprisingly, found little association (Wiessner 2009).

4.3.4 Concluding remarks

Findings from the PGG and salt decision agree with those from the UG (Chapter 3). There is significant variation in levels of cooperation across 16 populations of the same small-scale society, comparable to the variation previously found between 15 different small-scale societies. This variation is partly explained by demographic differences between populations, such as population size and age structures, which may affect the balance of cooperation and competition within each village (Doebeli et al. 1997; West et al. 2002). Congruent results from three measures of cooperative behaviour administered in up to 21 populations provide strong evidence that levels of cooperation vary substantially across populations of the same cultural group.

As discussed in Section 1.7, the first question I address in this thesis is: is there stable, heritable variation in levels of cooperation across human populations? My findings do not provide evidence that behavioural variation across populations is *stable or heritable*. Although there is behavioural variation across human populations, it is unlikely to be stable or heritable if environmental (demographic or ecological) factors, as opposed to cultural transmission, drive this variation.

4.4 Methods

4.4.1 *Public goods game set-up*

All games were played between February 2nd and May 16th, 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 one day. Mean age \pm SD of participants was 34.59 ± 12.13 years and 46% were female.

All participants collected at a common location in the village on the day of the games. They were instructed about the game rules and examples both collectively and then individually at the private location where they played the game (see Appendix A, Section A.2. for scripts). The PGG is a more complicated game than the UG. From prior experience piloting the UG in similar populations, I estimated that if I explained the PGG rules and examples to each player one at a time only, the total time required to obtain adequate sample sizes in each village would have been in the order of several days. This would have created ample opportunity for individuals who had played the game to discuss it with other village residents who were yet to play. To avoid such inevitable contamination, I first instructed all participants collectively (this usually took about 45 minutes) and then individually, in order to complete the games in one day. Participants were informed that the game would be discontinued if any discussion about the game ensued and two research assistants constantly monitored them to ensure that no such discussion occurred.

Players were tested both collectively and individually for their understanding of the game rules and of the anonymity of their decisions. Only a player who individually answered all test questions correctly played the game. Participants made their decisions by manipulating real five rupee coins and depositing their contributions into a money box.

Groups of six were constituted by randomly matching token numbers. Of the 52 games played across 16 villages, the total number of players was indivisible by six in nine games; six games had a group size less than six (three or four) and three games had a group size greater than six (seven or eight). These differences in group size do not change the relative

payoff structure of the game. Players always thought they were in a group of six players, including individuals who were actually in smaller or larger groups, as they were unaware of the number of people who did not play the game due to a failure to answer all test questions correctly.

Note that due to an oversight, data on the number of kin who participated in the PGG (Appendix B, Section B.1, questionnaire item 7g) were not collected in the first three villages visited namely, Kharranagar, Chipni Paani and Pareva Aara.

4.4.2 Salt decisions set-up

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. Moreover, they did not know how much salt was available to anyone else. Participants would have been unaware that the research team had brought large quantities of salt to the village as the salt was brought in opaque sacks with the other food rations distributed during the games.

All information about the salt was delivered by me from a standardised script (see Appendix A, Section A.3 for script) and a research assistant weighed the desired quantity. Participants were informed about their PGG earnings once they had stated their desired salt quantity. I used salt as the currency of the decision-frame as it is a commodity that is valued by the Pahari Korwa, can be measured on a continuous scale, is transported and stored without spoiling, and is unlikely to cause social repercussions after the games. The other obvious choice, rice, is often traded for or converted into alcohol if acquired in excess by Pahari Korwas. A recent ethnography (Srivastava 2007) confirms that salt is one of the top commodities that the Pahari Korwa are most likely to buy at market. It is very unlikely that limitations on physical strength affected the amount of salt that individuals took because

both Korwa women and men regularly carry large amounts of weight (tens of kilograms), in the form of wood, forest products, rice and other commodities, for long distances in hilly terrain, to and from the forest, markets and town.

4.4.3 Statistical analyses

Multilevel multivariate response models (Browne 2009; Rasbash et al. 2009; Snijders and Bosker 1999) were used to analyse the data. Models contained two response variables, PGG contribution and salt deviation, for individuals (level 1) nested within villages (level 2). They therefore allow simultaneous estimation of effects of explanatory variables on each response variable. I 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 co-variance 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. The analyses proceeded in four stages as described in Section 2.5.2.

SECTION II

SOCIAL LEARNING IN THE COOPERATIVE DOMAIN

CHAPTER 5

SOCIAL LEARNING IN THE COOPERATIVE DOMAIN: EVIDENCE FROM PUBLIC GOODS GAME EXPERIMENTS

5.1 Introduction

5.1.1 Background and related research

Cultural group selection models posit that social learning at the individual level - the non-genetic transfer of information from one individual to another via mechanisms such as teaching, imitation and language (Boyd and Richerson 1985; Mesoudi 2009) - can have population level consequences and maintain stable behavioural variation between populations (Boyd and Richerson 1985; Efferson and Richerson 2007; Henrich and Boyd 1998; Henrich and McElreath 2003; Richerson and Boyd 2005). The behavioural variation between populations may then be subject to natural selection. This process can lead to the evolution of large-scale cooperation if cooperative strategies are acquired via social learning (Boyd et al. 2003; Boyd and Richerson 1982; Boyd and Richerson 1985; Boyd and Richerson 2005; Gintis 2003; Guzmán et al. 2007; Henrich 2004; Henrich and Boyd 2001). In this chapter I present findings from public goods games experiments addressing whether people demonstrate any proclivity to acquire cooperative behavioural strategies via social learning. The experiments were conducted in 14 Pahari Korwa villages.

Social learning encompasses a variety of structurally different learning rules or strategies (Laland 2004). Individuals can employ various criteria in selecting the behaviour they should adopt, including the success or status of individuals exhibiting a behaviour (exemplars), the frequency of exemplars and the similarity between self and an exemplar (Boyd and Richerson 1985; Laland 2004; Mesoudi 2009). I focus on two social learning strategies, regarded as important for the evolution of large-scale cooperation due to their predicted population-level effects (Boyd and Richerson 1985; Henrich 2004). The first strategy I consider is payoff biased learning, the tendency to acquire behaviour that has produced the highest payoff or greatest success for an observed individual exhibiting the behaviour relative to other observed behaviours (Boyd and Richerson 1985; Henrich and Gil-White 2001; Richerson and Boyd 2005). The second strategy is conformity, the disproportionate tendency to acquire the behaviour exhibited with the highest frequency in a group of sampled individuals (Boyd and Richerson 1985).

Payoff biased learning has been extensively investigated in the theoretical literature and studies have examined the conditions under which it evolves, as well as its impact on the evolution of cooperation and other traits (e.g. Boyd et al. 2003; Boyd and Richerson 1985; Ellison and Fudenberg 1993, 1995; Gintis 2003; Guzmán et al. 2007; Henrich and Boyd 2001; Henrich and Gil-White 2001; Henrich and McElreath 2003; Kendal et al. 2009; Lehmann et al. 2008; McElreath et al. 2008; Schlag 1998, 1999; Vega-Redondo 1997); payoff biased learning can facilitate the evolution of cooperation in combination with some levels of conformity and/or punishment of defection (Boyd et al. 2003; Boyd and Richerson 1985; Gintis 2003; Guzmán et al. 2007; Henrich and Boyd 2001). Many social psychology studies find evidence that people tend to copy successful, high status or prestigious individuals (reviewed in Mesoudi 2009). Recent studies of cultural learning, guided directly by the theoretical literature on cultural evolution, provide evidence that people do employ payoff biased learning to some extent in complex laboratory task environments (Efferson et al. 2007; McElreath et al. 2008; Mesoudi 2008; Mesoudi and O'Brien 2008). There is also evidence from the experimental economics literature that payoff biased learning may play a role in determining the behaviour of firms in a market (e.g. Apesteguia et al. 2007; Offerman et al. 2002; Offerman and Sonnemans 1998; Selten and Apesteguia 2005); the extent to which it is employed may vary with informational and environmental parameters

(Bosch-Domènech and Vriend 2003). To my knowledge, no previous studies have investigated whether people use payoff biased learning in the context of a cooperative dilemma.

Conformity has been the subject of extensive theoretical research examining the conditions under which it evolves, as well as its impact on the evolution of cooperation and other traits (e.g. Boyd and Richerson 1985; Eriksson and Coultas 2009; Eriksson et al. 2007; Guzmán et al. 2007; Henrich and Boyd 1998; Henrich and Boyd 2001; Kendal et al. 2009; Nakahashi 2007; Wakano and Aoki 2007; Whitehead and Richerson 2009); conformity facilitates the evolution of cooperation (Boyd et al. 2003; Boyd and Richerson 1982; Boyd and Richerson 1985; Guzmán et al. 2007; Henrich 2004; Henrich and Boyd 2001). A multitude of empirical studies from social psychology demonstrate that individuals do tend to copy the majority (e.g. Asch 1951, 1955, 1956; Bond and Smith 1996; Sherif 1936). However, these studies do not unequivocally measure conformity as it is defined and implemented in cultural group selection models, i.e. the disproportionate tendency to copy the highest frequency behaviour (Boyd and Richerson 1985; Efferson et al. 2008; Mesoudi 2009). It is only such a disproportionate individual proclivity to acquire the most frequent behaviour that has demonstrable homogenising effects within populations, thus creating variation between them (Boyd and Richerson 1985; Efferson et al. 2008); a tendency to simply copy a behaviour with the likelihood of its occurrence in the population does not produce a homogenising effect within a population (Efferson et al. 2008; Henrich 2004). Furthermore, in the social psychology studies cited above, the experimental task was set up such that an individual experienced no clear benefit from attaining the correct solution to the task, as opposed to adopting the incorrect solution advocated by the majority. An exception is a study by Baron et al. (1996) which found that in a perceptual task of low difficulty, individuals' tendency to copy the majority decreased when incentives to make accurate judgements were introduced.

Jacobs and Campbell (1961) were the first to design experiments that can be used to investigate whether individuals demonstrate conformity as defined in cultural group selection models; these authors formed laboratory "micro-societies" consisting of varying numbers of individuals and demonstrated that the evaluations individuals made in an

estimation task were nonlinearly affected by the number of other individuals who had stated a particular estimate. More recent empirical work has been guided directly by theoretical models of cultural transmission in investigating whether individuals demonstrate conformity as defined in cultural group selection models (Coultas 2004; Efferson et al. 2008; Efferson et al. 2007; Eriksson and Coultas 2009; Eriksson et al. 2007; McElreath et al. 2008; McElreath et al. 2005). Some of these studies were implemented so that an individual's performance in the experimental task translated into proportionate monetary gains (Efferson et al. 2008; Efferson et al. 2007; McElreath et al. 2008; McElreath et al. 2005). These empirical studies find mixed support (Coultas 2004; Efferson et al. 2008; Eriksson et al. 2007; McElreath et al. 2008; McElreath et al. 2005), or no support (Efferson et al. 2007; Eriksson and Coultas 2009) for conformist learning.

Many studies have demonstrated that individuals' contributions to a public good correlate positively with the contributions of other individuals (e.g. Bardsley 2000; Croson 2007; Falk et al. 2003; Fischbacher and Gächter 2010; Fischbacher et al. 2001; Frey and Meier 2004; Gächter 2007; Weimann 1994); these studies cannot distinguish whether conformity or other strategic considerations explain such "conditional cooperation". Only a small number of studies have investigated whether individuals employ conformist learning in the context of a cooperative dilemma (Bardsley and Sausgruber 2005; Carpenter 2004; Samuelson and Messick 1986; Schroeder et al. 1983; Smith and Bell 1994; Velez et al. 2009). Although these studies find some evidence of social learning, they do not unequivocally demonstrate conformist learning as defined and implemented in cultural group selection models. While they show that individuals respond to information about other players' contributions to a PGG, they do not demonstrate that individuals preferentially make contributions that correspond to the most frequent contribution made by other players. Moreover, features of these studies, such as repeated interactions (Samuelson and Messick 1986; Schroeder et al. 1983; Smith and Bell 1994; Velez et al. 2009) and the measurement of conformity as individuals' responses to anticipated rather than real behaviour (Velez et al. 2009), cannot rule out other mechanisms (e.g. reciprocity) as explanations for the observed behaviour. Carpenter (2004) and Bardsley and Sausgruber (2005) provide the best evidence for social learning in a PGG. While the authors claim to observe conformity, what they demonstrate instead is that players' contributions in a PGG

positively co-vary with those of other players, even when the contributions of other players do not affect their own payoffs; they do not demonstrate that players contribute an amount that equals the contribution value made most frequently by other players. Thus, the current literature does not provide clear evidence that individuals employ conformist learning in the context of a cooperative dilemma.

A few studies have examined the effects on cooperative behaviour of other types of social information. Revealing the behaviour of only one other individual, who participated in a different session of the experiment to the focal individual, has little effect on the focal individual's allocation in the dictator game (Cason and Mui 1998), another economic game used to measure cooperation. Informing individuals playing a two-person PGG of the average contribution made by players in a previous session also does not affect game behaviour (Brandts and Fatás 2001).

Thus, one of the core assumptions of cultural group selection models of large-scale cooperation - that people use social learning to acquire behavioural strategies in a cooperative dilemma - is largely untested. I investigate whether individuals employ pay-off biased, conformist and individual learning when making decisions in a PGG. I compare the prevalence of different learning strategies across 14 Pahari Korwa villages and assess the association of properties of populations and individuals with the learning strategy employed by an individual.

5.1.2 Behavioural measures

Two rounds of an anonymous, one-shot PGG were played (see Section 2.4 for details of study set-up and Section 5.4.1 for details of the experimental set-up). Data from the first round of the PGG are presented in Chapter 4. Participants were only informed that there would be a second round after they had played the first round. For each round participants were divided into groups of six players. Groups were reconstituted in round two so that a player's group composition in round two was different to her group composition in round one. Players were explicitly informed about the reconstitution of groups in round two and

told that their group in round two would be different to their group from round one; all information and instructions about round two were provided only once round one had been completed. This process ensured that each round of the game was one-shot, i.e. there were no repeated interactions between players. Each player received an endowment of 20 rupees and decided how much of it she wished to contribute to a group pot in divisions of five rupees. Once all six players had 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-maximising strategy entails that a player contribute nothing to the group pot.

The difference between the first (PGG1) and second (PGG2) round is that in the second round each player was presented two pieces of information prior to deciding how much she wished to contribute to her new group pot. Each player was told i) the highest earner's contribution (HEC), i.e. the contribution made by the player who had earned the highest amount in her group from round one, and ii) the modal contribution (MC), i.e. the contribution made most frequently by the players in her group from round one. Once a player was told the HEC and MC for her group from round one, she decided how much of her new endowment she wished to contribute to her new group pot. Players were only informed of their earnings from each round at the end of both rounds. Hence, they did not know how much they or anyone else had earned in round one prior to making their decisions in round two.

To test whether individuals copied MCs and HECs in round two, i.e. whether they employed conformist and/or payoff biased learning respectively in making their PGG2 decisions, I compare variation in PGG1 and PGG2 contributions within and between villages. There is significant variation in PGG1 contributions between villages (Section 4.2.1). Each player received information about the MC and HEC derived from the PGG1 contributions of other players only from her village; hence, if individuals did copy the MC and/or HEC, we should expect the variance in PGG2 contributions to decrease within villages and increase between villages, compared to the within- and between-village variance in PGG1 contributions respectively. Although I did not provide players feedback

about their earnings from the PGG1 before they made their decisions in the PGG2, they did have opportunities for individual learning from prior experience with the game structure, since they were playing the game for the second time in the PGG2 (albeit with different players). However, such individual learning is not expected to increase between-village variance in contributions, even though it may decrease overall variance in contributions. Thus, if players employed conformist and/or payoff biased learning in the PGG2, we should expect a higher ratio of between-village to total (between-village and within-village) variance for PGG2 contributions, compared to PGG1 contributions.

I also examine frequencies of different learning strategies in my study populations. Each player is classified into one of four mutually exclusive categories: (i) ‘payoff copier’ if her PGG2 contribution equalled the HEC, (ii) ‘conformist’ if her PGG2 contribution equalled the MC, (iii) ‘individualist’ if her PGG2 contribution equalled neither the HEC nor the MC, and (iv) ‘unidentifiable’ if either (a) her PGG2 contribution equalled her PGG1 contribution as well as the HEC, MC or both, or (b) her PGG2 contribution equalled both the HEC and MC, i.e. when the HEC was equal to the MC. The ‘unidentifiable’ category thus includes players who cannot unambiguously be classified as ‘payoff copiers’ or ‘conformists’. Figure 5.1 provides a schematic representation of the criteria used to classify a player’s learning strategy. Although my experimental design cannot elucidate the strength of the conformist bias, i.e. the magnitude of the tendency to acquire the highest frequency behaviour (equivalent to the frequency dependent bias parameter D in (Boyd and Richerson 1985), p. 208), individuals who copy the MC demonstrate an explicit preference for adopting the highest frequency behaviour and are therefore classified as conformists.

Two sets of analyses are presented using two different classifications of player learning strategies. The first classification has four categories; individuals are either ‘payoff copiers’, ‘conformists’, ‘individualists’ or ‘unidentifiable’. The second classification has three categories; individuals are either ‘social learners’ (which includes ‘payoff copiers’, ‘conformists’ and those ‘unidentifiable’ players whose round two contribution equalled both the HEC and MC but not their round one contribution), ‘individualists’ (as defined previously), or ‘unidentifiable’ (which includes players whose round two contribution equalled their round one contribution as well as the HEC, MC or both). While the

‘unidentifiable’ category is included in all analyses, I do not test any hypotheses regarding these individuals. The distribution of different social learning strategies may vary across populations even though the overall frequencies of social learning do not or vice versa; the two sets of analyses were conducted to investigate this possibility.

Multilevel normal linear models (Browne 2009; Rasbash et al. 2009; Snijders and Bosker 1999) are used to explicitly analyse variation in PGG2 contributions at the village and individual levels. I employ non-parametric statistics to analyse the distribution of different learning strategies pooled across villages and to compare player contributions between the first and second round of the PGG. Multilevel multinomial logistic models (Browne 2009; Rasbash et al. 2009; Snijders and Roel 1999) are used to explicitly analyse variation in learning strategies at the village and individual levels.

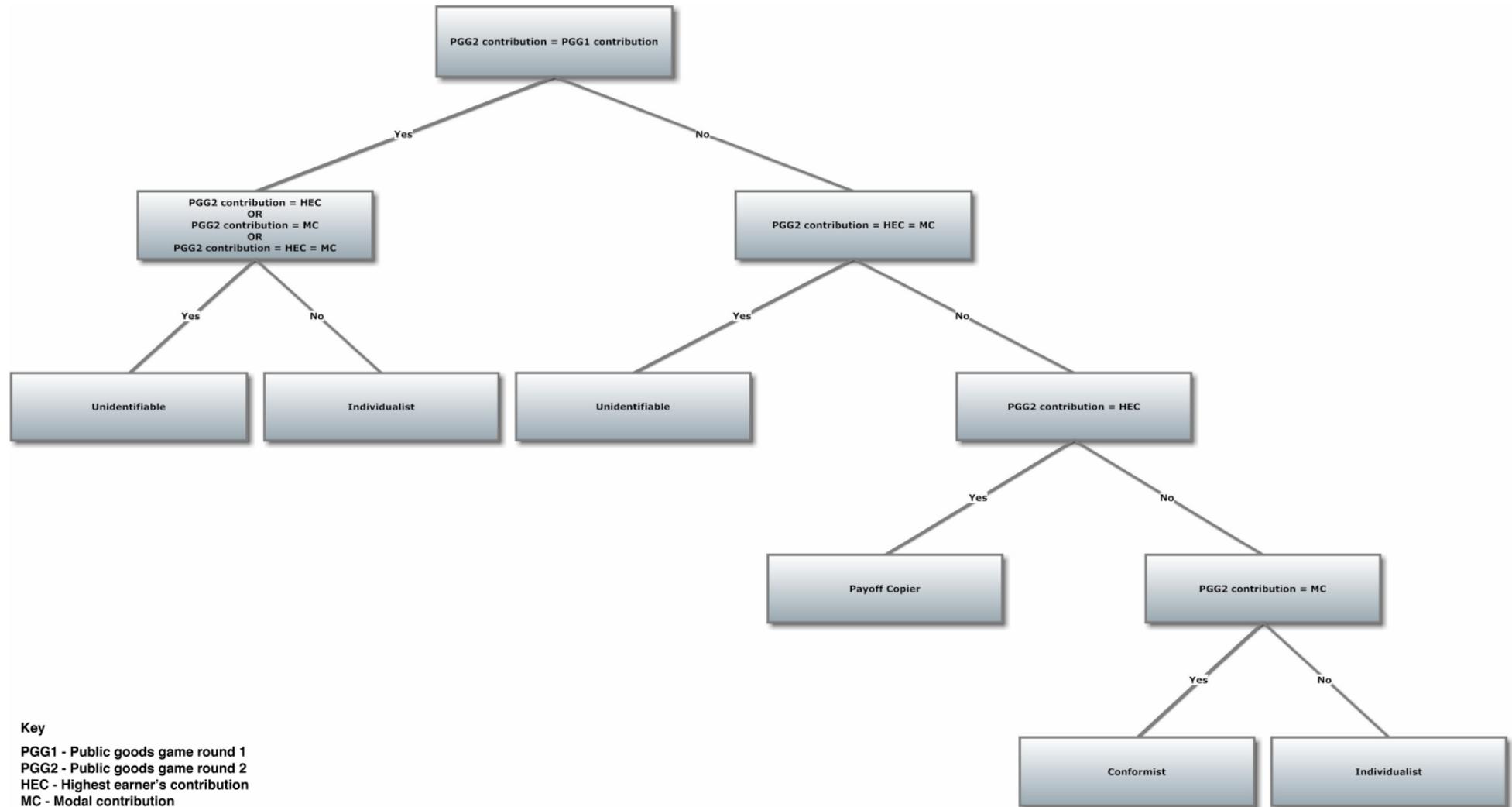


Figure 5.1 Classification of a player's learning strategy

5.2 Results

PGG1 was played in a total of 16 villages; these data are presented in Chapter 4. PGG2 was played in 14 of these 16 villages since in two villages (Jog Paani and Semar Kona) the total number of players who successfully played the PGG1 was under 12; therefore, since there were not enough players to form more than one group in round two, a second round would have entailed repeated interactions between players, as well as compromised players' anonymity. A total of 285 individuals played both PGG1 and PGG2 across all villages. Table 5.1 presents sample sizes of individuals who played both PGG1 and PGG2, for the 14 villages.

Table 5.1 Number (n) of players (total n = 285) who played both PGG1 and PGG2 from each of 14 study villages.

Village number	Village	PGG players (n)
1	Chipni Paani	12
2	Mahua Bathaan	18
3	Bihidaand	15
4	Khunta Paani	22
5	Kaua Daahi	18
6	Pareva Aara	24
7	Musakhhol	16
8	Kharranagar	24
9	Tedha Semar	19
10	Vesra Paani	22
11	Barghat	24
12	Aama Naara	30
13	Bakrataal	15
14	Ghatgaon	26

In Section 5.2.1 I examine whether there is evidence that players used information on the MC and HEC in making their PGG2 contributions. In Section 5.2.2 I compare the distribution of players classified as individualists versus social learners (payoff copiers and conformists) pooled across all villages. In Section 5.2.3 I examine whether the distribution of different learning strategies employed varies between villages and in Section 5.2.4 I examine whether properties of villages and/or individuals are associated with an individual's learning strategy. Finally, in Section 5.3.5 I investigate whether the learning

strategy employed is associated with a player's PGG2 contribution, i.e. whether the type of learning strategy employed affects the behavioural trait adopted by an individual.

5.2.1 Is there evidence that individuals use information on the MC and HEC in making their PGG2 contributions?

The overall distributions of PGG1 and PGG2 contributions pooled across all villages are significantly different (Wilcoxon signed ranks test: $Z = -2.143$, $n = 285$, Monte Carlo simulated $p = 0.032$). Players made smaller contributions in the PGG2 (mean \pm SD = 9.81 ± 4.60) than they did in the PGG1 (mean \pm SD = 10.51 ± 5.44).

Distributions of PGG2 contributions (Figure 5.2A) vary considerably across 14 villages, including the modes and means. 9.4% of the variance in PGG2 contributions occurs between villages [Table 5.3B; null model (multilevel)]. The DIC value for the null model with village level intercepts (multilevel) is about 13 units lower than for the null model without village level intercepts (single level), indicating that the multilevel model accounting for village effects provides a much better fit to the data (Table 5.3A; null models). Once village and individual descriptors are included in the model, the unexplained between-village variance in PGG2 contributions increases² to 10.3% [Table 5.3B; full model (multilevel)].

Total variance in PGG2 contributions is lower than that in PGG1 contributions, but a larger proportion of the total variance occurs between villages in PGG2 contributions as compared to PGG1 contributions (Table 5.2 summarises variance components for PGG1 and PGG2 contributions). 2% of the variance in PGG1 contributions is between villages as compared to 9.4% in PGG2 contributions across the same 14 villages (Figure 5.2B; Table 5.2). Hence, between-village variance in contributions increased by 7.4% between the PGG1 and the

²In multilevel models, the addition of a predictor variable can increase the residual variance at level 2 (villages), unlike in traditional regression models where residual variance always decreases when a predictor is added (Gelman & Hill 2007). A level 1 (individuals) predictor significantly associated with the response variable, such as sex, may be correlated with village level errors (due to differences in sex ratios between villages). Its inclusion in the model may therefore unmask the true underlying variation between villages (see Gelman & Hill (2007), Chapter 21, p. 480, for a detailed explanation).

PGG2. Variances of the absolute values of village level residuals differ significantly for PGG1 and PGG2 contributions (Table 5.2). These results suggest that some individuals did use information on the MC and HEC in making their PGG2 contributions.

Table 5.2 Null model (intercept only) variance components for PGG1 and PGG2 contributions. Variances of the absolute values of village level residuals differ significantly for PGG1 and PGG2 contributions (Levene's test for equality of variances: $F = 7.397$, $p = 0.011$).

Game	Variance \pm SE			VPC ¹
	Village level	Individual level	Total	
PGG1	0.603 \pm 1.006	29.341 \pm 2.548	29.944	0.020
PGG2	2.132 \pm 1.745	19.730 \pm 1.777	21.862	0.094

¹ VPC = village level variance/ (village level variance + individual level variance).

The only explanatory variables that have a significant association with PGG2 contributions are age and the number of full sisters aged under 15 years living in other villages; while age has a small positive effect, the number of young full sisters living in other villages has a small and marginally significant negative effect on PGG2 contributions (Table 5.3A; full model). Hence, the small, positive association between age and PGG contributions remains unaltered between rounds one (Section 4.2.2, Table 4.2) and two. However, a measure of social network size (the number of people invited to the harvest festival from other villages), the only other significant predictor of PGG1 contributions, is not an important predictor of PGG2 contributions; it is replaced by the number of young full sisters living in other villages.

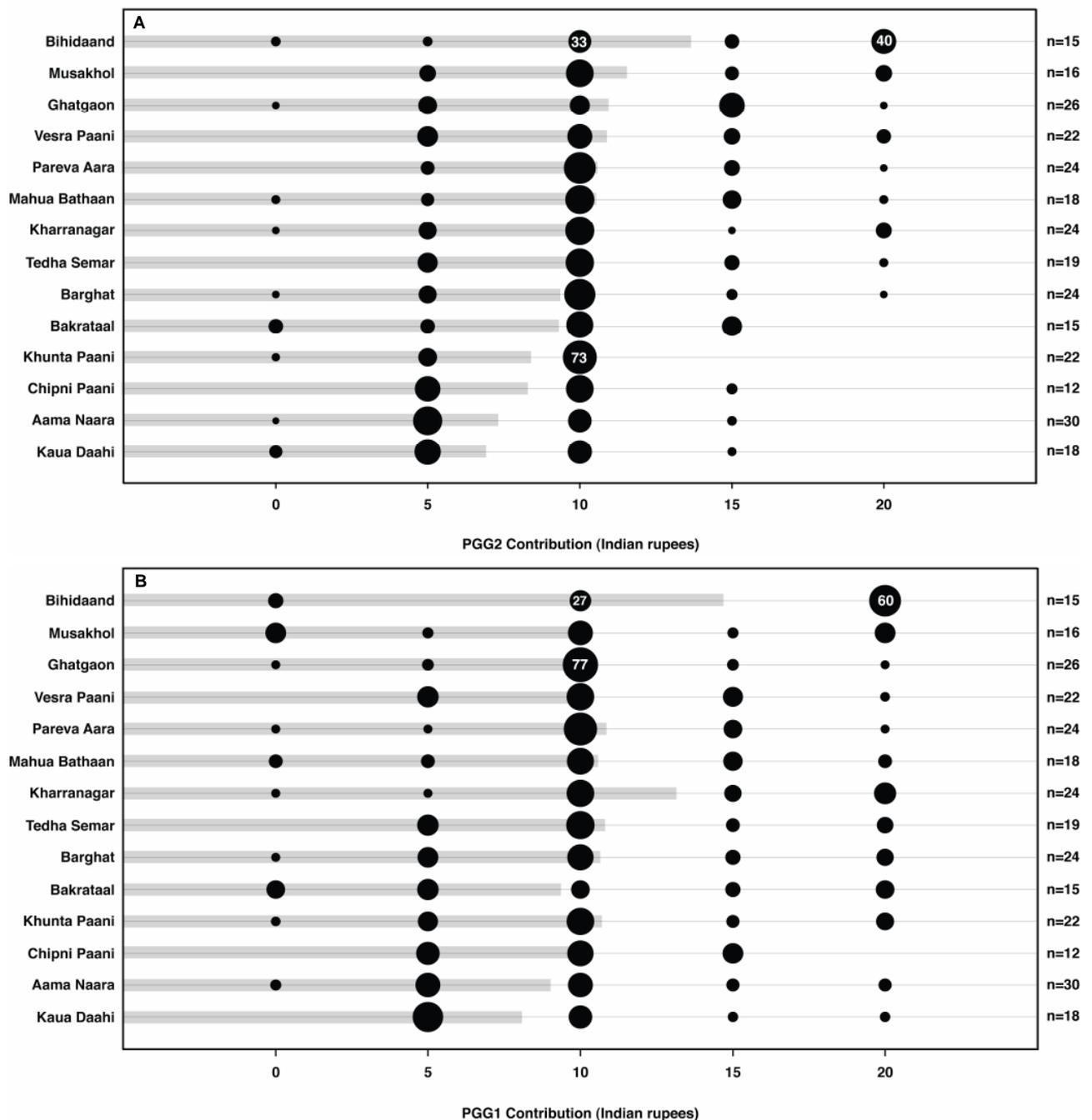


Figure 5.2 Distributions of (A) PGG2 contributions and (B) PGG1 contributions, across 14 villages. For each village on the y-axis, the areas of the black bubbles represent the proportion of individuals from the village who made a contribution of the value on the x-axis. To indicate scale, the numbers in some bubbles are the percentage proportions represented by those bubbles. Grey horizontal bars indicate the mean contributions for villages. Counts on the right (n) represent the number of players from each village (total n = 285). Villages in both graphs are ordered by their mean PGG2 contributions; the bottom village (Kaua Daahi) has the lowest mean PGG2 contribution. The overall mode across villages is 10 rupees for both PGG2 (mean \pm SD = 9.81 ± 4.60) and PGG1 (mean \pm SD = 10.51 ± 5.44) contributions.

5.2 RESULTS

Table 5.3 (A) Associations of each predictor term (fixed effect) with PGG2 contribution in the null (intercept only) and full models. **(B)** Village and individual level variance components for PGG2 contribution in the null and full models.¹ The variance partition coefficient [VPC = village level variance/ (village level variance + individual level variance)] is 0.094 ± 0.066 (95% BCI² = 0.000, 0.255) in the null model, and 0.103 ± 0.060 (95% BCI² = 0.018, 0.252) in the full model. ***p<0.01, **p<0.05, *p<0.10

A				
Fixed effect	PGG2 contribution (Indian rupees)		DIC ³	
	$\beta \pm SE$	95% BCI ²		
Null models				
Intercept (single level)	9.823 ± 0.272***	9.314, 10.370	1681.888	
Intercept (multilevel)	9.866 ± 0.499***	8.896, 10.891	1668.762	
Full model (multilevel)				
Intercept	8.572 ± 0.883***	6.773, 10.249	1662.890	
Age (years)	0.042 ± 0.022*	0.001, 0.088		
Full sisters aged < 15 years living in other villages	-1.286 ± 0.762*	-2.732, 0.209		
B				
	Village level		Individual level	
	Variance ± SE	95% BCI ²	Variance ± SE	95% BCI ²
Null model (multilevel)	2.132 ± 1.745	0.003, 6.518	19.730 ± 1.777	16.625, 23.517
Full model (multilevel)	2.282 ± 1.582	0.372, 6.341	19.206 ± 1.686	16.245, 22.877

¹ For the two multilevel models (null and full), fixed effect parameters in each model are specified in Table 5.3A, while Table 5.3B presents the village and individual level variances in PGG2 contributions for each model respectively. For instance, in Table 5.3A, the full model (multilevel) has three fixed effects including the intercept; for each fixed effect (column 1), the associated β value (column 2) and its 95% BCI² (column 3) can be read in the corresponding row. The DIC³ value (see Section 2.5.2 for details) for the model is presented in column 4 of Table 5.3A. The variance components for the full model (multilevel) can be read in the last row of Table 5.3B; column 2 represents the village level variance in PGG2 contributions with its 95% BCI² (column 3), and column 4 represents the individual level variance in PGG2 contributions with its 95% BCI² (column 5). The fixed effect parameters for the single level null model are presented in Table 5.3A; this model does not have variance components.

² Bayesian Credible Interval. Calculated from the posterior distribution, a k% interval contains k% of possible values of a parameter (Ellison 1996).

³ Deviance Information Criterion.

5.2.2. Do the overall frequencies of learning strategies vary?

Of the 285 individuals who played both the PGG1 and the PGG2 from 14 villages pooled together, 36.5% are individualists, 9.1% are payoff copiers, 14% are conformists and 40.4% are unidentifiable. There is significant variation in the frequencies of players with different learning strategies (Figure 5.3A; Table 5.4). Pair-wise tests confirm that the number of individualists is significantly greater than the number of payoff copiers and conformists respectively (Table 5.4). Although more players use a conformist rather than a payoff biased learning strategy, this difference is not significant (Table 5.4). Upon excluding the unidentifiable individuals, of the remaining 170 individuals, the percentage of individualists, payoff copiers and conformists is 61.2%, 15.3% and 23.5% respectively.

Using the second classification of player learning strategies, of the 285 individuals who played both the PGG1 and the PGG2 from 14 villages pooled together, 36.5% of individuals are individualists, 27% are social learners and 36.5% are unidentifiable (Figure 5.3B; Table 5.4). The number of individualists in the sample is greater than the number of social learners and this difference in frequencies is marginally significant at the $p < 0.05$ level (Table 5.4). Upon excluding the unidentifiable individuals, of the remaining 181 individuals, the percentage of individualists and social learners is 57.5% and 42.5% respectively.

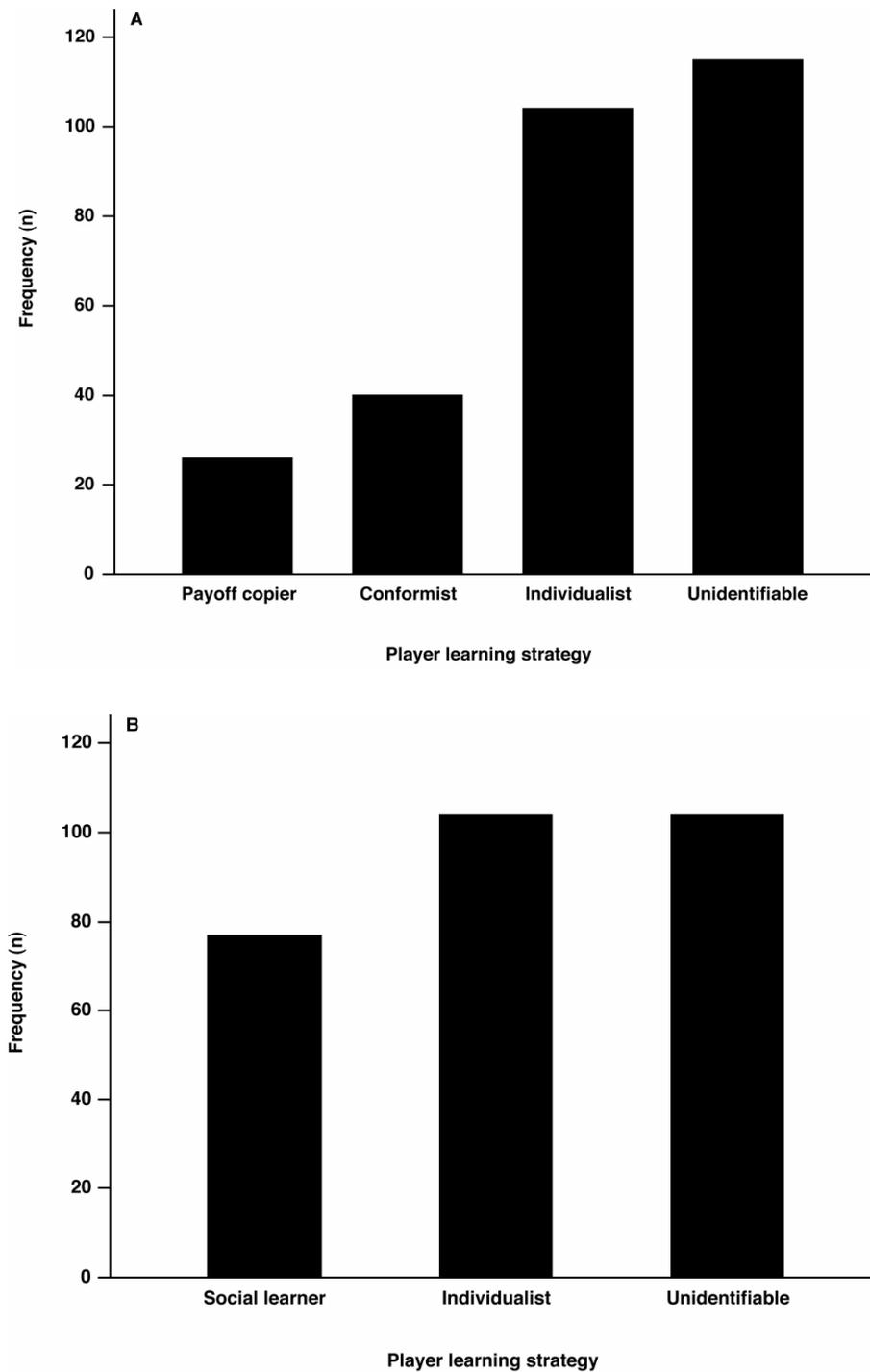


Figure 5.3 Frequencies of player learning strategies for individuals from 14 villages pooled together. Figures compare frequencies of, (A) payoff copiers, conformists, individualists and unidentifiable individuals and (B) social learners (payoff copiers, conformists and players whose round two contribution equalled both the HEC and MC but not their round one contribution), individualists and unidentifiable individuals (players whose round two contribution equalled their round one contribution as well as the HEC, MC or both).

Table 5.4 Results of chi-squared tests comparing frequencies of player learning strategies for individuals from 14 villages pooled together. Each test is reported in a similarly coloured block of rows and compares frequencies of all categories listed under ‘comparison categories’ in the same block.

Comparison categories	χ^2	df	Monte Carlo simulated p
Payoff copier Conformist Individualist Unidentifiable	84.361	3	<0.001
Individualist Payoff copier	46.800	1	<0.001 ^a
Individualist Conformist	28.444	1	<0.001 ^a
Payoff copier Conformist	2.970	1	0.324 ^a
Social learner Individualist Unidentifiable	5.116	2	0.080
Individualist Social learner	4.028	1	0.053

^a Bonferroni adjusted p value.

5.2.3. Does the distribution of learning strategies vary across populations?

Distributions of player learning strategies (Figure 5.4) vary considerably across the 14 villages. The odds of being a payoff copier relative to an individualist differ substantially between villages [Table 5.5B; null model (multilevel)]. 28.3% of the variance in the log odds of being a payoff copier (relative to an individualist) occurs between villages [Table 5.5B; null model (multilevel)]. The DIC value for the null model with village level intercepts (multilevel) is about 10 units lower than for the null model without village level intercepts (single level), indicating that the multilevel model accounting for village effects provides a much better fit to the data (Table 5.5A; null models). Once village and individual descriptors are included in the full model, the unexplained between-village variance in the log odds of being a payoff copier increases to 30.5% [Table 5.5B; full model (multilevel)].

Similarly, the odds of being a conformist relative to an individualist vary considerably between villages [Table 5.5; null model (multilevel)]. 15.5% of the variance in the log odds of being a conformist (relative to an individualist) occurs between villages [Table 5.5B;

null model (multilevel)]. Once village and individual descriptors are included in the full model, the unexplained between-village variance in the log odds of being a conformist decreases to 6.3% [Table 5.5B; full model (multilevel)].

11.9% of the variance in the log odds of being a social learner (relative to an individualist) occurs between villages [Table 5.6B; null model (multilevel)]. The unexplained between-village variance increases to 21% once individual descriptors are included in the full model [Table 5.6B; full model (multilevel)]. The DIC value for the null model with village level intercepts (multilevel) is about five units lower than for the null model without village level intercepts (single level), indicating that the multilevel model accounting for village effects provides a much better fit to the data (Table 5.6A; null models). Hence, populations vary in their relative distribution of individuals employing different learning strategies, as well as individuals employing social versus individual learning.

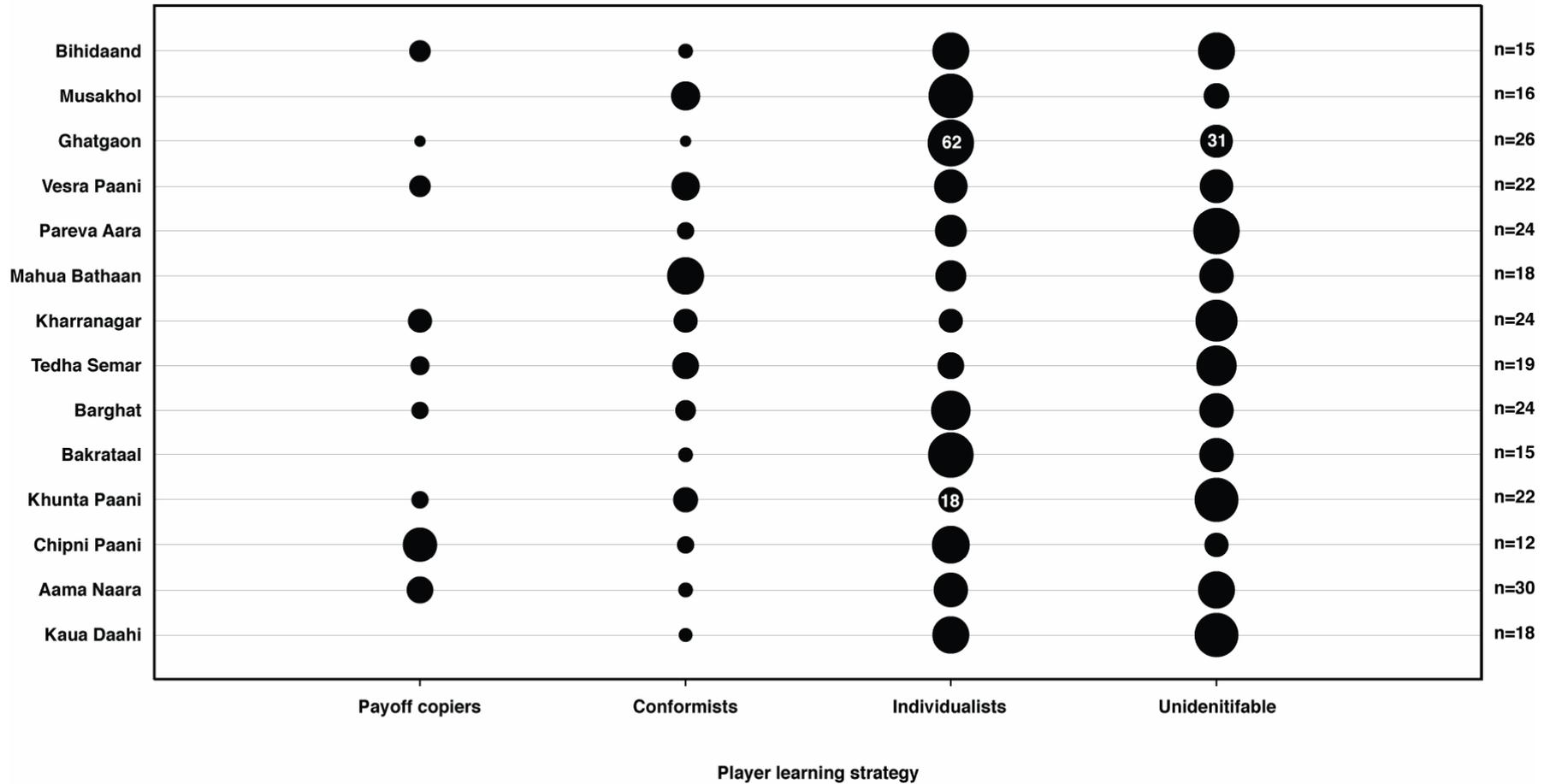


Figure 5.4 Distributions of player learning strategies across 14 villages. For each village on the y-axis, the areas of the black bubbles represent the proportion of individuals from the village with the learning strategy on the x-axis. To indicate scale, the numbers in some bubbles are the percentage proportions represented by those bubbles. Counts on the right (n) represent the number of players from each village (total $n = 285$). Villages are ordered by their mean PGG2 contributions; the bottom village (Kaua Daahi) has the lowest mean.

Table 5.5A Associations of each predictor term (fixed effect) with the odds of being a payoff copier, conformist or unidentifiable relative to an individualist respectively, in the null (intercept only) and full multinomial logistic models (see Table 5.5B for variance components of these models). Odds ratios less than, equal to, or greater than one represent lower, equal, or higher probabilities of occurrence (compared to the reference category) respectively.¹ ***p<0.001, **p<0.05, *p<0.10

Fixed effect	Payoff copier		Conformist		Unidentifiable		DIC ³
	exp (β) \pm SE	95% BCI ²	exp (β) \pm SE	95% BCI ²	exp (β) \pm SE	95% BCI ²	
Null models							
Intercept (single level)	0.251 \pm 0.056 ***	0.156, 0.371	0.386 \pm 0.069 ***	0.265, 0.540	1.114 \pm 0.147	0.843, 1.426	705.890
Intercept (multilevel)	0.201 \pm 0.084 ***	0.074, 0.406	0.385 \pm 0.111 ***	0.208, 0.643	1.148 \pm 0.245	0.752, 1.697	695.860
Full model (multilevel)							679.990
Intercept	0.127 \pm 0.154 **	0.008, 0.559	4.908 \pm 4.223 *	0.803, 15.730	2.923 \pm 1.658 *	0.933, 7.415	
Sex: female (ref: male)	1.530 \pm 0.858	0.462, 3.690	1.193 \pm 0.538	0.460, 2.514	2.304 \pm 0.749 **	1.202, 4.100	
Population size	0.998 \pm 0.002	0.993, 1.002	0.997 \pm 0.002 **	0.993, 0.999	0.999 \pm 0.001 *	0.997, 1.000	
Outstanding loans: yes (ref: no)	0.268 \pm 0.175 **	0.062, 0.721	0.546 \pm 0.252	0.207, 1.164	0.613 \pm 0.198 *	0.306, 1.086	
HEC	1.232 \pm 0.111 **	1.032, 1.477	0.903 \pm 0.063	0.783, 1.031	1.068 \pm 0.052	0.975, 1.178	
MC	1.065 \pm 0.062	0.944, 1.192	0.906 \pm 0.044 **	0.822, 0.993	0.923 \pm 0.030 **	0.863, 0.982	

¹ For the two multilevel models (null and full), fixed effect parameters in each model are specified in Table 5.5A, while Table 5.5B presents the village level variances in log odds of being a payoff copier, conformist or unidentifiable (relative to an individualist respectively) for each model respectively. For instance, in Table 5.5A, the full model (multilevel) has six fixed effects including the intercept; for each fixed effect (column 1), the associated exp (β) value for a payoff copier (column 2), conformist (column 4) and unidentifiable (column 6) and their respective 95% BCI² (columns 3, 5 and 7) can be read in the corresponding row. The DIC³ value (see Section 2.5.2 for details) for the model is presented in column 8 of Table 5.5A. The variance components for the full model (multilevel) can be read in the 12th, 13th and 14th, rows of Table 5.5B; column 2 represents the village level variance with its 95% BCI² (column 3), and column 4 represents the VPC with its 95% BCI² (column 5) for the corresponding rows. The last three rows of Table 5.5B present the residual covariances in the full (multilevel) model respectively; the associated values at the village level (column 2) and their 95% BCI² (column 3) can be read in the corresponding rows. The fixed effect parameters for the single level null model are presented in Table 5.5A; this model does not have variance components.

² Bayesian Credible Interval. Calculated from the posterior distribution, a k% interval contains k% of possible values of a parameter (Ellison 1996). For exp (β) values, 95% BCI not containing the value 1 indicates significance at p<0.05.

³ Deviance Information Criterion.

Table 5.5B Variance components for the log odds of being a payoff copier, conformist or unidentifiable relative to an individualist respectively in the null and full multinomial logistic models (see Table 5.5A for β parameters of these models and instructions on how to read this table).

	Village level variance		Variance partition coefficient (VPC) ²	
	Variance \pm SE	95% BCI ¹	VPC \pm SE	95% BCI ¹
Null model (multilevel)				
Payoff copier	1.481 \pm 1.140	0.363, 4.471	0.283 \pm 0.125	0.099, 0.576
Conformist	0.640 \pm 0.428	0.176, 1.738	0.155 \pm 0.077	0.051, 0.346
Unidentifiable	0.328 \pm 0.211	0.093, 0.856	0.088 \pm 0.048	0.027, 0.207
<i>Residual covariance:</i>				
Payoff copier - Conformist	0.282 \pm 0.443	-0.443, 1.315		
Payoff copier - Unidentifiable	0.346 \pm 0.346	-0.120, 1.193		
Conformist - Unidentifiable	0.347 \pm 0.250	0.045, 0.976		
Full model (multilevel)				
Payoff copier	1.663 \pm 1.241	0.404, 4.974	0.305 \pm 0.130	0.109, 0.602
Conformist	0.229 \pm 0.186	0.050, 0.733	0.063 \pm 0.044	0.015, 0.182
Unidentifiable	0.209 \pm 0.159	0.051, 0.632	0.058 \pm 0.039	0.015, 0.161
<i>Residual covariance:</i>				
Payoff copier - Conformist	-0.033 \pm 0.305	-0.657, 0.592		
Payoff copier - Unidentifiable	0.192 \pm 0.290	-0.269, 0.894		
Conformist - Unidentifiable	0.145 \pm 0.139	-0.017, 0.496		

¹ Bayesian Credible Interval. Calculated from the posterior distribution, a k% interval contains k% of possible values of a parameter (Ellison 1996).

² VPC = village level variance / (village level variance + 3.29). Level 1 (multinomial response variable) has a standard logistic distribution with variance $\pi^2/3 = 3.29$ (Hedeker 2003).

Table 5.6A Associations of each predictor term (fixed effect) with the odds of being a social learner or unidentifiable relative to an individualist respectively, in the null (intercept only) and full multinomial logistic models (see Table 5.6B for variance components of these models). Odds ratios less than, equal to, or greater than one represent lower, equal, or higher probabilities of occurrence (compared to the reference category) respectively.¹ *** $p < 0.001$, ** $p < 0.05$, * $p < 0.10$

Fixed effect	Social learner		Unidentifiable		DIC ³
	exp (β) \pm SE	95% BCI ²	exp (β) \pm SE	95% BCI ²	
Null models					
Intercept (single level)	0.771 \pm 0.123*	0.555, 1.032	0.992 \pm 0.146	0.733, 1.315	554.038
Intercept (multilevel)	0.754 \pm 0.189	0.436, 1.180	0.984 \pm 0.147	0.724, 1.307	549.661
Full Model (multilevel)					
Intercept	1.494 \pm 0.745	0.585, 3.527	0.960 \pm 0.417	0.406, 2.098	541.480
Sex: female (ref: male)	1.296 \pm 0.519	0.575, 2.541	2.672 \pm 0.976**	1.277, 5.038	
Outstanding loans: yes (ref: no)	0.407 \pm 0.185**	0.157, 0.840	0.572 \pm 0.223*	0.246, 1.117	
Father living in village: yes (ref: no)	0.262 \pm 0.147**	0.078, 0.645	0.980 \pm 0.431	0.407, 2.060	
Father participated in PGG: yes (ref: no)	6.551 \pm 7.392**	1.120, 21.090	2.728 \pm 2.311	0.628, 8.094	

¹ For the two multilevel models (null and full), fixed effect parameters in each model are specified in Table 5.6A, while Table 5.6B presents the village level variances in log odds of being a social learner or unidentifiable (relative to an individualist respectively) for each model respectively. For instance, in Table 5.6A, the full model (multilevel) has five fixed effects including the intercept; for each fixed effect (column 1), the associated exp (β) value for a social learner (column 2) and unidentifiable (column 4) and their respective 95% BCI² (columns 3 and 5) can be read in the corresponding row. The DIC³ value (see Section 2.5.2 for details) for the model is presented in column 6 of Table 5.6A. The variance components for the full model (multilevel) can be read in the 8th and 9th rows of Table 5.6B; column 2 represents the village level variance with its 95% BCI² (column 3), and column 4 represents the VPC with its 95% BCI² (column 5) for the corresponding rows. The last row of Table 5.6B presents the residual covariance in the full (multilevel) model at the village level (column 2) and its 95% BCI² (column 3). The fixed effect parameters for the single level null model are presented in Table 5.6A; this model does not have variance components.

² Bayesian Credible Interval. Calculated from the posterior distribution, a k% interval contains k% of possible values of a parameter (Ellison 1996). For exp (β) values, 95% BCI not containing the value 1 indicates significance at $p < 0.05$.

³ Deviance Information Criterion.

Table 5.6B Variance components for the log odds of being a social learner or unidentifiable relative to an individualist respectively in the null and full multinomial logistic models (see Table 5.6A for β parameters of these models and instructions on how to read this table).

	Village level variance		Variance partition coefficient (VPC) ²	
	Variance \pm SE	95% BCI ¹	VPC \pm SE	95% BCI ¹
Null model (multilevel)				
Social learner	0.470 \pm 0.354	0.097, 1.377	0.119 \pm 0.071	0.029, 0.295
Unidentifiable	0.006 \pm 0.012	0.000, 0.038	0.002 \pm 0.003	0.000, 0.012
<i>Residual covariance: Social learner - Unidentifiable</i>	0.018 \pm 0.045	-0.037, 0.124		
Full model (multilevel)				
Social learner	0.952 \pm 0.665	0.267, 2.612	0.210 \pm 0.097	0.075, 0.443
Unidentifiable	0.614 \pm 0.405	0.171, 1.667	0.150 \pm 0.075	0.049, 0.336
<i>Residual covariance: Social learner - Unidentifiable</i>	0.324 \pm 0.418	-0.205, 1.332		

¹ Bayesian Credible Interval. Calculated from the posterior distribution, a k% interval contains k% of possible values of a parameter (Ellison 1996).

² VPC = village level variance / (village level variance + 3.29). Level 1 (multinomial response variable) has a standard logistic distribution with variance $\pi^2/3 = 3.29$ (Hedeker 2003).

5.2.4. Are properties of populations and/or individuals associated with the learning strategies employed by individuals?

Five variables are significantly associated with the odds of being a payoff copier or a conformist (relative to an individualist), namely sex, village population size, outstanding loans, the value of the HEC, and the value of the MC. Sex was retained in the full model and women are more likely to be payoff copiers and conformists relative to individualists, but these relationships are not significant at conventional levels. The odds of being a conformist relative to an individualist significantly decrease as population size increases, as do the odds of being a payoff copier, although this latter relationship is not significant at conventional levels [Table 5.5A; full model (multilevel)].

Figure 5.5A presents the observed frequencies of the three strategies within each village; villages are ordered by increasing population size. The odds of being a conformist relative to an individualist decrease by about 3% for a ten person increase in population size.

The odds of being a payoff copier relative to an individualist are significantly lower for individuals with outstanding loans as compared to those with no loans [Table 5.5A; full model (multilevel)]. People with outstanding loans are about four times more likely to be individualists than payoff copiers. Outstanding loans also decrease the likelihood of a player being a conformist, but this relationship is not significant at conventional levels. The odds of being a payoff copier increase by about 23% for every one rupee increase in the value of the HEC. A one rupee increase in the HEC reduces the odds of being a conformist by about 10%. At the same time, the odds of being a conformist are about 9% lower for every one rupee increase in the value of the MC. Hence, players are more likely to be payoff copiers as the HEC increases and less likely to be conformists as the MC increases.

The odds of being a social learner relative to an individualist are significantly associated with four variables. Women are about 30% more likely to be social learners than men are, but this relationship is not significant at conventional levels. Outstanding loans and the co-

residence of the father in the village both make individuals less likely to be social learners [Table 5.6A; full model (multilevel)]. On the other hand, the participation of the father in the PGG on the day of the games makes individuals 6.5 times more likely to be social learners [Table 5.6A; full model (multilevel)].

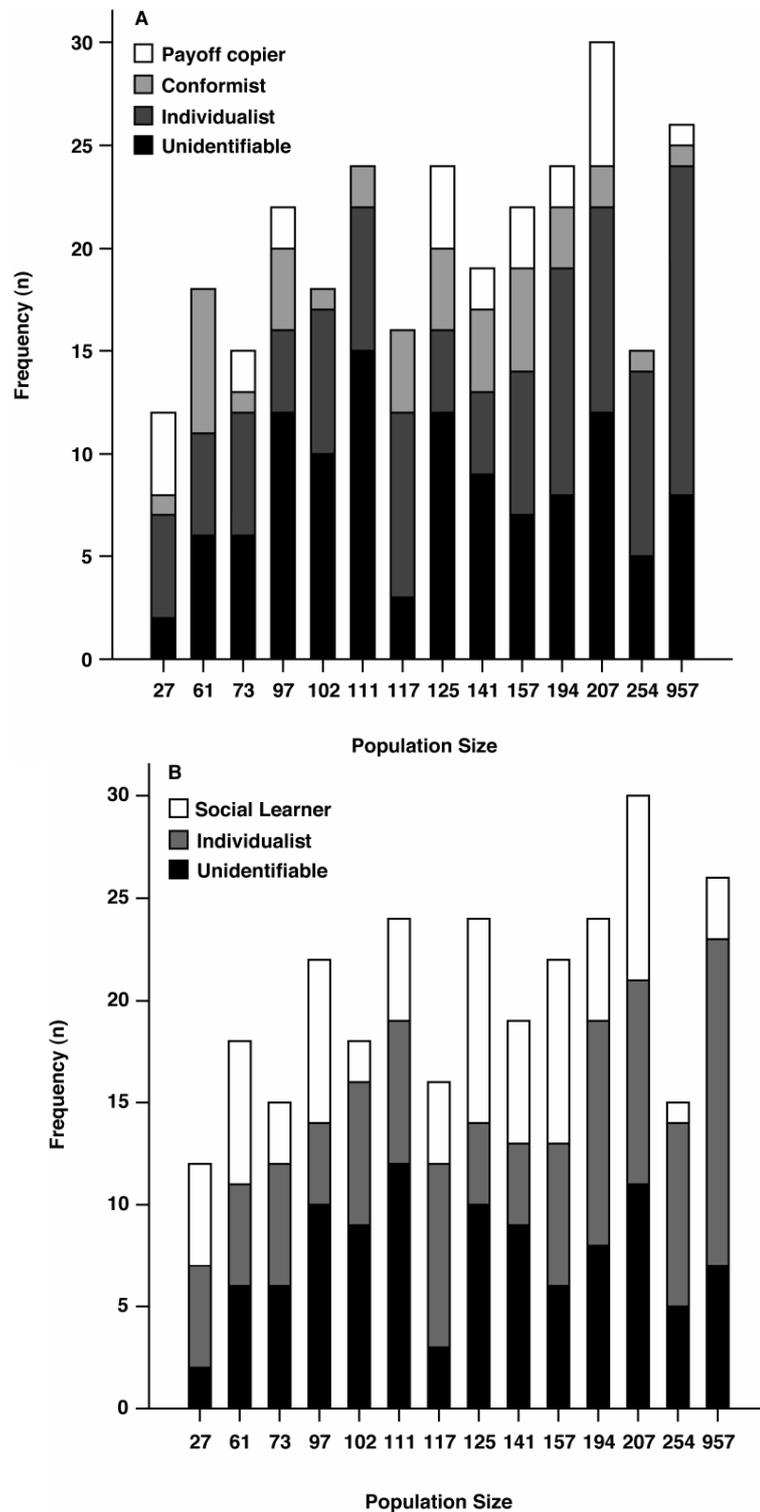


Figure 5.5 Frequencies of player learning strategies within each village. Villages are arranged by increasing population size. Figures compare frequencies of (A) payoff copiers, conformists, individualists and unidentifiable individuals, and (B) social learners, individualists and unidentifiable individuals.

5.2.5. Do different learning strategies result in the acquisition of different behavioural traits?

Players employing different learning strategies made significantly different contributions to their respective group pots in both the PGG2 (Figure 5.6, unfilled bars; Table 5.1) and the PGG1 (Figure 5.6, filled bars; Table 5.7). However, pair-wise comparisons reveal that individuals whose behaviour is most affected by their learning strategy are payoff copiers (Figure 5.6A; Table 5.7). Individualists made much higher PGG2 contributions than payoff copiers; the mean PGG2 contribution for individualists is about six rupees higher than that for payoff copiers. However, individualists' PGG2 contributions did not differ from those of conformists. Conformists made much higher PGG2 contributions than payoff copiers; the mean PGG2 contribution for conformists is about six rupees higher than that for payoff copiers.

On the other hand, individualists' PGG1 contributions are on average about 1.5 rupees lower than those of payoff copiers, although this difference is not statistically significant. Individualists' PGG1 contributions are about 2.5 rupees higher on average than those of conformists; this difference is marginally significant. Conformists made significantly lower PGG1 contributions than payoff copiers; the mean PGG1 contribution for conformists is about four rupees lower than that for payoff copiers.

Hence, individualists did not change their contributions significantly between rounds one and two (Wilcoxon signed ranks test: $Z = -0.26$, $n = 104$, Monte Carlo simulated $p = 0.803$). Payoff copiers dramatically changed their behaviour between round one and two of the PGG, lowering their contributions in round two by about seven rupees on average (Wilcoxon signed ranks test: $Z = -4.65$, $n = 26$, Monte Carlo simulated $p < 0.001$). While conformists did increase their contributions in round two compared to their contributions in round one, this difference in their behaviour between rounds is not significant (Wilcoxon signed ranks test: $Z = -1.49$, $n = 40$, Monte Carlo simulated $p = 0.128$).

Social learners made PGG2 contributions that were lower than those of individualists by about two rupees on average (Figure 5.6B; Table 5.7), although their PGG1 contributions

did not differ from those of individualists (Figure 5.6B; Table 5.7). Social learners made significantly lower PGG2 contributions as compared to their PGG1 contributions (Wilcoxon signed ranks test: $Z = -2.673$, $n = 77$, Monte Carlo simulated $p = 0.007$). Individualists did not change their contributions between rounds one and two (Wilcoxon signed ranks test: $Z = -0.256$, $n = 104$, Monte Carlo simulated $p = 0.800$).

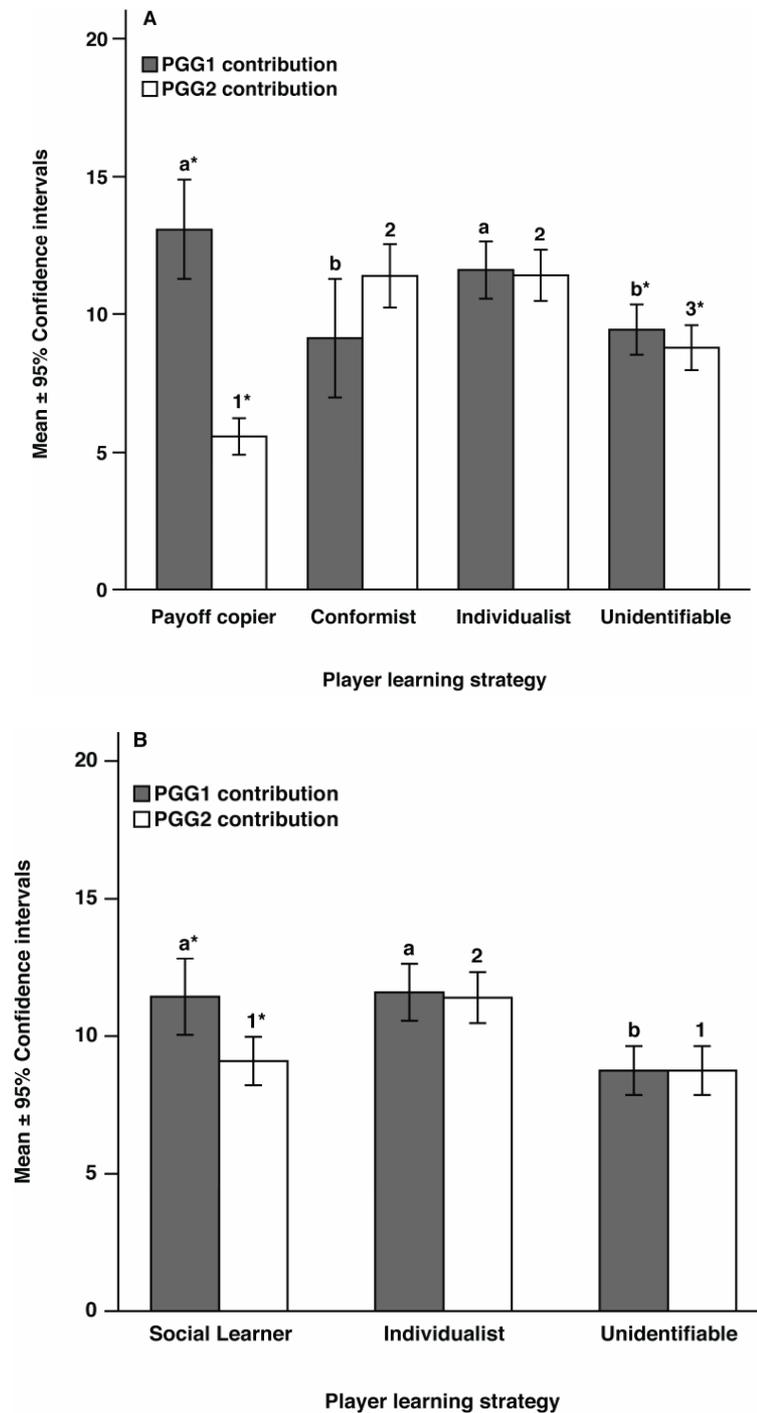


Figure 5.6 Mean contributions to the group pot in the PGG1 (PGG1 contribution; filled bars) and PGG2 (PGG2 contribution; unfilled bars) pooled across 14 villages for **(A)** payoff copiers, conformists, individualists and unidentifiable individuals respectively, and **(B)** social learners, individualists and unidentifiable individuals respectively. Different letters indicate a significant difference between the filled bars. Different numbers indicate a significant difference between the unfilled bars. Asterisks indicate a significant difference between the filled and unfilled bars within the same category of player learning strategy.

Table 5.7 Results of Kruskal-Wallis and Mann-Whitney tests comparing the PGG1 and PGG2 contributions of players with different learning strategies from 14 villages pooled together.

Comparison categories	Test variable	Test statistic	df or n	Monte Carlo simulated p
Payoff copier Conformist Individualist Unidentifiable	PGG1 contribution	Kruskal-Wallis $\chi^2 = 18.230$	3	<0.001
	PGG2 contribution	Kruskal-Wallis $\chi^2 = 57.072$	3	<0.001
Payoff copier Individualist	PGG1 contribution	Mann-Whitney U = 1160.500	130	0.726 ^a
	PGG2 contribution	Mann-Whitney U = 407.500	130	<0.001 ^a
Conformist Individualist	PGG1 contribution	Mann-Whitney U = 1578.000	144	0.057 ^a
	PGG2 contribution	Mann-Whitney U = 1946.500	144	1.000 ^a
Payoff copier Conformist	PGG1 contribution	Mann-Whitney U = 321.500	66	0.018 ^a
	PGG2 contribution	Mann-Whitney U = 62.500	66	<0.001 ^a
Social learner Individualist Unidentifiable	PGG1 contribution	Kruskal-Wallis $\chi^2 = 18.489$	2	<0.001
	PGG2 contribution	Kruskal-Wallis $\chi^2 = 24.074$	2	<0.001
Social learner Individualist	PGG1 contribution	Mann-Whitney U = 3976.500	181	0.935
	PGG2 contribution	Mann-Whitney U = 2739.000	181	<0.001

^a Bonferroni adjusted p value.

5.3 Discussion

5.3.1 Evidence for social learning in a cooperative dilemma

Variation in contributions between villages increased significantly by 7.4% in round two compared to round one of the PGG. In other words, individuals were behaviourally more similar within villages and less similar between villages in round two of the PGG. These results suggest that at least some individuals used the information that was provided in round two about the behaviour of other players from their respective villages. I thus infer that some individuals did employ social learning in making decisions in a cooperative dilemma. However, only 27% of the 285 individuals who participated in this study across 14 populations can clearly be identified as social learners, while the number of individualists is about 10% higher at 37%. Only 14% of all participants can clearly be identified as conformists and an even lower proportion (9%) as payoff copiers. Hence, individualists significantly outnumber social learners.

It is possible that the analyses presented here overestimate the number of social learners in the study populations and that the number of individualists may be even greater than currently estimated; some individuals classified as payoff copiers or conformists may in fact be individualists who independently decided on an amount for their PGG2 contribution that corresponded with the HEC or MC. A Bayesian model fit approach, comparing candidate models of social and individual learning to the observed distribution of behaviour may provide more accurate estimates of levels of social learning in my study populations (e.g. Efferson et al. 2008; Efferson et al. 2007; McElreath et al. 2008; McElreath et al. 2005 and see Camerer 2003 for an overview of this approach as applied to studying individual learning in economic games). However, since the number of social learners can only be lower than estimated in the present analyses, we can be confident in inferring that most individuals in my study populations do not appear to employ payoff biased and conformist social learning in a cooperative dilemma. It remains a possibility that individuals use social learning strategies other than the ones investigated in this study.

5.3.2 Correlates of learning strategies

The relative distribution of different learning strategies varies considerably across populations. Properties of villages and individuals that systematically explain some of the variation in patterns of learning across 14 populations are population size, which has a negative association with the likelihood of being a conformist, and outstanding loans, which have a negative association with the likelihood of being a payoff copier.

At least three hypotheses may explain the negative association between population size and conformity. First, the lower prevalence of conformity in larger populations may be a response to an increased likelihood of adopting the wrong or maladaptive behaviour in larger populations, if individuals sample the behaviour of only a fraction of the population. A theoretical model has demonstrated that conformist transmission is disfavoured when the costs of adopting a maladaptive behaviour are high (Nakahashi 2007). In another theoretical study Kendal et al. (2009) find that the probability of conforming is negatively affected by population size when the frequency of individuals possessing the adaptive behaviour for an environment is less than half. Behavioural tracking of the environment may be less accurate in larger populations if most people are conformists sampling from a subset of the population and the proportion of individual learners in the population is small. My results are consistent with the theoretical finding that social learning is less likely to fixate in larger populations (Whitehead and Richerson 2009); however, this study examined the likelihood of fixation only in populations of 500 individuals or more, whereas my study populations are smaller.

A second hypothesis is that large or growing populations may contribute to environmental instability, which in turn disfavours conformist learning. Large populations may experience accelerated consumption of local resources (like wood and water) and greater competition for them. This may be especially true for populations, like those of the Pahari Korwa, that rely heavily on locally available resources for their subsistence and survival. If conformist transmission is disfavoured in rapidly changing, unstable environments, the prevalence of conformity would decline in large or growing populations. The current theoretical literature exploring the effects of environmental instability on the frequency of conformity provides

mixed predictions. While most authors are in agreement that environmental instability has a negative effect on the frequency of unbiased social learning (copying a randomly selected phenotype from the parental generation; Aoki et al. 2005; Borenstein et al. 2009; Boyd and Richerson 1985; Feldman et al. 1996; Rogers 1988; Wakano and Aoki 2006; Wakano et al. 2004), some authors suggest that it negatively affects the strength of conformity (Henrich and Boyd 1998), while others argue the opposite (Kendal et al. 2009; Nakahashi 2007; Wakano and Aoki 2007).

The third hypothesis reverses the direction of causality; populations with fewer conformists (or more individualists) may be more productive and therefore grow to be larger. Support for this hypothesis requires identifying mechanisms that counter “Rogers’ paradox”, the theoretical expectation that the mean fitness of a population (or individual) with social learning should be no different to one without it (Rogers 1988). A recent theoretical study finds that when learning is structured, i.e. individuals learn only from a set of neighbours and do not disperse far, social learning can become common and negatively affect fitness and thus population size (Rendell et al. 2009).

I propose two hypotheses that potentially explain the relationship between outstanding loans and a reduced dependence on social learning. Outstanding loans may reflect long-term financial stress and instability, making individuals more risk-averse and therefore less willing to chance adopting a non-optimum costly behaviour via social learning. Alternatively, that outstanding loans are associated with a lower likelihood of being a payoff copier may indicate that individuals who are more likely to receive help via loans are also more willing to reciprocate by contributing to a public good.

It is notable that a player’s likelihood of being a conformist decreases as the actual value of the MC increases, indicating that the conformist strategy may be flexible; individuals may avoid conforming if it is too expensive to do so. It is, however, puzzling that individuals are more likely to be payoff copiers as the HEC increases; if payoff copiers are motivated by a desire to increase payoffs, then they should favour lower HEC values which, given the structure of the PGG, will provide higher payoffs. Nonetheless, these results raise the

possibility that conformist or payoff biased learning is conditional on the cost incurred by adopting a trait.

Players whose fathers live in the same village as them are less likely to be social learners, whereas those whose fathers participate with them in the games are more likely to be social learners. These seemingly contradictory results may indicate that fathers are important models of socially learned behaviour. A co-resident father may make individuals less sensitive to the behaviour of others. However, when the father is part of an aggregate behavioural pool being sampled (such as when a player's father participates in the games), individuals may pay more attention to information derived from this pool than they would otherwise. These are speculations to guide future research.

Together, my results support the idea that individuals' learning strategies are sensitive to the relative costs of individual versus social learning and the relative likelihood that each of these strategies will result in the adoption of the optimal behaviour in different environments. Certainly they suggest that people do not use a single learning strategy across all environments and irrespective of their circumstances. Thus, my findings challenge the suggestion by some authors (Boyd and Richerson 1985; Gintis 2003) that conformity evolved as an all-purpose learning strategy that individuals employ across task-domains, even though it leads to the acquisition of sub-optimal behaviour in some domains. These authors argue that conformity is advantageous to individuals averaged across several domains; its averaged benefit across domains mitigates the costs incurred on account of it in some domains. Indeed, there has been a tendency to take as given the as yet unconfirmed theoretical assumption that people acquire behavioural traits via conformist learning (Gintis 2007; Henrich 2004; Henrich and Boyd 2001). It is, however, more likely that whether social learning is employed at all or not depends on the task domain (Eriksson and Coultas 2009; Eriksson et al. 2007; Rowthorn et al. 2009), its cost-benefit outcomes with respect to the current environment, as well as the circumstances of the individual. The specific learning strategy used should depend on many factors, including, among others, the availability of information about the choice of cultural/behavioural variants and the number of different variants available (Eriksson et al. 2007).

It is noteworthy that demographic factors such as migration (Aoki and Nakahashi 2008; Boyd and Richerson 1985; Boyd and Richerson 1988b) and population size (Whitehead and Richerson 2009) are expected to inversely affect the prevalence of social learning in populations; the same factors, i.e. large populations and high rates of migration, impede the evolution of cooperation (reviewed in Grafen 1984 and Henrich 2004). Hence, while cultural group selection models invoke social learning to explain the evolution of cooperation in large populations with high rates of migration, social learning itself is less likely to be employed in such populations.

5.3.3 The impact of learning on the distribution of trait variants

Models of cultural evolution predict that social learning should influence the distribution of trait variants within and across populations by affecting which variants are acquired by individuals (Boyd and Richerson 1985). I find evidence that employing a payoff biased learning strategy unsurprisingly led to the acquisition of more selfish behaviour in a one-shot, anonymous PGG, and instrumented a change in players' behaviour between round one and two of the game. Alternatively, although a conformist learning strategy is associated with a statistically non-significant increase in a player's PGG2 contribution as compared to her PGG1 contribution, this small increase in contribution eliminated the difference between conformists' and individualists' behaviour in round one. Most individualists in the population maintain stable behaviour between rounds one and two. Overall, these data suggest that the learning strategies employed by individuals do influence the distribution of trait variants within the population. However, how social learning affects trait variation between populations in the real world depends greatly on whether social learners selectively sample the behaviour of only those residing in their population, thus increasing trait variation between populations, or not, thus decreasing trait variation between populations. Moreover, while players in this study were told the values of the MC and HEC, individuals in the real world must estimate these values by sampling the behaviour of others over time; individual errors in estimation are likely to increase behavioural variance, whether it is within or between populations.

The mean contribution is lower in round two as compared to round one of the PGG. Previous studies have found that contributions in a PGG decline when the game is played repeatedly, even when individuals play with a different set of players each time (e.g. Fehr and Gächter 2002). While the decrease in individuals' contributions between round one and two in this study may be explained by repeated play (albeit with a different set of players) in part, it is likely that at least some of this effect is the consequence of payoff biased learning.

5.3.4 Unidentifiable strategies

A potential drawback of the current study design is the large number of unidentifiable individuals; individuals who could not unequivocally be classified as payoff copiers, conformists or individualists. This category of individuals most likely contains not only an assortment of payoff copiers, conformists and individualists, but also players using complex or alternative learning strategies. While the analyses presented here take account of these unidentifiable individuals, their large number warrants a closer investigation of how best we may identify their strategies. One way that the number of unidentifiable individuals could have been eliminated is by presenting players with false values for the MC or HEC in games where the two were equal, or where either or both of these values was equal to a player's PGG1 contribution. This was avoided as I did not wish to deceive participants, a policy adopted throughout this work. However, it is not obvious that eliminating this category by design would improve the inferences of this study. Several individuals in the unidentifiable category may genuinely possess complex strategies, such as using social information to confirm the benefit of a behavioural strategy they already possess (the "confirmation" strategy modelled by McElreath et al. 2005). Indeed, 90% of the unidentifiable individuals in my sample are those who contributed the same amount in round two as they did in round one and this amount was also the same as the HEC, MC or both. The current study design thus allows the separation, if not explicit identification, of such complex strategy learners, instead of forcing them to use one of three pure learning strategies; it also likely captures a more real-world decision making environment.

Hence, the distribution of learning strategies captured in this study may be a more accurate representation of the true distribution of strategies in the study populations, than if individuals had been provided incomplete information. Although studies have modelled complex learning strategies (e.g. Borenstein et al. 2009; Boyd and Richerson 1995; Boyd and Richerson 1996; Enquist et al. 2007; Kameda and Nakanishi 2003; McElreath et al. 2008; McElreath et al. 2005; Rendell et al. 2009), my results highlight the need for both more theoretical and empirical work, focussing not only on the effects of complex learning strategies on individual behaviour, but also their population level consequences; this work is particularly important if complex strategy learners are relatively numerous in populations.

5.3.5 Concluding remarks

The second question I address in this thesis is: do people use social learning to acquire cooperative strategies? My findings suggest that some minority of individuals do employ social learning in the context of a cooperative dilemma, although most individuals do not. The frequencies of different learning strategies are highly variable across populations; this variation is partly explained by demographic differences between populations, most notably population size. Theoretical work is required to clarify whether these low and variable levels of social learning can maintain stable behavioural differences between populations, given the high rates of migration between my study villages (see Section 2.3.2.2, Table 2.1). Furthermore, whether social learning increases or decreases behavioural variation between populations depends crucially on whether social learners selectively sample the behaviour of only those residing in their population or not respectively; empirical work in real-world populations will shed light on this matter.

5.4 Methods

5.4.1 Experimental set-up

All games were played between February 2nd and May 16th, 2008. All games in most villages were administered on the third day after arrival in the village (the second day in two villages and the fourth day in one village) and completed in one day. Mean age \pm SD of participants was 34.59 ± 12.13 years and 46% were female.

All participants collected at a common location in the village on the day of the games. They were instructed about the game rules and examples both collectively and then individually at the private location where they played the game (see Appendix A, Sections A.2 and A.4 for scripts). Players were tested both collectively and individually for their understanding of the game rules and of the anonymity of their decisions in each round of the game. Only a player who individually answered all test questions correctly played the game in round one. Only a player who had played in round one and answered all test questions for round two correctly played in round two. In all 14 villages where both rounds of the PGG were played, all individuals ($n = 285$) who understood the game rules in round one did so in round two; they therefore played in both rounds. Participants made their decisions in each round by manipulating real five rupee coins and depositing their contribution into a money box. In round two, prior to making their contribution decisions, players were informed about the HEC and the MC for their group from round one; this was done by placing five rupee coins summing to the relevant amount on the right and left side of the money box respectively. 11 of 49 round one groups across 14 villages generated two MCs. Players from three such groups were presented both MCs; these groups were in the first two villages the PGG2 was implemented in. In the remaining 12 villages, for players from nine such groups, I presented the MC that was most different to the HEC. For the three groups where both MCs were presented, a player is classified as a conformist if her PGG2 contribution equalled either of these MCs.

Groups of six players³ were constituted in each round by randomly matching token numbers. Of the 49 games played in each round across 14 villages, the total number of players was indivisible by six in seven games; five games had a group size less than six (three or four) and two games had a group size greater than six (seven or eight). These differences in group size do not change the relative payoff structure of the game. Players always thought they were in a group of six players as they were unaware of the number of people who did not play the game due to a failure to answer all test questions correctly.

Note that due to an oversight, data on the number of kin who participated in the PGG (Appendix B, Section B.1, questionnaire item 7g) were not collected in the first three villages visited namely, Kharranagar, Chipni Paani and Pareva Aara.

5.4.2 Statistical analyses

Multilevel normal linear models (Browne 2009; Rasbash et al. 2009; Snijders and Bosker 1999) were used to explicitly analyse variation in PGG2 contributions at the village and individual levels. Non-parametric statistics were used to analyse the distribution of different learning strategies pooled across villages and to compare player PGG1 and PGG2 contributions. Multilevel multinomial logistic models (Browne 2009; Rasbash et al. 2009; Snijders and Bosker 1999) were used to analyse variation in learning strategies between villages, and the relationship of population and individual descriptors with an individual's likelihood of possessing a particular learning strategy. Individuals (level 1) were nested within villages (level 2). Two sets of models were run, each based on a different classification of player learning strategies. For the first set of models, the response variable was categorical with four categories for individuals classified as either 'payoff copier', 'conformist', 'individualist' or 'unidentifiable'. For the second set of models, the response variable was categorical with three categories for individuals classified as either 'social learner', 'individualist' or 'unidentifiable'. The inclusion of the 'unidentifiable' category

³ Group size was chosen as six because player contributions could assume five possible values (0, 5, 10, 15, 20), so a minimum group size of six was required to ensure that there was a clear mode in every group. Larger group sizes were avoided in order to minimise the likelihood that an individual played again with any of the members of her group from round one, once groups were reconstituted in round two.

reduces biases that may be introduced in the analyses by the exclusion of players who have complex strategies and thus affords more conservative analyses. For each set of models, the analyses proceeded in four stages as described in Section 2.5.2. However, for the first set of models (response variable with four categories), an additional fourth block of variables was included in the fourth stage of analyses (full model fitting); this block contained two predictor variables, the values of a player's group one MC and HEC.

SECTION III

CONCLUSION

CHAPTER 6

CONCLUSION

The work presented in this thesis makes an empirical contribution towards understanding the evolution of large-scale cooperation in humans. There has been intense debate over the extent to which such cooperation results from natural selection acting not only on individuals, but also on groups of individuals (West et al. submitted; West et al. 2007, 2008; Wilson 2008; Wilson and Sober 1994; Wilson and Wilson 2007). The substantive contributions of this thesis are (i) to systematically outline theoretical assumptions and predictions that require validation for cultural group selection models of large-scale cooperation to find support in nature, and (ii) to establish an empirical research programme that tests these assumptions and predictions in real-world populations. The findings of this thesis have implications not only for an understanding of the evolution of large-scale cooperation in humans, but also for an understanding of the structure of a cultural inheritance system; I conclude by discussing these implications.

6.1 Implications for an understanding of the evolution of large-scale cooperation in humans

Cultural group selection models posit that social learning at the individual level can maintain stable, heritable behavioural variation between populations; this variation may then be subject to natural selection, enabling the evolution of large-scale cooperation if cooperative strategies are acquired via social learning (reviewed in Henrich 2004). Hence,

6.1 IMPLICATIONS FOR AN UNDERSTANDING OF THE EVOLUTION OF LARGE-SCALE COOPERATION IN HUMANS

to demonstrate support for cultural group selection models of large-scale cooperation we need to establish that there is stable, heritable behavioural variation between populations, maintained as a consequence of individuals acquiring cooperative behavioural strategies via social learning (Section 1.6.2).

The first major question addressed in this thesis is: is there *stable, heritable* variation in levels of cooperation across human populations? Current empirical data on cooperation in real-world populations, from previous studies and this study, together do not provide evidence that variation across populations is *stable* or *heritable*. In Chapters 3 and 4 I demonstrate that variation in levels of cooperation across populations of the same cultural group is equivalent to that found previously across populations of different cultural groups (Henrich et al. 2004; Henrich et al. 2005; Herrmann et al. 2008). If the cultural group is a unit of selection, then assuming that the strength of selection between cultural groups is not very much higher than the strength of selection within groups, we must establish that there is greater behavioural variation between different endogamous cultural groups than between populations of the same endogamous cultural group (Section 1.6.2). I do not find support for this prediction. Moreover, I identify demographic factors, such as population size and age, explaining part of the variation between my study populations (Chapters 3 and 4). Together, these results suggest that behavioural variation across my study populations, which belong to the same cultural group, is driven by environmental (ecological and demographic) differences between them. While variation driven by cultural transmission is heritable, variation driven by demographic or ecological factors is not necessarily stable or heritable; environmental drivers of behavioural variation are less likely to maintain stable differences essential for selection at the population level. I address whether populations of the same cultural group are likely to be units of selection later in this chapter.

I find significant variation across populations living in broadly similar environments; the populations compared in most cross-cultural studies, on the other hand, often exist in wildly different ecologies. For example, Henrich et al.'s (2005) study compared populations spanning a considerable range of ecologies including tropical rainforest (e.g. Machiguenga, Quichua, Tsimane), temperate plains (e.g. Mapuche), high latitude desert (e.g. Torguuds, Kazakhs) and tropical islands (e.g. Lamalera). The costs of cooperation are likely to vary

6.1 IMPLICATIONS FOR AN UNDERSTANDING OF THE EVOLUTION OF LARGE-SCALE COOPERATION IN HUMANS

substantially across different ecologies. For instance, cooperation may not be as expensive where subsistence is based wholly on hunting large game (which cannot be done alone) versus gathering small fruit. In fact, Henrich et al. (2005) constructed a variable called “payoffs to cooperation” which explained a significant amount of variation in ultimatum game behaviour (47% together with the variable “market integration”) between the 15 cultural groups in their study; this variable purportedly captures the degree to which “economic life depend[s] on cooperation with non-immediate kin”, such as in different subsistence activities. That “payoffs to cooperation” explain substantial variation across their study populations supports the proposition made here: ecological factors affecting the cost of cooperation drive much of the behavioural variation across populations.

The second major question addressed in this thesis is: do people use social learning to acquire cooperative strategies? In Chapter 5 I present evidence that while some individuals do employ social learning in the context of a cooperative dilemma, the majority do not use conformist or payoff biased learning. There is considerable variation across populations in the frequencies of different learning strategies used; population size and an individual’s economic status are associated with the learning strategy (payoff copying, conformity, individual learning) employed (Chapter 5).

The frequency of social or conformist learning required to maintain behavioural variation between populations depends on several factors, including rates of migration between populations and the degree of environmental stability, as well as the strength of homogenising forces within populations, such as conformity and punishment of norm violation (e.g. Boyd et al. 2003; Boyd and Richerson 1985; Guzmán et al. 2007; Henrich and Boyd 2001). It is not apparent whether the levels of social learning observed in my study can maintain stable between-population variation; to clarify this requires constructing theoretical models that incorporate these real-world estimates of levels of social learning, as well as estimates of levels of migration between populations. However, rates of migration between villages in my study are high; about 38% of individuals across my study populations are living in a village they were not born in (Section 2.3.2.2, Table 2.1). Hence, forces generating behavioural homogeneity within these populations, such as conformity or punishment of norm violation, must be strong enough to counter the variation introduced

6.1 IMPLICATIONS FOR AN UNDERSTANDING OF THE EVOLUTION OF LARGE-SCALE COOPERATION IN HUMANS

by migration in each generation; only then can stable variation be maintained between villages. Only about 14% of individuals across my study populations can be identified as conformists in the cooperative domain (Section 5.2.2). Furthermore, the frequency of conformity varies considerably across populations. It is therefore unlikely that stable variation can be maintained between villages under these conditions of high migration and low and variable levels of conformity.

It has been suggested that cultural transmission may occur at the level of the village unit, rather than at the level of the endogamous cultural unit (Gurven 2004a; Henrich et al. 2005). If between-village variation is maintained by cultural transmission within villages, cultural group selection could occur, the village being the unit of selection instead of the cultural group. We should then expect substantial behavioural variation between villages of the same cultural group and significantly lower variation between individuals of the same village. Although there is substantial behavioural variation between villages in my study, there is much greater variation at the individual level than at the village level (Chapters 3 and 4). Moreover, as mentioned previously, it is unlikely that the levels of social learning observed in these populations can maintain stable behavioural variation given the high rates of migration between populations. However, even if the observed levels of conformity are theoretically sufficient to maintain variation between villages, whether they do so depends greatly on whether individuals sample and acquire behaviour only from members of the same village; sampling the behaviour of those belonging to other villages will decrease between-village variance. Since there is considerable migration between villages (see Section 2.3.2.2, Table 2.1), and individuals often visit other villages (personal observation), they frequently encounter people from other villages; it is, therefore, unlikely that individuals sample only the behaviour of members of their respective villages. Empirical work will clarify whether individuals selectively socially learn only from members of their populations, an assumption made by all existing cultural group selection models. While it seems less likely that inter-marrying villages of the same endogamous, cultural group are units of selection, for reasons outlined above, this hypothesis needs to be empirically tested. However, that behavioral variation between populations is at least partly contingent on environmental differences between them, questions the existence of stable norms of cooperation.

6.1 IMPLICATIONS FOR AN UNDERSTANDING OF THE EVOLUTION OF LARGE-SCALE COOPERATION IN HUMANS

My findings call for re-interpretation of existing cross-cultural studies on cooperation that endorse the existence of culturally learned ‘cooperative norms’ based on samples from one (or few) populations per culture (Henrich et al. 2005; Henrich et al. 2010; Henrich et al. 2006; Herrmann et al. 2008; Roth et al. 1991). A failure to account for the fact that the environment in which any organism lives provides the landscape for adaptation, and is thus a major source of variation between organisms and populations, can lead to grossly incorrect inferences about the origin and function of traits. For instance, as discussed in Section 4.3.2, two recent studies (Henrich et al. 2010; Marlowe et al. 2008) infer that societal complexity, including religious institutions, played an important role in the evolution of large-scale cooperation by promoting the enforcement of cooperative norms; this inference is based on the finding that individuals from large populations are more willing to punish defectors. Since in both these studies the authors sampled behaviour from one or a few populations per society, they confound population size and societal complexity. My results challenge the conclusions of these studies since I demonstrate an association between population size and cooperation that is independent of variation in structural features of populations, such as socio-political complexity or religion.

Population level replicates from each cultural group are crucial to determine whether there is behavioural variation between cultural groups in addition to variation between populations within a cultural group. However, if the cultural groups being compared are found in extremely dissimilar environments, such as different ecosystems, simply demonstrating that variation at the cultural group level is greater than that at the population level is also not sufficient to infer that this variation is driven by cultural transmission rather than environmental differences between populations; in this case culture is confounded with ecosystem, and populations existing in the same ecosystem may be more similar than populations living in different ecosystems due to an effect of environment rather than culture. To demonstrate that behaviour is acquired via cultural transmission independent of environmental conditions, we need to establish that there is greater behavioural variation between cultural groups than between populations of the same cultural group, when all compared populations live in the same ecosystem.

6.1 IMPLICATIONS FOR AN UNDERSTANDING OF THE EVOLUTION OF LARGE-SCALE COOPERATION IN HUMANS

As discussed previously (Section 1.6.2), individually costly cooperation may be favoured by selection at the level of the cultural group even when variation across populations of the same cultural group is equal to or greater than variation between cultural groups; for this to occur the strength of selection between cultural groups would have to be very much higher than the strength of selection within groups. While this constraint is generally considered too stringent to be satisfied often in nature (Henrich 2004), it nonetheless remains a theoretical possibility.

In sum, my findings empirically challenge cultural group selection models of the evolution of large-scale cooperation. While we cannot yet discard evolutionary accounts of large-scale cooperation based on cultural group selection, we must continue to look for other possible explanations. One hypothesis that I propose for the evolution of large-scale cooperation is as follows. Mechanisms that maintain environmental stability can allow the inheritance of selection pressures across generations, the idea of an “ecological inheritance” (Odling-Smee et al. 2003). For instance, beavers colonising new habitat produce long-term changes in the habitat by constructing dams that create swampland; this process of “niche construction” (Odling-Smee et al. 2003) ensures that generations of beavers are born into a similar environment and therefore face selection pressures that are similar to those faced by their ancestors. It is therefore possible that mechanisms that maintain environmental (ecological and demographic) stability across generations ensure that the selection pressures acting for or against cooperation within a population remain constant across generations. In this case, behavioural variation may be maintained between populations if populations live in varying environments but the environmental differences are stable across generations. Selection on between-population variation may then lead to the evolution of large-scale cooperation. However, the plausibility of this ‘ecological group selection’ hypothesis depends on whether we can identify mechanisms that can maintain environmental stability across generations such that the selection pressures acting for or against cooperation remain constant within populations.

While the theoretical literature on the evolution of cooperation is vast, more often than not theoreticians have paid little attention to empirical observation and the validity of their assumptions. Much of the theoretical debate on the evolution of cooperation (see references

6.1 IMPLICATIONS FOR AN UNDERSTANDING OF THE EVOLUTION OF LARGE-SCALE COOPERATION IN HUMANS

cited in the first paragraph of this chapter) may be futile, once we reject particular models on the basis of assumptions that they make and which do not reflect reality. A tighter integration of theory and empiricism is essential if our ultimate aim is to provide a rigorous scientific framework explaining phenomena in the real world.

6.2 Implications for an understanding of the structure of cultural inheritance systems

This study demonstrates that frequencies of different learning strategies are highly variable across populations and the prevalence of social learning is influenced by demographic features of populations (Chapter 5). These findings suggest that whether individuals use social learning in the cooperative domain or not, and the extent to which they do so, depends considerably on the environment they live in; individuals do not use a uniform learning strategy across all environments and irrespective of their circumstances.

It is not surprising that the use of social learning in the cooperative domain may be particularly sensitive to environmental parameters. Social learning should be favoured if it saves learners the cost of individual trial and error learning in acquiring the optimum behaviour for an environment (Boyd and Richerson 1988b). Cooperation by definition is costly. Hence, factors that make individual learning more costly and/or cooperation less costly should favour the social learning of cooperative behaviour; however, these factors may vary greatly in different environments.

In their 1985 book, Boyd and Richerson (p. 16) state that, “The evolution of the structure of cultural transmission in humans is analogous to the evolution of the genetic system. Changes in the structure of cultural transmission simultaneously affect all the characters that are culturally transmitted. If we want to understand the evolution of the structure of cultural inheritance itself, we have to average over all these effects. On the other hand, if we want to understand the evolution of social behaviour in humans, we take the structure of the cultural inheritance system as fixed.” The authors speak of the issue that lies at the

6.2 IMPLICATIONS FOR AN UNDERSTANDING OF THE STRUCTURE OF CULTURAL INHERITANCE SYSTEMS

centre of a comprehensive understanding of the processes of cultural evolution, its impact on the evolution of human behaviour and the differences between cultural and acultural animals (see Hoppitt et al. 2008, Laland 2008 and Laland and Janik 2006 for reviews of evidence for culture in non-human animals); what factors shape and determine the structure of a cultural inheritance system? Do systems of inheritance, cultural or genetic, evolve as all-purpose mechanisms according to their averaged effects on multiple traits or domains? Or can they evolve to incorporate some degree of mechanistic variation with different inheritance rules applying to different traits or task domains?

There are no *a priori* grounds to believe that all the components of a cultural inheritance system evolved as all-purpose mechanisms averaged over many domains. Even genetic inheritance systems demonstrate variation in inheritance mechanisms, certainly across species and even across traits within a species. For instance, most antibiotic resistance genes are more frequently transmitted via horizontal gene transfers between bacteria of the same and different species than via vertical transmission (Davies 1994; Neu 1992; Salyers and Amabile-Cuevas 1997). Moreover, the horizontal gene transfer can occur via an assortment of mechanisms: for example, transformation involves the uptake of DNA from the physical environment, transduction involves the transfer of DNA between bacteria by a virus, and conjugation involves the direct physical exchange of DNA between two bacteria. As Ochman et al. (2000, p. 301) point out, “it is not surprising that antibiotic resistance genes are associated with highly mobile genetic elements, because the benefit to a microorganism derived from antibiotic resistance is transient, owing to the temporal and spatial heterogeneity of antibiotic bearing environments.”

A ‘clever’ learning strategy that selectively learns from others only in domains where the cost of adopting the suboptimal behaviour is low should outcompete a strategy that does not discriminate between more and less costly domains (Nakahashi 2007; Rowthorn et al. 2009). Richard McElreath found evidence that the Sangu of Tanzania employ social learning in acquiring their beliefs about witchcraft but not their beliefs about the importance of kin versus friends or the role of elders in society (McElreath 2004b); adopting incorrect beliefs about the importance of kin, friends and elders who directly

6.2 IMPLICATIONS FOR AN UNDERSTANDING OF THE STRUCTURE OF CULTURAL INHERITANCE SYSTEMS

impact individuals' lives may be much more costly for individuals than adopting incorrect beliefs about witchcraft which likely have no real repercussions.

The structure of cultural inheritance systems and the learning mechanisms associated with them need to be considered on a trait by trait, domain by domain basis. Investigations of the repercussions of cultural transmission must not "take the structure of the cultural inheritance system as fixed"; this was a reasonable first assumption in a project (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981; Rogers 1988) that significantly advanced the theoretical study of cultural evolution. In light of both the empirical and theoretical work that has followed, studies of the evolutionary repercussions of cultural transmission must be accompanied by investigations of the underlying inheritance structures themselves. A comprehensive science of the evolution of behaviour must (1) describe and explain the origin of the inheritance systems, be they genetic or cultural, governing the transmission of traits between organisms, and (2) take account of the central role of the environment in determining the traits favoured by natural selection; this will provide a unifying framework that explains both systematic or mechanistic continuity between species, as well as the diversity of behaviour within and across species.

REFERENCES

- Aamodt, M. G. and Custer, H. (2006). Who can best catch a liar?: A meta-analysis of individual differences in detecting deception. *The Forensic Examiner*, 15(1), 6-11.
- Alexander, R. (1987). *The biology of moral systems*. New York, NY: Aldine de Gruyter.
- Allen-Arave, W., Gurven, M., and Hill, K. (2008). Reciprocal altruism, rather than kin selection, maintains nepotistic food transfers on an Ache reservation. *Evolution and Human Behavior*, 29(5), 305-318.
- Alpizar, F., Carlsson, F., and Johansson-Stenman, O. (2008). Anonymity, reciprocity, and conformity: Evidence from voluntary contributions to a national park in Costa Rica. *Journal of Public Economics*, 92(5-6), 1047-1060.
- Alvard, M. (2003). Kinship, lineage, and an evolutionary perspective on cooperative hunting groups in Indonesia. *Human Nature*, 14(2), 129-163.
- Alvard, M. and Gillespie, A. (2004). Good Lamalera whale hunters accrue reproductive benefits: Re-evaluating the hunting hypothesis. *Research in Economic Anthropology*, 23, 225-247.
- Anderson, K. G., Kaplan, H., Lam, D., and Lancaster, J. (1999). Paternal care by genetic fathers and stepfathers II: Reports by Xhosa high school students. *Evolution and Human Behavior*, 20(6), 433-451.
- Andreoni, J. (1988). Why free ride?: Strategies and learning in public goods experiments. *Journal of Public Economics*, 37(3), 291-304.

- Andreoni, J. and Croson, R. (2008). Partners versus strangers: The effect of random rematching in public goods experiments. In C. Plott and V. Smith (Eds.), *The handbook of experimental economic results* (pp. 776–783). Amsterdam, The Netherlands: Elsevier.
- Aoki, K. (1983). A quantitative genetic model of reciprocal altruism: A condition for kin or group selection to prevail. *Proceedings of the National Academy of Sciences of the United States of America*, 80(13), 4065-4068.
- Aoki, K. and Nakahashi, W. (2008). Evolution of learning in subdivided populations that occupy environmentally heterogeneous sites. *Theoretical Population Biology*, 74(4), 356-368.
- Aoki, K., Wakano, Joe Y., and Feldman, Marcus W. (2005). The emergence of social learning in a temporally changing environment: A theoretical model. *Current Anthropology*, 46(2), 334-340.
- Apesteguia, J., Huck, S., and Oechssler, J. (2007). Imitation-theory and experimental evidence. *Journal of Economic Theory*, 136(1), 217-235.
- ArcGIS. (2006). ArcGIS version 9.2. Environmental Systems Research Institute, Inc., Redlands, CA.
- Asch, S. E. (1951). Effects of group pressure on the modification and distortion of judgments. In H. Guetzkow (Ed.), *Groups, leadership and men* (pp. 177–190). Pittsburgh, PA: Carnegie.
- Asch, S. E. (1955). Opinions and social pressure. *Scientific American*, 193(5), 31-35.
- Asch, S. E. (1956). Studies of independence and conformity: A minority of one against a unanimous majority. *Psychological Monographs*, 70(9), 1-70.
- Axelrod, R. (1984). *The evolution of cooperation*. New York, NY: Basic Books.
- Axelrod, R. and Hamilton, W. D. (1981). The evolution of cooperation. *Science*, 211(4489), 1390-1396.

- Axelrod, R., Hammond, R. A., and Grafen, A. (2004). Altruism via kin-selection strategies that rely on arbitrary tags with which they coevolve. *Evolution*, 58(8), 1833-1838.
- Bandura, A. (1977). *Social learning theory*. Oxford, England: Prentice-Hall.
- Bardsley, N. (2000). *Control without deception*. Tinbergen Institute Discussion Papers 00-107/1, Tinbergen Institute.
- Bardsley, N. and Sausgruber, R. (2005). Conformity and reciprocity in public good provision. *Journal of Economic Psychology*, 26(5), 664-681.
- Baron, R. S., Vandello, J. A., and Brunsman, B. (1996). The forgotten variable in conformity research: Impact of task importance on social influence. *Journal of Personality & Social Psychology*, 71(5), 915-927.
- Barr, A. (2001). Social dilemmas and shame-based sanctions: Experimental results from rural Zimbabwe. *Center for the Study of African Economies Working Paper*. WPS2001.11.
- Barr, A., Wallace, C., Ensminger, J., Henrich, J., Barrett, C., Bolyanatz, A. et al. (2009). *Homo aequalis: A cross-society experimental analysis of three bargaining games*. Documento CEDE No. 2009-09. Available at SSRN: <http://ssrn.com/abstract=1485862>.
- Bernhard, H., Fischbacher, U., and Fehr, E. (2006). Parochial altruism in humans. *Nature*, 442(7105), 912-915.
- Birkás, B., Bereczkei, T., and Kerekes, Z. (2006). Generosity, reputation, and costly signaling: A preliminary study of altruism toward unfamiliar people. *Journal of Cultural and Evolutionary Psychology*, 4(2), 173-181.
- Blaustein, A. R. (1983). Kin recognition mechanisms: Phenotypic matching or recognition alleles? *The American Naturalist*, 121(5), 749-754.
- Bolton, G. E. and Ockenfels, A. (2000). ERC: A theory of equity, reciprocity, and competition. *The American Economic Review*, 90(1), 166-193.

- Bond, R. and Smith, P. B. (1996). Culture and conformity: A meta-analysis of studies using Asch's (1952b, 1956) line judgement task. *Psychological Bulletin*, 119, 111-137.
- Borenstein, E., Feldman, M. W., Aoki, K., and Wolf, J. (2009). Evolution of learning in fluctuating environments: When selection favors both social and exploratory individual learning. *Evolution*, 62(3), 586-602.
- Bosch-Domènech, A. and Vriend, N. J. (2003). Imitation of successful behaviour in cournot markets. *The Economic Journal*, 113(487), 495-524.
- Bowles, S. and Posel, D. (2005). Genetic relatedness predicts South African migrant workers' remittances to their families. *Nature*, 434(7031), 380-383.
- Boyd, R., Gintis, H., Bowles, S., and Richerson, P. J. (2003). The evolution of altruistic punishment. *Proceedings of the National Academy of Sciences*, 100(6), 3531-3535. doi: 10.1073/pnas.0630443100
- Boyd, R. and Richerson, P. J. (1982). Cultural transmission and the evolution of cooperative behavior. *Human Ecology*, 10(3), 325-351.
- Boyd, R. and Richerson, P. J. (1985). *Culture and the evolutionary process*. Chicago: University of Chicago Press.
- Boyd, R. and Richerson, P. J. (1988a). The evolution of reciprocity in sizable groups. *Journal of Theoretical Biology*, 132(3), 337-356.
- Boyd, R. and Richerson, P. J. (1988b). An evolutionary model of social learning: The effects of spatial and temporal variation. In T. R. Zentall and B. G. Galef (Eds.), *Social learning: Psychological and biological perspectives* (pp. 29-48). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Boyd, R. and Richerson, P. J. (1995). Why does culture increase human adaptability? *Ethology and Sociobiology*, 16(2), 125-143.
- Boyd, R. and Richerson, P. J. (1996). Why culture is common, but cultural evolution is rare. *Proceedings of the British Academy*, 88, 77-93.

- Boyd, R. and Richerson, P. J. (2005). Solving the puzzle of human cooperation. In S. Levinson (Ed.), *Evolution and culture* (pp. 105–132). Cambridge, MA: MIT Press.
- Brandts, J. and Fatás, E. (2001). Social information and social influence in an experimental dilemma game. *LINEES Working Paper 29/00*. University of València.
- Brandts, J. and Schram, A. (2001). Cooperation and noise in public goods experiments: Applying the contribution function approach. *Journal of Public Economics*, 79(2), 399-427.
- Breden, F. (1990). Partitioning of covariance as a method for studying kin selection. *Trends in Ecology & Evolution*, 5(7), 224-228.
- Brewer, M. B. and Schneider, S. K. (1990). Social identity and social dilemmas: A double-edged sword. In D. Abrams and M. A. Hogg (Eds.), *Social identity theory: Constructive and critical advances* (pp. 169-184). London: Harvester Wheatsheaf.
- Brown, J. S., Sanderson, M. J., and Michod, R. E. (1982). Evolution of social behavior by reciprocation. *Journal of Theoretical Biology*, 99(2), 319-339.
- Browne, W. J. (2009). MCMC estimation in MLwiN, v2.13: Centre for Multilevel Modelling, University of Bristol.
- Burnham, K. P. and Anderson, D. R. (1998). *Model selection and inference*. New York, NY: Springer.
- Burnham, K. P. and Anderson, D. R. (2002). *Model selection and multi-model inference: A practical information-theoretic approach. 2nd ed.* New York, NY: Springer-Verlag.
- Burton-Chellew, M. N., Ross-Gillespie, A., and West, S. A. (2010). Cooperation in humans: Competition between groups and proximate emotions. *Evolution and Human Behavior*, 31(2), 104-108.
- Camerer, C. F. (2003). *Behavioral game theory: Experiments in strategic interaction*. Princeton, NJ: Princeton University Press.

- Cameron, L. A. (1999). Raising the stakes in the ultimatum game: Experimental evidence from Indonesia. *Economic Inquiry*, 37, 47-59.
- Cardenas, J. C. and Carpenter, J. P. (2005). *Experiments and economic development: Lessons from field labs in the developing world. Middlebury College working paper series*. Middlebury College, Department of Economics.
- Cardenas, J. C. and Jaramillo, C. R. (2007). Cooperation in large networks. An experimental approach. *Documento CEDE 2007-06 (Edición Electrónica)*. Bogotá, Colombia: Universidad de los Andes.
- Carpenter, J. P. (2004). When in Rome: Conformity and the provision of public goods. *Journal of Socio-Economics*, 33(4), 395-408.
- Carpenter, J. P. (2007). Punishing free-riders: How group size affects mutual monitoring and the provision of public goods. *Games and Economic Behavior*, 60(1), 31-51.
- Cason, T. N. and Mui, V. L. (1998). Social influence in the sequential dictator game. *Journal of Mathematical Psychology*, 42, 248-265.
- Cavalli-Sforza, L. L. and Feldman, M. W. (1981). *Cultural transmission and evolution: a quantitative approach*. Princeton, NJ: Princeton University Press.
- Chagnon, N. A. and Bugos, P. (1979). Kin selection and conflict: An analysis of a Yanomamö ax fight. In N. A. Chagnon and W. Irons (Eds.), *Evolutionary biology and human social behavior: An anthropological perspective*. North Scituate, MA: Duxbury Press.
- Choi, J.K. and Bowles, S. (2007). The coevolution of parochial altruism and war. *Science*, 318(5850), 636-640. doi: 10.1126/science.1144237
- Clark, K. and Sefton, M. (2001). The sequential prisoner's dilemma: Evidence on reciprocation. *The Economic Journal*, 111(468), 51-68.
- Clark, P. J. and Evans, F. C. (1954). Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology*, 35(4), 445-453.

-
- Coultas, J. C. (2004). When in Rome... An evolutionary perspective on conformity. *Group Processes Intergroup Relations*, 7(4), 317-331. doi: 10.1177/1368430204046141
- Croson, R. T. A. (1996). Partners and strangers revisited. *Economics Letters*, 53(1), 25-32.
- Croson, R. T. A. (2007). Theories of commitment, altruism and reciprocity: Evidence from linear public goods games. *Economic Inquiry*, 45(2), 199-216.
- Daly, M. and Wilson, M. (1988a). Evolutionary social psychology and family homicide. *Science*, 242(4878), 519-524.
- Daly, M. and Wilson, M. (1988b). *Homicide*. New York, NY: Aldine de Gruyter.
- Darwin, C. (1859). *The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. 6th ed., with additions and corrections. London: J. Murray.
- Davies, J. (1994). Inactivation of antibiotics and the dissemination of resistance genes. *Science*, 264 375-382.
- Davis, D. D. and Holt, C. (1993). *Experimental economics*. Princeton, N.J: Princeton University Press.
- Dawkins, R. (1976). *The selfish gene*. Oxford: Oxford University Press.
- de Cremer, D. and van Vugt, M. (1999). Social identification effects in social dilemmas: A transformation of motives. *European Journal of Social Psychology*, 29, 871-893.
- DePaulo, B. M. (1994). Spotting lies: Can humans learn to do better? *Current Directions in Psychological Science*, 3(3), 83-86.
- DePaulo, B. M., Stone, J., and Lassiter, D. (1985). Deceiving and detecting deceit. In B. R. Schlenker (Ed.), *The self and social life* (pp. 323-370). New York, NY: McGraw-Hill.
- Doebeli, M., Blarer, A., and Ackermann, M. (1997). Population dynamics, demographic stochasticity, and the evolution of cooperation. *Proceedings of the National Academy of Sciences*, 94, 5167-5171

- Dugatkin, L. A. (2002). Animal cooperation among unrelated individuals. *Naturwissenschaften*, 89(12), 533-541.
- Dugatkin, L. A. (1999). *Cheating monkeys and citizen bees: The nature of cooperation in animals and humans*. New York, NY: The Free Press.
- Efferson, C., Lalive, R., Richerson, P. J., McElreath, R., and Lubell, M. (2008). Conformists and mavericks: The empirics of frequency-dependent cultural transmission. *Evolution and Human Behavior*, 29(1), 56-64.
- Efferson, C. and Richerson, P. J. (2007). A prolegomenon to nonlinear empiricism in the human behavioral sciences. *Biology and Philosophy*, 22(1), 1-33.
- Efferson, C., Richerson, P. J., McElreath, R., Lubell, M., Edsten, E., Waring, T. M., Paciotti, B., Baum, W. (2007). Learning, productivity, and noise: An experimental study of cultural transmission on the Bolivian Altiplano. *Evolution and Human Behavior*, 28(1), 11-17.
- Egas, M. and Riedl, A. (2008). The economics of altruistic punishment and the maintenance of cooperation. *Proceedings of the Royal Society B: Biological Sciences*, 275, 871-878. doi: 10.1098/rspb.2007.1558
- Ekman, P. and O'Sullivan, M. (1991). Who can catch a liar? *American Psychologist*, 46(9), 913-920.
- Ellison, A. M. (1996). An introduction to bayesian inference for ecological research and environmental decision-making. *Ecological Applications*, 6, 1036-1046.
- Ellison, G. and Fudenberg, D. (1993). Rules of thumb for social learning. *Journal of Political Economy*, 101(4), 612-643. doi: 10.1086/261890
- Ellison, G. and Fudenberg, D. (1995). Word-of-mouth communication and social learning. *The Quarterly Journal of Economics*, 110(1), 93-125.
- Enquist, M., Eriksson, K., and Ghirlanda, S. (2007). Critical social learning: A solution to Rogers's paradox of nonadaptive culture. *American Anthropologist*, 109(4), 727-734.

- Eriksson, K. and Coultas, J. (2009). Are people really conformist-biased? An empirical test and a new mathematical model. *Journal of Evolutionary Psychology*, 7(1), 5-21.
- Eriksson, K., Enquist, M., and Ghirlanda, S. (2007). Critical points in current theory of conformist social learning. *Journal of Evolutionary Psychology*, 5(1), 67-87.
- Etzioni, A. (1986). The case for a multiple utility conception. *Economics and Philosophy*, 2, 159–183.
- Falk, A., Fischbacher, U., and Gächter, S. (2003). *Living in two neighborhoods: Social interactions in the lab. IEW working paper no. 150. Institute of Empirical Research in Economics*. University of Zurich.
- Fehr, E. and Fischbacher, U. (2003). The nature of human altruism. *Nature*, 425, 785-791.
- Fehr, E. and Gächter, S. (2000). Cooperation and punishment in public goods experiments. *The American Economic Review*, 90(4), 980-994.
- Fehr, E. and Gächter, S. (2002). Altruistic punishment in humans. *Nature*, 415(6868), 137-140.
- Fehr, E. and Gächter, S. (1998). Reciprocity and economics: The economic implications of *Homo reciprocans*. *European Economic Review*, 42(3-5), 845-859.
- Fehr, E. and Schmidt, K. M. (1999). A theory of fairness, competition, and cooperation. *Quarterly Journal of Economics*, 114(3), 817-868. doi: 10.1162/003355399556151
- Feldman, M. W., Aoki, K., and Kumm, J. (1996). Individual versus social learning: Evolutionary analysis in a fluctuating environment. *Anthropological Science*, 104, 209-232.
- Festinger, L. (1954). A theory of social comparison processes. *Human Relations*, 7(2), 117-140.
- Fetchenhauer, D., Grootuis, T., and Pradel, J. (2010). Not only states but traits - humans can identify permanent altruistic dispositions in 20 s. *Evolution and Human Behavior*, 31(2), 80-86

- Fischbacher, U. and Gächter, S. (2010). Social preferences, beliefs, and the dynamics of free riding in public goods experiments. *The American Economic Review*, 100, 541-556.
- Fischbacher, U., Gächter, S., and Fehr, E. (2001). Are people conditionally cooperative? Evidence from a public goods experiment. *Economics Letters*, 71(3), 397-404.
- Fletcher, J. A. and Doebeli, M. (2009). A simple and general explanation for the evolution of altruism. *Proceedings of the Royal Society B: Biological Sciences*, 276(1654), 13-19.
- Fletcher, J. A. and Zwick, M. (2006). Unifying the theories of inclusive fitness and reciprocal altruism. *The American Naturalist*, 168(2), 252-262.
- Fletcher, J. A. and Zwick, M. (2007). The evolution of altruism: Game theory in multilevel selection and inclusive fitness. *Journal of Theoretical Biology*, 245(1), 26-36.
- Flinn, M. V. (1988). Step- and genetic parent/offspring relationships in a Caribbean village. *Ethology and Sociobiology*, 9(6), 335-369.
- Frank, S. A. (1998). *Foundations of social evolution*. Princeton, NJ: Princeton University Press.
- Frey, B. S. and Meier, S. (2004). Social comparisons and pro-social behavior: Testing "Conditional cooperation" in a field experiment. *The American Economic Review*, 94(5), 1717-1722.
- Gächter, S. (2007). Conditional cooperation: Behavioral regularities from the lab and the field and their policy implications. In B. S. Frey and A. Stutzer (Eds.), *Psychology and economics: A promising new cross-disciplinary field* (pp. 19-50). Cambridge, MA: MIT Press.
- Gächter, S. and Falk, A. (2002). Reputation and reciprocity: Consequences for the labour relation. *Scandinavian Journal of Economics*, 104(1), 1-26.
- Gächter, S. and Herrmann, B. (in press). The limits of self-governance when cooperators get punished: Experimental evidence from urban and rural Russia. *European Economic Review*. doi: 10.1016/j.eurocorev.2010.04.003

- Gächter, S. and Herrmann, B. (2009). Reciprocity, culture and human cooperation: Previous insights and a new cross-cultural experiment. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1518), 791-806. doi: 10.1098/rstb.2008.0275
- Gächter, S., Herrmann, B., and Thöni, C. (2004). Trust, voluntary cooperation, and socio-economic background: Survey and experimental evidence. *Journal of Economic Behavior & Organization*, 55(4), 505-531.
- Gächter, S., Renner, E., and Sefton, M. (2008). The long-run benefits of punishment. *Science*, 322(5907), 1510. doi: 10.1126/science.1164744
- Gardner, A. and West, S. A. (2006). Demography, altruism, and the benefits of budding. *Journal of Evolutionary Biology*, 19(5), 1707-1716. doi: 10.1111/j.1420-9101.2006.01104.x
- Gelman, A. and Hill, J. (2007). *Data analysis using regression and multilevel/hierarchical models*. Cambridge: Cambridge University Press.
- Gintis, H. (2003). The hitchhiker's guide to altruism: Gene-culture coevolution, and the internalization of norms. *Journal of Theoretical Biology*, 220(4), 407-418.
- Gintis, H. (2007). A framework for the unification of the behavioral sciences. *Behavioral and Brain Sciences*, 30(01), 1-16. doi: 10.1017/S0140525X07000581
- Gintis, H., Smith, E.A., Bowles, S. (2001). Costly signalling and cooperation. *Journal of Theoretical Biology*, 213(1), 103-119.
- Goeree, J. K., Holt, C. A., and Laury, S. K. (2002). Private costs and public benefits: Unraveling the effects of altruism and noisy behavior. *Journal of Public Economics*, 83(2), 255-276.
- Grafen, A. (1984). Natural selection, kin selection and group selection. In J. R. Krebs and N. B. Davies (Eds.), *Behavioural ecology. An evolutionary approach* (pp. 62–84). Oxford: Blackwell Scientific Publications.

- Grafen, A. (1985). A geometric view of relatedness. *Oxford Surveys in Evolutionary Biology*, 2, 28-89.
- Grafen, A. (2006). Optimization of inclusive fitness. *Journal of Theoretical Biology*, 238(3), 541-563.
- Grafen, A. (2007). Detecting kin selection at work using inclusive fitness. *Proceedings of the Royal Society B: Biological Sciences*, 274(1610), 713-719.
- Grafen, A. (2009). Formalizing Darwinism and inclusive fitness theory. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364(1533), 3135-3141.
- Granovetter, M. (2005). The impact of social structure on economic outcomes. *The Journal of Economic Perspectives*, 19(1), 33-50.
- Gurerk, O., Irlenbusch, B., and Rockenbach, B. (2006). The competitive advantage of sanctioning institutions. *Science*, 312(5770), 108-111. doi: 10.1126/science.1123633
- Gurven, M. (2004a). Economic games among the Amazonian Tsimane: Exploring the roles of market access, costs of giving, and cooperation on pro-social game behavior. *Experimental Economics*, 7(1), 5-24.
- Gurven, M. (2004b). Reciprocal altruism and food sharing decisions among Hiwi and Ache hunter-gatherers. *Behavioral Ecology and Sociobiology*, 56(4), 366-380.
- Gurven, M. (2004c). To give and to give not: The behavioral ecology of human food transfers. *Behavioral and Brain Sciences*, 27(04), 543-559
- Gurven, M., Allen-Arave, W., Hill, K., and Hurtado, M. (2000a). "It's a wonderful life": Signaling generosity among the Ache of Paraguay. *Evolution and Human Behavior*, 21(4), 263-282.
- Gurven, M., Hill, K., and Kaplan, H. (2002). From forest to reservation: Transitions in food-sharing behavior among the Ache of Paraguay. *Journal of Anthropological Research*, 58(1), 93-120.

- Gurven, M., Hill, K., Kaplan, H., Hurtado, A., and Lyles, R. (2000b). Food transfers among Hiwi foragers of Venezuela: Tests of reciprocity. *Human Ecology*, 28(2), 171-218.
- Gurven, M., Zanolini, A., and Schniter, E. (2008). Culture sometimes matters: Intra-cultural variation in pro-social behavior among Tsimane Amerindians. *Journal of Economic Behavior & Organization*, 67(3-4), 587-607.
- Güth, W., Schmittberger, R., and Schwarze, B. (1982). An experimental analysis of ultimatum bargaining. *Journal of Economic Behavior & Organization*, 3(4), 367-388.
- Guzmán, R. A., Rodríguez-Sickert, C., and Rowthorn, R. (2007). When in Rome, do as the Romans do: The coevolution of altruistic punishment, conformist learning, and cooperation. *Evolution and Human Behaviour*, 28, 112-117.
- Haig, D. (1997). The social gene. In J. R. Krebs and N. B. Davies (Eds.), *Behavioural ecology, fourth edition* (pp. 284-304). Oxford: Blackwell Scientific.
- Hamilton, W. D. (1964a). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, 7(1), 1-16.
- Hamilton, W. D. (1964b). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*, 7(1), 17-52.
- Hamilton, W. D. (1975). Innate social aptitudes in man: An approach from evolutionary genetics. In R. Fox (Ed.), *Biosocial anthropology*. New York, NY: John Wiley & Sons.
- Hardin, G. (1968). The tragedy of the commons. *Science*, 162(3859), 1243-1248. doi: 10.1126/science.162.3859.1243
- Hawkes, K. and Bird, R. B. (2002). Showing off, handicap signaling, and the evolution of men's work. *Evolutionary Anthropology: Issues, News, and Reviews*, 11(2), 58-67.
- Hedeker, D. (2003). A mixed-effects multinomial logistic regression model. *Statistics in Medicine*, 22, 1433-1446.
- Henrich, J. (2004). Cultural group selection, coevolutionary processes and large-scale cooperation. *Journal of Economic Behavior & Organization*, 53(1), 3-35.

- Henrich, J. and Boyd, R. (1998). The evolution of conformist transmission and the emergence of between-group differences. *Evolution and Human Behavior*, 19(4), 215-241.
- Henrich, J. and Boyd, R. (2001). Why people punish defectors: Weak conformist transmission can stabilize costly enforcement of norms in cooperative dilemmas. *Journal of Theoretical Biology*, 208(1), 79-89.
- Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., and Gintis, H. (2004). *Foundations of human sociality: Economic experiments and ethnographic evidence from fifteen small-scale societies*. Oxford: Oxford University Press.
- Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., McElreath, R. (2001). In search of *Homo economicus*: Behavioral experiments in 15 small-scale societies. *The American Economic Review*, 91(2), 73-78.
- Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., McElreath, R., Alvard, M., Barr, A., Ensminger, J., Henrich, N. S., Hill, K., Gil-White, F., Gurven, M., Marlowe, F. W., Patton, J. Q., Tracer, D. (2005). In cross-cultural perspective: Behavioral experiments in 15 small-scale societies. *Behavioral and Brain Sciences*, 28(06), 795-815. doi: 10.1017/S0140525X05000142
- Henrich, J., Ensminger, J., McElreath, R., Barr, A., Barrett, C., Bolyanatz, A., Cardenas, J. C., Gurven, M., Gwako, E., Henrich, N. S., Lesorogol, C., Marlowe, F. W., Tracer, D., Ziker, J. (2010). Markets, religion, community size, and the evolution of fairness and punishment. *Science*, 327(5972), 1480-1484.
- Henrich, J. and Gil-White, F. J. (2001). The evolution of prestige: Freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior*, 22(3), 165-196.
- Henrich, J. and McElreath, R. (2003). The evolution of cultural evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, 12(3), 123-135.

- Henrich, J., McElreath, R., Barr, A., Ensminger, J., Barrett, C., Bolyanatz, A., Cardenas, J. C., Gurven, M., Gwako, E., Henrich, N. S., Lesorogol, C., Marlowe, F. W., Tracer, D., Ziker, J. (2006). Costly punishment across human societies. *Science*, 312(5781), 1767-1770. doi: 10.1126/science.1127333
- Herrmann, B., Thoni, C., and Gächter, S. (2008). Antisocial punishment across societies. *Science*, 319(5868), 1362-1367. doi: 10.1126/science.1153808
- Hill Korwa Development Agency Report. (2003). Ambikapur, Chhattisgarh.
- Holmes, W. G. and Sherman, P. W. (1982). The ontogeny of kin recognition in two species of ground squirrels. *Integrative and Comparative Biology*, 22(3), 491-517.
- Hoppitt, W. J. E., Brown, G. R., Kendal, R., Rendell, L., Thornton, A., Webster, M. M., Laland, K. N. (2008). Lessons from animal teaching. *Trends in Ecology & Evolution*, 23(9), 486-493.
- Hornstein, H. A., Fisch, E., and Holmes, M. (1968). Influence of a model's feeling about his behavior and his relevance as a comparison other on observers' helping behaviour. *Journal of Personality and Social Psychology*, 10, 222-226.
- Indian Census report. (1991).
- Irwin, A. J. and Taylor, P. D. (2001). Evolution of altruism in stepping-stone populations with overlapping generations. *Theoretical Population Biology*, 60(4), 315-325.
- Isaac, R. M. and Walker, J. M. (1988). Group size effects in public goods provision: The voluntary contributions mechanism. *The Quarterly Journal of Economics*, 103(1), 179-199.
- Isaac, R. M., Walker, J. M., and Williams, A. W. (1994). Group size and the voluntary provision of public goods: Experimental evidence utilizing large groups. *Journal of Public Economics*, 54(1), 1-36.
- Jacobs, R. C. and Campbell, D. T. (1961). The perpetuation of an arbitrary tradition through several generations of a laboratory microculture. *Journal of Abnormal and Social Psychology*, 62, 649-658.

-
- Jansen, V. A. A. and van Baalen, M. (2006). Altruism through beard chromodynamics. *Nature*, 440(7084), 663-666.
- Jaramillo, C. R. (2004). *The role of networks in collective action with costly communication*. Documentos CEDE 2005-34.
- Kagel, J. H. and Roth, A. E. (Eds.). (1995). *The handbook of experimental economics*. Princeton: Princeton University Press.
- Kameda, T. and Nakanishi, D. (2003). Does social/cultural learning increase human adaptability?: Rogers's question revisited. *Evolution and Human Behavior*, 24(4), 242-260.
- Kaplan, H. and Hill, K. (1985). Food sharing among Ache foragers: Tests of explanatory hypotheses. *Current Anthropology*, 26(2), 223.
- Karp, D., Jin, N., Yamagishi, T., and Shinotsuka, H. (1993). Raising the minimum in the minimal group paradigm. *Japanese Journal of Experimental Social Psychology*, 32(3), 231-240.
- Keller, L. and Ross, K. G. (1998). Selfish genes: A green beard in the red fire ant. *Nature*, 394(6693), 573-575.
- Kendal, J., Giraldeau, L.-A., and Laland, K. (2009). The evolution of social learning rules: Payoff-biased and frequency-dependent biased transmission. *Journal of Theoretical Biology*, 260(2), 210-219.
- Kerr, B., Godfrey-Smith, P., and Feldman, M. W. (2004). What is altruism? *Trends in Ecology & Evolution*, 19(3), 135-140.
- Knack, S. (2001). Trust, associational life and economic performance. Paper presented at the OECD/HRDC conference Quebec, March 19–21, 2000, HDRC, Ottawa.
- Kocher, M. G., Martinsson, P. and Visser, M. (2008). Does stake size matter for cooperation and punishment? *Economics Letters*, 99, 508-511.

- Kollock, P. (2003). Social dilemmas: The anatomy of cooperation. *Annual Review of Sociology*, 24(1), 183-214.
- Kümmerli, R., Gardner, A., West, S. A., and Griffin, A. S. (2009). Limited dispersal, budding dispersal, and cooperation: An experimental study. *Evolution*, 63(4), 939-949.
- Lacy, R. C. and Sherman, P. W. (1983). Kin recognition by phenotype matching. *The American Naturalist*, 121(4), 489-512.
- Laland, K. (2004). Social learning strategies. *Learning & Behavior*, 32, 4-14.
- Laland, K. N. (2008). Animal cultures. *Current Biology*, 18(9), R366-R370.
- Laland, K. N. and Janik, V. M. (2006). The animal cultures debate. *Trends in Ecology & Evolution*, 21(10), 542-547.
- Lamba, S. and Mace, R. (2010). People recognise when they are really anonymous in an economic game. *Evolution and Human Behavior*, 31(4), 271-278.
- Ledyard, J. O. (1995). Public goods: A survey of experimental research. In J. H. Kagel and A. E. Roth (Eds.), *The handbook of experimental economics* (pp. 111-181). Princeton, NJ: Princeton University Press.
- Lehmann, L., Feldman, M. W., and Foster, K. R. (2008). Cultural transmission can inhibit the evolution of altruistic helping. *The American Naturalist*, 172(1), 12-24. doi: 10.1086/587851
- Lehmann, L. and Keller, L. (2006). The evolution of cooperation and altruism - a general framework and a classification of models. *Journal of Evolutionary Biology*, 19(5), 1365-1376.
- Lehmann, L. and Perrin, N. (2002). Altruism, dispersal, and phenotype-matching kin recognition. *The American Naturalist*, 159(5), 451-468.
- Leimar, O. and Hammerstein, P. (2001). Evolution of cooperation through indirect reciprocity. *Proceedings of the Royal Society B: Biological Sciences*, 268(1468), 745-753.

- Li, C. C. (1967). Fundamental theorem of natural selection. *Nature*, 214(5087), 505-506.
- Lieberman, E., Hauert, C., and Nowak, M. A. (2005). Evolutionary dynamics on graphs. *Nature*, 433(7023), 312-316.
- List, J. A. (2004). Young, selfish and male: Field evidence of social preferences. *The Economic Journal*, 114(492), 121-149.
- Loewenstein, G. (1999). Experimental economics from the vantage-point of behavioural economics. *The Economic Journal*, 109(453), F25-F34.
- Lotem, A., Fishman, M. A., and Stone, L. (1999). Evolution of cooperation between individuals. *Nature*, 400, 226-227.
- Macfarlan, S. and Quinlan, R. (2008). Kinship, family, and gender effects in the ultimatum game. *Human Nature*, 19, 294-309.
- Madsen, E. A., Tunney, R. J., Fieldman, G., Plotkin, H. C., Dunbar, R. I. M., Richardson, J.-M., McFarland, D. (2007). Kinship and altruism: A cross-cultural experimental study. *British Journal of Psychology*, 98, 339-359.
- Marlowe, F. W. (1999). Male care and mating effort among Hadza foragers. *Behavioral Ecology and Sociobiology*, 46(1), 57-64.
- Marlowe, F. W. (2004). Dictators and ultimatums in an egalitarian society of hunter-gatherers - the Hadza of Tanzania. In J. Henrich, R. Boyd, S. Bowles, C. Camerer, E. Fehr and H. Gintis (Eds.), *Foundations of human sociality: Economic experiments and ethnographic evidence from fifteen small-scale societies*. Oxford: Oxford University Press.
- Marlowe, F. (2010). *The Hadza: Hunter-gatherers of Tanzania (Origins of human behavior and culture)* Berkeley, CA: University of California Press.
- Marlowe, F. W., Berbesque, J. C., Barr, A., Barrett, C., Bolyanatz, A., Cardenas, J. C., Ensminger, J., Gurven, M., Gwako, E., Henrich, J., Henrich, N. S., Lesorogol, C., McElreath, R., Tracer, D. (2008). More 'altruistic' punishment in larger societies.

-
- Proceedings of the Royal Society B: Biological Sciences*, 275(1634), 587-592. doi: 10.1098/rspb.2007.1517
- Marwell, G. and Ames, R. E. (1979). Experiments on the provision of public goods. I. Resources, interest, group size, and the free-rider problem. *American Journal of Sociology*, 84(6), 1335. doi: 10.1086/226937
- Maynard Smith, J. (1964). Group selection and kin selection. *Nature*, 201(4924), 1145-1147.
- Mayr, E. (1997). The objects of selection. *Proceedings of the National Academy of Sciences of the United States of America*, 94(6), 2091-2094.
- McAndrew, F. T. (2002). New evolutionary perspectives on altruism: Multilevel-selection and costly-signaling theories. *Current Directions in Psychological Science*, 11(2), 79-82.
- McElreath, R. (2004a). Community structure, mobility, and the strength of norms in an African society: The Sangu of Tanzania. In J. Henrich, R. Boyd, S. Bowles, C. Camerer, E. Fehr and H. Gintis (Eds.), *Foundations of human sociality: Economic experiments and ethnographic evidence from fifteen small-scale societies* (pp. 335-355). Oxford: Oxford University Press.
- McElreath, R. (2004b). Social learning and the maintenance of cultural variation: An evolutionary model and data from East Africa. *American Anthropologist*, 106(2), 308-321.
- McElreath, R., Bell, A. V., Efferson, C., Lubell, M., Richerson, P. J., and Waring, T. (2008). Beyond existence and aiming outside the laboratory: Estimating frequency-dependent and pay-off-biased social learning strategies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363(1509), 3515-3528. doi: 10.1098/rstb.2008.0131
- McElreath, R., Lubell, M., Richerson, P. J., Waring, T. M., Baum, W., Edsten, E., Efferson, C., Paciotti, B. (2005). Applying evolutionary models to the laboratory study of social learning. *Evolution and Human Behavior*, 26(6), 483-508.

- Mesoudi, A. (2008). An experimental simulation of the "copy-successful-individuals" cultural learning strategy: Adaptive landscapes, producer-scrouter dynamics, and informational access costs. *Evolution and Human Behavior*, 29(5), 350-363.
- Mesoudi, A. (2009). How cultural evolutionary theory can inform social psychology and vice versa. *Psychological Review*, 116(4), 929-952.
- Mesoudi, A. and O'Brien, M. J. (2008). The cultural transmission of great basin projectile-point technology I: An experimental simulation. *American Antiquity*, 73(1), 3-28.
- Michod, R. E. and Hamilton, W. D. (1980). Coefficients of relatedness in sociobiology. *Nature*, 288(5792), 694-697.
- Microsoft Corporation. (2003). Microsoft Office Excel 2003 (version 11). Redmond, WA.
- Milinski, M., Semmann, D., Bakker, T. C. M., and Krambeck, H.-J. (2001). Cooperation through indirect reciprocity: Image scoring or standing strategy? *Proceedings of the Royal Society B: Biological Sciences*, 268(1484), 2495-2501.
- Milinski, M., Semmann, D., and Krambeck, H.-J. (2002a). Donors to charity gain in both indirect reciprocity and political reputation. *Proceedings of the Royal Society B: Biological Sciences*, 269(1494), 881-883.
- Milinski, M., Semmann, D., and Krambeck, H.-J. (2002b). Reputation helps solve the 'tragedy of the commons'. *Nature*, 415(6870), 424-426.
- Miller, G. F. (2007). Sexual selection for moral virtues. *The Quarterly Review of Biology*, 82(2), 97-125.
- Mitteldorf, J. and Wilson, D. S. (2000). Population viscosity and the evolution of altruism. *Journal of Theoretical Biology*, 204(4), 481-496.
- Mohtashemi, M. and Mui, L. (2003). Evolution of indirect reciprocity by social information: The role of trust and reputation in evolution of altruism. *Journal of Theoretical Biology*, 223, 523-531.

- Morgan, C. J. (1979). Eskimo hunting groups, social kinship, and the possibility of kin selection in humans. *Ethology and Sociobiology*, 1(1), 83-86.
- Nakahashi, W. (2007). The evolution of conformist transmission in social learning when the environment changes periodically. *Theoretical Population Biology*, 72(1), 52-66.
- Neu, H. C. (1992). The crisis in antibiotic resistance. *Science*, 257, 1064-1073.
- Nowak, M. A., Bonhoeffer, S., and May, R. M. (1994). Spatial games and the maintenance of cooperation. *Proceedings of the National Academy of Sciences of the United States of America*, 91(11), 4877-4881.
- Nowak, M. A. and May, R. M. (1992). Evolutionary games and spatial chaos. *Nature*, 359(6398), 826-829.
- Nowak, M. A. and Sigmund, K. (1998a). The dynamics of indirect reciprocity. *Journal of Theoretical Biology*, 194, 561-574.
- Nowak, M. A. and Sigmund, K. (1998b). Evolution of indirect reciprocity by image scoring. *Nature*, 393(6685), 573-577.
- Ochman, H., Lawrence, J. G., and Groisman, E. A. (2000). Lateral gene transfer and the nature of bacterial innovation. *Nature*, 405, 299-304.
- Odling-Smee, F. J., Laland, K. N., and Feldman, M. F. (2003). *Niche construction: The neglected process in evolution*. Monographs in Population Biology, 37. New Jersey: Princeton University Press.
- Offerman, T., Potters, J., and Sonnemans, J. (2002). Imitation and belief learning in an oligopoly experiment. *The Review of Economic Studies*, 69(4), 973-997.
- Offerman, T. and Sonnemans, J. (1998). Learning by experience and learning by imitating successful others. *Journal of Economic Behavior & Organization*, 34(4), 559-575.
- Ohtsuki, H., Hauert, C., Lieberman, E., and Nowak, M. A. (2006). A simple rule for the evolution of cooperation on graphs and social networks. *Nature*, 441(7092), 502-505.

-
- Oosterbeek, H., Sloof, R., and van de Kuilen, G. (2004). Cultural differences in ultimatum game experiments: Evidence from a meta-analysis. *Experimental Economics*, 7(2), 171-188.
- Orlove, M. J. and Wood, C. L. (1978). Coefficients of relationship and coefficients of relatedness in kin selection: A covariance form for the rho formula. *Journal of Theoretical Biology*, 73(4), 679-686.
- Ostrom, E., Walker, J., and Gardner, R. (1992). Covenants with and without a sword: Self-governance is possible. *The American Political Science Review*, 86(2), 404-417.
- Panchanathan, K. and Boyd, R. (2003). A tale of two defectors: The importance of standing for evolution of indirect reciprocity. *Journal of Theoretical Biology*, 224(1), 115-126.
- Panchanathan, K. and Boyd, R. (2004). Indirect reciprocity can stabilize cooperation without the second-order free rider problem. *Nature*, 432(7016), 499-502.
- Pradel, J., Euler, H. A., and Fetchenhauer, D. (2009). Spotting altruistic dictator game players and mingling with them: The elective assortment of classmates. *Evolution and Human Behavior*, 30(2), 103-113.
- Price, G. R. (1970). Selection and covariance. *Nature*, 227(5257), 520-521.
- Price, G. R. (1972). Extension of covariance selection mathematics. *Annals of Human Genetics*, 35(4), 485-490.
- Puurttinen, M. and Mappes, T. (2009). Between-group competition and human cooperation. *Proceedings of the Royal Society B: Biological Sciences*, 276(1655), 355-360. doi: 10.1098/rspb.2008.1060
- Queller, D. C. (1985). Kinship, reciprocity and synergism in the evolution of social behaviour. *Nature*, 318(6044), 366-367.
- Queller, D. C. (1992). A general model for kin selection. *Evolution*, 46(2), 376-380.

- Queller, D. C., Ponte, E., Bozzaro, S., and Strassmann, J. E. (2003). Single-gene greenbeard effects in the social amoeba *Dictyostelium discoideum*. *Science*, 299(5603), 105-106.
- Rasbash, J., Steele, F., Browne, W. J., and Goldstein, H. (2009a). A user's guide to MLwiN, v2.10. Centre for Multilevel Modelling, University of Bristol.
- Reeve, H. K. (1989). The evolution of conspecific acceptance thresholds. *The American Naturalist*, 133(3), 407.
- Rendell, L., Fogarty, L., and Laland, K. N. (2009). Rogers' paradox recast and resolved: Population structure and the evolution of social learning strategies *Evolution*, 64(2), 534-548.
- Richerson, P. J. and Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution*. Chicago: University of Chicago Press.
- Riolo, R. L., Cohen, M. D., and Axelrod, R. (2001). Evolution of cooperation without reciprocity. *Nature*, 414(6862), 441-443.
- Rizvi, B. R. (1989). *Hill Korwas of Chhattisgarh*. New Delhi: Gian Publishing House
- Roberts, G. (1998). Competitive altruism: From reciprocity to the handicap principle. *Proceedings of the Royal Society B: Biological Sciences*, 265(1394), 427-431.
- Robertson, A. (1966). A mathematical model of the culling process in dairy cattle. *Animal Production*, 8, 95-108.
- Rockenbach, B. and Milinski, M. (2006). The efficient interaction of indirect reciprocity and costly punishment. *Nature*, 444(7120), 718-723.
- Rogers, A. R. (1988). Does biology constrain culture? *American Anthropologist*, 90(4), 819-831.
- Roth, A. E. (1995a). Bargaining experiments. In J. Kagel and A. E. Roth (Eds.), *The handbook of experimental economics* (pp. 253-348). Princeton, NJ: Princeton University Press.

- Roth, A. E. (1995b). Introduction to experimental economics. In J. H. Kagel and A. E. Roth (Eds.), *The handbook of experimental economics* (pp. 3-109). Princeton, NJ: Princeton University Press.
- Roth, A. E., Prasnikar, V., Okuno-Fujiwara, M., and Zamir, S. (1991). Bargaining and market behavior in Jerusalem, Ljubljana, Pittsburgh, and Tokyo: An experimental study. *The American Economic Review*, 81(5), 1068-1095.
- Rowthorn, R. E., Guzmán, R. A., and Rodríguez-Sickert, C. (2009). Working paper: Theories of the evolution of cooperative behaviour: A critical survey plus some new results. *Working paper (MPRA Paper No. 12574)*. Faculty of Economics, University of Cambridge; Escuela de Administración, Pontificia Universidad Católica de Chile.
- Sally, D. (1995). Conversation and cooperation in social dilemmas: A meta-analysis of experiments from 1958 to 1992. *Rationality and Society*, 7(1), 58-92. doi: 10.1177/1043463195007001004
- Salyers, A. A. and Amabile-Cuevas, C. F. (1997). Why are antibiotic resistance genes so resistant to elimination? *Antimicrobial Agents and Chemotherapy*, 41, 2321-2325.
- Samuelson, C. D. and Messick, D. M. (1986). Alternative structural solutions to resource dilemmas. *Organizational Behavior and Human Decision Processes*, 37(1), 139-155.
- Santos, F. C. and Pacheco, J. M. (2005). Scale-free networks provide a unifying framework for the emergence of cooperation. *Physical Review Letters*, 95(9), 098104.
- Santos, F. C., Rodrigues, J. F., and Pacheco, J. M. (2006). Graph topology plays a determinant role in the evolution of cooperation. *Proceedings of the Royal Society B: Biological Sciences*, 273(1582), 51-55. doi: 10.1098/rspb.2005.3272
- Schlag, K. H. (1998). Why imitate, and if so, how?: A boundedly rational approach to multi-armed bandits. *Journal of Economic Theory*, 78(1), 130-156.
- Schlag, K. H. (1999). Which one should I imitate? *Journal of Mathematical Economics*, 31(4), 493-522.

- Schroeder, D. A., Jensen, T. D., Reed, A. J., Sullivan, D. K., and Schwab, M. (1983). The actions of others as determinants of behavior in social trap situations. *Journal of Experimental Social Psychology*, 19(6), 522-539.
- Seeger, J. (1981). Kinship and covariance. *Journal of Theoretical Biology*, 91(1), 191-213.
- Seinen, I. and Schram, A. (2006). Social status and group norms: Indirect reciprocity in a repeated helping experiment. *European Economic Review*, 50(3), 581-602.
- Selten, R. and Apesteguia, J. (2005). Experimentally observed imitation and cooperation in price competition on the circle. *Games and Economic Behavior*, 51(1), 171-192.
- Sharma, S. (2007). *Hill Korwas: Biology & behaviour*. Delhi: Academic Excellence.
- Sherif, M. (1936). *The psychology of social norms*. New York, NY: Harper and Brothers.
- Sherman, P. W., Reeve, H. K., and Pfennig, D. W. (1997). Recognition systems. In J. R. Krebs and N. B. Davies (Eds.), *Behavioural ecology*, 4th edn. (pp. 69–96). Oxford: Blackwell.
- Smith, J. M. and Bell, P. A. (1994). Conformity as a determinant of behavior in a resource dilemma. *Journal of Social Psychology*, 134(2), 191-200.
- Snijders, T. A. B. and Bosker, R. J. (1999). *Multilevel analysis: An introduction to basic and advanced multilevel modeling*. London: Sage Publications.
- Sosis, R. (2000). Costly signaling and torch fishing on Ifaluk atoll. *Evolution and Human Behavior*, 21(4), 223-244.
- Spiegelhalter, D. J., Best, N. G., Carlin, B. P., and van der Linde, A. (2002). Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society. Series B (Statistical Methodology)*, 64(4), 583-639.
- SPSS Inc. (2008). SPSS 16.0.2 for Windows. Chicago, IL.
- Srivastava, V. K. (2007). *The Pahari Korwas. Socio-economic condition and their development*. New Delhi: Sonali Publications.

- Summers, K. and Crespi, B. (2005). Cadherins in maternal-foetal interactions: Red queen with a green beard? *Proceedings of the Royal Society B: Biological Sciences*, 272(1563), 643-649.
- Tajfel, H., Billig, M. G., Bundy, R. P., and Flament, C. (1971). Social categorization and intergroup behaviour. *European Journal of Social Psychology*, 1(2), 149-178.
- Taylor, P. D., Day, T., and Wild, G. (2007). Evolution of cooperation in a finite homogeneous graph. *Nature*, 447(7143), 469-472.
- Taylor, P. D. and Irwin, A. J. (2000). Overlapping generations can promote altruistic behavior. *Evolution*, 54(4), 1135-1141.
- Traulsen, A. and Nowak, M. A. (2006). Evolution of cooperation by multilevel selection. *Proceedings of the National Academy of Sciences*, 103(29), 10952-10955. doi: 10.1073/pnas.0602530103
- Trivers, R. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology*, 46, 35-57.
- UN FAO report. (1998). <http://www.fao.org/docrep/007/ae393e/ae393e00.htm>.
- Vega-Redondo, F. (1997). The evolution of Walrasian behavior. *Econometrica*, 65(2), 375-384.
- Velez, M. A., Stranlund, J. K., and Murphy, J. J. (2009). What motivates common pool resource users? Experimental evidence from the field. *Journal of Economic Behavior & Organization*, 70(3), 485-497.
- Verplaetse, J., Vanneste, S., and Braeckman, J. (2007). You can judge a book by its cover: The sequel.: A kernel of truth in predictive cheating detection. *Evolution and Human Behavior*, 28(4), 260-271.
- Wade, M. J. (1978). Kin selection: A classical approach and a general solution. *Proceedings of the National Academy of Sciences of the United States of America*, 75(12), 6154-6158.

- Wade, M. J. (1980). Kin selection: Its components. *Science*, 210(4470), 665-667.
- Wade, M. J. (1985). Soft selection, hard selection, kin selection, and group selection. *The American Naturalist*, 125(1), 61-73.
- Wakano, J. Y. and Aoki, K. (2006). A mixed strategy model for the emergence and intensification of social learning in a periodically changing natural environment. *Theoretical Population Biology*, 70(4), 486-497.
- Wakano, J. Y. and Aoki, K. (2007). Do social learning and conformist bias coevolve? Henrich and Boyd revisited. *Theoretical Population Biology*, 72(4), 504-512.
- Wakano, J. Y., Aoki, K., and Feldman, M. W. (2004). Evolution of social learning: A mathematical analysis. *Theoretical Population Biology*, 66(3), 249-258.
- Walker, J. M. and Halloran, M. A. (2004). Rewards and sanctions and the provision of public goods in one-shot settings. *Experimental Economics*, 7(3), 235-247.
- Wedekind, C. and Braithwaite, V. A. (2002). The long-term benefits of human generosity in indirect reciprocity. *Current Biology*, 12(12), 1012-1015.
- Wedekind, C. and Milinski, M. (2000). Cooperation through image scoring in humans. *Science*, 288(5467), 850-852.
- Weimann, J. (1994). Individual behaviour in a free riding experiment. *Journal of Public Economics*, 54(2), 185-200.
- West, S. A., El Mouden, C., and Gardner, A. (submitted). *Social evolution theory and its application to the evolution of cooperation in humans*.
- West, S. A. and Gardner, A. (2010). Altruism, spite, and greenbeards. *Science*, 327(5971), 1341-1344. doi: 10.1126/science.1178332
- West, S. A., Griffin, A. S., and Gardner, A. (2007). Social semantics: Altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology*, 20(2), 415-432.

- West, S. A., Griffin, A. S., and Gardner, A. (2008). Social semantics: How useful has group selection been? *Journal of Evolutionary Biology*, 21(1), 374-385.
- West, S. A., Pen, I., and Griffin, A. S. (2002). Cooperation and competition between relatives. *Science*, 296(5565), 72-75.
- Whitehead, H. and Richerson, P. J. (2009). The evolution of conformist social learning can cause population collapse in realistically variable environments. *Evolution and Human Behavior*, 30(4), 261-273.
- Wiessner, P. (2009). Experimental games and games of life among the Ju/'hoan bushmen. *Current Anthropology*, 50(1), 133-138.
- Wilson, D. S. (1979). Structured demes and trait-group variation. *The American Naturalist*, 113(4), 606-610.
- Wilson, D. S. (1990). Weak altruism, strong group selection. *Oikos*, 59(1), 135-140.
- Wilson, D. S. (2008). Social semantics: Toward a genuine pluralism in the study of social behaviour. *Journal of Evolutionary Biology*, 21(1), 368-373.
- Wilson, D. S. and Dugatkin, L. A. (1997). Group selection and assortative interactions. *The American Naturalist*, 149(2), 336.
- Wilson, D. S. and Sober, E. (1994). Reintroducing group selection to the human behavioral sciences. *Behavioral and Brain Sciences*, 17(04), 585-608. doi: 10.1017/S0140525X00036104
- Wilson, D. S. and Wilson, E. O. (2007). Rethinking the theoretical foundation of sociobiology. *The Quarterly Review of Biology*, 82(4), 327-348.
- Yad Vashem - The Holocaust Martyrs' and Heroes' Remembrance Authority. (2010). Righteous among the nations - per country & ethnic origin January 1, 2010: http://www1.yadvashem.org/righteous_new/statistics.html.
- Yamagishi, T. and Kiyonari, T. (2000). The group as the container of generalized reciprocity. *Social Psychology Quarterly*, 63(2), 116-132.

- Yamagishi, T. and Mifune, N. (2008). Does shared group membership promote altruism?: Fear, greed, and reputation. *Rationality and Society*, 20(1), 5-30. doi: 10.1177/1043463107085442
- Yamagishi, T., Mifune, N., Liu, J. H., and Pauling, J. (2008). Exchanges of group-based favours: Ingroup bias in the prisoner's dilemma game with minimal groups in Japan and New Zealand. *Asian Journal of Social Psychology*, 11(3), 196-207.
- Zahavi, A. and Zahavi, A. (1997). *The handicap principle: A missing piece of Darwin's puzzle*. New York, NY: Oxford University Press.
- Zelmer, J. (2003). Linear public goods experiments: A meta-analysis. *Experimental Economics*, 6(3), 299-310.
- Zuckerman, M. and Driver, R. E. (1985). Telling lies: Verbal and nonverbal correlates of deception. In W. A. Siegman and S. Feldstein (Eds.), *Multichannel integration of non-verbal behavior* (pp. 129-147). Hillsdale, NJ: Erlbaum.

APPENDIX A

GAME SCRIPTS

A.1 Ultimatum game (UG)

A.1.1 Script read collectively to all assembled UG participants

Thank you for attending this study. For the time that you are taking out from work to spend here, we will give each of you Rs30. This money is yours to keep, is being given to you in place of your day's wages and will be given to you at the end of the programme. We have also made arrangements for a meal for you.

We would like to play a game with each individual assembled here. Please play this game seriously because you can earn more money in this game. The money earned in this game will be given to you, along with your Rs30, one at a time at the end of this programme. Hence, at the end of the programme, you will anyway receive Rs30 but along with that you will also receive the money that you have earned in the game.

For this programme you must remember three things (*literally talk*):

First thing (*talk*) – Each person present here will play this game with another person from the village. But you will never know who the other person playing the game with you is. And this other person will also never know who you are. You two will never meet and neither will you be able to know each others name. Neither during the programme, nor after it.

I will give you a token of this kind. Each token has a different symbol on it. For this programme, only this token will be your identity. Even I will not ask you for your name. Your complete identity is in this token and with the exception of me and X (RA) you should not show this token to anyone else here. Therefore even I cannot tell anyone here about what decisions you made in the game since I only know your token and not your name, and besides me no one else here knows your token.

Which two people from the village will play this game with each other will be determined by pairing tokens. For instance, four of you please come here.

(4 individuals were called forth and handed a token each. It was explained that the tokens would be randomly matched to determine who played with whom but that any two individuals would never meet each other or know each others' identity either during or after the game.)

Now, through these tokens we will determine who will play this game with whom. But these two people will never meet and will never be able to know each others' names or anything about each other. Of these two people, one will be called the 'first player' and one will be called the 'second player'. You will come into this room one by one where I will tell you the rules of the game and will tell you whether you are the first or the second player of the game.

You will never know who took what decision in the game from amongst the other people here, either during the programme or after it. At the end of the programme, you will give me your token one at a time in the room and in exchange will receive the money you have earned in the game.

Second thing (talk) - All the decisions you will make in the game will be for REAL money. At the end of the programme you will receive your earnings in the game in real money.

Third thing (*talk*) - This money that you are receiving today does not belong to me. It has been given to me by the school to conduct this programme. It does not matter to the school whether this money gets spent or not.

All of you will come into the room one at a time where I will be seated. I will give you a token. Then I will tell you the rules of the game and you will play the game. After that, you will come out of the room and go to X (RA) who will ask you some questions. Upon answering X's questions you will sit on this side (*point out where*). After this you will not be able to talk to or meet with all the remaining people assembled here who have not yet played the game. When everyone has played the game, you will come into the room one at a time, give me your token and take the money you earned in the game along with Rs30. Then this programme will end.

Now we will give you this information one more time so you can fully understand the programme.

Questions asked collectively:

Now I will ask you some questions to check whether you have understood the information about the programme or not. Please raise your hand if you know the answer to the question.

1. Will this game be played for real money? Will you get real money in it?
2. Why are you being given Rs30?
3. Is this yours to keep and for your use?
4. Besides this Rs30, can you earn more money? How?
5. Who has given the money for this programme?
6. How will we determine who will play with whom?
7. Can you ever know who the other person playing the game with you is, either during the programme or after it?
8. Why are you being given the token?
9. Will I ask for your name?
10. Can I tell any other person in the village what decision you made in the game?

Does anybody want to leave this programme?

Now we will begin. You will come into the room one by one. X (*research assistant*) will tell you when it is your turn to come into the room. The rest of you will have to sit here until your turn. There are arrangements for food and water for you.

A.1.2 Script read individually to UG proposers

Thank you for coming here.

You will play this game with another person from your village. But you two will never meet and you will never know each other's name or identity. I will give you a token and for me only this token will be your identity. Therefore, the decisions you will take here cannot be known by anyone else in the village.

This game will be played for 5 'kori'⁴ meaning Rs100, in 20 Rs5 coins. I will give this 5 kori or Rs100 to the first player. Of this 5 kori or Rs100, the first player may keep as much as s/he likes and can give away as much as s/he likes to the second player playing with him. Afterwards, I will show the second player how much the first player wants to give away from the 5 kori or Rs100 and what part he wants to keep himself. I will not tell the second player the first player's name, token or anything else about him. The second player can either accept this share or not accept it. If the second player accepts the share, then both players will be given money according to the decision of the first player. If the second player does not accept the share, then both players will receive no money from this 5 kori or Rs100. Neither the first player, nor the second player.

Note that the first players' role is to make two shares of the Rs100 according to his own wishes, one for himself and one for the second player. And the second player's role is to determine whether s/he accepts the two shares that the first player has made of the 5 kori or Rs100. If the second player accepts it, then both players will be given their shares

⁴1 'kori' = 20 units.

according to the division made by the first player. If the second player does not accept it, then both players will receive nothing. All decisions will only be taken once.

Now I will ask you some questions to check if you have understood the rules or not.

1. What is the role of the first player in this game?
2. If the second player accepts the share then what will happen?
3. If the second player does not accept the share then what will happen?
4. Does the second player know that his share is being given out of Rs100?
5. Can the other player playing with you know your name or who you are?

Remember that:

1. These decisions are for real money. The person playing with you and you will receive real money according to the outcome of both your decisions.
2. You will never find out who the other person playing with you is and this other player will also never find out who you are; neither during the programme, nor after it.

You are the first player in the game.

Now show me how much money you want to give to the second player out of this 5 kori or Rs100 and how much you want to keep for yourself. Place the amount you want to give away to him on this side of the rope. Place the amount you want to keep for yourself on this side of the rope.

(The coins were placed in the middle of two strings to start with. The player was therefore instructed to place the share he wanted to keep on one side of one string and to place the share he wanted to give away on one side of the second string.)

If the second player accepts this then you will receive and he will receive If he does not accept it, then both of you will receive nothing.

This is your token, keep it safe and do not show it to anyone. At the end of the programme you will come here again, give me your token, and I will give you Rs30 and the money you have earned in this programme.

Now you can leave the room, meet X and answer his questions.

Thank you.

Note: The words 'he' and 'she' used in this script do not translate as such into Hindi and Sargujia since the word 'player' in Hindi and Sargujia is a neutral gender word.

A.1.3 Script read individually to UG responders

Thank you for coming here.

You will play this game with another person from your village. But you two will never meet and you will never know each other's name or identity. I will give you a token and for me only this token will be your identity. Therefore, the decisions you will take here cannot be known by anyone else in the village.

This game will be played for 5 'kori' meaning Rs100, in 20 Rs5 coins. I will give this 5 kori or Rs100 to the first player. Of this 5 kori or Rs100, the first player may keep as much as s/he likes and can give away as much as s/he likes to the second player playing with him. Afterwards, I will show the second player how much the first player wants to give away from the 5 kori or Rs100 and what part he wants to keep himself. I will not tell the second player the first player's name, token or anything else about him. The second player can either accept this share or not accept it. If the second player accepts the share, then both players will be given money according to the decision of the first player. If the second player does not accept the share, then both players will receive no money from this 5 kori or Rs100. Neither the first player, nor the second player.

Note that the first players' role is to make two shares of the Rs100 according to his own wishes, one for himself and one for the second player. And the second players' role is to

determine whether s/he accepts the two shares that the first player has made of the 5 kori or Rs100. If the second player accepts it, then both players will be given their shares according to the division made by the first player. If the second player does not accept it, then both players will receive nothing. All decisions will only be taken once.

Now I will ask you some questions to check if you have understood the rules or not.

1. What is the role of the first player in this game?
2. If the second player accepts the share then what will happen?
3. If the second player does not accept the share then what will happen?
4. Does the second player know that his share is being given out of Rs100?
5. Can the other player playing with you know your name or who you are?

Remember that:

1. These decisions are for real money. The person playing with you and you will receive real money according to the outcome of both your decisions.
2. You will never find out who the other person playing with you is and this other player will also never find out who you are; neither during the programme, nor after it.

You are the second player in the game.

The first player wants to giveout of Rs100.

The first player wants to give youcoins and wants to keepcoins for himself.

(The two piles of coins made by the first player were recreated, counted out and shown to the second player)

Now tell me if you accept this share or not?

You will receive And the first player will receive

This is your token, keep it safe and do not show it to anyone. At the end of the programme you will come here again, give me your token, and I will give you Rs30 and the money you have earned in this programme.

Now you can leave the room, meet X and answer his questions.

Thank you.

A.2 Public goods game round 1 (PGG1)

A.2.1 Script read collectively to all assembled PGG1 participants

Thank you for attending this study. For the time that you are taking out from work to spend here, we will give each of you 30 rupees. This money is yours to keep, is being given to you in place of your day's wages and will be given to you at the end of the programme. We have also made arrangements for a meal for you.

Please remember that if at any time you feel that you do not wish to participate in this study, you are free to leave whether we have started the programme or not.

We would like to play a game with every person assembled here. Please play this game seriously because you can earn more money in this game. The money earned in this game, along with your 30 rupees, will be given to you one at a time at the end of this programme. Hence, at the end of the programme, you will receive 30 rupees but on top of that you will also receive the money that you have earned in the game.

For this programme you must remember four points:

First point – The game we will play today is different from the game played earlier. For this game, you will be divided into groups of six players. These six players will play the game with each other. However, you will never know who the other 5 players in your group are, either during or after the game. These other 5 players will also never know who you are, either during or after the game. You will never meet the other players in your group or be able to know their names either during or after the game.

I will give you a token like this. Every token has a different symbol (number) on it. In this programme, this token will be your only identity. Even I will not ask you your name. Your complete identity will be in this token. Besides me and X (*research assistant*), do not show

this token to anyone assembled here. And even I will not be able to tell anyone what decisions you have taken since I only know your token numbers and not your names. And besides me, no one else will know your token numbers. Which six people from the village play the game with each other will be determined by randomly matching token numbers.⁵

Second point - All the decisions you will make in the game will be for real money. You will receive real money at the end of the programme in accordance with the decisions you have made and how much you have earned.

Third point - The money that you are receiving today does not belong to me. It has been given to me by the school to conduct this programme. It does not matter to the school whether this money is spent or not.

Fourth point – Once I have told you the rules of the game, please do not discuss the game between yourselves and also do not discuss it with other people from the village who are yet to play the game. This is very important. You cannot ask questions or talk about the game until this programme is over. You will get a chance to ask questions when you are in the private room. Please be sure that you obey this rule, because even one person disobeying can spoil the game for everyone. If even one person starts talking about the game while sitting here, then we will not be able to play the game in your village. Once you have played the game, you will not be able to talk to or meet with all the remaining people assembled here who have not yet played the game.

I will now tell you the rules of this game⁶. It is important that you listen carefully and understand these rules, because only those people who understand the rules will be able to play.

⁵Since the PGG was played in each village after the ultimatum game had already been played, participants were familiar with the use of tokens to anonymise identities as well as to randomly match players in the games. This procedure had been demonstrated in great detail with real tokens and models pulled up from among the participants. Participants were also familiar with procedural details such as the fact that the games were all played individually at a private location and that the tokens would be exchanged for earnings in the game.

⁶All game rules and examples were demonstrated with real money and a money box.

For this game you will all be divided into groups of six players and each group will be given a group pot. Each individual in the group will receive an endowment of 20 rupees (meaning one kori⁷) in rupee 5 coins. These 20 rupees (one kori) are yours. Now, you can deposit as much of these 20 rupees (one kori) as you wish to the group pot, in 5 rupee increments. This means that if you wish you can deposit nothing in the group pot, or you can deposit 5, 10, 15 or 20 rupees (one kori) in your group pot. The money that you do not deposit in the pot will be yours to keep and to take home. Once each of the 6 people in your group have decided how much of their 20 rupees they want to deposit in the group pot, then I will count the money deposited in your group pot, double the total amount of money deposited, and then divide this doubled amount equally between the six people in your group. Hence at the end of the game, you will receive the amount of money that you did not deposit in the group pot, plus an equal share of double the total amount of money accumulated in the group pot. Therefore in this game you have to decide how much of your 20 rupees (one kori) you wish to keep for yourself, and how much you wish to deposit in your group pot. Note that you will make your decision independently and in private so that none of the other members of your group can ever know your decision. All decisions will only be taken once.

Now I will give you some examples so that you can understand the game properly:

First example - If all the women and men in your group deposit their whole 20 rupees (one kori) in the group pot, then the pot will accumulate a total of 20 multiplied by 6 meaning 120 rupees (six koris). 120 rupees (six koris) doubled is 240 rupees (twelve koris). If 240 rupees (twelve koris) are divided into 6 equal shares, then one share will contain 40 rupees (two koris). Therefore each group player will receive 40 rupees (two koris). If no one in your group deposits anything in the pot, then you will each receive only your endowment of 20 rupees (two koris).

Second example - If everyone in your group deposits nothing in the group pot, then the pot will contain nothing and each of your group players will receive only your endowment of 20 rupees (two koris).

⁷1 kori = 20 units.

Third example - If one group player does not deposit anything in the pot and the remaining five group players deposit their whole 20 rupees (one kori) in the group pot, then the pot will accumulate a total of 20 multiplied by 5 meaning 100 rupees (five koris). 100 rupees (five koris) doubled is 200 rupees (ten koris). And if 200 rupees (ten koris) are divided into 6 equal shares, then one share will contain 33 rupees (one kori and thirteen). Therefore each of the 5 group players who deposited their whole 20 rupees (one kori) into the pot will receive 33 rupees (one kori and thirteen) and the one group player who deposited nothing in the pot will receive 33 rupees (one kori and thirteen) plus his endowment of 20 rupees which he kept for himself. Therefore he will receive a total of 53 rupees (two koris and thirteen). Hence, if one group player does not deposit anything in the pot, and the remaining 5 group players deposit their whole endowment of 20 rupees (one kori), then this first player will earn more money than the remaining five players and will also earn more money than he would have earned if all six players had deposited their whole endowment of 20 rupees into the group pot as illustrated in the first example.

Fourth example - If one group player deposits 20 rupees (one kori) in the group pot and all the other players deposit nothing, then the pot will accumulate a total of 20 rupees (one kori). 20 rupees (one kori) doubled is 40 rupees (two koris). And if the 40 rupees (two koris) are divided into 6 equal shares, then each share will contain 6.5 rupees (six rupees and eight annas). Hence the group player who deposited his whole endowment of 20 rupees (one kori) in the group pot will receive 6.5 rupees (six rupees and eight annas) and the remaining five group players will receive 6.5 rupees (six rupees and eight annas) plus their endowments of 20 rupees which they kept for themselves. Therefore they will each receive a total of 26.5 rupees (one kori, six rupees and eight annas). Hence if only one group player deposited his whole endowment of 20 rupees (one kori) into the group pot but the remaining five group players do not deposit anything, then this first player will earn less money than the remaining five players and will also earn less money than he would have earned in the other three examples given so far.

Hence,

1. If all 6 group players deposit some money in the group pot, then they will earn more money than if no one deposits anything in the pot.
2. If most group players deposit some money in the group pot, but a few group players do not deposit any money, then the few players who did not deposit any money earn more than the players who did deposit money.
3. If most group players do not deposit any money in the pot, and a few players do deposit some money, then these few group players earn the least amount of money.

Now I will ask you some questions to check whether you have understood the rules of the game or not.

1. How many players are there in each group?
2. Can you ever know who the other players in your group are?
3. Can the other players in your group ever know your identity?
4. What is the endowment that each player of the group receives at the beginning of the game?
5. What decision must each player take about these 20 rupees (one kori)?
6. If you so wish, can you take the decision to deposit nothing in the group pot?
7. If you so wish, can you take the decision to deposit the whole 20 rupees (one kori) into the group pot?
8. Once all 6 group players have decided how much money they want to deposit in the group pot, then what will I do?
9. What will your total earnings consist of?
10. Will you be given your earnings in real money at the end of the game?
11. Why are each of you being given a token?
12. Will I ask for your name while you are playing this game?
13. Can I tell any other person in the village what decision you made in the game? Why not?

Does anybody want to leave this programme? Is everyone happy to participate?

Now we will begin. You will each pick a number out of this bowl to determine the order in which you will play the game. You will come into the private room one by one. Y (*research assistant*) will tell you when it is your turn to come into the room. Then I will ask you some questions to check whether you have understood the rules of the game or not. If you answer my questions correctly then you will play the game. Arrangements for a meal have been made for you all.

A.2.2 Script read individually to PGG1 participants

Now I will explain the rules of this game to you one more time⁸. For this game you will all be divided into groups of six players and each group will receive a group pot. Each player in the group will receive an endowment of 20 rupees (meaning one kori) in rupee 5 coins. Each person has to decide how much of their 20 rupees (one kori) they want to deposit in their group pot and how much they want to keep for themselves. The money that you do not deposit in the pot will be yours to keep.

Meaning,

If you deposit 5 rupees in the group pot then how much money remains?

If you deposit 10 rupees in the group pot then how much money remains?

If you deposit 15 rupees in the group pot then how much money remains?

If you deposit 20 rupees in the group pot then how much money remains?

If you deposit nothing in the group pot then how much money remains?

⁸All game rules and test question examples were demonstrated with real money and a money box. Participants made their decisions by physically manipulating real money.

So the money that you do not deposit in your group pot, the money that remains, will be yours to keep. And on top of that once each of the 6 people in your group have decided how much money they want to deposit in the group pot and how much they want to keep for themselves, then I will count the money deposited in your group pot, double the total amount of money deposited and then divide this doubled amount equally between the six people in your group. Hence at the end of the game, you will receive the amount of money out of your endowment of 20 rupees (one kori) that you did not deposit in the group pot, plus an equal share of double the total amount of money accumulated in the group pot. You cannot know what decisions the remaining five people in your group have taken and they cannot know what decision you have taken.

Now I will ask you some questions to check whether you have understood the rules of the game or not.

First question – If all the six players in your group want to keep their 20 rupees (one kori) for themselves and do not want to deposit any money in the group pot then no money will accumulate in the group pot. If nothing accumulates in the pot then no one gets any share out of the pot but all you six group players have kept your endowment of 20 rupees (one kori) for yourselves.

So,

- i. How much money will you earn?
- ii. How much money will each of the other players in your group earn?

Second question - If each of the six players in your group deposit their endowments of 20 rupees (one kori) into the group pot, then the group pot will accumulate 120 rupees (six koris). 120 rupees (six koris) doubled is 240 rupees (twelve koris). If I divide 240 rupees (twelve koris) equally between six people, then each share will contain 40 rupees (two koris).

So,

- i. How much money will you earn?

- ii. How much money will each of the other players in your group earn?

Third question - If all the other five players of your group want to keep their 20 rupees (one kori) for themselves and do not want to deposit anything in the group pot and you want to deposit your 20 rupees (one kori) in the group pot, then the group pot will accumulate only 20 rupees (one kori). 20 rupees (one kori) doubled is 40 rupees (two koris). And if I divide 40 rupees (two koris) equally between six people, then each share will contain 6.5 rupees (six rupees and eight annas).

So,

- i. How much money will you earn?
ii. How much money will each of the other players in your group earn?

Therefore if all the six players in your group keep their 20 rupees (one kori) for themselves and do not deposit anything in the group pot, the group pot will accumulate no money and each player will only receive their endowment of 20 rupees (one kori). If all six players in your group deposit their 20 rupees (one kori) in the group pot, then the group will accumulate 120 rupees (six koris). 120 rupees (six koris) doubled is 240 rupees (twelve koris) and if I divide 240 rupees (twelve koris) equally between six people, then each share will contain 40 rupees (two koris). So all six players in your group will receive 40 rupees (two koris) each. But you cannot know whether the remaining five players in your group have deposited anything in the group pot or not. So if the remaining five players do not deposit anything in your group pot and you deposit your whole endowment of 20 rupees (one kori) then you will earn less money and they will earn more money.

Now tell me, can you know who the other five players in your group are or what decision they have made?

Can any of the other players know your name or the decision you have made?

Now you will play the game. Remember that you must take your decision independently and there is no right or wrong answer in this game. Here are your 20 rupees (one kori) in

four Rs 5 coins. You must decide how much of these 20 rupees (one kori) you want to deposit in your group pot and how much of it you want to keep for yourself. Remember that if you so wish you can deposit nothing in the pot, or 5, 10, 15 or the whole 20 rupees. Please put the amount you want to deposit in the pot into the pot and keep the rest on this side. Thank you.

A.3 Salt decision

Script read individually to each participant when collecting her payment.

I have brought some salt with me to give to everyone who participated in this study. I have a total of x^9 kg of salt remaining, and you are y (see footnote 9) people remaining. Therefore I have got z kg (see footnote 9) of salt per person. But you can take as much of this x kg (see footnote 9) of salt as you wish. Now tell me how much of this x kg (see footnote 9) of salt you would like to take home and I will give you that much salt.

⁹In each village I started with a total quantity of salt (x) in kilograms equal to the total number of participants so that the initial amount available per person (z) was 1 kg. I recalculated and updated the total amount available (x), the number of people remaining (y), and the amount available per person ($z = x/y$) to the nearest 100 g for each person based on how much salt remained after the preceding person had taken their desired salt quantity.

A.4 Public goods game round 2 (PGG2)

A.4.1 Script read collectively to all assembled PGG2 participants

Now we will play another game with you. This game is very similar to the first game you have played today. The rules of this game are the same as the rules of the previous game¹⁰. Again, you will be divided into groups of six players but this time, you will not be grouped with the same people you played with the previous time. This time new groups will be made in which you will be grouped with a new set of players. The six players in the each new group will play the game with each other. This time too you will never know who the other five players in your group are, either during or after the game. These other five players will also never know who you are, either during or after the game. You will never meet the other players in your group or be able to know their names either during or after the game. Your token¹¹ will be your only identification and even I will not be able to tell anyone what decision you made in the game because I will not know your names.

This time too for this game you will all be divided into groups of six players and each group will be given a group pot. Each individual in the group will receive an endowment of 20 rupees (meaning one kori¹²) in rupee 5 coins. These 20 rupees (one kori) are yours. Now, you can deposit as much of these 20 rupees (one kori) as you wish to the group pot, in 5 rupee increments. This means that if you wish you can deposit nothing in the group pot, or you can deposit 5, 10, 15 or 20 rupees (one kori) in your group pot. The money that you do not deposit in the pot will be yours to keep and to take home. Once each of the 6 people in your group have decided how much of their 20 rupees they want to deposit in the group pot, then I will count the money deposited in your group pot, double the total amount of money

¹⁰All game rules and examples were demonstrated with real money and a money box. Participants made their decisions by physically manipulating real money.

¹¹Since both rounds of the PGG were played in each village after the ultimatum game had already been played, participants were familiar with the use of tokens to anonymise identities as well as to randomly match players in the games. This procedure had been demonstrated in great detail with real tokens and models pulled up from among the participants. Participants were also familiar with procedural details such as the fact that the games were all played individually at a private location and that the tokens would be exchanged for earnings in the game.

¹²1 kori = 20 units.

deposited, and then divide this doubled amount equally between the six people in your group. Hence at the end of the game, you will receive the amount of money that you did not deposit in the group pot, plus an equal share of double the total amount of money accumulated in the group pot. Therefore in this game you have to decide how much of your 20 rupees (one kori) you wish to keep for yourself, and how much you wish to deposit in your group pot. However, this time before you take your decision I will tell you two things:

First thing - I will tell you the amount of money that was contributed to the group pot by the player who earned the most money in your previous group in the previous game that you played. You will not find out who this player was, what his/her name is or how much money he/she earned. You will only be told how much money this player, who earned the most money in your previous group, contributed to your previous group pot.

Second thing – After this I will tell you the amount of the contribution that was made by the majority of people in your previous group of players. For example, if four out of the six players in your group contributed 5 rupees to the group pot, then you will be told this amount. Or if three out of the six players in your group contributed 10 rupees, two players contributed 5 rupees and 1 player contributed 20 rupees, then since the majority of players in the group contributed 10 rupees you will be told this amount. This time too you will not be told who these players are, what their names are or how much money they earned. You will only be told what amount the majority of people contributed.

Once you have been given these two pieces of information, you will be asked to make your decision about how much of your 20 rupee endowment you wish to contribute to your new group pot and how much you want to keep for yourself. Note that you will make your decision independently and in private so that none of the other members of your group can ever know your decision. All decisions will only be taken once.

Remember,

1. All the decisions you will make in the game will be for real money. You will receive real money at the end of the programme in accordance with the decisions you have made and how much you have earned.
2. Please do not discuss the game between yourselves and also do not discuss it with other people from the village who are yet to play the game. This is very important. You cannot ask questions or talk about the game until this programme is over. You will get a chance to ask questions when you are in the private room. Please be sure that you obey this rule, because even one person disobeying can spoil the game for everyone. If even one person starts talking about the game while sitting here, then we will not be able to play the game in your village. Once you have played the game, you will not be able to talk to or meet with all the remaining people assembled here who have not yet played the game.

Note that you will only find out how much you have earned in the previous game and this new game, after you have finished playing both games.

Now I will ask you some questions to check whether you have understood the rules of the game or not.

14. What is the difference between this game and the game you played previously?
15. Are the rules of this game the same as the rules of the game you played previously?
16. What are the two things you will be told before you make your decision?
17. Will you play this game with the players from your old group or with the new players in a new group?
18. Can you ever know who the other players in your group are?
19. Can the other players in your group ever know your identity?
20. Will I ask for your name while you are playing this game?

21. Can I tell any other person in the village what decision you made in the game? Why not?

Does anybody want to leave this programme?

Now we will begin. You will each pick a number out of this bowl to determine the order in which you will play the game. You will come into the private room one by one. Y (*research assistant*) will tell you when it is your turn to come into the room. Then I will ask you some questions to check whether you have understood the rules of the game or not. If you answer my questions correctly then you will play the game.

A.4.2 Script read individually to PGG2 participants

Have you understood the rules of the game?

Now I will ask you some questions to check whether you have understood the rules of the game or not. If you answer the questions correctly then you will play the game.

1. Are the rules of this new game the same as the rules of the game you played previously?
2. Will you play this game with the players from your old group or with the new players in a new group?
3. Can you ever know who the other players in your new group are?
4. Can the other players in your new group ever know your identity?

Now I will tell you two things.

The first thing I will tell you is the amount of money that was contributed to the group pot by the player who earned the most money in your previous group in the previous game that you played.

The second thing I will tell you is the amount of the contribution that was made by the majority of people in your previous group of players.

So from your previous group in the previous game, the player who earned the most money contributed rupees to the group pot¹³.

And, the majority of people from your previous group of players contributed ... rupees to the group pot¹⁴.

1. How much did the player who earned the most money contribute to the group pot?

2. How much did the majority of people contribute to the group pot?

Now you will play the game. Remember that you must take your decision independently and there is no right or wrong answer in this game.

Here are your 20 rupees (one kori) in four Rs 5 coins. You must decide how much of these 20 rupees (one kori) you want to deposit in your group pot and how much of it you want to keep for yourself. Please put the amount you want to deposit in the pot into the pot and keep the rest on this side.

Thank you.

¹³The appropriate amount of money was placed in rupee 5 coins to the left of the money box.

¹⁴The appropriate amount of money was placed in rupee 5 coins to the right of the money box.

APPENDIX B

DATA SHEETS

B.1 Individual data sheet

Tola:
Village:
Block:
District:

Recorder:
Date:
Game:

1. Token number:

2. Tribe: P. Korwa Other:

3. Age¹⁵:

4. Gender: Male Female

5. Education

Illiterate	Literate	Primary 1-5	Middle 6-8	High 9-10	Higher Secondary	University

6. Occupation

Agriculture	Gathering	Daily wage Labour	Other

¹⁵ Many individuals did not know their exact age. We estimated their age by using a combination of the following criteria: (a) whether they were married (b) the number of children they had (c) whether they had been born and experienced a major festival that occurred in the region in the 1950's and if so whether they had been a child, adolescent or a married adult at the time (d) whether they had been born and experienced a major drought that occurred in the region in the 1980's and if so whether they had been a child, adolescent or a married adult at the time (e) physical appearance.

B.1 INDIVIDUAL DATA SHEET

g) Relatives

Relative	Total number	Number participated in the game	Number living in this village		Number living in other villages	
			Under 15 years	Over 15 years	Under 15 years	Over 15 years
Sons						
Daughters						
Grandchildren						
Mother						
Father						
Full brothers born of mother			Under 15 years		Under 15 years	
			Over 15 years		Over 15 years	
Children of full brothers born of mother						
Wives of full brothers born of mother						
Full sisters born of mother			Under 15 years		Under 15 years	
			Over 15 years		Over 15 years	
Children of full sisters born of mother						
Husbands of full sisters born of mother						
Half brothers born of mother			Under 15 years		Under 15 years	
			Over 15 years		Over 15 years	
Children of half brothers born of mother						
Wives of half brothers born of mother						
Half sisters born of mother			Under 15 years		Under 15 years	
			Over 15 years		Over 15 years	
Children of half sisters born of mother						
Husbands of half sisters born of mother						
Half brothers born of father			Under 15 years		Under 15 years	
			Over 15 years		Over 15 years	
Children of half brothers born of father						
Wives of half brothers born of father						
Half sisters born of father			Under 15 years		Under 15 years	
			Over 15 years		Over 15 years	

B.1 INDIVIDUAL DATA SHEET

Relative	Total number	Number participated in the game	Number living in this village	Number living in other villages
Children of half sisters born of father				
Husbands of half sisters born of father				
Mothers' siblings				
Mothers' siblings children				
Fathers' siblings				
Fathers' siblings' children				

8. Migration status

a)	Place of birth	
b)	Time lived in this village	
c)	Number of times village changed since birth ¹⁷	

9. Income

- a) How many major wage earners are there in your family?
- b) How many months in the year do you eat self grown rice?
- c) How much outstanding loan money have you taken in all from any source¹⁸?
- d) How much do you earn for one day's labour?

10. Markets

- a) How many times a month do you visit the weekly tribal market?
- b) How many times a month do you visit your nearest city to buy or sell something?

11. Network data

How many people did you invite to your home last Cherta:

- a) From this village:
- b) From other villages:

¹⁷ If the individual was currently residing in the natal village this was recorded as 0.

¹⁸ This is a record of the total amount of outstanding loans an individual had at the time of the survey.

B.2 VILLAGE DATA SHEET**Amenities:**

Type	Present in village Y/N	Closest place of access	GPS Reading
School			
Hospital/health care centre			
Post office			
Railway Station			
Inter-state bus service			
Inter-village/district bus service			
Village Panchayat Office			
Presence of NGO's working with them			

Resource Distribution: Water bodies, markets (tribal & city), grazing grounds

S No.	Resource Type	Identification name	GPS reading	Additional notes

Information from local land ownership records:

a) Total registered land in the village ('Patte valee'):

Additional Comments on village:

B.3 Housing data sheet

Recorder:

Date:

Tola:

Village:

Block:

District:

House	Latitude	Longitude	Altitude	Male head	Female head	Salt used	Number of residents

B.4 Qualitative data sheet

Village

1. How old is this village? How long has it been here?
2. Have you always practiced agriculture here or has there been any other main source of income and living in the last two generations?
3. In what generation according to your memory, did you primarily hunt and gather and practice Jhoom?
4. How much movement is there between villages? What villages do people most visit in the neighboring areas in their lifetimes?
5. How often do you normally change your place of residence? Why?
6. Do you use the grazing land? How much do people use the grazing land? How do you decide when and how it should be used? How do you make sure that it isn't over-grazed?
7. What are the daily wages in the area?
8. How many people in the village engage in daily wage labour?
9. What do people identify themselves with? The 'tola' or the village?

General ethnographic survey

Kinship:

10. Who do people marry? Those within the village or those in other villages?
11. Do people marry other members of the family?
12. Do people look after their parents when they are old and provide them a roof and food?
13. Up to what age do people look after their children?

14. Do sisters and brothers help each other to do things (e.g. tend fields, fish, hunt, gather, build houses etc)?
15. What about aunts and uncles and their children?
16. Do the above relatives help each other when:
 - a. They don't have food
 - b. Need care when they are ill
 - c. Need help in the field
 - d. Hunting or fishing
 - e. Collecting water
 - f. Building houses
 - g. Anything else?
17. Who lives in a household? What relatives? Your mother, father, children, siblings, grand parents etc?
18. Do grandmothers look after their grandchildren? From the mothers' side, from the fathers' side?
19. What is the in laws' role:
 - a. From the girls side?
 - b. From the boys side?

Subsistence:

20. What is the main source of subsistence?
 - a. Self grown food
 - b. Bought food
 - c. Wages used to buy food
 - d. Gathered food (fruit, vegetables, roots, honey etc?)
 - e. Hunted food (fishing, other meat)?

21. Are there any subsistence related activities that are communal in nature?
- a. Farming related
 - b. Fishing
 - c. Gathering
 - d. Hunting
 - e. Tending to animals
 - f. Honey gathering
 - g. Other?

Communal Activities:

22. What types of activities do people do together?

APPENDIX C

STATISTICAL ANALYSES

This appendix presents the univariate and domain-wise models, and a step-wise summary of the full model fitting process implemented in the fourth stage, for all analyses presented in this thesis. Section C.1 presents analyses for UG proposer offers (Chapter 3, Section 3.2.1) and Section C.2 presents analyses for UG responder MAOs (Chapter 3, Section 3.2.2). Section C.3 presents analyses for PGG1 contributions and salt deviations (Chapter 4, Section 4.2). Section C.4 presents analyses for PGG2 contributions (Chapter 5, Section 5.2.1). Section C.5 presents analyses for learning strategies in the PGG2 (Chapter 5, Sections 5.2.3 and 5.2.4). For a description of a variable in any of the following tables see Chapter 2, Section 2.4.2, Table 2.5).

C.1 UG Proposer offer (Chapter 3, Section 3.2.1)

C.1.1 Univariate Models

Table C.1 Univariate associations between each predictor term (fixed effect) and UG offer (models include constants). A Bonferroni correction has not been applied to these models as they were used for exploratory analyses. Values in bold are significant. *** $p < 0.01$; ** $p < 0.05$; * $p < 0.10$.

Model	Fixed effect	UG offer (Indian rupees) $\beta \pm SE$	-2 Log likelihood			n
			Current model	Null model	Δ^1	
Village descriptors						
1	Population size	-0.001 \pm 0.005	2553.279	2553.267	-0.012	344
2	Proportion of migrants	-0.189 \pm 7.178	2553.324	2553.267	-0.057	344
3	Proportion of non-Korwas	15.156 \pm 7.378**	2549.147	2553.267	4.120	344
4	Household dispersion	-0.883 \pm 4.514	2553.288	2553.267	-0.021	344
5A	Distance from major town (km)	0 \pm 0	2553.171	2553.267	0.096	344
5B	Distance from major town: 25-35 km (ref: 0-25 km)	-2.608 \pm 2.932				
	35-45 km (ref: 0-25 km)	-0.409 \pm 3.206	2552.279	2553.267	0.988	344
	45+ km (ref: 0-25 km)	-1.111 \pm 3.371				
Individual descriptors						
<i>Basic individual descriptors</i>						
6	Age (years)	-0.061 \pm 0.045	2551.380	2553.267	1.887	344
7	Sex: female (ref: male)	0.365 \pm 1.062	2553.148	2553.267	0.119	344
8	Education:					
	Illiterate (ref: some schooling)	0.383 \pm 1.348	2553.128	2553.267	0.139	344
	Literate (ref: some schooling)	0.687 \pm 1.803				
9	Household size (individuals)	-0.402 \pm 0.219*	2549.947	2553.267	3.320	344
10	Marriage: ever married (ref: never married)	-3.918 \pm 2.274*	2550.286	2553.267	2.981	344
11	Day on which game was played: day 2+ (ref: day 1)	5.034 \pm 1.153***	2534.616	2553.267	18.651	344
<i>Residence and migration</i>						
12	Birthplace: this village (ref: other village)	-0.278 \pm 1.079	2539.669	2539.732	0.063	343
13	Time resident in this village (years)	-0.032 \pm 0.035	2545.707	2546.562	0.855	343
14	Number of times migrated	0.638 \pm 0.752	2552.540	2553.267	0.727	344
15	Post-marital residence: natal village (ref: other village)	-0.924 \pm 1.113	2411.147	2411.837	0.690	325
<i>Wealth, markets and social networks</i>						

C.1 UG PROPOSER OFFER

16	Proportion of earners in household	3.623 ± 2.490	2551.227	2553.267	2.040	344
17	Months per year household eats self-grown rice	-0.209 ± 0.204	2552.238	2553.267	1.029	344
18	Outstanding loans: yes (ref: no)	-0.992 ± 1.223	2545.980	2546.646	0.666	343
19	Number of monthly visits to local bazaar	-0.116 ± 0.621	2553.241	2553.267	0.026	344
20	Number of monthly visits to nearest town	0.076 ± 0.115	1779.497	1779.934	0.437	253
21	People invited to harvest festival from own village	-0.037 ± 0.066	2553.029	2553.267	0.238	344
22	People invited to harvest festival from other villages	0.143 ± 0.126	2551.948	2553.267	1.319	344
<i>Children and grandchildren</i>						
23	Children living	-0.352 ± 0.275	2551.632	2553.267	1.635	344
24	Children living together	-0.116 ± 0.276	1779.761	1779.934	0.173	253
25	Grandchildren living	-0.081 ± 0.249	1779.834	1779.934	0.100	253
26	Grandchildren living in village	-0.082 ± 0.371	2553.220	2553.267	0.047	344
<i>Kin</i>						
27	Mother living: yes (ref: no)	1.458 ± 1.047	1777.992	1779.934	1.942	253
28	Mother living in village: yes (ref: no)	1.398 ± 1.108	2551.688	2553.267	1.579	344
29	Mother participated in UG: yes (ref: no)	0.182 ± 2.002	1779.931	1779.934	0.003	253
30	Father living: yes (ref: no)	0.245 ± 1.031	1779.883	1779.934	0.051	253
31	Father living in village: yes (ref: no)	-0.494 ± 1.186	2553.111	2553.267	0.156	344
32	Father participated in UG: yes (ref: no)	0.153 ± 1.908	1779.933	1779.934	0.001	253
33	Full brothers living	0.075 ± 0.446	1779.911	1779.934	0.023	253
34	Full brothers living in village	-0.183 ± 0.491	1779.800	1779.934	0.134	253
35	Full brothers aged < 15 years living in village	-0.134 ± 0.991	1779.921	1779.934	0.013	253
36	Full brothers aged ≥ 15 years living in village	-0.183 ± 0.542	1779.825	1779.934	0.109	253
37	Full brothers living in other villages	0.327 ± 0.545	1779.577	1779.934	0.357	253
38	Full brothers aged < 15 years living in other villages	0.252 ± 1.004	1779.876	1779.934	0.058	253
39	Full brothers aged ≥ 15 years living in other villages	0.361 ± 0.651	1779.630	1779.934	0.304	253
40	Full brothers participated in UG	-1.353 ± 0.856	1777.433	1779.934	2.501	253
41	Full sisters living	-0.500 ± 0.435	1778.611	1779.934	1.323	253
42	Full sisters living in village	-1.314 ± 0.656**	1775.932	1779.934	4.002	253
43	Full sisters aged < 15 years living in village	-0.819 ± 1.061	1779.339	1779.934	0.595	253
44	Full sisters aged ≥ 15 years living in village	-1.847 ± 0.893**	1775.666	1779.934	4.268	253
45	Full sisters living in other villages	0.099 ± 0.516	1779.902	1779.934	0.032	253
46	Full sisters aged < 15 years living in other villages	0.169 ± 1.238	1779.921	1779.934	0.013	253
47	Full sisters aged ≥ 15 years living in other villages	0.104 ± 0.630	1779.912	1779.934	0.022	253
48	Full sisters participated in UG	-2.422 ± 1.348*	1776.705	1779.934	3.229	253

¹ Δ = -2 Log Likelihood of null model – (-2 Log likelihood of current model)

C.1.2 Domain-wise models

Table C.2 Multivariate associations between domains of predictor terms (fixed effects) and UG offer (models include constants). Values in bold are significant. *** $p < 0.01$; ** $p < 0.05$; * $p < 0.10$.

Model	Fixed effect	UG offer (Indian rupees) $\beta \pm SE$	-2 Log likelihood			n
			Current model	Null model	Δ^1	
1	Village descriptors					
A	Population size	0.002 \pm 0.009	2549.370	2553.267	3.897	344
	Proportion of migrants	2.329 \pm 9.258				
	Proportion of non-Korwas	17.636 \pm 9.967*				
	Household dispersion	-1.805 \pm 5.746				
	Distance from major town (km)	0 \pm 0				
B	Population size	0.000 \pm 0.010	2547.432	2553.267	5.835	344
	Proportion of migrants	-1.238 \pm 9.350				
	Proportion of non-Korwas	17.943 \pm 9.086**				
	Household dispersion	-1.163 \pm 6.257				
	Distance from major town: 25-35 km (ref: 0-25 km)	-3.147 \pm 3.432				
	35-45 km (ref: 0-25 km)	-0.342 \pm 4.024				
	45+ km (ref: 0-25 km)	0.098 \pm 4.543				
	Individual descriptors					
2	Basic individual descriptors					
	Age (years)	-0.068 \pm 0.048	2525.618	2553.267	27.649	344
	Sex: female (ref: male)	0.062 \pm 1.120				
	Education:					
	Illiterate (ref: some schooling)	1.232 \pm 1.478				
	Literate (ref: some schooling)	1.015 \pm 1.854				
	Household size (individuals)	-0.440 \pm 0.215**				
	Marriage: ever married (ref: never married)	-3.648 \pm 2.433				
	Day on which game was played: day 2+ (ref: day 1)	4.962 \pm 1.160***				
3	Residence and migration					
	Birthplace: this village (ref: other village)	1.449 \pm 4.170	2389.506	2390.929	1.423	323
	Time resident in this village (years)	-0.011 \pm 0.044				
	Number of times migrated	0.990 \pm 1.044				

C.1 UG PROPOSER OFFER

	Post-marital residence: natal village (ref: other village)	-1.004 ± 3.982				
4	<i>Wealth, markets and social networks</i>					
	Proportion of earners in household	1.585 ± 2.462	1772.629	1779.932	7.303	253
	Months per year household eats self-grown rice	-0.058 ± 0.206				
	Outstanding loans: yes (ref: no)	-1.239 ± 1.101				
	Number of monthly visits to local bazaar	-1.028 ± 0.710				
	Number of monthly visits to nearest town	0.127 ± 0.122				
	People invited to harvest festival from own village	-0.034 ± 0.043				
	People invited to harvest festival from other villages	0.203 ± 0.108*				
5	<i>Children and grandchildren</i>					
	Children living	0.413 ± 0.852	1779.180	1779.932	0.752	253
	Children living together	-0.562 ± 0.918				
	Grandchildren living	-0.027 ± 0.627				
	Grandchildren living in village	-0.248 ± 0.809				
6	<i>Kin</i>					
A	Mother living: yes (ref: no)	-0.569 ± 1.493	1771.790	1779.932	8.142	253
	Mother living in village: yes (ref: no)	4.052 ± 1.873**				
	Mother participated in UG: yes (ref: no)	-1.501 ± 2.500				
	Father living: yes (ref: no)	2.313 ± 1.583				
	Father living in village: yes (ref: no)	-4.750 ± 2.049**				
	Father participated in UG: yes (ref: no)	1.548 ± 2.412				
B	Full siblings living	-0.529 ± 0.459	1774.809	1779.932	5.123	253
	Full brothers aged < 15 years living in village	0.796 ± 1.258				
	Full brothers aged ≥ 15 years living in village	1.400 ± 0.904				
	Full brothers aged < 15 years living in other villages	0.959 ± 1.208				
	Full brothers aged ≥ 15 years living in other villages	0.873 ± 0.870				
	Full brothers participated in UG	-2.151 ± 1.204*				
C	Full siblings living	0.161 ± 0.461	1775.044	1779.932	4.888	253
	Full sisters aged < 15 years living in village	-0.920 ± 1.265				
	Full sisters aged ≥ 15 years living in village	-1.541 ± 1.426				
	Full sisters aged < 15 years living in other villages	-0.331 ± 1.388				
	Full sisters aged ≥ 15 years living in other villages	-0.207 ± 0.854				
	Full sisters participated in UG	-0.894 ± 2.027				

¹ Δ = -2 Log Likelihood of null model – (-2 Log likelihood of current model)

C.1.3 Full model fitting summary

Table C.3 Summary of model-fitting process in the fourth stage of analyses. Variables in bold are significant predictors of UG offer at $p < 0.05$ and were retained in the next listed model.

Model	Fixed effect	n	p	DIC ¹	NM DIC ²	Δ DIC ³
Block 1						
1	Proportion of non-Korwas	344	<0.05	2546.12	2546.07	-0.05
	Age ⁴		>0.05			
	Sex ⁴		>0.05			
	Household size		<0.05			
	Marriage		>0.05			
	People invited to harvest festival from other villages		>0.05			
2	Proportion of non-Korwas	344	<0.05	2545.38	2546.07	0.69
	Age ⁴		>0.05			
	Sex ⁴		>0.05			
	Household size		<0.05			
Block 2						
3	Proportion of non-Korwas	344	<0.05	2545.38	2546.07	0.69
	Age ⁴		>0.05			
	Sex ⁴		>0.05			
	Household size		<0.05			
Block 3						
4	Proportion of non-Korwas	253	>0.05	1788.74	1784.55	-4.19
	Age ⁴		>0.05			
	Sex ⁴		>0.05			
	Household size		>0.05			
	Mother living in village		<0.05			
	Father living in village		>0.05			
	Full brothers participated in UG		>0.05			
5	Proportion of non-Korwas	344	<0.05	2545.94	2546.07	0.13
	Age ⁴		>0.05			
	Sex ⁴		>0.05			
	Household size		<0.05			
	Mother living in village		>0.05			
	Father living in village		>0.05			
6	Proportion of non-Korwas	344	<0.05	2543.34	2546.07	2.73
	Household size		=0.059			
7	Proportion of non-Korwas	344	<0.05	2545.44	2546.07	0.63
8	Proportion of non-Korwas	344	=0.057	2528.60	2546.07	17.47
	Household size		=0.060			
	Day on which game was played: day 2+ (ref: day 1)		<0.05			

¹ Deviance information criterion

² DIC value for the null model (NM) with only an intercept

³ Δ DIC = NM DIC – Model DIC

⁴ The variables age and sex were carried forward to the last block even if they did not reach significance at $p < 0.05$. They were only eliminated at the very end if they did not reach significance at the $p < 0.05$ level (see Section 2.5.2).

C.2 UG Responder MAO (Chapter 3, Section 3.2.2)

C.2.1 Univariate Models

C.2.1.1 Normal linear models

Table C.4 Univariate associations between each predictor term (fixed effect) and UG MAO (models include constants). A Bonferroni correction has not been applied to these models as they were used for exploratory analyses. Values in bold are significant. *** $p < 0.01$; ** $p < 0.05$; * $p < 0.10$.

Model	Fixed effect	UG MAO (Indian rupees) $\beta \pm SE$	-2 Log likelihood			n
			Current model	Null model	Δ^1	
Village descriptors						
1	Population size	0.007 \pm 0.003*	1820.548	1825.341	4.793	248
2	Proportion of migrants	-4.458 \pm 5.652	1824.736	1825.341	0.605	248
3	Proportion of non-Korwas	-7.332 \pm 8.505	1824.588	1825.341	0.753	248
4	Household dispersion	-4.405 \pm 3.293	1823.534	1825.341	1.807	248
5A	Distance from major town (km)	0 \pm 0	1822.706	1825.341	2.635	248
5B	Distance from major town: 25-35 km (ref: 0-25 km)	-4.663 \pm 2.406*	1820.353	1825.341	4.988	248
	35-45 km (ref: 0-25 km)	-4.876 \pm 2.317**				
	45+ km (ref: 0-25 km)	-3.192 \pm 2.404				
Individual descriptors						
<i>Basic individual descriptors</i>						
6	Age (years)	0.005 \pm 0.049	1825.340	1825.341	0.001	248
7	Sex: female (ref: male)	-2.810 \pm 1.216**	1820.011	1825.341	5.330	248
8	Education:					
	Illiterate (ref: some schooling)	-3.900 \pm 1.454***	1817.996	1825.341	7.345	248
	Literate (ref: some schooling)	-2.086 \pm 1.888				
9	Household size (individuals)	0.245 \pm 0.249	1824.414	1825.341	0.927	248
10	Marriage: ever married (ref: never married)	-0.213 \pm 2.433	1825.336	1825.341	0.005	248
11	Day on which game was played: day 2+ (ref: day 1)	-0.514 \pm 1.231	1825.169	1825.341	0.172	248
<i>Residence and migration</i>						
12	Birthplace: this village (ref: other village)	1.643 \pm 1.272	1823.684	1825.341	1.657	248
13	Time resident in this village (years)	0.010 \pm 0.042	1825.295	1825.341	0.046	248
14	Number of times migrated	-0.128 \pm 0.831	1825.322	1825.341	0.019	248
15	Post-marital residence: natal village (ref: other village)	-0.125 \pm 1.339	1704.502	1704.504	0.002	231
<i>Wealth, markets and social networks</i>						
16	Proportion of earners in household	1.988 \pm 2.435	1824.665	1825.341	0.676	248
17	Months per year household eats self-grown rice	0.111 \pm 0.354	1825.265	1825.341	0.076	248
18	Outstanding loans: yes (ref: no)	0.878 \pm 1.356	1810.491	1810.897	0.406	246
19	Number of monthly visits to local bazaar	1.012 \pm 0.693	1823.508	1825.341	1.833	248
20	Number of monthly visits to nearest town	-0.156 \pm 0.219	1824.809	1825.341	0.532	248
21	People invited to harvest festival from own village	-0.011 \pm 0.054	1825.323	1825.341	0.018	248
22	People invited to harvest festival from other villages	0.250 \pm 0.119**	1821.166	1825.341	4.175	248
<i>Children and grandchildren</i>						
23	Children living	0.046 \pm 0.282	1825.320	1825.341	0.021	248
24	Children living together	0.135 \pm 0.299	1825.148	1825.341	0.193	248
25	Grandchildren living	0.109 \pm 0.290	1825.197	1825.341	0.144	248
26	Grandchildren living in village	0.093 \pm 0.364	1825.278	1825.341	0.063	248

<i>Kin</i>						
27	Mother living: yes (ref: no)	2.281 ± 1.218*	1821.819	1825.341	3.522	248
28	Mother living in village: yes (ref: no)	2.915 ± 1.273**	1820.112	1825.341	5.229	248
29	Mother participated in UG: yes (ref: no)	0.540 ± 1.983	1825.263	1825.341	0.078	248
30	Father living: yes (ref: no)	0.265 ± 1.229	1825.292	1825.341	0.049	248
31	Father living in village: yes (ref: no)	0.311 ± 1.332	1825.280	1825.341	0.061	248
32	Father participated in UG: yes (ref: no)	1.314 ± 2.242	1824.984	1825.341	0.357	248
33	Full brothers living	0.544 ± 0.546	1824.322	1825.341	1.019	248
34	Full brothers living in village	-0.345 ± 0.597	1825.059	1825.341	0.282	248
35	Full brothers aged < 15 years living in village	0.609 ± 1.771	1825.227	1825.341	0.114	248
36	Full brothers aged ≥ 15 years living in village	-0.457 ± 0.624	1824.877	1825.341	0.464	248
37	Full brothers living in other villages	1.575 ± 0.760**	1821.030	1825.341	4.311	248
38	Full brothers aged < 15 years living in other villages	0.905 ± 1.589	1825.013	1825.341	0.328	248
39	Full brothers aged ≥ 15 years living in other villages	2.021 ± 0.924**	1820.547	1825.341	4.794	248
40	Full brothers participated in UG	-0.150 ± 0.977	1825.332	1825.341	0.009	248
41	Full sisters living	0.053 ± 0.529	1825.333	1825.341	0.008	248
42	Full sisters living in village	0.226 ± 0.781	1825.253	1825.341	0.088	248
43	Full sisters aged < 15 years living in village	0.593 ± 1.371	1825.146	1825.341	0.195	248
44	Full sisters aged ≥ 15 years living in village	0.054 ± 1.009	1825.347	1825.341	-0.006	248
45	Full sisters living in other villages	-0.082 ± 0.676	1825.333	1825.341	0.008	248
46	Full sisters aged < 15 years living in other villages	2.847 ± 2.331	1823.839	1825.341	1.502	248
47	Full sisters aged ≥ 15 years living in other villages	-0.349 ± 0.705	1825.104	1825.341	0.237	248
48	Full sisters participated in UG	1.408 ± 1.612	1824.559	1825.341	0.782	248
49	Proposer offer	0.015 ± 0.075	1825.304	1825.341	0.037	248

¹ $\Delta = -2 \text{ Log Likelihood of null model} - (-2 \text{ Log likelihood of current model})$

C.2.1.2 Ordinal multinomial models

Table C.5 Univariate associations between each predictor term (fixed effect) and logit (probability of UG MAO Indian Rupees 10+ or below) (models include constants). A Bonferroni correction has not been applied to these models as they were used for exploratory analyses. Values in bold are significant. ***p<0.01; **p<0.05; *p<0.10.

Model	Fixed effect	Logit (probability of UG MAO Indian Rupees 10+ or below) $\beta \pm SE$	-2 Log likelihood			n
			Current model	Null model	Δ^1	
Village descriptors						
1	Population size	-0.001 ± 0.001**	536.391	548.483	12.092	248
2	Proportion of migrants	0.085 ± 1.066	548.320	548.483	0.163	248
3	Proportion of non-Korwas	1.228 ± 1.579	544.717	548.483	3.766	248
4	Household dispersion	0.843 ± 0.615	539.327	548.483	9.156	248
5A	Distance from major town (km)	0 ± 0	543.568	548.483	4.915	248
5B	Distance from major town: 25-35 km (ref: 0-25 km)	0.984 ± 0.450**	534.864	548.483	13.619	248
	35-45 km (ref: 0-25 km)	0.753 ± 0.430*				
	45+ km (ref: 0-25 km)	0.547 ± 0.444				
Individual descriptors						
<i>Basic individual descriptors</i>						
6	Age (years)	0.013 ± 0.010	547.619	548.483	0.864	248
7	Sex: female (ref: male)	0.688 ± 0.248***	529.969	548.483	18.514	248
8	Education:					
	Illiterate (ref: some schooling)	1.170 ± 0.297***	514.761	548.483	33.722	248
	Literate (ref: some schooling)	0.341 ± 0.374				
9	Household size (individuals)	-0.103 ± 0.050**	543.523	548.483	4.960	248
10	Marriage: ever married (ref: never married)	0.444 ± 0.473	547.800	548.483	0.683	248
11	Day on which game was played: day 2+ (ref: day 1)	0.147 ± 0.243	548.390	548.483	0.093	248
<i>Residence and migration</i>						
12	Birthplace: this village (ref: other village)	-0.242 ± 0.252	546.228	548.483	2.255	248
13	Time resident in this village (years)	0.009 ± 0.008	547.637	548.483	0.846	248
14	Number of times migrated	-0.072 ± 0.163	548.214	548.483	0.269	248
15	Post-marital residence: natal village (ref: other village)	-0.087 ± 0.261	509.702	509.643	-0.059	231
<i>Wealth, markets and social networks</i>						

C.2 UG RESPONDER MAO

16	Proportion of earners in household	-0.091 ± 0.479	548.168	548.483	0.315	248
17	Months per year household eats self-grown rice	-0.060 ± 0.069	547.978	548.483	0.505	248
18	Outstanding loans: yes (ref: no)	-0.452 ± 0.264*	535.036	540.463	5.427	246
19	Number of monthly visits to local bazaar	-0.203 ± 0.137	544.196	548.483	4.287	248
20	Number of monthly visits to nearest town	0.098 ± 0.044**	541.811	548.483	6.672	248
21	People invited to harvest festival from own village	-0.004 ± 0.010	549.287	548.483	-0.804	248
22	People invited to harvest festival from other villages	-0.042 ± 0.024*	543.02	548.483	5.463	248
<i>Children and grandchildren</i>						
23	Children living	-0.011 ± 0.055	548.509	548.483	-0.026	248
24	Children living together	-0.025 ± 0.059	548.547	548.483	-0.064	248
25	Grandchildren living	-0.009 ± 0.057	548.289	548.483	0.194	248
26	Grandchildren living in village	0.016 ± 0.072	548.73	548.483	-0.247	248
<i>Kin</i>						
27	Mother living: yes (ref: no)	-0.491 ± 0.245**	527.873	532.095	4.222	248
28	Mother living in village: yes (ref: no)	-0.684 ± 0.256***	523.11	532.095	8.985	248
29	Mother participated in UG: yes (ref: no)	-0.435 ± 0.389	530.996	532.095	1.099	248
30	Father living: yes (ref: no)	-0.222 ± 0.243	530.438	532.095	1.657	248
31	Father living in village: yes (ref: no)	-0.399 ± 0.263	529.439	532.095	2.656	248
32	Father participated in UG: yes (ref: no)	-0.721 ± 0.440	528.507	532.095	3.588	248
33	Full brothers living	-0.266 ± 0.347	530.864	532.095	1.231	248
34	Full brothers living in village	0.015 ± 0.118	531.901	532.095	0.194	248
35	Full brothers aged < 15 years living in village	-0.266 ± 0.347	530.864	532.095	1.231	248
36	Full brothers aged ≥ 15 years living in village	0.054 ± 0.124	531.426	532.095	0.669	248
37	Full brothers living in other villages	-0.159 ± 0.150	529.944	532.095	2.151	248
38	Full brothers aged < 15 years living in other villages	-0.164 ± 0.311	531.164	532.095	0.931	248
39	Full brothers aged ≥ 15 years living in other villages	-0.178 ± 0.183	530.751	532.095	1.344	248
40	Full brothers participated in UG	-0.116 ± 0.192	531.253	532.095	0.842	248
41	Full sisters living	0.011 ± 0.105	532.023	532.095	0.072	248
42	Full sisters living in village	0.095 ± 0.156	531.397	532.095	0.698	248
43	Full sisters aged < 15 years living in village	-0.099 ± 0.269	531.902	532.095	0.193	248
44	Full sisters aged ≥ 15 years living in village	0.206 ± 0.203	529.398	532.095	2.697	248
45	Full sisters living in other villages	-0.051 ± 0.133	531.624	532.095	0.471	248
46	Full sisters aged < 15 years living in other villages	-0.336 ± 0.457	530.584	532.095	1.511	248
47	Full sisters aged ≥ 15 years living in other villages	-0.032 ± 0.139	532.013	532.095	0.082	248
48	Full sisters participated in UG	-0.114 ± 0.317	531.954	532.095	0.141	248

¹ Δ = -2 Log Likelihood of null model – (-2 Log likelihood of current model)

C.2.2 Domain-wise models

C.2.2.1 Normal linear models

Table C.6 Multivariate associations between domains of predictor terms (fixed effects) and UG MAO (models include constants). Values in bold are significant. ***p<0.01; **p<0.05; *p<0.10.

Model	Fixed effect	UG MAO (Indian rupees) $\beta \pm SE$	-2 Log likelihood			n
			Current model	Null model	Δ^1	
1	Village descriptors					
A	Population size	0.001 \pm 0.007	1819.636	1825.341	5.705	248
	Proportion of migrants	-0.493 \pm 7.105				
	Proportion of non-Korwas	-5.713 \pm 10.222				
	Household dispersion	-2.954 \pm 5.594				
	Distance from major town (km)	0 \pm 0				
B	Population size	-0.001 \pm 0.010	1820.073	1825.341	5.268	248
	Proportion of migrants	0.898 \pm 7.617				
	Proportion of non-Korwas	7.522 \pm 13.456				
	Household dispersion	-6.366 \pm 8.358				
	Distance from major town: 25-35 km (ref: 0-25 km)	-5.640 \pm 4.736				
	35-45 km (ref: 0-25 km)	-5.683 \pm 4.857				
	45+ km (ref: 0-25 km)	-4.106 \pm 5.241				
	Individual descriptors					
2	Basic individual descriptors					
	Age (years)	0.051 \pm 0.058	1813.546	1825.341	11.795	248
	Sex: female (ref: male)	-1.967 \pm 1.367				
	Education:					
	Illiterate (ref: some schooling)	-3.762 \pm 1.682**				
	Literate (ref: some schooling)	-3.221 \pm 2.017				
	Household size (individuals)	0.270 \pm 0.250				
	Marriage: ever married (ref: never married)	0.180 \pm 2.603				
	Day on which game was played: day 2+ (ref: day 1)	-0.489 \pm 1.227				
3	Residence and migration					
	Birthplace: this village (ref: other village)	5.646 \pm 2.490**	1699.290	1704.472	5.182	231
	Time resident in this village (years)	0.008 \pm 0.052				

	Number of times migrated	0.180 ± 1.178				
	Post-marital residence: natal village (ref: other village)	-4.826 ± 2.763*				
4	<i>Wealth, markets and social networks</i>					
	Proportion of earners in household	2.187 ± 2.451	1801.629	1810.866	9.237	246
	Months per year household eats self-grown rice	0.150 ± 0.359				
	Outstanding loans: yes (ref: no)	0.416 ± 1.401				
	Number of monthly visits to local bazaar	1.152 ± 0.723				
	Number of monthly visits to nearest town	-0.140 ± 0.239				
	People invited to harvest festival from own village	-0.061 ± 0.062				
	People invited to harvest festival from other villages	0.310 ± 0.132**				
5	<i>Children and grandchildren</i>					
	Children living	-1.794 ± 1.136	1822.448	1825.341	2.893	248
	Children living together	2.015 ± 1.214*				
	Grandchildren living	0.971 ± 0.804				
	Grandchildren living in village	-0.473 ± 0.846				
6	<i>Kin</i>					
A	Mother living: yes (ref: no)	0.080 ± 1.897	1818.261	1825.341	7.080	248
	Mother living in village: yes (ref: no)	4.000 ± 2.267*				
	Mother participated in UG: yes (ref: no)	-2.357 ± 2.512				
	Father living: yes (ref: no)	1.027 ± 2.044				
	Father living in village: yes (ref: no)	-2.243 ± 2.481				
	Father participated in UG: yes (ref: no)	1.693 ± 2.791				
B	Full siblings living	0.007 ± 0.549	1820.043	1825.341	5.298	248
	Full brothers aged < 15 years living in village	0.991 ± 2.011				
	Full brothers aged ≥ 15 years living in village	-0.297 ± 1.030				
	Full brothers aged < 15 years living in other villages	0.538 ± 1.800				
	Full brothers aged ≥ 15 years living in other villages	1.993 ± 1.114*				
	Full brothers participated in UG	0.553 ± 1.296				
C	Full siblings living	0.536 ± 0.566	1820.985	1825.341	4.356	248
	Full sisters aged < 15 years living in village	0.257 ± 1.592				
	Full sisters aged ≥ 15 years living in village	-1.658 ± 1.544				
	Full sisters aged < 15 years living in other villages	2.307 ± 2.455				
	Full sisters aged ≥ 15 years living in other villages	-0.890 ± 0.906				
	Full sisters participated in UG	2.671 ± 2.119				

¹ Δ = -2 Log Likelihood of null model – (-2 Log likelihood of current model)

C.2.2.2 Ordinal multinomial models

Table C.7 Multivariate associations between domains of predictor terms (fixed effects) and logit (probability of UG MAO Indian Rupees 10+ or below) (models include constants). Values in bold are significant. ***p<0.01; **p<0.05; *p<0.10.

Model	Fixed effect	Logit (probability of UG MAO Indian Rupees 10+ or below) $\beta \pm SE$	-2 Log likelihood			n
			Current model	Null model	Δ^1	
1	Village descriptors					
A	Population size	-0.001 \pm 0.001	533.175	548.483	15.308	248
	Proportion of migrants	-1.505 \pm 1.335				
	Proportion of non-Korwas	-0.301 \pm 1.906				
	Household dispersion	0.513 \pm 1.040				
	Distance from major town (km)	0 \pm 0				
B	Population size	-0.001 \pm 0.002	526.452	548.483	22.031	248
	Proportion of migrants	-1.572 \pm 1.305				
	Proportion of non-Korwas	-2.559 \pm 2.263				
	Household dispersion	1.256 \pm 1.385				
	Distance from major town: 25-35 km (ref: 0-25 km)	1.082 \pm 0.803				
	35-45 km (ref: 0-25 km)	0.743 \pm 0.822				
	45+ km (ref: 0-25 km)	0.512 \pm 0.883				
	Individual descriptors					
2	Basic individual descriptors					
	Age (years)	-0.003 \pm 0.012	501.301	548.483	47.182	248
	Sex: female (ref: male)	0.382 \pm 0.280				
	Education:					
	Illiterate (ref: some schooling)	1.025 \pm 0.343***				
	Literate (ref: some schooling)	0.448 \pm 0.403				
	Household size (individuals)	-0.100 \pm 0.051*				
	Marriage: ever married (ref: never married)	0.315 \pm 0.525				
	Day on which game was played: day 2+ (ref: day 1)	0.092 \pm 0.250				
3	Residence and migration					
	Birthplace: this village (ref: other village)	-1.164 \pm 0.526**	495.772	509.643	13.871	231
	Time resident in this village (years)	0.008 \pm 0.010				
	Number of times migrated	-0.224 \pm 0.231				

	Post-marital residence: natal village (ref: other village)	0.702 ± 0.574				
4	Wealth, markets and social networks					
	Proportion of earners in household	-0.124 ± 0.494	512.903	540.463	27.560	246
	Months per year household eats self-grown rice	-0.079 ± 0.072				
	Outstanding loans: yes (ref: no)	-0.388 ± 0.280				
	Number of monthly visits to local bazaar	-0.312 ± 0.148**				
	Number of monthly visits to nearest town	0.101 ± 0.051**				
	People invited to harvest festival from own village	0.006 ± 0.012				
	People invited to harvest festival from other villages	-0.045 ± 0.028				
5	Children and grandchildren					
	Children living	0.307 ± 0.245	545.231	548.483	3.252	248
	Children living together	-0.344 ± 0.261				
	Grandchildren living	-0.224 ± 0.164				
	Grandchildren living in village	0.183 ± 0.168				
6	Kin					
A	Mother living: yes (ref: no)	-0.085 ± 0.381	520.415	548.483	28.068	248
	Mother living in village: yes (ref: no)	-0.607 ± 0.451				
	Mother participated in UG: yes (ref: no)	0.282 ± 0.495				
	Father living: yes (ref: no)	0.017 ± 0.410				
	Father living in village: yes (ref: no)	-0.022 ± 0.495				
	Father participated in UG: yes (ref: no)	-0.534 ± 0.550				
B	Full siblings living	0.033 ± 0.109	523.802	548.483	24.681	248
	Full brothers aged < 15 years living in village	-0.371 ± 0.396				
	Full brothers aged ≥ 15 years living in village	0.099 ± 0.207				
	Full brothers aged < 15 years living in other villages	-0.206 ± 0.354				
	Full brothers aged ≥ 15 years living in other villages	-0.212 ± 0.220				
	Full brothers participated in UG	-0.313 ± 0.258				
C	Full siblings living	-0.089 ± 0.112	522.835	548.483	25.648	248
	Full sisters aged < 15 years living in village	-0.087 ± 0.312				
	Full sisters aged ≥ 15 years living in village	0.576 ± 0.319*				
	Full sisters aged < 15 years living in other villages	-0.195 ± 0.478				
	Full sisters aged ≥ 15 years living in other villages	0.067 ± 0.179				
	Full sisters participated in UG	-0.620 ± 0.427				

¹ Δ = -2 Log Likelihood of null model – (-2 Log likelihood of current model)

C.2.3 Full model fitting summary

C.2.3.1 Normal linear models

Table C.8 Summary of model-fitting process in the fourth stage of analyses. Variables in bold are significant predictors of UG MAO at $p < 0.05$ and were retained in the next listed model.

Model	Fixed effect	n	p	DIC ¹	NM DIC ²	Δ DIC ³
Block 1						
1	Age ⁴	231	>0.05	1704.07	1708.77	4.7
	Sex ⁴		>0.05			
	Education: illiterate		>0.05			
	literate (ref: some schooling)		>0.05			
	Birthplace		=0.069			
	Post-marital residence		=0.057			
People invited to harvest festival from other villages						
<hr/>						
2A	Age ⁴	231	>0.05	1706.95	1708.77	1.82
	Sex		<0.05			
	Post-marital residence		>0.05			
	People invited to harvest festival from other villages		>0.05			
<hr/>						
2B	Age ⁴	248	>0.05	1827.46	1829.94	2.48
	Sex ⁴		>0.05			
	Birthplace		>0.05			
	People invited to harvest festival from other villages		=0.051			
<hr/>						
2C	Age ⁴	231	>0.05	1704.39	1708.77	4.38
	Sex		<0.05			
	Birthplace		<0.05			
	Post-marital residence		<0.05			
	People invited to harvest festival from other villages		>0.05			
<hr/>						
3	Age ⁴	231	>0.05	1706.41	1708.77	2.36
	Sex		<0.05			
	Birthplace		<0.05			
	Post-marital residence		<0.05			
<hr/>						
4	Age ⁴	248	>0.05	1826.46	1829.94	3.48
	Sex		<0.05			
	People invited to harvest festival from other villages		=0.058			
	Block 2					
<hr/>						
5	Age ⁴	231	>0.05	1706.37	1708.77	2.4
	Sex		<0.05			
	Birthplace		<0.05			
	Post-marital residence		<0.05			
	People invited to harvest festival from other villages		>0.05			
	Children living together		>0.05			
<hr/>						
6	Age ⁴	231	>0.05	1706.41	1708.77	2.36
	Sex		<0.05			
	Birthplace		<0.05			
	Post-marital residence		<0.05			
Block 3						
<hr/>						
7	Age ⁴	231	>0.05	1697.93	1708.77	10.84
	Sex		<0.05			
	Birthplace		<0.05			
	Post-marital residence		<0.05			
	Mother living in village		<0.05			
	Full brothers aged \geq 15 years living in other villages		<0.05			
<hr/>						
8	Sex	231	<0.05	1695.83	1708.77	12.94
	Birthplace		<0.05			
	Post-marital residence		<0.05			
	Mother living in village		<0.05			
	Full brothers aged \geq 15 years living in other villages		<0.05			

¹Deviance information criterion ²DIC value for the null model (NM) with only an intercept. ³ Δ DIC = NM DIC – Model DIC

⁴The variables age and sex were carried forward to the last block even if they did not reach significance at $p < 0.05$. They were only eliminated at the very end if they did not reach significance at the $p < 0.05$ level (see Section 2.5.2).

C.2.3.2 Ordinal multinomial models

Table C.9 Summary of model-fitting process in the fourth stage of analyses. Variables in bold are significant predictors of the logit (probability of UG MAO Indian rupees 10+ or below) at $p < 0.05$ and were retained in the next listed model.

Model	Fixed effect	n	p	DIC ¹	NM DIC ²	Δ DIC ³
Block 1						
1	Age ⁴	248	>0.05	509.17	523.27	14.1
	Sex ⁴		>0.05			
	Education: illiterate		<0.05			
	literate (ref: some schooling)		>0.05			
	Household size		=0.076			
	Birthplace		>0.05			
	Number of monthly visits to local bazaar		>0.05			
	Number of monthly visits to town		<0.05			
2A	Age ⁴	248	>0.05	506.88	523.27	16.39
	Sex ⁴		>0.05			
	Education: illiterate		<0.05			
	literate (ref: some schooling)		>0.05			
	Number of monthly visits to town		<0.05			
2B	Age ⁴	248	>0.05	507.76	523.27	15.51
	Sex ⁴		>0.05			
	Education: illiterate		<0.05			
	literate (ref: some schooling)		>0.05			
	Household size		=0.086			
	Birthplace		>0.05			
	Number of monthly visits to town		<0.05			
Block 2						
3	Age ⁴	248	>0.05	506.88	523.27	16.39
	Sex ⁴		>0.05			
	Education: illiterate		<0.05			
	literate (ref: some schooling)		>0.05			
	Number of monthly visits to town		<0.05			
Block 3						
4	Age ⁴	248	>0.05	507.16	523.27	16.11
	Sex ⁴		>0.05			
	Education: illiterate		<0.05			
	literate (ref: some schooling)		>0.05			
	Number of monthly visits to town		<0.05			
	Full sisters aged ≥ 15 years living in village		>0.05			
5	Education: illiterate	248	<0.05	506.08	523.27	17.19
	literate (ref: some schooling)		>0.05			
	Number of monthly visits to town		<0.05			

¹ Deviance information criterion² DIC value for the null model (NM) with only an intercept.³ Δ DIC = NM DIC – Model DIC⁴ The variables age and sex were carried forward to the last block even if they did not reach significance at $p < 0.05$. They were only eliminated at the very end if they did not reach significance at the $p < 0.05$ level (see Section 2.5.2).

C.3 Salt decision and PGG1 contribution (Chapter 4, Section 4.2)

C.3.1 Univariate Models

Table C.10 Univariate associations between each predictor term (fixed effect) and Salt deviation & PGG1 contribution respectively (models include constants). A Bonferroni correction has not been applied to these models as they were used for exploratory analyses. Values in bold are significant. *** $p < 0.01$; ** $p < 0.05$; * $p < 0.10$.

Model	Fixed effect	Salt deviation (g) $\beta \pm SE$	PGG1 contribution (Indian rupees) $\beta \pm SE$	Residual correlation ¹		-2 Log likelihood			n
				Village level	Individual level	Current model	Null model	Δ^2	
Village descriptors									
1	Population size	-3.245 ± 1.188***	-0.001 ± 0.002	0.480	0.046	7461.692	7467.740	6.048	413
2	Proportion of migrants	3165.609 ± 1669.468*	0.799 ± 2.461	0.455	0.044	7464.459	7467.740	3.281	413
3	Proportion of non-Korwas	2300.910 ± 2966.843	2.069 ± 3.994	0.432	0.042	7467.020	7467.740	0.720	413
4	Household dispersion	1388.781 ± 1141.639	0.020 ± 1.559	0.476	0.044	7466.227	7467.740	1.513	413
5A	Distance from major town (km)	-0.006 ± 0.024	0 ± 0	0.463	0.042	7467.658	7467.740	0.082	413
5B	Distance from major town: 25-35 km (ref: 0-25 km)	532.815 ± 903.751	1.622 ± 1.192	0.373	0.043	7465.421	7467.740	2.319	413
	35-45 km (ref: 0-25 km)	322.370 ± 870.015	1.357 ± 1.111						
	45+ km (ref: 0-25 km)	412.317 ± 909.118	0.790 ± 1.174						
Individual descriptors									
<i>Basic individual descriptors</i>									
6	Age (years)	-12.019 ± 11.946	0.075 ± 0.027***	0.473	0.058	7458.949	7467.740	8.791	413
7	Sex: female (ref: male)	542.688 ± 289.246*	0.213 ± 0.639	0.439	0.042	7464.179	7467.740	3.561	413
Education:									
8	Illiterate (ref: some schooling)	-276.510 ± 349.900	1.012 ± 0.701	0.315	0.053	7462.818	7467.740	4.922	413
	Literate (ref: some schooling)	-704.591 ± 485.786	1.285 ± 0.919						
9	Household size (individuals)	-52.645 ± 59.464	-0.108 ± 0.126	0.411	0.040	7466.310	7467.740	1.430	413
10	Marriage: ever married (ref: never married)	-469.919 ± 575.016	1.134 ± 1.184	0.419	0.044	7466.148	7467.740	1.592	413
<i>Residence and migration</i>									
11	Birthplace: this village (ref: other village)	-231.720 ± 291.530	0.118 ± 0.640	0.470	0.043	7467.065	7467.740	0.675	413
12	Time resident in this village (years)	-9.485 ± 9.509	0.044 ± 0.022**	0.557	0.048	7462.624	7467.740	5.116	413
13	Number of times migrated	-56.339 ± 192.869	0.161 ± 0.430	0.433	0.045	7467.512	7467.740	0.228	413
14	Post-marital residence: natal village (ref: other village)	-250.573 ± 310.788	0.166 ± 0.657	0.869	0.048	6971.787	6973.534	1.747	385
<i>Wealth, markets and social networks</i>									
15	Proportion of earners in household	814.478 ± 612.807	0.268 ± 1.380	0.474	0.038	7465.961	7467.740	1.779	413
16	Months per year household eats self-grown rice	111.572 ± 66.553*	-0.144 ± 0.137	0.454	0.041	7463.755	7467.740	3.985	413
17	Outstanding loans: yes (ref: no)	-550.810 ± 365.483	-0.327 ± 0.684	0.437	0.034	7465.479	7467.740	2.261	413

C.3 SALT DECISION AND PGG1 CONTRIBUTION

18	Number of monthly visits to local bazaar	-73.300 ± 193.511	-0.270 ± 0.371	0.467	0.041	7467.100	7467.740	0.640	413
19	Number of monthly visits to nearest town	43.051 ± 49.455	-0.019 ± 0.077	0.499	0.040	7466.877	7467.740	0.863	413
20	People invited to harvest festival from own village	22.057 ± 17.414	-0.001 ± 0.033	0.423	0.047	7466.133	7467.740	1.607	413
21	People invited to harvest festival from other villages	15.584 ± 25.830	0.125 ± 0.054**	0.699	0.042	7463.002	7467.740	4.738	413
Children and grandchildren									
22	Children living	-141.195 ± 67.358**	0.047 ± 0.152	0.513	0.042	7463.276	7467.740	4.464	413
23	Children living together	-124.866 ± 71.553*	-0.027 ± 0.165	0.491	0.037	7464.708	7467.740	3.032	413
24	Grandchildren living	29.056 ± 67.334	0.248 ± 0.197	0.445	0.039	7466.022	7467.740	1.718	413
25	Grandchildren living in village	23.401 ± 91.542	0.311 ± 0.280	0.461	0.041	7466.463	7467.740	1.277	413
Kin									
26	Mother living yes: (ref: no)	280.509 ± 293.872	-0.658 ± 0.633	0.520	0.043	7465.704	7467.740	2.036	413
27	Mother living in village: yes (ref: no)	-133.129 ± 315.666	-0.522 ± 0.655	0.462	0.045	7466.953	7467.740	0.787	413
28	Mother participated in PGG: yes (ref: no)	349.917 ± 696.689	-2.464 ± 1.196**	0.257	0.043	5647.886	5652.436	4.550	328
29	Father living yes: (ref: no)	57.966 ± 287.120	-0.679 ± 0.628	0.411	0.045	7466.559	7467.740	1.181	413
30	Father living in village: yes (ref: no)	-176.809 ± 322.733	-0.270 ± 0.670	0.436	0.043	7467.292	7467.740	0.448	413
31	Father participated in PGG: yes (ref: no)	411.534 ± 650.924	-1.507 ± 1.158	0.069	0.048	5650.278	5652.436	2.158	328
32	Full brothers living	81.218 ± 128.101	-0.168 ± 0.273	0.390	0.044	7466.961	7467.740	0.779	413
33	Full brothers living in village	-106.153 ± 143.357	-0.010 ± 0.304	0.467	0.044	7467.195	7467.740	0.545	413
34	Full brothers aged < 15 years living in village	98.398 ± 318.446	-0.339 ± 0.731	0.457	0.043	7467.421	7467.740	0.319	413
35	Full brothers aged ≥ 15 years living in village	-152.268 ± 157.041	0.057 ± 0.326	0.494	0.045	7466.770	7467.740	0.970	413
37	Full brothers living in other villages	218.516 ± 148.075	-0.309 ± 0.361	0.408	0.048	7464.785	7467.740	2.955	413
36	Full brothers aged < 15 years living in other villages	45.137 ± 311.478	-1.184 ± 0.636*	0.419	0.046	7464.288	7467.740	3.452	413
38	Full brothers aged ≥ 15 years living in other villages	286.578 ± 173.034	0.117 ± 0.452	0.409	0.044	7464.981	7467.740	2.759	413
39	Full brothers participated in PGG	-493.519 ± 383.162	-0.109 ± 0.678	0.047	0.042	5650.721	5652.436	1.715	328
40	Full sisters living	-89.077 ± 118.029	0.069 ± 0.269	0.466	0.043	7467.089	7467.740	0.651	413
41	Full sisters living in village	-290.202 ± 180.151	0.244 ± 0.413	0.539	0.045	7464.757	7467.740	2.983	413
42	Full sisters aged < 15 years living in village	62.580 ± 272.562	0.554 ± 0.688	0.462	0.039	7467.054	7467.740	0.686	413
43	Full sisters aged ≥ 15 years living in village	-682.429 ± 261.379***	0.054 ± 0.536	0.587	0.043	7461.019	7467.740	6.721	413
44	Full sisters living in other villages	49.205 ± 141.726	-0.044 ± 0.323	0.468	0.042	7467.599	7467.740	0.141	413
45	Full sisters aged < 15 years living in other villages	238.391 ± 370.545	-0.268 ± 0.920	0.454	0.045	7467.230	7467.740	0.510	413
46	Full sisters aged ≥ 15 years living in other villages	18.423 ± 159.939	-0.014 ± 0.360	0.462	0.042	7467.725	7467.740	0.015	413
47	Full sisters participated in PGG	-2121.181 ± 687.743***	0.694 ± 1.286	0.030	0.032	5642.745	5652.436	9.691	328
48	Total amount of salt available³	-1.233 ± 0.498***				5588.363	5593.843	5.480	302

¹ Correlation between Salt deviation and PGG1 contribution. ² $\Delta = -2 \text{ Log Likelihood of null model} - (-2 \text{ Log likelihood of current model})$

³ This is a univariate response model; salt deviation is the response variable and total amount of salt available is the only fixed effect.

C.3 SALT DECISION AND PGG1 CONTRIBUTION

C.3.2 Domain-wise models

Table C.11 Multivariate associations between domains of predictor terms (fixed effects) and Salt deviation & PGG1 contribution respectively (models include constants). Values in bold are significant. ***p<0.01; **p<0.05; *p<0.10.

Mode l	Fixed effect	Salt deviation (g) $\beta \pm SE$	PGG1 contribution (Indian rupees) $\beta \pm SE$	Residual correlation ¹		-2 Log likelihood		Δ^2	n
				Village level	Individual level	Current model	Null model		
1	Village descriptors								
A	Population Size	-6.626 ± 2.035**	-0.001 ± 0.003	0.663	0.039	7454.254	7467.740	13.486	413
	Proportion of migrants	1486.957 ± 1706.084	1.746 ± 3.509						
	Proportion of non-Korwas	865.413 ± 2475.859	3.659 ± 5.127						
	Household dispersion	-3239.822 ± 1459.157*	-1.813 ± 2.724						
	Distance from major town (km)	-0.062 ± 0.027*	0 ± 0						
B	Population size	-6.279 ± 2.503**	0.004 ± 0.004	1.072	0.045	7452.569	7467.740	15.171	413
	Proportion of migrants	2622.388 ± 1773.903	2.062 ± 3.23						
	Proportion of non-Korwas	4854.912 ± 3352.811	-2.764 ± 5.918						
	Household dispersion	-4211.28 ± 2223.623*	2.015 ± 3.381						
	Distance from major town: 25-35 km (ref: 0-25 km)	-1708.313 ± 1185.381	3.322 ± 2.044						
	35-45 km (ref: 0-25 km)	-2046.77 ± 1253.946	3.133 ± 2.057						
	45+ km (ref: 0-25 km)	-2027.191 ± 1322.038	2.488 ± 2.183						
	Individual descriptors								
2	Basic individual descriptors								
	Age (years)	-0.592 ± 14.083	0.070 ± 0.032**	0.373	0.055	7451.441	7467.740	16.299	413
	Sex: female (ref: male)	680.289 ± 329.782**	0.371 ± 0.695						
	Education:								
	Illiterate (ref: some schooling)	-470.939 ± 410.184	0.187 ± 0.802						
	Literate (ref: some schooling)	-526.473 ± 506.037	0.515 ± 0.981						
	Household size (individuals)	-55.824 ± 59.494	-0.081 ± 0.126						
	Marriage: ever married (ref: never married)	-504.254 ± 626.889	-0.174 ± 1.267						
3	Residence and migration								
	Birthplace: this village (ref: other village)	-87.644 ± 763.658	-0.394 ± 1.844	1.154	0.058	6965.558	6973.534	7.976	385
	Time resident in this village (years)	-5.654 ± 12.372	0.056 ± 0.026**						
	Number of times migrated	-281.327 ± 264.675	0.517 ± 0.609						
	Post-marital residence: natal village (ref: other village)	-341.197 ± 797.520	0.254 ± 1.880						

C.3 SALT DECISION AND PGG1 CONTRIBUTION

4	Wealth, markets and social networks								
	Proportion of earners in household	930.744 ± 615.681	0.273 ± 1.383	0.483	0.027	7450.606	7467.740	17.134	413
	Months per year household eats self-grown rice	124.113 ± 67.654*	-0.133 ± 0.139						
	Outstanding loans: yes (ref: no)	-594.728 ± 374.409	-0.527 ± 0.683						
	Number of monthly visits to local bazaar	-216.445 ± 202.518	-0.158 ± 0.384						
	Number of monthly visits to nearest town	52.431 ± 52.454	-0.004 ± 0.079						
	People invited to harvest festival from own village	20.248 ± 18.665	-0.021 ± 0.033						
	People invited to harvest festival from other villages	15.453 ± 27.291	0.136 ± 0.06**						
5	Children and grandchildren								
	Children living	-560.996 ± 266.918**	0.482 ± 0.644	0.466	0.037	7457.890	7467.740	9.850	413
	Children living together	449.501 ± 283.232	-0.511 ± 0.694						
	Grandchildren living	323.256 ± 202.462	-0.013 ± 0.436						
	Grandchildren living in village	-278.531 ± 240.7	0.189 ± 0.489						
6	Kin								
A	Mother living: yes (ref: no)	468.45 ± 553.937	-0.138 ± 1.138	0.190	0.055	5642.114	5652.436	10.322	328
	Mother living in village: yes (ref: no)	-514.912 ± 717.56	-0.658 ± 1.368						
	Mother participated in PGG: yes (ref: no)	522.792 ± 827.285	-1.865 ± 1.419						
	Father living: yes (ref: no)	242.37 ± 585.558	-0.904 ± 1.162						
	Father living in village: yes (ref: no)	-792.477 ± 818.813	0.976 ± 1.426						
	Father participated in PGG: yes (ref: no)	870.913 ± 822.807	-0.636 ± 1.409						
B	Full siblings living	-230.256 ± 164.268	0.104 ± 0.322	-0.139	0.058	5642.497	5652.436	9.939	328
	Full brothers aged < 15 years living in village	468.845 ± 522.5	-0.632 ± 1.014						
	Full brothers aged ≥ 15 years living in village	116.896 ± 357.981	-0.072 ± 0.62						
	Full brothers aged < 15 years living in other villages	423.853 ± 482.909	-1.464 ± 0.843*						
	Full brothers aged ≥ 15 years living in other villages	567.546 ± 324.858*	0.335 ± 0.727						
	Full brothers participated in PGG	-301.817 ± 482.11	-0.210 ± 0.913						
C	Full siblings living	-25.604 ± 187.973	-0.230 ± 0.354	-0.337	0.047	5634.698	5652.436	17.738	328
	Full sisters aged < 15 years living in village	438.874 ± 472.594	0.898 ± 0.987						
	Full sisters aged ≥ 15 years living in village	-1388.38 ± 576.35**	-0.444 ± 0.926						
	Full sisters aged < 15 years living in other villages	133.034 ± 537.277	-0.222 ± 1.177						
	Full sisters aged ≥ 15 years living in other villages	59.674 ± 293.866	0.339 ± 0.540						
	Full sisters participated in PGG	-756.291 ± 868.241	1.305 ± 1.540						

¹ Correlation between Salt deviation and PGG1 contribution. ²Δ = -2 Log Likelihood of null model - (-2 Log likelihood of current model)

C.3 SALT DECISION AND PGG1 CONTRIBUTION

C.3.3 Full model fitting summary

Table C.12 Summary of model-fitting process in the fourth stage of analyses. Variables in bold are significant predictors of either PGG1 contribution or Salt deviation at $p < 0.05$ and were retained in the next listed model.

Model	Fixed effect	n	p	DIC ¹	NM DIC ²	Δ DIC ³
Block 1						
1	Population size Age ⁴ Sex ⁴ Household dispersion Distance from major town Time resident in this village Months per year household eats self-grown rice People invited to harvest festival from other villages	413	<0.05 >0.05 >0.05 >0.05 <0.05 >0.05 >0.05 <0.05	12832.04	12832.15	0.11
2	Population size Age Sex ⁴ Distance from major town People invited to harvest festival from other villages	413	<0.05 <0.05 >0.05 >0.05 <0.05	12827.67	12832.15	4.48
3	Population size Age Sex ⁴ People invited to harvest festival from other villages	413	<0.05 <0.05 >0.05 <0.05	12825.40	12832.15	6.75
Block 2						
4	Population size Age Sex ⁴ People invited to harvest festival from other villages Children living	413	<0.05 <0.05 >0.05 <0.05 >0.05	12824.89	12832.15	7.26
Block 3						
5	Population size Age Sex ⁴ People invited to harvest festival from other villages Full brothers aged < 15 years living in other villages Full brothers aged \geq 15 years living in other villages Full sisters aged \geq 15 years living in village	413	<0.05 <0.05 >0.05 <0.05 >0.05 >0.05 <0.05	12826.00	12832.15	6.15
6	Population size Age Sex People invited to harvest festival from other villages Full sisters aged \geq 15 years living in village	413	<0.05 <0.05 >0.05 <0.05 <0.05	12821.46	12832.15	10.69
7	Population size Age People invited to harvest festival from other villages Full sisters aged \geq 15 years living in village	413	<0.05 <0.05 <0.05 <0.05	12822.35	12832.15	9.8

¹ Deviance information criterion

² DIC value for the null model (NM) with only an intercept.

³ Δ DIC = NM DIC – Model DIC

⁴ The variables age and sex were carried forward to the last block even if they did not reach significance at $p < 0.05$. They were only eliminated at the very end if they did not reach significance at the $p < 0.05$ level (see Section 2.5.2).

C.4 PGG2 contribution (Chapter 5, Section 5.2.1)

C.4.1 Univariate Models

Table C.13 Univariate associations between each predictor term (fixed effect) and PGG2 contribution (models include constants). A Bonferroni correction has not been applied to these models as they were used for exploratory analyses. Values in bold are significant. *** $p < 0.01$; ** $p < 0.05$; * $p < 0.10$.

Model	Fixed effect	PGG2 contribution (Indian rupees) $\beta \pm SE$	-2 Log likelihood			n
			Current model	Null model	Δ^1	
Village descriptors						
1	Population size	0.001 \pm 0.002	1667.703	1667.800	0.097	285
2	Proportion of migrants	-2.477 \pm 2.856	1667.071	1667.800	0.729	285
3	Proportion of non-Korwas	7.846 \pm 4.561*	1664.812	1667.800	2.988	285
4	Household dispersion	-0.032 \pm 1.996	1667.918	1667.800	-	285
					0.118	
5A	Distance from major town (km)	0 \pm 0*	1664.879	1667.800	2.921	285
5B	Distance from major town: 25-35 km (ref: 0-25 km)	1.372 \pm 1.127				
	35-45 km (ref: 0-25 km)	-0.193 \pm 1.066	1659.178	1667.800	8.622	285
	45+ km (ref: 0-25 km)	-1.707 \pm 1.143				
Individual descriptors						
<i>Basic individual descriptors</i>						
6	Age (years)	0.049 \pm 0.023**	1663.300	1667.800	4.500	285
7	Sex: female (ref: male)	-0.086 \pm 0.538	1667.736	1667.800	0.064	285
8	Education:					
	Illiterate (ref: some schooling)	1.359 \pm 0.593**	1661.501	1667.800	6.299	285
	Literate (ref: some schooling)	1.526 \pm 0.779*				
9	Household size (individuals)	-0.112 \pm 0.107	1666.680	1667.800	1.120	285
10	Marriage: ever married (ref: never married)	1.693 \pm 1.021*	1665.049	1667.800	2.751	285
<i>Residence and migration</i>						
11	Birthplace: this village (ref: other village)	-0.234 \pm 0.544	1667.578	1667.800	0.222	285
12	Time resident in this village (years)	0.015 \pm 0.019	1667.172	1667.800	0.628	285
13	Number of times migrated	0.130 \pm 0.364	1667.634	1667.800	0.166	285
14	Post-marital residence: natal village (ref: other village)	0.400 \pm 0.557	1545.770	1546.282	0.512	265
<i>Wealth, markets and social networks</i>						
15	Proportion of earners in household	-1.130 \pm 1.190	1666.864	1667.800	0.936	285
16	Months per year household eats self-grown rice	-0.206 \pm 0.122*	1664.927	1667.800	2.873	285
17	Outstanding loans: yes (ref: no)	0.675 \pm 0.605	1666.550	1667.800	1.250	285
18	Number of monthly visits to local bazaar	-0.196 \pm 0.322	1667.400	1667.800	0.400	285
19	Number of monthly visits to nearest town	0.031 \pm 0.071	1667.571	1667.800	0.229	285
20	People invited to harvest festival from own village	0.029 \pm 0.031	1666.993	1667.800	0.807	285
21	People invited to harvest festival from other villages	-0.003 \pm 0.048	1667.757	1667.800	0.043	285
<i>Children and grandchildren</i>						
22	Children living	0.239 \pm 0.127*	1664.263	1667.800	3.537	285
23	Children living together	0.224 \pm 0.139	1665.173	1667.800	2.627	285
24	Grandchildren living	0.141 \pm 0.168	1667.056	1667.800	0.744	285
25	Grandchildren living in village	0.216 \pm 0.232	1666.901	1667.800	0.899	285
<i>Kin</i>						
26	Mother living: yes (ref: no)	0.390 \pm 0.533	1667.229	1667.800	0.571	285

C.4 PGG2 CONTRIBUTION

27	Mother living in village: yes (ref: no)	0.066 ± 0.557	1667.747	1667.800	0.053	285
28	Mother participated in PGG: yes (ref: no)	-0.902 ± 0.990	1439.000	1439.828	0.828	247
29	Father living: yes (ref: no)	-0.196 ± 0.532	1667.629	1667.800	0.171	285
30	Father living in village: yes (ref: no)	-0.514 ± 0.569	1666.964	1667.800	0.836	285
31	Father participated in PGG: yes (ref: no)	-1.787 ± 0.972*	1474.025	1477.368	3.343	252
32	Full brothers living	0.157 ± 0.230	1667.293	1667.800	0.507	285
33	Full brothers living in village	-0.023 ± 0.255	1667.753	1667.800	0.047	285
34	Full brothers aged < 15 years living in village	0.283 ± 0.629	1667.560	1667.800	0.240	285
35	Full brothers aged ≥ 15 years living in village	-0.079 ± 0.272	1667.678	1667.800	0.122	285
36	Full brothers living in other villages	0.255 ± 0.300	1667.042	1667.800	0.758	285
37	Full brothers aged < 15 years living in other villages	-0.674 ± 0.533	1666.170	1667.800	1.630	285
38	Full brothers aged ≥ 15 years living in other villages	0.726 ± 0.372*	1663.977	1667.800	3.823	285
39	Full brothers participated in PGG	0.371 ± 0.539	1431.934	1432.405	0.471	245
40	Full sisters living	-0.098 ± 0.232	1667.582	1667.800	0.218	285
41	Full sisters living in village	-0.209 ± 0.367	1667.439	1667.800	0.361	285
42	Full sisters aged < 15 years living in village	0.464 ± 0.634	1667.228	1667.800	0.572	285
43	Full sisters aged ≥ 15 years living in village	-0.568 ± 0.457	1666.228	1667.800	1.572	285
44	Full sisters living in other villages	-0.021 ± 0.275	1667.755	1667.800	0.045	285
45	Full sisters aged < 15 years living in other villages	-1.610 ± 0.748**	1663.169	1667.800	4.631	285
46	Full sisters aged ≥ 15 years living in other villages	0.249 ± 0.309	1667.126	1667.800	0.674	285
47	Full sisters participated in PGG	0.322 ± 1.119	1418.484	1418.567	0.083	242

¹ Δ = -2 Log Likelihood of null model – (-2 Log likelihood of current model)

C.4.2 Domain-wise models

Table C.14 Multivariate associations between domains of predictor terms (fixed effects) and PGG2 contribution (models include constants). Values in bold are significant. ***p<0.01; **p<0.05; *p<0.10.

Model	Fixed effect	PGG2 contribution (Indian rupees) $\beta \pm SE$	-2 Log likelihood			n
			Current model	Null model	Δ^1	
1	Village descriptors					
A	Population size	-0.004 ± 0.003	1659.517	1667.800	8.283	285
	Proportion of migrants	-3.288 ± 3.668				
	Proportion of non-Korwas	4.328 ± 5.052				
	Household dispersion	-2.458 ± 2.529				
	Distance from major town (km)	0 ± 0**				
B	Population size	-0.006 ± 0.005	1656.7	1667.800	11.100	285
	Proportion of migrants	-4.966 ± 3.864				
	Proportion of non-Korwas	1.601 ± 6.032				
	Household dispersion	-3.161 ± 2.948				
	Distance from major town: 25-35 km (ref: 0-25 km)	-1.372 ± 2.555				
	35-45 km (ref: 0-25 km)	-3.166 ± 2.595				
	45+ km (ref: 0-25 km)	-4.911 ± 2.644*				
	Individual descriptors					
2	Basic individual descriptors					
	Age (years)	0.019 ± 0.027	1658.594	1667.800	9.206	285
	Sex: female (ref: male)	-0.342 ± 0.587				
	Education:					
	Illiterate (ref: some schooling)	1.154 ± 0.684*				
	Literate (ref: some schooling)	1.097 ± 0.837				
	Household size (individuals)	-0.075 ± 0.107				
	Marriage: ever married (ref: never married)	0.922 ± 1.090				
3	Residence and migration					
	Birthplace: this village (ref: other village)	0.550 ± 1.511	1545.044	1546.282	1.238	265
	Time resident in this village (years)	0.015 ± 0.023				
	Number of times migrated	-0.098 ± 0.515				
	Post-marital residence: natal village (ref: other village)	-1.219 ± 1.543				
4	Wealth, markets and social networks					
	Proportion of earners in household	-1.206 ± 1.178	1660.791	1667.800	7.009	285
	Months per year household eats self-grown rice	-0.222 ± 0.124*				
	Outstanding loans: yes (ref: no)	0.704 ± 0.604				
	Number of monthly visits to local bazaar	-0.162 ± 0.327				
	Number of monthly visits to nearest town	0.053 ± 0.071				
	People invited to harvest festival from own village	0.037 ± 0.032				
	People invited to harvest festival from other villages	-0.024 ± 0.050				
5	Children and grandchildren					
	Children living	0.363 ± 0.547	1663.434	1667.800	4.366	285
	Children living together	-0.137 ± 0.588				
	Grandchildren living	-0.117 ± 0.379				
	Grandchildren living in village	0.294 ± 0.423				
6	Kin					
A	Mother living: yes (ref: no)	0.197 ± 0.915	1383.836	1397.091	13.255	237
	Mother living in village: yes (ref: no)	0.282 ± 1.126				
	Mother participated in PGG: yes (ref: no)	-0.393 ± 1.204				

C.4 PGG2 CONTRIBUTION

	Father living: yes (ref: no)	-0.297 ± 0.937				
	Father living in village: yes (ref: no)	0.085 ± 1.167				
	Father participated in PGG: yes (ref: no)	-1.699 ± 1.189				
B	Full siblings living	0.002 ± 0.253	1427.948	1445.476	17.528	245
	Full brothers aged < 15 years living in village	0.094 ± 0.830				
	Full brothers aged ≥ 15 years living in village	-0.217 ± 0.499				
	Full brothers aged < 15 years living in other villages	-0.890 ± 0.662				
	Full brothers aged ≥ 15 years living in other villages	0.585 ± 0.575				
	Full brothers participated in PGG	0.690 ± 0.733				
C	Full siblings living	0.039 ± 0.271	1411.670	1418.567	6.897	242
	Full sisters aged < 15 years living in village	0.147 ± 0.886				
	Full sisters aged ≥ 15 years living in village	-0.241 ± 0.737				
	Full sisters aged < 15 years living in other villages	-2.101 ± 0.925**				
	Full sisters aged ≥ 15 years living in other villages	0.417 ± 0.429				
	Full sisters participated in PGG	0.536 ± 1.314				

¹ $\Delta = -2 \text{ Log Likelihood of null model} - (-2 \text{ Log likelihood of current model})$

C.4.3 Full model fitting summary

Table C.15 Summary of model-fitting process in the fourth stage of analyses. Variables in bold are significant predictors of PGG2 contribution at $p < 0.05$ and were retained in the next listed model.

Model	Fixed effect	n	p	DIC ¹	NM DIC ²	Δ DIC ³
Block 1						
1	Distance from major town: 25-35km (ref: 0-25km) 35-45km (ref: 0-25km) 45+km (ref: 0-25km)	285	>0.05 >0.05 >0.05	1668.02	1668.76	0.74
	Age ⁴		>0.05			
	Sex ⁴		>0.05			
	Education: illiterate literate (ref: some schooling)		>0.05 >0.05			
	Number of months in a year household eats self-grown rice		>0.05			
2	Age ⁴ Sex ⁴	285	>0.05 >0.05	1668.02	1668.76	0.74
Block 2						
3	Age ⁴ Sex ⁴	285	>0.05 >0.05	1665.98	1668.76	2.78
Block 3						
4	Age ⁴ Sex ⁴	285	>0.05 >0.05	1665.06	1668.76	3.7
	Full sisters aged < 15 years living in other villages		=0.07			
5	Full sisters aged < 15 years living in other villages	285	<0.05	1663.90	1668.76	4.86
6	Age	285	<0.05	1663.95	1668.76	4.81
7	Age Full sisters aged < 15 years living in other villages	285	=0.06 =0.09	1662.89	1668.76	5.87

¹ Deviance information criterion

² DIC value for the null model (NM) with only an intercept.

³ Δ DIC = NM DIC – Model DIC

⁴ The variables age and sex were carried forward to the last block even if they did not reach significance at $p < 0.05$. They were only eliminated at the very end if they did not reach significance at the $p < 0.05$ level (see Section 2.5.2).

C.5 PGG2 learning strategies (Chapter 5, Sections 5.2.3 and 5.2.4)

C.5.1 Univariate Models

C.5.1.1 Four category classification of learning strategies (payoff copier, conformist, individualist and unidentifiable)

Table C.16 Univariate associations between each predictor term (fixed effect) and the log-odds of being a payoff copier, conformist or unidentifiable relative to an individualist respectively (models include constants). A Bonferroni correction has not been applied to these models as they were used for exploratory analyses. Values in bold are significant. *** $p < 0.01$; ** $p < 0.05$; * $p < 0.10$.

Model	Fixed effect	Payoff copier	Conformist	Unidentifiable	-2 Log likelihood			n
		$\beta \pm SE$	$\beta \pm SE$	$\beta \pm SE$	Current model	Null model	Δ^1	
Village descriptors								
1	Population size	-0.002 \pm 0.002	-0.003 \pm 0.001**	-0.001 \pm 0.001*	543.479	542.902	-0.577	285
2	Proportion of migrants	2.141 \pm 1.695	-0.549 \pm 1.734	0.143 \pm 1.065	553.279	542.902	-10.377	285
3	Proportion of non-Korwas	-2.360 \pm 3.410	3.346 \pm 2.276	-0.190 \pm 1.750	543.342	542.902	-0.440	285
4	Household dispersion	1.807 \pm 1.232	0.939 \pm 0.998	-0.294 \pm 0.731	539.841	542.902	3.061	285
5A	Distance from major town (km)	0 \pm 0	0 \pm 0	0 \pm 0**	541.137	542.902	1.765	285
5B	Distance from major town: 25-35 km (ref: 0-25 km)	-0.793 \pm 1.332	1.199 \pm 0.950	0.325 \pm 0.482	484.124	542.902		285
	35-45 km (ref: 0-25 km)	-0.422 \pm 1.274	1.901 \pm 0.913**	1.228 \pm 0.446*				
	45+ km (ref: 0-25 km)	0.318 \pm 1.301	1.097 \pm 0.990	1.164 \pm 0.471**				
Individual descriptors								
<i>Basic individual descriptors</i>								
6	Age (years)	-0.015 \pm 0.020	-0.001 \pm 0.015	-0.014 \pm 0.011	522.992	542.902	19.910	285
7	Sex: female (ref: male)	0.508 \pm 0.448	0.225 \pm 0.361	0.840 \pm 0.250***	518.602	542.902	24.300	285
8	Education:							
	Illiterate (ref: some schooling)	-0.228 \pm 0.514	0.520 \pm 0.415	-0.062 \pm 0.272	519.728	542.902	23.174	285
	Literate (ref: some schooling)	0.074 \pm 0.600	0.120 \pm 0.545	-0.451 \pm 0.371				
9	Household size (individuals)	0.051 \pm 0.090	-0.048 \pm 0.072	0.045 \pm 0.049	524.66	542.902	18.242	285
10	Marriage: ever married (ref: never married)	-0.304 \pm 1.022	0.167 \pm 1.061	-1.745 \pm 0.548***	494.268	542.902	48.634	285
<i>Residence and migration</i>								

C.5 PGG2 LEARNING STRATEGIES

11	Birthplace: this village (ref: other village)	-0.866 ± 0.445*	-0.047 ± 0.358	-0.324 ± 0.248	522.239	542.902	20.663	285
12	Time resident in this village (years)	-0.015 ± 0.016	0.002 ± 0.012	-0.013 ± 0.009	519.465	542.902	23.437	285
13	Number of times migrated	0.518 ± 0.231**	0.020 ± 0.242	0.043 ± 0.169	517.644	542.902	25.258	285
14	Post-marital residence: natal village (ref: other village)	-0.668 ± 0.456	0.119 ± 0.369	-0.470 ± 0.258*	512.001	516.789	4.788	265
<i>Wealth, markets and social networks</i>								
15	Proportion of earners in household	1.969 ± 0.884**	0.036 ± 0.803	0.563 ± 0.542	501.764	542.902	41.138	285
16	Months per year household eats self-grown rice	0.068 ± 0.108	0.093 ± 0.072	0.041 ± 0.057	533.591	542.902	9.311	285
17	Outstanding loans: yes (ref: no)	-1.286 ± 0.559**	-0.795 ± 0.398**	-0.612 ± 0.268**	487.985	542.902	54.917	285
18	Number of monthly visits to local bazaar	0.162 ± 0.261	0.132 ± 0.197	-0.093 ± 0.146	526.704	542.902	16.198	285
19	Number of monthly visits to nearest town	0.041 ± 0.049	0.035 ± 0.037	-0.039 ± 0.033	530.852	542.902	12.050	285
20	People invited to harvest festival from own village	0.017 ± 0.027	0.023 ± 0.017	-0.009 ± 0.014	516.148	542.902	26.754	285
21	People invited to harvest festival from other villages	0.061 ± 0.035*	0.056 ± 0.027**	0.055 ± 0.022**	532.807	542.902	10.095	285
<i>Children and grandchildren</i>								
22	Children living	-0.178 ± 0.113	0.022 ± 0.081	-0.144 ± 0.061**	503.93	542.902	38.972	285
23	Children living together	-0.149 ± 0.120	0.063 ± 0.087	-0.121 ± 0.066*	512.774	542.902	30.128	285
24	Grandchildren living	-0.036 ± 0.141	0.040 ± 0.101	-0.085 ± 0.084	526.832	542.902	16.070	285
25	Grandchildren living in village	-0.157 ± 0.249	0.035 ± 0.144	-0.060 ± 0.111	524.117	542.902	18.785	285
<i>Kin</i>								
26	Mother living: yes (ref: no)	-0.125 ± 0.445	0.731 ± 0.361**	0.405 ± 0.247	517.528	542.902	25.374	285
27	Mother living in village: yes (ref: no)	-0.292 ± 0.494	0.227 ± 0.358	0.080 ± 0.256	526.103	542.902	16.799	285
28	Mother participated in PGG: yes (ref: no)	-0.511 ± 1.152	0.584 ± 0.592	0.457 ± 0.450	483.255	489.464	6.209	247
29	Father living: yes (ref: no)	-0.168 ± 0.444	-0.655 ± 0.356*	-0.028 ± 0.245	523.656	542.902	19.246	285
30	Father living in village: yes (ref: no)	0.227 ± 0.453	-1.352 ± 0.507***	-0.138 ± 0.262	488.127	542.902	54.775	285
31	Father participated in PGG: yes (ref: no)	1.420 ± 0.628**	0.501 ± 0.650	0.614 ± 0.443	462.977	462.621	-0.356	252
32	Full brothers living	0.023 ± 0.196	0.177 ± 0.145	0.236 ± 0.105**	523.337	542.902	19.565	285
33	Full brothers living in village	-0.184 ± 0.251	0.113 ± 0.164	0.184 ± 0.117	512.637	542.902	30.265	285
34	Full brothers aged < 15 years living in village	0.151 ± 0.564	-0.255 ± 0.654	0.641 ± 0.316**	516.847	542.902	26.055	285
35	Full brothers aged ≥ 15 years living in village	-0.222 ± 0.271	0.135 ± 0.168	0.086 ± 0.124	517.966	542.902	24.936	285
36	Full brothers living in other villages	0.189 ± 0.222	0.139 ± 0.185	0.129 ± 0.136	524.976	542.902	17.926	285
37	Full brothers aged < 15 years living in other villages	0.669 ± 0.300**	-0.064 ± 0.453	0.199 ± 0.245	517.561	542.902	25.341	285
38	Full brothers aged ≥ 15 years living in other villages	0.056 ± 0.318	0.249 ± 0.214	0.174 ± 0.169	527.597	542.902	15.305	285
39	Full brothers participated in PGG	-1.026 ± 0.737	0.005 ± 0.341	-0.281 ± 0.257	428.149	444.808	16.659	245
40	Full sisters living	0.059 ± 0.187	0.048 ± 0.148	0.072 ± 0.105	529.686	542.902	13.216	285
41	Full sisters living in village	-0.043 ± 0.308	-0.206 ± 0.287	0.172 ± 0.165	516.88	542.902	26.022	285

C.5 PGG2 LEARNING STRATEGIES

42	Full sisters aged < 15 years living in village	0.248 ± 0.509	-0.559 ± 0.847	0.507 ± 0.306*	509.596	542.902	33.306	285
43	Full sisters aged ≥ 15 years living in village	-0.118 ± 0.363	-0.168 ± 0.315	0.014 ± 0.204	525.7	542.902	17.202	285
44	Full sisters living in other villages	0.097 ± 0.218	0.129 ± 0.164	-0.001 ± 0.126	525.956	542.902	16.946	285
45	Full sisters aged < 15 years living in other villages	1.470 ± 0.452***	0.964 ± 0.441**	0.799 ± 0.352**	542.731	542.902	0.171	285
46	Full sisters aged ≥ 15 years living in other villages	-0.125 ± 0.275	0.106 ± 0.184	-0.048 ± 0.142	527.714	542.902	15.188	285
47	Full sisters participated in PGG	-0.184 ± 1.182	0.927 ± 0.569	-0.288 ± 0.535	472.944	477.667	4.723	242
48	Modal contribution (MC)	0.052 ± 0.048	-0.078 ± 0.047*	-0.075 ± 0.030**	490.009	542.902	52.893	285
49	Highest earner's contribution (HEC)	0.168 ± 0.074**	-0.112 ± 0.057**	0.049 ± 0.036	441.118	542.902	101.784	285

¹ Δ = -2 Log Likelihood of null model – (-2 Log likelihood of current model)

C.5.1.2 Three category classification of learning strategies (social learner, individualist and unidentifiable)

Table C.17 Univariate associations between each predictor term (fixed effect) and the log-odds of being a social learner or unidentifiable relative to an individualist respectively (models include constants). A Bonferroni correction has not been applied to these models as they were used for exploratory analyses. Values in bold are significant. ***p<0.01; **p<0.05; *p<0.10.

Model	Fixed effect	Social learner	Unidentifiable	-2 Log likelihood			n
		$\beta \pm SE$	$\beta \pm SE$	Current Model	Null model	Δ^1	
Village descriptors							
1	Population size	-0.002 ± 0.001**	-0.001 ± 0.001**	653.584	666.843	13.259	285
2	Proportion of migrants	0.638 ± 1.412	0.329 ± 1.072	668.084	666.843	-1.241	285
3	Proportion of non-Korwas	1.151 ± 2.404	-0.353 ± 1.848	667.825	666.843	-0.982	285
4	Household dispersion	1.113 ± 0.927	-0.119 ± 0.754	664.668	666.843	2.175	285
5A	Distance from major town (km)	0 ± 0*	0 ± 0***	658.429	666.843	8.414	285
5B	Distance from major town: 25-35 km (ref: 0-25 km)	0.211 ± 0.621	0.361 ± 0.464	652.039	666.843	14.804	285
	35-45 km (ref: 0-25 km)	0.913 ± 0.582	1.206 ± 0.428***				
	45+ km (ref: 0-25 km)	0.850 ± 0.623	1.160 ± 0.450***				
Individual descriptors							
<i>Basic individual descriptors</i>							
6	Age (years)	-0.003 ± 0.012	-0.016 ± 0.011	664.448	666.843	2.395	285
7	Sex: female (ref: male)	0.429 ± 0.276	0.735 ± 0.251***	657.962	666.843	8.881	285
8	Education:						
	Illiterate (ref: some schooling)	0.047 ± 0.309	-0.084 ± 0.271	664.328	666.843	2.515	285
	Literate (ref: some schooling)	0.075 ± 0.396	-0.425 ± 0.378				
9	Household size (individuals)	-0.027 ± 0.055	0.059 ± 0.048	663.090	666.843	3.753	285
10	Marriage: ever married (ref: never married)	-0.076 ± 0.683	-1.625 ± 0.500**	649.299	666.843	17.544	285
<i>Residence and migration</i>							
11	Birthplace: this village (ref: other village)	-0.412 ± 0.275	-0.303 ± 0.250	663.575	666.843	3.268	285
12	Time resident in this village (years)	-0.003 ± 0.010	-0.015 ± 0.009*	663.022	666.843	3.821	285
13	Number of times migrated	0.215 ± 0.178	0.062 ± 0.170	664.687	666.843	2.156	285
14	Post-marital residence: natal village (ref: other village)	0.287 ± 0.282	0.401 ± 0.263	619.143	621.883	2.74	265
<i>Wealth, markets and social networks</i>							
15	Proportion of earners in household	0.709 ± 0.596	0.498 ± 0.542	664.890	666.843	1.953	285
16	Months per year household eats self-grown rice	0.044 ± 0.061	0.027 ± 0.056	666.602	666.843	0.241	285

C.5 PGG2 LEARNING STRATEGIES

17	Outstanding loans: yes (ref: no)	-0.778 ± 0.310**	-0.506 ± 0.256**	657.936	666.843	8.907	285
18	Number of monthly visits to local bazaar	0.159 ± 0.159	-0.093 ± 0.147	663.903	666.843	2.940	285
19	Number of monthly visits to nearest town	0.042 ± 0.031	-0.025 ± 0.030	661.095	666.843	5.748	285
20	People invited to harvest festival from own village	0.009 ± 0.014	-0.011 ± 0.013	663.085	666.843	3.758	285
21	People invited to harvest festival from other villages	0.080 ± 0.024	0.079 ± 0.020	671.57	666.843	-4.727	285
<i>Children and grandchildren</i>							
22	Children living	-0.055 ± 0.065	-0.133 ± 0.062**	661.773	666.843	5.070	285
23	Children living together	-0.014 ± 0.070	-0.111 ± 0.067*	663.839	666.843	3.004	285
24	Grandchildren living	-0.004 ± 0.083	-0.086 ± 0.086	664.675	666.843	2.168	285
25	Grandchildren living in village	0.038 ± 0.119	-0.080 ± 0.113	666.064	666.843	0.779	285
<i>Kin</i>							
26	Mother living: yes (ref: no)	0.339 ± 0.276	0.279 ± 0.249	665.030	666.843	1.813	285
27	Mother living in village: yes (ref: no)	-0.114 ± 0.287	-0.013 ± 0.257	666.564	666.843	0.279	285
28	Mother participated in PGG: yes (ref: no)	0.095 ± 0.533	0.471 ± 0.450	573.727	574.976	1.249	247
29	Father living: yes (ref: no)	-0.542 ± 0.271**	0.063 ± 0.247	661.108	666.843	5.735	285
30	Father living in village: yes (ref: no)	-0.783 ± 0.319**	-0.019 ± 0.262	652.648	666.843	14.195	285
31	Father participated in PGG: yes (ref: no)	0.591 ± 0.474	0.656 ± 0.443	587.609	589.419	1.810	252
32	Full brothers living	0.098 ± 0.114	0.239 ± 0.104**	663.566	666.843	3.277	285
33	Full brothers living in village	0.010 ± 0.131	0.161 ± 0.115	665.502	666.843	1.341	285
34	Full brothers aged < 15 years living in village	-0.195 ± 0.434	0.654 ± 0.317**	660.203	666.843	6.64	285
35	Full brothers aged ≥ 15 years living in village	-0.030 ± 0.140	-0.003 ± 0.125	666.777	666.843	0.066	285
36	Full brothers living in other villages	0.122 ± 0.151	0.172 ± 0.136	664.866	666.843	1.977	285
37	Full brothers aged < 15 years living in other villages	0.114 ± 0.272	0.180 ± 0.243	666.342	666.843	0.501	285
38	Full brothers aged ≥ 15 years living in other villages	0.161 ± 0.187	0.211 ± 0.169	664.998	666.843	1.845	285
39	Full brothers participated in PGG	-0.280 ± 0.292	-0.323 ± 0.263	568.254	570.239	1.985	245
40	Full sisters living	0.047 ± 0.118	0.089 ± 0.105	665.885	666.843	0.958	285
41	Full sisters living in village	-0.084 ± 0.193	0.148 ± 0.161	664.334	666.843	2.509	285
42	Full sisters aged < 15 years living in village	0.063 ± 0.375	0.546 ± 0.298*	663.154	666.843	3.689	285
43	Full sisters aged ≥ 15 years living in village	-0.134 ± 0.226	-0.026 ± 0.201	668.520	666.843	-1.677	285
44	Full sisters living in other villages	0.107 ± 0.136	0.024 ± 0.127	665.743	666.843	1.100	285
45	Full sisters aged < 15 years living in other villages	0.768 ± 0.345**	0.548 ± 0.345	662.047	666.843	4.796	285
46	Full sisters aged ≥ 15 years living in other villages	0.038 ± 0.155	-0.024 ± 0.143	666.501	666.843	0.342	285
47	Full sisters participated in PGG	0.496 ± 0.518	-0.480 ± 0.584	560.166	563.994	3.828	242

¹ Δ = -2 Log Likelihood of null model – (-2 Log likelihood of current model)

C.5.2 Domain-wise models

C.5.2.1 Four category classification of learning strategies (payoff copier, conformist, individualist and unidentifiable)

Table C.18 Multivariate associations between domains of predictor terms (fixed effects) and the log-odds of being a payoff copier, conformist or unidentifiable relative to an individualist respectively (models include constants). Values in bold are significant. ***p<0.01; **p<0.05; *p<0.10.

Model	Fixed effect	Payoff copier	Conformist	Unidentifiable	-2 Log likelihood			n
		$\beta \pm SE$	$\beta \pm SE$	$\beta \pm SE$	Current model	Null model	Δ^1	
1	Village descriptors							
A	Population size	0.003 ± 0.005	-0.004 ± 0.002*	-0.002 ± 0.002	430.506	542.902	112.396	285
	Proportion of migrants	-1.942 ± 5.499	-2.946 ± 2.540	0.357 ± 2.062				
	Proportion of non-Korwas	-5.619 ± 7.629	0.649 ± 3.583	0.918 ± 2.810				
	Household dispersion	5.871 ± 4.096	-0.579 ± 1.884	-1.533 ± 1.420				
	Distance from major town (km)	0 ± 0	0 ± 0	0 ± 0				
B	Population size	0.002 ± 0.009	-0.006 ± 0.004	0 ± 0.002	428.47	542.902	114.432	285
	Proportion of migrants	-0.999 ± 6.686	-3.676 ± 3.193	1.72 ± 2.022				
	Proportion of non-Korwas	-3.783 ± 10.783	3.844 ± 4.934	3.144 ± 3.139				
	Household dispersion	5.391 ± 5.598	-1.303 ± 2.283	-1.287 ± 1.54				
	Distance from major town: 25-35 km (ref: 0-25 km)	0.541 ± 4.721	-2.233 ± 2.385	0.034 ± 1.341				
	35-45 km (ref: 0-25 km)	1.064 ± 4.619	-1.356 ± 2.286	1.091 ± 1.371				
	45+ km (ref: 0-25 km)	2.357 ± 4.658	-1.752 ± 2.226	1.236 ± 1.392				
	Individual descriptors							
2	Basic individual descriptors							
	Age (years)	-0.010 ± 0.024	-0.006 ± 0.017	0.011 ± 0.013	452.84	542.902	90.062	285
	Sex: female (ref: male)	0.753 ± 0.509	0.008 ± 0.402	1.075 ± 0.289***				
	Education:							
	Illiterate (ref: some schooling)	-0.403 ± 0.603	0.525 ± 0.471	-0.331 ± 0.331				
	Literate (ref: some schooling)	0.333 ± 0.661	0.166 ± 0.574	-0.148 ± 0.405				
	Household size (individuals)	0.036 ± 0.092	-0.033 ± 0.073	0.037 ± 0.051				
	Marriage: ever married (ref: never married)	-0.411 ± 1.001	0.339 ± 1.174	-2.008 ± 0.595***				
3	Residence and migration							
	Birthplace: this village (ref: other village)	0.766 ± 0.650	-0.240 ± 0.714	0.195 ± 0.355	444.524	542.902	98.378	285
	Time resident in this village (years)	-0.031 ± 0.020	-0.036 ± 0.016**	-0.006 ± 0.010				
	Number of times migrated	-0.235 ± 0.406	-1.063 ± 0.614*	-0.081 ± 0.226				

C.5 PGG2 LEARNING STRATEGIES

	Post-marital residence: natal village (ref: other village)	-0.789 ± 0.462*	0.011 ± 0.369	-0.512 ± 0.263*				
4	Wealth, markets and social networks							
	Proportion of earners in household	3.653 ± 1.051***	0.620 ± 0.813	1.224 ± 0.554**	386.685	542.902	156.217	285
	Months per year household eats self-grown rice	0.045 ± 0.122	0.088 ± 0.071	0.064 ± 0.058				
	Outstanding loans: yes (ref: no)	-1.843 ± 0.611***	-0.916 ± 0.399**	-0.793 ± 0.272***				
	Number of monthly visits to local bazaar	0.527 ± 0.268**	0.141 ± 0.209	0.023 ± 0.152				
	Number of monthly visits to nearest town	0.054 ± 0.054	0.027 ± 0.038	-0.042 ± 0.032				
	People invited to harvest festival from own village	0.035 ± 0.031	0.024 ± 0.017	-0.014 ± 0.015				
	People invited to harvest festival from other villages	-0.005 ± 0.063	0.017 ± 0.031	0.036 ± 0.023				
5	Children and grandchildren							
	Children living	-1.711 ± 0.930*	-1.693 ± 0.633***	-0.417 ± 0.323	462.744	542.902	80.158	285
	Children living together	1.614 ± 0.961*	1.821 ± 0.663***	0.313 ± 0.342				
	Grandchildren living	1.076 ± 0.477**	0.887 ± 0.312***	0.056 ± 0.266				
	Grandchildren living in village	-1.048 ± 0.491**	-0.554 ± 0.304*	-0.022 ± 0.270				
6	Kin							
A	Mother living: yes (ref: no)	0.049 ± 0.780	0.457 ± 0.568	0.306 ± 0.421	383.795	459.738	75.943	237
	Mother living in village: yes (ref: no)	-0.447 ± 0.981	0.651 ± 0.691	-0.035 ± 0.519				
	Mother participated in PGG: yes (ref: no)	-0.755 ± 1.149	0.000 ± 0.753	0.185 ± 0.554				
	Father living: yes (ref: no)	0.291 ± 0.830	0.614 ± 0.573	0.471 ± 0.431				
	Father living in village: yes (ref: no)	-0.153 ± 1.006	-2.495 ± 0.953***	-0.787 ± 0.544				
	Father participated in PGG: yes (ref: no)	1.750 ± 0.833**	1.802 ± 0.990*	0.834 ± 0.555				
B	Full siblings living	-0.097 ± 0.207	-0.172 ± 0.171	-0.160 ± 0.118	424.642	542.902	118.260	285
	Full brothers aged < 15 years living in village	0.289 ± 0.606	-0.158 ± 0.645	0.348 ± 0.374				
	Full brothers aged ≥ 15 years living in village	-0.044 ± 0.347	-0.091 ± 0.291	0.275 ± 0.186				
	Full brothers aged < 15 years living in other villages	1.029 ± 0.537*	1.162 ± 0.381***	1.109 ± 0.306***				
	Full brothers aged ≥ 15 years living in other villages	-0.157 ± 0.479	0.065 ± 0.315	0.272 ± 0.229				
	Full brothers participated in PGG	-0.987 ± 0.708	0.018 ± 0.334	-0.291 ± 0.261				
C	Full siblings living	-0.111 ± 0.210	0.181 ± 0.141	0.175 ± 0.107	509.127	542.902	33.775	285
	Full sisters aged < 15 years living in village	0.575 ± 0.509	-0.770 ± 0.866	0.345 ± 0.339				
	Full sisters aged ≥ 15 years living in village	0.075 ± 0.433	-0.342 ± 0.353	-0.208 ± 0.244				
	Full sisters aged < 15 years living in other villages	1.748 ± 0.569***	0.489 ± 0.526	0.644 ± 0.379*				
	Full sisters aged ≥ 15 years living in other villages	-0.265 ± 0.380	-0.072 ± 0.235	-0.264 ± 0.187				

¹ Δ = -2 Log Likelihood of null model – (-2 Log likelihood of current model)

C.5.2.2 Three category classification of learning strategies (social learner, individualist and unidentifiable)

Table C.19 Multivariate associations between domains of predictor terms (fixed effects) and the log-odds of being a social learner or unidentifiable relative to an individualist respectively (models include constants). Values in bold are significant. ***p<0.01; **p<0.05; *p<0.10.

Model	Fixed effect	Social learner $\beta \pm SE$	Unidentifiable $\beta \pm SE$	-2 Log likelihood			n
				Current model	Null model	Δ^1	
1	Village descriptors						
A	Population size	-0.001 ± 0.003	-0.001 ± 0.002	656.403	666.843	10.440	285
	Proportion of migrants	-0.585 ± 2.908	0.668 ± 2.212				
	Proportion of non-Korwas	0.613 ± 4.005	1.243 ± 3.016				
	Household dispersion	1.296 ± 2.012	-1.123 ± 1.508				
	Distance from major town (km)	0 ± 0	0 ± 0				
B	Population size	-0.004 ± 0.003	0 ± 0.002	632.482	666.843	34.361	285
	Proportion of migrants	-1.998 ± 2.427	1.403 ± 1.632				
	Proportion of non-Korwas	3.946 ± 3.673	2.338 ± 2.466				
	Household dispersion	-0.265 ± 1.746	-0.973 ± 1.205				
	Distance from major town: 25-35 km (ref: 0-25 km)	-2.269 ± 1.696	0.034 ± 1.104				
	35-45 km (ref: 0-25 km)	-1.343 ± 1.634	0.975 ± 1.121				
	45+ km (ref: 0-25 km)	-0.899 ± 1.614	1.071 ± 1.131				
	Individual descriptors						
2	Basic individual descriptors						
	Age (years)	0 ± 0.014	0.007 ± 0.013	637.958	666.843	28.885	285
	Sex: female (ref: male)	0.526 ± 0.309*	0.941 ± 0.287***				
	Education:						
	Illiterate (ref: some schooling)	-0.166 ± 0.358	-0.263 ± 0.325				
	Literate (ref: some schooling)	0.155 ± 0.423	-0.116 ± 0.41				
	Household size (individuals)	-0.045 ± 0.057	0.038 ± 0.05				
	Marriage: ever married (ref: never married)	-0.141 ± 0.726	-1.758 ± 0.546***				
3	Residence and migration						
	Birthplace: this village (ref: other village)	-0.767 ± 0.754	-0.520 ± 0.730	614.39	666.843	52.453	285
	Time resident in this village (years)	0.007 ± 0.011	-0.003 ± 0.011				
	Number of times migrated	0.178 ± 0.244	-0.206 ± 0.286				
	Post-marital residence: natal village (ref: other village)	0.511 ± 0.764	-0.097 ± 0.748				

4	Wealth, markets and social networks					
	Proportion of earners in household	1.139 ± 0.602*	0.956 ± 0.548*	640.765	666.843	26.078 285
	Months per year household eats self-grown rice	0.061 ± 0.061	0.067 ± 0.058			
	Outstanding loans: yes (ref: no)	-1.002 ± 0.322***	-0.802 ± 0.269***			
	Number of monthly visits to local bazaar	0.183 ± 0.168	-0.032 ± 0.154			
	Number of monthly visits to nearest town	0.031 ± 0.033	-0.021 ± 0.031			
	People invited to harvest festival from own village	0.002 ± 0.015	-0.022 ± 0.014			
	People invited to harvest festival from other villages	0.075 ± 0.026***	0.084 ± 0.023***			
5	Children and grandchildren					
	Children living	-1.304 ± 0.452***	-0.394 ± 0.302	639.763	666.843	27.080 285
	Children living together	1.345 ± 0.474***	0.294 ± 0.323			
	Grandchildren living	0.633 ± 0.241***	0.113 ± 0.222			
	Grandchildren living in village	-0.410 ± 0.240*	-0.115 ± 0.231			
6	Kin					
A	Mother living: yes (ref: no)	0.354 ± 0.454	0.299 ± 0.429	531.035	556.167	25.132 237
	Mother living in village: yes (ref: no)	0.191 ± 0.560	-0.018 ± 0.528			
	Mother participated in PGG: yes (ref: no)	-0.417 ± 0.635	0.220 ± 0.553			
	Father living: yes (ref: no)	0.316 ± 0.468	0.562 ± 0.437			
	Father living in village: yes (ref: no)	-1.470 ± 0.659**	-0.742 ± 0.547			
	Father participated in PGG: yes (ref: no)	1.803 ± 0.659***	0.887 ± 0.554			
B	Full siblings living	-0.047 ± 0.084	-0.018 ± 0.076	565.884	570.269	4.385 245
	Full brothers aged < 15 years living in village	-0.123 ± 0.463	0.451 ± 0.351			
	Full brothers aged ≥ 15 years living in village	0.206 ± 0.221	0.448 ± 0.193**			
	Full brothers aged < 15 years living in other villages	0.207 ± 0.302	0.261 ± 0.276			
	Full brothers aged ≥ 15 years living in other villages	0.578 ± 0.256**	0.769 ± 0.238***			
	Full brothers participated in PGG	-0.367 ± 0.394	-0.581 ± 0.355			
C	Full siblings living	0.013 ± 0.147	0.201 ± 0.128	545.945	563.994	18.049 242
	Full sisters aged < 15 years living in village	-0.224 ± 0.550	-0.298 ± 0.414			
	Full sisters aged ≥ 15 years living in village	-0.350 ± 0.473	0.159 ± 0.340			
	Full sisters aged < 15 years living in other villages	0.944 ± 0.458**	0.191 ± 0.474			
	Full sisters aged ≥ 15 years living in other villages	-0.053 ± 0.227	-0.249 ± 0.207			
	Full sisters participated in PGG	0.898 ± 0.706	-0.814 ± 0.678			

¹ Δ = -2 Log Likelihood of null model – (-2 Log likelihood of current model)

C.5.3 Full model fitting summary

C.5.3.1 Four category classification of learning strategies (payoff copier, conformist, individualist and unidentifiable)

Table C.20 Summary of model-fitting process in the fourth stage of analyses. Variables in bold are significant predictors of either the log-odds of being a payoff copier, conformist or unidentifiable, relative to an individualist respectively, at $p < 0.05$ and were retained in the next listed model.

Model	Fixed effect	n	p	DIC ¹	NM DIC ²	Δ DIC ³
Block 1⁴						
1	Age ⁵	285	>0.05	706.35	695.86	-10.49
	Sex		<0.05			
	Population size		<0.05			
	Time resident in this village		>0.05			
	Number of times migrated		<0.05			
	Proportion of earners in household		<0.05			
	Outstanding loans		<0.05			
	Number of monthly visits to local bazaar		>0.05			
2	Age ⁵	285	>0.05	698.96	695.86	-3.10
	Sex		<0.05			
	Population size		<0.05			
	Number of times migrated		>0.05			
	Proportion of earners in household		<0.05			
	Outstanding loans		<0.05			
3	Age ⁵	285	>0.05	696.75	695.86	-0.89
	Sex		<0.05			
	Population size		<0.05			
	Proportion of earners in household		>0.05			
	Outstanding loans		<0.05			
4	Age ⁵	285	>0.05	695.12	695.86	0.74
	Sex		<0.05			
	Population size		<0.05			
	Outstanding loans		<0.05			
Block 2						
5	Age ⁵	285	>0.05	710.34	695.86	-14.48
	Sex		<0.05			
	Population size		<0.05			
	Outstanding loans		<0.05			
	Children living		<0.05			
	Children living together		<0.05			
	Grandchildren living		<0.05			
	Grandchildren living in village		>0.05			
6	Age ⁵	285	>0.05	703.42	695.86	-7.56
	Sex		<0.05			
	Population size		<0.05			
	Outstanding loans		<0.05			
	Children living		<0.05			
	Children living together		<0.05			
	Grandchildren living		>0.05			
7	Age ⁵	285	>0.05	700.89	695.86	-5.03
	Sex		<0.05			
	Population size		<0.05			
	Outstanding loans		<0.05			

C.5 PGG2 LEARNING STRATEGIES

	Children living		>0.05			
	Children living together		>0.05			
8	Age ⁵	285	> 0.05	695.12	695.86	0.74
	Sex		< 0.05			
	Population size		< 0.05			
	Outstanding loans		< 0.05			
Block 3						
9	Age ⁵	237	>0.05	587.61	582.20	-5.41
	Sex		< 0.05			
	Population size		< 0.05			
	Outstanding loans		< 0.05			
	Mother in village		>0.05			
	Mother participated in PGG		>0.05			
	Father participated in PGG		>0.05			
	Full brothers aged < 15 years living in other villages		>0.05			
	Full sisters aged < 15 years living in other villages		< 0.05			
10	Age ⁵	285	>0.05	697.44	695.86	-1.58
	Sex		< 0.05			
	Population size		= 0.056			
	Outstanding loans		< 0.05			
	Full sisters aged < 15 years living in other villages		>0.05			
Block 4						
11	Age ⁵	285	>0.05	688.15	695.86	7.71
	Sex		< 0.05			
	Population size		< 0.05			
	Outstanding loans		< 0.05			
	Highest earner's contribution (HEC)		< 0.05			
12	Age ⁵	285	>0.05	682.51	695.86	13.35
	Sex		< 0.05			
	Population size		< 0.05			
	Outstanding loans		< 0.05			
	Highest earner's contribution (HEC)		< 0.05			
	Modal contribution (MC)		< 0.05			
13	Sex	285	< 0.05	670.99	695.86	24.87
	Population size		< 0.05			
	Outstanding loans		< 0.05			
	Highest earner's contribution (HEC)		< 0.05			
	Modal contribution (MC)		< 0.05			

¹ Deviance information criterion

² DIC value for the null model (NM) with only an intercept.

³ Δ DIC = NM DIC – Model DIC

⁴ Both the ‘number of times migrated’ and ‘post-marital residence’ were significant at $p < 0.01$ in the domain-wise analyses. Since the ‘number of times migrated’ variable includes migrations by individuals who have moved residence after marriage and is available for all individuals (unlike data on post-marital residence which are incomplete for individuals who are not married), I included the ‘number of times migrated’ in the model here. An alternative set of analyses were conducted including ‘post-marital residence’ and produced the same results (see Table C.21). Models including both the ‘number of times migrated’ and ‘post-marital residence’ produce inconsistent results which change between repeated runs of the model, perhaps because most people in the dataset have migrated only once, post-marriage, and so the two variables capture the same migratory history.

⁵ The variables age and sex were carried forward to the last block even if they did not reach significance at $p < 0.05$. They were only eliminated at the very end if they did not reach significance at the $p < 0.05$ level (see Section 2.5.2).

Table C.21 Alternative Block 1 analyses for model-fit summary presented in Table C.20; the analyses include predictor term ‘post-marital residence’ and exclude the variable ‘number of times migrated’. Variables in bold are significant predictors of either the log-odds of being a payoff copier, conformist or unidentifiable, relative to an individualist respectively, at $p < 0.05$ and were retained in the next listed model.

Model	Fixed effect	n	p	DIC ¹	NM DIC ²	Δ DIC ³
Block 1						
1	Age ⁴	265	>0.05	662.17	656.67	-5.50
	Sex		<0.05			
	Population size		<0.05			
	Time resident in this village		>0.05			
	Post-marital residence		<0.05			
	Proportion of earners in household		>0.05			
	Outstanding loans		<0.05			
	Number of monthly visits to local bazaar		>0.05			
2	Age ⁴	265	>0.05	653.12	656.67	3.55
	Sex		<0.05			
	Population size		<0.05			
	Post-marital residence		>0.05			
	Outstanding loans		<0.05			
3	Age ⁴	285	>0.05	695.12	695.86	0.74
	Sex		<0.05			
	Population size		<0.05			
	Outstanding loans		<0.05			

¹ Deviance information criterion

² DIC value for the null model (NM) with only an intercept.

³ Δ DIC = NM DIC – Model DIC

⁴ The variables age and sex were carried forward to the last block even if they did not reach significance at $p < 0.05$. They were only eliminated at the very end if they did not reach significance at the $p < 0.05$ level (see Section 2.5.2).

C.5.3.2 Three category classification of learning strategies (social learner, individualist and unidentifiable)

Table C.22 Summary of model-fitting process in the fourth stage of analyses. Variables in bold are significant predictors of either the log-odds of being a social learner or unidentifiable, relative to an individualist respectively, at $p < 0.05$ and were retained in the next listed model.

Model	Fixed effect	n	p	DIC ¹	NM DIC ²	Δ DIC ³
Block 1						
1	Age ⁴	285	>0.05	626.86	623.70	-3.16
	Sex		<0.05			
	Proportion of earners in household		>0.05			
	Outstanding loans		<0.05			
	People invited to harvest festival from other villages		>0.05			
2	Age ⁴	285	>0.05	622.60	623.70	1.10
	Sex		<0.05			
	Outstanding loans		<0.05			
Block 2						
3	Age ⁴	285	>0.05	629.18	623.70	-5.48
	Sex		<0.05			
	Outstanding loans		<0.05			
	Children living		<0.05			
	Children living together		<0.05			
	Grandchildren living		<0.05			
	Grandchildren living in village		>0.05			
4	Age ⁴	285	>0.05	628.03	623.70	-4.33
	Sex		<0.05			
	Outstanding loans		<0.05			
	Children living		<0.05			
	Children living together		<0.05			
	Grandchildren living		>0.05			
5	Age ⁴	285	>0.05	625.57	623.70	-1.87
	Sex		<0.05			
	Outstanding loans		<0.05			
	Children living		>0.05			
	Children living together		>0.05			
6	Age ⁴	285	>0.05	622.60	623.70	1.10
	Sex		<0.05			
	Outstanding loans		<0.05			
Block 3						
7	Age ⁴	252	<0.05	545.01	549.66	4.65
	Sex		<0.05			
	Outstanding loans		<0.05			
	Father living in village		<0.05			
	Father participated in PGG		<0.05			
	Full brothers aged \geq over 15 years living in other villages		>0.05			
	Full sisters aged < 15 years living in other villages		>0.05			
8	Sex	252	<0.05	541.48	549.66	8.18
	Outstanding loans		<0.05			
	Father living in village		<0.05			
	Father participated in PGG		<0.05			

¹ Deviance information criterion

² DIC value for the null model (NM) with only an intercept.

³ Δ DIC = NM DIC – Model DIC

⁴ The variables age and sex were carried forward to the last block even if they did not reach significance at $p < 0.05$. They were only eliminated at the very end if they did not reach significance at the $p < 0.05$ level (see Section 2.5.2).