The Dynamics of Human Cooperative Groups

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I, Matthew Gwynfryn Thomas, 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 work.

Abstract

Humans live in cooperative groups of varying scales and composition, from families to nations and international communities. Segregating into groups can provide benefits by alleviating individual costs. However, individuals also face a dilemma between following their own interests and those of the group, which can lead to a breakdown in cooperation. The evolutionary benefits and costs of cooperation are well-understood theoretically, but the real-world dynamics of cooperative behaviour remain unclear. This thesis investigates cooperation in two populations, employing field experiments and social network methods grounded in a human behavioural ecology framework.

Part I centres on Saami reindeer pastoralists, an indigenous minority who live and work in cooperative herding groups around northern Norway. I collected survey and experimental data, using gift games to test whether herders acted cooperatively towards genetic relatives or to their herding group, or both. I also played public goods games to understand how herders respond to and solve social dilemmas. Cooperative behaviours were biased towards the herding group, although kinship also had a positive effect on gift-giving. Smaller groups were more cooperative, although this pattern was not driven by relatedness.

Part II analyses demographic and experimental data collected by others from a population of Mosuo farmers living in rural southwest China. The Mosuo are a minority whose social system traditionally revolved around matrilineal households but which is changing in response to increased tourism. The results show how affinal relationships encourage a real-word measure of cooperation: labouring on farms. Some Mosuo people were considered witches. I test whether witchcraft accusations act as a form of costless punishment, al-

lowing people to withhold help from witches. Witches were somewhat isolated within their villages but clustered together and did not suffer significantly lowered reproductive success.

These results underline the importance of studying cooperation in real-world groups in addition to laboratories.

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Chapter 1

Introduction

Cooperation is rife in nature. Trillions of cells forgo their own reproductive interests to keep you alive; individual slime molds clump together into stalks, producing a specialised fruiting body that releases only a handful of their number as spores to reproduce elsewhere; ants protect aphids in exchange for their 'milk'.

Since Hamilton's (1964) insight of widening the focus from an individual's genes to encompass relatives—other individuals containing copies of your genes—evolutionary scientists have been able to account for the abundance of social creatures backed by a theory of evolution incorporating 'inclusive fitness' – one's personal genetic fitness combined with fitness derived through genes shared with others. Since an organism's strategies can be understood as having been shaped by evolution to maximise its inclusive fitness (Grafen 2002), cooperation can evolve as an optimal strategy. When coupled with theories explaining social interactions among non-kin (see section 1.4.2), the existence of cooperation becomes less puzzling.

Humans have been called 'super-cooperators' (Nowak 2012b) for our apparent willingness to go above and beyond the genetic duty of maximising reproductive success in order to cooperate promiscuously. There are many circumstances in which we cooperate despite self-interest conflicting with the welfare of the wider group – known as a 'social dilemma' or 'collective action problem' (Kollock 1998). When we cooperate, we cooperate in all manner of ways on all manner of scales, investing time and energy into adopting and raising other people's children; debating, drafting and protesting laws on be-

half of a wider populace; donating not only money to anonymous others in acts of charity but also donating blood, kidneys and even slices of liver while still alive. We run races to raise money for charities supporting carers supporting those in need, we teach skills and share knowledge with others, and we strive for PhDs and contribute to the public good known as science.

This thesis investigates cooperation in two human societies. The research presented conducts an evolutionary investigation into cooperative behaviour in real-world situations, testing predictions derived from an inclusive fitness perspective of evolution. I will use a combination of experiments and survey data in order to analyse the patterns and outcomes of meaningful social relationships. In doing so, I aim to further our understanding of how evolutionary forces shape our cooperative interactions.

1.1 The diversity of human cooperation

In this section, I briefly discuss cooperative behaviours in the two types of society studied in this thesis: pastoralists and small-scale farmers. I will outline their main forms of cooperation, the social institutions supporting such behaviours, and the collective action problems they face.

Pastoralism (the focus of Part I) is a mode of subsistence in which wealth is embodied in livestock and, thus, kept on the hoof. Pastoralists live in a range of ecologies—from Arctic tundra to African savannah—and stock many different animals, not least reindeer, cows, goats, yak, sheep, and arguably bees. Despite pastoralist societies engaging in a wide range of kinship, marriage and inheritance systems, many have in common the coalescence of households into cooperative groups. These household clusters aid in herding tasks, protect livestock from predators or raiders, protect pastureland from encroachers, and pool resources in order to spread risk (Dyson-Hudson & Dyson-Hudson 1980; Næss 2012).

Herding groups are typically formed of several families and households—not all related, necessarily—working together in varying combinations and to varying extents depending on the season, migration patterns, and yearly trends of livestock needs. Pastoralists also have livestock-sharing partners

(called 'stock friends') with whom they can gift animals according to need (Cronk 2007). The Saami reindeer herders of Norway have a form of relationship known as *verdde* (roughly: guest-friend) which allows for reciprocal, needs-based cooperation with people who are not themselves pastoralists (Paine 1994).

Farmers in small-scale societies (the focus of Part II) tend to live with a greater number of relatives compared to more mobile groups (Dyble et al. 2015), which may more readily prompt explanation for their cooperation in terms of kin selection (see Section 1.4.1). However, since trading goods and services beyond the family, as well as dispersal upon marriage and links to other families arising from marriage, tend to occur in these populations, researchers cannot ignore the potential importance of other explanations, such as the various types of reciprocity (see Section 1.4.2). Indeed, living with kin can create its own problems, namely competition among relatives for local resources and mates (Platt & Bever 2009), or reproductive competition among communally breeding sisters (Ji et al. 2013), all potentially having negative effects on cooperativeness (and reproductive success; see Appendix A). Resource competition can also lead to a breakdown in reciprocal cooperation between unrelated people (West et al. 2006).

Regardless of the extent or intensiveness, or whether growing edibles or ornamentals, all farmers have in common the need to align interests over long cycles of growing and harvesting; that is, people must cooperate in order to solve collective action problems. Some of the most famous cases of successful collective action—the management of common pool resources—have been documented in farming populations, for example the scheduled use of waterways for irrigation organised around a ritualised system of water temples in Bali (Lansing 1991) or on the terraces of western Nepal (Agrawal & Ostrom 2001).

The examples given above suggest that flexibility is a keystone of human cooperation, especially when it comes to cooperating on a large scale with non-kin. In order to understand this kind of cooperation, researchers have begun to transplant laboratory experiments into their field sites. These quantitative

studies of flexible and extensive cooperation as it exists in a range of societies have shed light on the dynamics of social behaviour. However, much remains to be done in order to fully understand how evolutionary forces shape patterns of social behaviours within and between human groups at various levels of organisation, from nuclear families to communities of households.

This thesis makes use of field experiments to investigate: (i) how cooperative relationships are shaped by kin selection (see Section 1.4.1) and reciprocal cooperation (see Section 1.4.2.1); (ii) how pastoralists balance individual and collective interests to solve social dilemmas; (iii) whether behaviour in experimental games corresponds to a real-world measure of cooperation; and (iv) how cooperation based around reputations (see Section 1.4.2.2) can affect reproductive success for people with poor standing in their community. In doing so, I aim to further our empirical understanding of human cooperation in a variety of salient contexts.

In the next two sections, I define the concepts that are central to this thesis and introduce the theoretical framework underpinning the research. The remainder of this chapter goes on to review the evolutionary theories of cooperation. Finally, I present an overview of chapters to come.

1.2 Definitions of key terms

The scientific (and non-scientific) literature is swarming with definitions for the key terms I employ in this thesis, namely *cooperation* and *groups*. These words are also laden with intuitive folk definitions (and in the case of cooperation, laden with value) that do not necessarily or fully reflect their academic usages. In the following subsections, I will briefly cover how other researchers use these terms, and settle on definitions pertinent to the work presented in this thesis.

1.2.1 What is cooperation?

In evolutionary science, cooperation broadly refers to social behaviours that have evolved for their beneficial effects beyond the individuals performing those behaviours (Bergmüller et al. 2007; West et al. 2007a). Many groups of

researchers have produced hierarchical frameworks of cooperation focussing on various factors, such as inclusive fitness (Lehmann & Rousset 2010; West et al. 2007a), investment (Bergmüller et al. 2007), and interdependence (Roberts 2005). This section will briefly review the evolutionary definitions of cooperation.

Cooperation is a beneficial outcome of interactions between two or more individuals, as distinct from 'cooperative behaviours', which are the actions of an individual (Connor 2010; Cronk & Leech 2013). This distinction highlights the difference between an individual's tendencies or characteristics and their emergent consequences within dyads and beyond. Through focussing on cooperation as multi-party interactions, we can begin to explore nuances that may lead to a breakdown in cooperation, such as where individuals act solely in their own interests or where it is difficult to align the interests of group members.

The term 'altruism' is commonly confused for cooperation when it should really be thought of more as a type of cooperation in which an actor suffers a fitness cost in order to benefit others (Hamilton 1964; West et al. 2007a). Some researchers emphasise the need for an actor to incur costs in order for behaviours to count as cooperation (Bowles & Gintis 2003; Henrich & Henrich 2007; Nowak 2006); however, this view is not shared by all (e.g. Bergmüller et al. 2007; Connor 2010; West et al. 2007a) and will not be central to the definition of cooperation used here.

The work presented in this thesis analyses the cooperative behaviours of individuals (e.g. in the form of gift-giving, as presented in Chapters 4 and 7) as well as the outcomes of cooperative interactions, including group productivity (Chapter 5) and fitness (Chapter 8). I will investigate social behaviour through proximate factors that theoretically mediate cooperation and will analyse fitness through proxies such as fertility and wealth.

1.2.2 What is a group?

When looking at cooperation beyond the dyad, we enter the realm of groups. As with 'cooperation', 'group' is an intuitive and flexible concept that, for the

purposes of scientific enquiry, requires narrowing down in order to have any explanatory power.

Groups may be bound by ancestry, descent, politics, inclusion and exclusion (e.g. ethnicity might be covered by all five), by accidents of birth (e.g. age cohorts within schools and universities), proximity (neighbours and community groups – although proximity is not a prerequisite, e.g. 'world' religions or internet hordes). In some societies, such groupings allowed partitioning into sets of people you can marry (or, perhaps more importantly, people you absolutely cannot). The social group may also be a nexus for encouraging normative behaviours ("we do things *this* way").

Group membership can be heritable (e.g. family, royalty, Judaism, feudal lords) or non-heritable (e.g. football teams, universities, Hell's Angels), and membership might be permanent or changeable (e.g. football teams). In the latter case, groups may be more or less easy to join – for example, some groups might impose costly behaviours such as sanctions or signals in order to become a member, e.g. paying fees, wearing tattoos or through hazing new initiates.

Families have shared interests in shared genes – indeed, in humans, pairs of unrelated individuals often find their interests aligned in the form of offspring. Families and factions within families might also find themselves in conflict, despite their common reproductive interests, for example when kin come into competition due to limited resources and potential mates (West et al. 2006). Thus, I will use an "ultra-liberal definition" (Okasha 2006: 184) by counting families as groups, *contra* Williams (1966: 93).

Groups are important loci for collective action and their structure matters. Increasing membership can boost (Zhang & Zhu 2011) or diminish (Soetevent 2005) the amount of cooperation within a group. Favouring what we might call an in-group can promote or bolster collective action through emphasising and aligning shared interests or triggering motivations for helping the group (e.g. through self-identification with other group members). In-group bias would also allow longer-term association between members, which may allow trust and reciprocity to flourish (Carpenter 2000) in the context of reputational systems (Yamagishi & Mifune 2009).

1.3 Theoretical perspectives on understanding social evolution

The work presented in this thesis relies predominantly on human behavioural ecology, a sub-discipline of evolutionary anthropology (EA). Like many other social sciences, EA is concerned, in part, with analysing human decision-making. Unlike many social sciences, EA takes an explicitly theory-driven approach, generating hypotheses from evolutionary theory, developing models and testing them empirically. In the words of Cronk & Leech (2013: 11): "Evolutionary theory can provide a theoretically grounded set of expectations about what motivates humans to act."

Human behaviour operates at a number of interlocking levels. Many behaviours can be affected by culture, and in turn culture can be shaped by behaviours. Human behavioural researchers often use an 'ideational' definition of culture as, in the words of Barkow (1989: 140), "a system of socially transmitted information," (see also Boyd & Richerson 1988; Cronk 1995; Durham 1991). This narrowed concept of culture—one that "includes less and reveals more" (Keesing 1974: 73)—separates it from its manifestations in behaviour (Cronk 1995) and thus allows researchers to explain behaviour in terms of culture and vice versa. I will employ this conceptual definition of culture in the analysis chapters. Although culture *per se* is not the target of enquiry here, I will explore how facets of culture—such as reputation systems, taboos, perceptions of wealth, and ideas of kinship outside of genealogical relatedness—affect cooperation.

1.3.1 Human behavioural ecology

Human behavioural ecology (HBE) emerged from the more animal-focussed discipline of behavioural ecology (Davies et al. 2012) but extended to include factors seemingly unique to humans such as marriage systems, as well as mating systems; friendship, affinal kinship, and other fictive forms of kinship (see Section 1.4.1.2); an extraordinary diversity in subsistence and home range; unique aspects of life history such as childhood and extended post-reproductive lifespan; extreme niche construction; and cumulative culture. As

such, research in this area bridges between the natural and social sciences. HBE has tended to focus on the classic topics of anthropology such as kinship, marriage, inheritance, and subsistence. Today, the discipline reaches beyond its original home within anthropology to engage with demography, economics, epidemiology, political science, psychology, and public health, among others (Borgerhoff Mulder 2013).

HBE provides a theoretical framework for explaining how and why behaviour becomes adapted to social and physical environments – and how behaviour can in turn shape environments (Bliege Bird 2015). The discipline's traditional focus on small-scale societies such as hunter-gatherer or horticulturalist populations has shifted somewhat, with many researchers now exploring behaviour in industrialised and 'post-industrial' (e.g. service economy) societies, as well as attempting to understand societies in transition that combine traditional ways of life with the encroaching demands of a globalising world (such as the two populations studied in this thesis).

The core tenet of HBE is that natural selection has shaped (and continues to shape) human behaviour, psychology and physiology in order to maximise inclusive fitness. Through whittling down genetic variation in a population depending on how well genotypes survive and reproduce relative to one another, natural selection is the only evolutionary force that can produce complex adaptations, giving the appearance of design in organisms (Dawkins 1986). The concept of adaptation refers to heritable traits that have been shaped by selection on variation within populations; an adaptive trait increases the fitness of its bearer relative to the mean fitness in the population. For creatures capable of cumulative culture, such as humans, the processes of cultural evolution can also produce adaptations (Richerson & Boyd 2005).

Evolutionary dynamics—changes in gene frequencies—can be described in terms of selection and transmission (Gardner et al. 2011). This partitioning is captured by the Price equation (Price 1970), a theorem describing how the frequency of a trait changes relative to the mean fitness within a population, given the covariance between the trait and fitness, and the expected fitness given the change. The equation accounts for genetic and non-genetic (or more generally,

replicative and non-replicative) sources of change. Biases in the transmission of genes affect evolutionary dynamics, e.g. through behaviours such as assortative mating or genes with the ability to represent themselves in gametes at a greater-than-average rate (e.g. meiotic drive). When transmission biases are low or absent, selection become the key driver of evolutionary change (Panchanathan 2011).

Selection can be further partitioned into two components: direct fitness and indirect fitness (see Section 1.4.1). Inclusive fitness is the additive effect of direct fitness (one's own genes) and indirect fitness (copies of genes shared by other individuals) (Hamilton 1964). HBE emphasises the role of natural selection as an optimiser of traits and posits that selection shapes behaviours, physiology and reaction norms to make individuals act as if maximising their inclusive fitness (Grafen 2002).

HBE uses optimality models as a starting point for predicting which behaviours evolution should favour in particular environments. Optimality, in the HBE sense, is based on the microeconomics framework of rational choice theory, in which actors make decisions based on cost-benefit ratios and their underlying preferences. When examining social behaviour through an evolutionary lens, we must be careful not to conflate strategies produced through the optimising nature of selection with an individual's strategies, which are a product of her psychology. Optimality models can give insight into the strategies favoured by natural selection (all else equal), but it is not necessarily reasonable to apply these models to predict what an individual 'should' do. As Binmore (2010: 3) wrote, the latter is "the dogma that people actually do have utility functions in their heads that they seek to optimize when interacting with others."

Life entails a balance of costs and benefits. Evolutionarily, both are defined in terms of fitness: an individual's long-term genetic contribution to future generations. Fitness is difficult to measure in the real world (Orr 2009), especially in long-lived species such as humans. Proxies of fitness—such as the survival of offspring to reproductive age, completed fertility, number of children or grandchildren (controlling for age)—give some insight into the survival

and reproductive behaviours of individuals following particular strategies.

Given the strictures of ethics, it is difficult to marshal evidence for adaptation by conducting controlled experiments on human marriage, reproduction or subsistence systems. Instead, HBE relies on an explicitly promiscuous approach involving theoretical models and simulations, surveys, statistics, opportunism such as natural experiments, and 'natural-field' experiments in which subjects are not aware they are taking part in an experiment. Through converging lines of evidence from various methods, human behavioural ecologists are able to test their adaptive hypotheses. This thesis will use a variety of statistical approaches to analyse behaviour in field-based quasi-experiments, survey data collected for this thesis, data collected for a separate project, and governmental data.

Behavioural ecologists tend to be unconcerned with the exact genetics or psychological mechanisms underlying behaviour and assume that neither constrain the adaptation of behaviour (known, respectively, as the phenotypic and behavioural gambits; Nettle et al. 2013). Following Tinbergen (1963), HBE categorises two kinds of explanation: proximate and ultimate. Proximate questions ask about the mechanisms of a trait in terms of its development (e.g. how people learn in which situations they should cooperate) and physiology (e.g. the emotional glow of doing something nice). However, warm, fuzzy feelings are not an answer to evolutionary questions, which ultimately ask why traits have come to exist, in terms of their phylogenetic history (e.g. which other species cooperate in similar situations) and their function (e.g. nice people have higher inclusive fitness). When attempting to scrutinise the dynamics of cooperation through the lens of evolution, we must bear in mind the type of question – i.e. whether we are asking proximate or ultimate questions. Within the literature on cooperation, as I shall discuss in the next section, these two types of question often become conflated (see also e.g. West et al. 2010).

1.4 Evolutionary theories of cooperation

I will begin this section by examining the ultimate explanations for cooperation alongside the proximate mechanisms, discussing general as well as human-

centric frameworks. I will first introduce two seminal theories of cooperation—kin selection and reciprocal altruism—before moving on to discuss more recent attempts to extend and provide alternatives to these theories.

Evolutionary theories of cooperation require non-random interactions between potential cooperators. The idea of assortment among cooperators is becoming central to the field, encompassing kin selection and the various reciprocities (discussed below) as well as mechanisms such as partner choice (Barclay 2013), mobility (Aktipis 2004, 2011; Lewis et al. 2014) and demographic factors such as population structure (Lion et al. 2011; Nowak & May 1992; see Chapter 9 for further elaboration of these topics).

1.4.1 Kin selection

As with much in evolution, Darwin discussed the possibility of kin selection first, pondering the sterile castes found in eusocial insects (Darwin 1859). The idea that costly behaviours such as sterility had not evolved for the good of the species gained traction in the 1930s with the work of Fisher and Haldane. It was not until Hamilton's formal model analysing the circumstances under which social behaviours can evolve that the concept of inclusive fitness—an approach based on a "gene's-eye view" of evolution (Dawkins 1976; Williams 1966)—gained widespread acceptance among most evolutionary biologists.

Hamilton's key insight was to extend Fisher's genetical theorem of natural selection—"which represents the mathematical foundation of Darwinian theory itself" (Gardner et al. 2011: 18)—by partitioning selection into direct and indirect fitness components. Under kin selection, a gene should increase in frequency despite deleterious effects on its carrier's fitness if it benefits others carrying copies of the same gene(s); in all cases, the benefits to others, tempered by the degree of relatedness, must outweigh the costs to the carrier. This dynamic is summarised in the following inequality, known as Hamilton's rule (HR):

$rB > C$

Here, r is the degree of relatedness between the actor and the recipient (see section 1.4.1.1 for definition of relatedness); B is the fitness benefit gained by

the recipient; and *C* is the fitness cost suffered by the performer of the social behaviour. Since evolution by natural selection is a population-level statistical process, fitness effects (the benefits and costs in HR) should properly be understood in statistical terms (Gardner et al. 2011). It is important to remember that an inclusive fitness approach is as mechanism-free as natural selection; regardless of the mechanisms at play, the outcome of natural selection can be understood in terms of costs, benefits and relatedness (Gardner et al. 2011).

Since Hamilton's original formalisation (Hamilton 1964), theoreticians have increasingly generalised the concept of inclusive fitness. In essence, the benefit and cost terms have remained the same, although confusion is still rife regarding their exact definition and how best to measure them empirically; the major shifts towards generalisation has been with regards to relatedness (Fletcher & Zwick 2006).

1.4.1.1   Concepts of relatedness

The relatedness parameter, *r*, in Hamilton's rule was originally defined by Wright (1922) as the probability that alleles at any randomly chosen locus in two individuals will be identical by descent. Thus, siblings will share, on average, 50% of their genomes (although the exact proportions shared will vary due to random processes such as recombination), grandparents and grandchildren will share 25% and so on, exponentially decreasing as the most recent common ancestor of two individuals becomes more distant.

This consanguineal approach to relatedness is intuitive but theoreticians, including Hamilton (1972), have generalised the concept to measure assortment on genotype regardless of descent (Fletcher & Zwick 2006). Relatedness was redefined as a statistical term to reflect the benefit and cost parameters in Hamilton's rule (which, as discussed above, are also statistical terms). This new definition of relatedness measures the genetic similarity of any two individuals with respect to the average relatedness in each individual's neighbourhood. Where Wright's (1922) relatedness by descent is a coefficient bounded between zero and one, relatedness as a statistical concept can take negative values. Negative relatedness captures the possibility that two individuals can

be less related to one another than each is to its local population, while positive values of relatedness describe a situation in which an actor is more likely to share alleles with a recipient than with the recipient's neighbourhood (Krupp & Taylor 2015).

Importantly, neighbourhood relatedness allows for genetic similarity between non-kin. While this approach, based on quantitative genetics, has value in theoretical models, it is difficult to measure empirically, especially in humans, where the experimental setup needed to measure genotype-phenotype covariance, given current methods, involves artificial selection and is thus ethically dubious. As genome sequencing technology matures and becomes more affordable, relatedness as identity by descent will likely be dropped in favour of directly measuring genome similarity (Speed & Balding 2015).

For the time being, pedigree data are relatively straightforward for human behavioural ecologists to collect and analyse compared to genomic data. Techniques for ensuring accuracy in pedigrees have been well-developed in anthropology and will be employed in this thesis. In Chapter 9, I will outline how evolutionary anthropologists might begin to test kin selection hypotheses using the statistical concept of relatedness.

1.4.1.2   Unrelated relatives: fictive and affinal kin

Colloquially, we hear people (often youthful) talk of brothers from other mothers, sisters from different misters, or refer to one another as 'cuz', 'blood' or 'fam'. Political groups speak of motherlands and brotherhoods, organised crime syndicates describe themselves as families, and some religions tell us we are the children of their gods. These examples have in common the treating of people who are unrelated as family. Extending the status of 'family' to friends and others expands social networks, forging deep ties of mutual obligation, ameliorating social isolation and perhaps substituting for absent biological family (Chatters et al. 1994; Freed 1963; MacRae 1992; Norbeck & Befu 1958). Fictive kinship can be important among pastoralists who herd in cooperative groups (see Chapter 4). For example, *khot ail*—nomadic groups of Mongolian herders—include not only family but also fictive kin (Conte 2013).

Marriage ties create fictive kinship relations between families (e.g. sisters-in-law); affinal kin are unlikely to be related, except in cases such as cousin marriage. Humans appear to be unique in recognising not only a vast range of distant relatives (e.g. the Saami pastoralists of Part I know who their third cousins are) but also in how we extend our kinship systems to encompass the family of our spouses. Language enables us to distinguish a wider circle of kin compared to other animals, as well as giving us the tools to treat non-relatives as fictive kin.

Cooperation among fictive kin would, on the surface, preclude an inclusive fitness explanation; however, Hamilton's rule is theoretically capable of accounting for cooperative behaviour between individuals who might share genes at particular loci without being genealogically related, as well as among true non-kin (Queller 2011). Since shared genes are fundamental to an inclusive fitness understanding of social evolution, this thesis will quantify the effects of relatedness on cooperation in each of the research chapters.

1.4.2 The reciprocities

Practically all life in society includes and implies reciprocities, and reciprocity has been seen as the basic glue that makes people constitute groups or societies.

(Serge-Christophe Kolm, quoted in Frey & Meier (2004))

1.4.2.1 Reciprocal altruism

In his seminal paper, Trivers (1971) formalised how cooperation may be conditioned upon long-term reciprocal interactions between individuals providing benefits to one another, regardless of whether or not they are related. Trivers's model of reciprocal altruism (RA) shows how cooperation can be enforced through actors and recipients promoting each other's cooperation with cooperation of their own or, conversely, punishing betrayal with betrayal. As such, RA explains how non-relatives can solve social dilemmas.

RA, on an ultimate level, should be more correctly thought of as reciprocal cooperation since nobody is being altruistic when they ultimately receive long-term fitness benefits despite paying short-term fitness costs. On a proximate

level, however, cooperation can be altruistic if an individual helps another, selflessly, without expectation of repayment (assuming no one else is around to witness the event and the recipient will not spread word of the kindness); altruistic psychologies might be shaped for genetically selfish reasons (Barclay 2012). Therefore a full evolutionary understanding of reciprocal altruism must include both levels of analysis. Throughout this thesis, I will use 'reciprocal altruism' and 'reciprocal cooperation' interchangeably and will mention explicitly if I mean 'true' altruism from a fitness point of view.

The idea of reciprocity as an essential component of cooperation has a long history within social anthropology, parallel to its history within the evolutionary sciences. Lévi-Strauss (1969) understood human relations as being based around norms of reciprocity and exchange in three realms: words (language); women (kinship); and resources (economics). Mauss (1925) discussed three obligations that come with cooperative, rewarding behaviours such as gifts: to give, to receive, and to reciprocate. Exchanges, by this account, create obligation – the burden to repay and the risk of not being able to do so, which may lead those reneging to lose face and prestige, thus potentially losing out on future cooperative encounters. Not all gifts engender debt, however: some can be free, e.g. urban passers-by giving change to beggars, tipping in a restaurant you will never revisit, or 'Indian gifts' expressly given to not be repaid (Parry 1986).

Sahlins (1972) outlined a similar tripartite typology of reciprocity: generalised, balanced, and negative. In his account, generalised reciprocity refers to a seemingly altruistic giving of gifts without prescribing specific terms of redress; balanced reciprocity is an immediate-return exchange; and negative reciprocity can be thought of as barter, where each party seeks to increase its own self-interest without creating or tending to social relationships (much like the evolutionary idea of pseudo-reciprocity; see section 1.4.2.3). These social theories correspond to proximate explanations in the evolutionary sciences, albeit particularly human-centric mechanisms: exchange relationships imbued with meaning and poised on reputational concerns.

The Prisoner's Dilemma became the canonical model of cooperation (Ax-

elrod & Hamilton 1981), pitting self-interested actors against one another in an artificial, inhospitable world. The abstractness of the basic model—two players, each with limited options (to either cooperate or defect), subjected to the outcome of their own and their opponent's decision—provides a rich ground for exploring the dynamics of cooperation. Indeed, theoreticians are still discovering hidden corners of this well-explored mathematical terrain, such as the class of 'zero determinant strategies' which allow one player to determine her opponent's payoffs regardless of how the opponent plays (Press & Dyson 2012; Stewart & Plotkin 2012).

Repeated interactions are the key to reciprocity. Although a single round of the PD (a 'one-shot game') inexorably leads to a failure in cooperation for economically rational actors, repeating the game with the same players can foster cooperation. Cooperation can also emerge from a PD situation if players have the ability to 'parcel' their investments into smaller, less costly acts – essentially turning a one-shot interaction into a repeated, perhaps indefinite, game (Raihani & Bshary 2015). However, despite the PD's prominence in theoretical work, it is less clear how often this form of social dilemma occurs in nature. For humans, social norms and institutions might evolve in order to solve dilemmas through changing or ameliorating individual incentives. Shifting payoff structures alter the terms of the game, potentially reorienting the dilemma into a situation more conducive to cooperation (Archetti & Scheuring 2012).

'Network reciprocity' refers to a form of reciprocal altruism that accounts for population structure (Nowak & May 1992). This form of reciprocity involves situations where individuals interact in a biased, limited manner based on patterns of social ties (Nowak 2006), in a similar manner to the assortment discussed at the beginning of this section. The networks of farm labour presented in Chapter 7 are spatially structured within villages; I will analyse the effect of geographical proximity alongside kinship and reciprocal relationships hypothesised to predict cooperation.

1.4.2.2 Indirect reciprocity and reputation-based cooperation

Reputation has been posited as a factor underlying cooperation, whereby individuals cooperate with those who have previously helped others, even if the potential co-operator has no previous experience with the helper (Nowak & Sigmund 1998, 2005). Indirect reciprocity—so called to contrast with the 'direct reciprocity' of RA—is a form of reputation-based cooperation that is contingent on an individual's image score; some theoreticians also emphasise the need for being seen to make appropriate, justified decisions ("standing"; Panchanathan & Boyd 2003). The original models of indirect reciprocity (Nowak & Sigmund 1998) made the unrealistic assumption that individuals cannot interact with the same partner more than once (Roberts 2008). Later work suggests that the ability to choose partners for repeated interactions based on their reputation is essential for reputation-based cooperation to evolve (Roberts 2015b).

Potential cooperative partners can distinguish themselves through their reputations. Laboratory studies of public goods games in which participants are able to build up good reputations show that players with a history of donating, or a willingness to sacrifice earnings, can increase their probability of being chosen to join groups (Barclay & Willer 2007; Stiff & Van Vugt 2008; Wedekind & Milinski 2000). Cooperation plummets or disappears altogether when reputation systems are removed (Yamagishi & Mifune 2009) or when reputations can be earned easily, e.g. by paying for a good reputation (Pfeiffer et al. 2012). The ability to choose social partners based on their reputation can lead to a form of 'competitive' cooperation whereby individuals cooperate to strategically invest in building good reputations, increasing their chances of being chosen for future cooperative interactions (Sylwester & Roberts 2013), including mating (Raihani & Smith 2015).

Evidence from the field provides support for the importance of indirect reciprocity in human societies. A study of Quechua agro-pastoralists living in the highlands of Peru found that households helping with cooperative tasks such as harvesting and husbandry had larger support networks as a result of reputational boons (Lyle & Smith 2014). A good reputation was defined in terms of being known as a reliable and hardworking person, who was also

respected, influential and generous.

Better reputations can also translate into fitness benefits. Upper-body strength was the strongest predictor of a good hunting reputation for Hadza men, which also boosted their reproductive success (Apicella 2013); other, less easily quantified ideals such as 'heart' and 'intelligence' were also cited as desirable traits. Similarly for Meriam people in Australia, those who were known as better turtle hunters also had greater reproductive success (Smith et al. 2003).

In Chapter 8, I look at reputation for witchcraft to analyse how poor standing in a community might lead to isolation and the withholding of cooperation, and how these might negatively affect reproductive success. The definitions of desirable and objectionable reputations will be valued differently in particular societies at particular times. This potentially makes truly comparative studies of reputation systems difficult if researchers must rely on emic understandings of reputation that might be hard to translate to different places. Further elaboration of this point is beyond what is possible in this thesis, although it is something researchers should bear in mind when designing field-based studies in future.

1.4.2.3 Other reciprocities

There are three other 'kinds' of reciprocity that will not be covered further in this thesis, but I mention them here for completeness. 'Pseudo-reciprocity' describes a situation in which one individual invests in another, at a cost to themselves, boosting the fitness of the recipient who continues to follow their own self-interest rather than directly reciprocating the investment, e.g. honeyguide birds leading humans to beehives and eating the leftovers (Bergmüller et al. 2007; Connor 2010; Leimar & Connor 2003; Raihani et al. 2012; Sachs et al. 2004). 'Generalised reciprocity', in an evolutionary sense, means to help someone if you have previously been helped by anyone (Barta et al. 2011), and thus is not really reciprocity at all (Cronk & Leech 2013).

'Strong reciprocity' is the idea that cooperation evolves through biological or cultural group selection. Strong reciprocators are individuals who favour other cooperators and are willing to bear a cost in punishing transgressors and

violators of social norms (Gintis 2000). Although strong reciprocity appears to be important in theory and laboratory experiments, evidence of its importance in the real world is equivocal (Balafoutas & Nikiforakis 2012; Guala 2012; Winking & Mizer 2013). Experimental evidence suggests that individuals will not pay a cost to punish norm violators (Bone et al. 2014) and third-party punishment is more prevalent in larger-scale societies (Marlowe et al. 2008), although coordinated collective punishment (e.g. mobs) might be present in many societies, regardless of scale (Moya, pers. comm.). In addition, reputation systems might function as a means of cheap collective punishment (see Chapter 8).

Of the reciprocities, the work presented in this thesis focusses mainly on reciprocal altruism (direct reciprocity) and indirect reciprocity (reputation). I will not, therefore, concentrate further on generalised, pseudo or strong cooperation.

1.4.3 Kin selection versus reciprocal altruism?

On occasion, researchers have sought to show the primacy of kin selection over reciprocal altruism (or vice versa), unnecessarily opposing the two theories. Such attempts at finding 'silver bullet' explanations for cooperation ignore the fact that these theories are not mutually exclusive and can operate in concert (Carter 2014; Rothstein 1980; Schino & Aureli 2010). A simple thought experiment shows how this can be the case: if there is any genetic proclivity for reciprocal cooperation, reciprocators are likely to share these genes and thus within-species reciprocity cannot be distinct from kin selection (Rothstein 1980).

According to Schino & Aureli (2010: 562), researchers "have been adopting a double standard" where they control for relatedness when statistically testing reciprocity but not vice versa. In a meta-analysis of primate allo-grooming, Schino (2007) looked at the relative effect sizes of kin selection and reciprocity, each controlling for the other. He found that, across 14 primate species, reciprocity had a stronger effect on allo-grooming compared to kinship, although both predictors were positive (Schino 2007). A similar technique was applied to observations of food sharing in humans and other primates, which again found that reciprocity had a stronger effect on average than kinship, although

the differences were not statistically significant (Jaeggi & Gurven 2013). Chapters 4 and 7 will analyse how kin selection and reciprocal altruism can have complementary, positive effects on cooperative behaviour.

1.5 Overview of thesis structure

This thesis investigates cooperative behaviour in real-world situations. The following chapters explore kin and non-kin cooperation using datasets from two field studies, including one which was collected for this thesis. The groups in these chapters range from nuclear families living in households, to villages of households and larger communities.

Part I of this thesis focusses on a population of reindeer herders living around the Arctic tundra of northern Europe, while Part II focusses on a small-scale farming community in rural China. While the two study populations lead quite different lifestyles in very different environments, they have in common the fact that they are ethnic minorities trying to keep alive their traditional cultures that are, to varying extents, at odds with the nations in which they find themselves. The research presented here will analyse the social dynamics and the kinds of cooperation these two populations engage in, in the absence of more formalised state institutions.

Within Part I, Chapter 4 uses social network analysis on a gift game played among Saami reindeer herders in order to investigate the relative importance of kin selection and reciprocal altruism in explaining cooperation. Chapter 5 analyses behaviour in a public goods game to understand how groups of Saami herders cooperate in order to solve social dilemmas.

In Part II, Chapter 7 combines a real-world measure of cooperation—working on the farm of another household—with two gift games played by a population of Mosuo farmers in order to understand the factors affecting observed social relationships. Chapter 8 focusses on how having a poor reputation might lead to social isolation and detrimental effects on reproductive success.

Finally, Chapter 9 discusses the overarching results of these analyses in the context of the wider literature and concludes with suggestions for future work.

Chapter 2

Methods

This chapter will introduce experimental economics games—a key methodology for understanding cooperative behaviour in this thesis—and review how researchers have used these games to understand real-world cooperation. Finally, I provide an overview of the statistical methods used throughout this thesis.

2.1 Measuring social relationships with experimental games

Scientific approaches to testing predictions derived from the theories of cooperation reviewed in Chapter 1 have several features in common. Theoretical work constructs stylised games that are mathematically precise yet general (Camerer 2011a); real-world situations that potentially lead to social dilemmas are distilled into highly abstracted models. Their general, abstract nature means that the games are analytically tractable and their structure can potentially be applied to a number of situations. Empirical studies attempt to translate these stylised games into relevant, real-world situations in order to understand how individuals actually behave.

A core assumption of the empirical work presented in this thesis is that experimental games can reveal meaningful underlying social relationships. While abstract games involving anonymous interactions are of great use and aid cross-cultural comparison of studies, I will argue that researchers should not feel bound by them. It might prove equally enlightening to toy with a

game's structure in order to make it more contextual and relevant to particular ecologies (including subsistence mode, kinship system, etc.), thus increasing the value of conducting games in field studies. Accordingly, the empirical work presented in this thesis is centred on games framed such that a participant's decisions reveal their underlying social relationships.

Models of humans as rational actors seeking to maximise their utility (where utility may be fitness, money, happiness, etc.) do not adequately explain observed levels of cooperation in many situations across many societies. Our constant and widespread economic irrationality has led some researchers to consider human cooperativeness as non-adaptive (Gintis 2000), maladaptive (Burnham & Johnson 2005) or adapted to ancestral conditions (Tooby & Cosmides 1996).

I will leave aside the debate surrounding the applicability of economic rationality versus ecological rationality – the latter suggesting that our apparent and 'predictable' (Ariely 2009) biases are in fact rational when accounting for context (Fawcett et al. 2014; Gigerenzer 2010). Suffice to say, *Homo economicus* has led many researchers to concentrate on our cognitive biases and seemingly irrational behaviours at the expense of understanding sociality in ecologies laden with context (McNamara & Houston 2009). While it is not an aim of this thesis to develop these distinctions further, it is worth bearing in mind that seemingly irrational behaviour, when analysed with the tools of evolution in meaningful contexts, may turn out to make sense after all.

In recent years, researchers have taken the methods of experimental economics and begun to apply them to situations that are salient to local groups (Camerer 2011b; Cárdenas & Carpenter 2008; Harrison & List 2004). Early work in this area used context-free games in order to explore variability in behaviour across societies (Henrich et al. 2001). However, field experiments tend now to involve games framed in terms of relevant social institutions that promote particular norms (Cronk 2007; Gerkey 2013), games involving amounts of money with high purchasing power (perhaps making up a large proportion of a participant's wages), or games played using goods relevant to the field situation, such as salt or honey rather than money (Apicella et al. 2012; Chaudhary

et al. 2015; Lamba & Mace 2011). This enables researchers to study cooperative behaviour in contextually relevant situations using a quasi-experimental approach that will form the backbone of this thesis. I will use experimental games as one method of testing evolutionary hypotheses about cooperation in the real world.

The research reviewed in the following sections will be limited to studies in which laboratory methods have been transposed to field sites (i.e. the kinds of societies that are the traditional fodder of human behavioural ecology). Thus, I will ignore experiments carried out among students at Western universities and elsewhere, although I include experiments conducted among other urban dwellers in Western(ised) nations. I will also ignore online experiments such as those conducted via the Amazon Mechanical Turk labour market. For brevity, I do not include field experiments designed to capture behaviour towards common pool resources rather than public goods (e.g. Ruffle & Sosis 2006; Vollan 2008).

2.1.1   Games with gifts

Many field experiments that explore individual-level rather than group-level cooperative behaviour tend to do so with ultimatum, dictator or trust games (Camerer 2011a). The trust (or investment) game involves one participant giving part (or all or none) of an endowment to another player, who can then send some, all or none back. The ultimatum game (UG) is a simpler version of the trust game in which one player offers a split of their endowment to another player who then chooses to accept or reject the offer; in the case of rejection, neither player receives anything. The dictator game (DG) is simpler still: one player gives a split of their endowment (or nothing) to another, often anonymous, player.

While undeniably useful as a proxy for understanding pro-social behaviour and fairness norms, I argue that the DG and UG exhibit shortcomings that make them inappropriate tools for the purposes of this thesis, which is to understand social relationships between individuals. The main criticism involves how to interpret the seemingly irrational and variable behaviours ob-

served worldwide in these games (Henrich et al. 2001; Lamba & Mace 2011). The sub-game perfect Nash equilibrium strategy—i.e. the strategy arrived at by a rational player working through backward induction—in the DG is to donate nothing and in the UG is to offer the smallest possible split. However, researchers tend to ignore the fact that any donations in the DG and any split of the endowment in the UG, no matter how big or small, are also Nash equilibria and, thus, rational strategies.

Here, I make use of a simpler, more intuitive experiment: the gift game. Gift-giving is likely to be a human universal found in all societies, as well as being classic grist to the anthropological mill (Mauss 1925). In a gift game, participants are endowed with an amount which they must give away to one or more people, not keeping any for themselves.

Gift games were first employed, to the best of my knowledge, by Apicella et al. (2012) in their study of Hadza hunter-gatherer social networks, in which they found that people gave gifts of honey to relatives as well as to spouses and friends (who also considered the giver a friend). Chaudhary et al. (2015) used this method, including the honey sticks, among a group of BaYaka hunter-gatherers. They found that men who received more gifts (i.e. were more popular) were also more likely to be in polygynous relationships, which in turn was associated with greater reproductive success. In addition, men who were the appointed spokespeople for their camps received the highest number of gifts, suggesting there were also reputational factors at play.

Gift-giving can also be leveraged for a different purpose. Researchers working for an international charity based in Switzerland found that including gifts with letters soliciting donations led to a substantial increase in charity giving (Falk 2004), perhaps sparking norms of obligation and reciprocity in potential donors. Similarly, tourists visiting a Costa Rican national park gave slightly larger donations after they were given a refrigerator magnet, although the marginal increase was less than the cost of the gift itself (Alpizar et al. 2008).

In an interesting reversal of gift-giving, Rucas et al. (2010) played a 'social strategy game' in which Tsimane forager-horticulturalist women from three communities in Bolivia were given the opportunity to anonymously take

coloured plastic beads (a favoured commodity in the area) away from other women. They took fewer beads from neighbours, friends and enemies, but more beads from distant relatives (although still some from close relatives).

In my experience (see Chapter 4 and Thomas et al. 2015), gift games require little explanation and so are an easy yet efficacious way of revealing meaningful social relationships between individuals. Chapter 4 uses a gift game to explicitly compare the relative importance of genealogical relatedness and social group membership, while Chapter 7 tests whether patterns of gift-giving predict a real-world cooperative behaviour: helping on the farms of other households during planting and harvesting seasons.

2.1.2   Public goods games

How group-level cooperation emerges from individual decisions is also important for understanding cooperative dynamics across human societies. The canonical model of group-level cooperation is a social dilemma known as the public goods game (PGG). PGG participants are given an initial endowment and they must choose a proportion to donate to the public good (often a pot of money), keeping any remainder for themselves. Once everyone has made their decision, the group pot is multiplied—either by a fixed amount (linear PGG) or as a function of donations (nonlinear PGG)—and the total is distributed equally to all group members, regardless of their donations.

A social dilemma arises because the structure of the PGG forces group members to balance their own self-interest (following an individually rational, income-maximising strategy, which is to donate nothing) with the collective interest of maximising everyone's welfare by all members donating their full endowments. Thus, if everybody behaves in a self-interested manner, the public good does not get provisioned. However, when deployed in laboratory experiments, the majority of people donate (Ledyard 1995).

2.1.2.1   Variation in cooperativeness within and across cultures

PGGs played in the field have uncovered a wide variation in cooperative behaviours. One review of PGGs involving non-student samples found that donations ranged from 23% to 81% of the initial endowments (mean = 51%;

Cárdenas & Carpenter 2008). In a study of 15 small-scale societies, the differences in contributions were larger between groups than within (Henrich et al. 2005). However, Lamba & Mace (2011) found considerable variation in contributions across villages in a single society in Pahari Korwa, India. Similarly, among Hadza hunter-gatherers there was substantial variation between camps, while people donated similar amounts to a PGG within camps (Apicella et al. 2012). A study in southwest China found large variation in PGG contributions across eight ethnic groups (including Mosuo people – the focus of Part II), associated with differing norms of female-biased dispersal. Populations featuring low rates of female dispersal contributed less, while individuals gave more when they lived in their natal villages (Wu et al. 2015).

Researchers disagree over whether this variation is primarily driven by market integration and stable society-wide cultural norms (Henrich et al. 2005), localised and changing expectations of fairness and trust resulting from social dynamics (Gurven et al. 2008), or village-level demography and ecology (Lamba & Mace 2011). While measuring and explaining intra-cultural and inter-cultural variation in cooperative behaviour is beyond the scope of this thesis, I attempt to minimise confounding factors in PGG donations by playing them only among herding groups within a single district in northern Norway (Chapter 5).

2.1.2.2 Group size affects contributions

The number of people in a group can affect cooperativeness by changing the returns each player can expect from their donations. This is known as the marginal per-capita return rate (MPCR; Ledyard 1995). When a player would receive less than they put in—e.g. for every one monetary unit (MU) contributed, they receive less than one MU in return, meaning MPCR < 1—a social dilemma exists by which every player has a self-interested incentive to contribute nothing (the Nash Equilibrium), despite the welfare-maximising strategy being to donate the full endowment (Pareto optimality). The vast majority of PGG experiments employ MPCR < 1, although exact rates vary from study to study.

Different studies have found positive (Zhang & Zhu 2011), negative (Soetevent 2005) and curvilinear (Yang et al. 2013) responses to group size, and one study found no effect of group size at all (Baldassarri 2014). Overall, there appears to be a 'Goldilocks zone': groups that are not too big and not too small are the most cooperative (Aaron MacNeil & Cinner 2013; Agrawal & Goyal 2001; Poteete & Ostrom 2004).

A meta-analysis of the effects of punishment on cooperation reported across 18 countries found that group size (and thus MPCR) did not have a statistically significant effect (Balliet & Lange 2013). In other cases, people contribute despite low MPCR; for example, most Hadza people donated more than half their endowment despite a very low marginal return where people would receive a maximum of 0.27 honey sticks for each honey stick they donated (Apicella et al. 2012). In Chapter 5, I exploit the natural variation in the size of meaningful social groups in order to test whether perceived returns affect donations to PGGs.

2.1.2.3   Individual characteristics

Age affects cooperativeness. Some studies have found that older people are more likely to donate to the public good or contribute more, e.g. evacuees from Hurricane Katrina (Whitt & Wilson 2007); in rural Vietnam (Carpenter et al. 2004); Kamchatka, Russia (Gerkey 2013); and Pahari Korwa, India (Lamba & Mace 2011). In some places, age may have a curvilinear relationship with donating; for example, Rieger & Mata (2013) found that donations in rural Morocco peaked for people aged between 41 and 50 years, although $50-60\%$ of the youngest and eldest people also contributed.

Sex also affects contributions in some studies. Women were found to contribute more in rural Zimbabwe (Barr 2001); Nairobi, Kenya (Greig & Bohnet 2009); Maharashtra, India (Bouma et al. 2014); and in Vietnam, although women contributed less in Thailand (Carpenter et al. 2004). In PGGs played with Ache forager-horticulturalists, 70% of women contributed their entire stake, although men contributed slightly more to the group overall (Hill & Gurven 2004). Males across eight ethnic groups in southwest China con-

tributed more than women (Wu et al. 2015). A meta-analysis of public goods games (and other social dilemmas) found no sex effects, although the majority of studies involved students in laboratories (Balliet et al. 2011). The PGGs presented in Chapter 5 will thus control for the age and sex of participants.

2.1.2.4   Group composition shapes cooperation

A group's composition—its level of homogeneity or heterogeneity on a particular measure—can affect cooperation. Here, I will discuss three of the most salient: sex ratio, ethnic diversity and relatedness.

A study of people living in slums in Nairobi, Kenya, found no difference in contributions between sexes when they were placed in same-sex groups. However, women contributed more to all-female groups compared to mixed-sex groups, but contributed less than men in mixed sex groups, while men were not affected by group composition (Greig & Bohnet 2009). Males also expected others in mixed-sex groups to donate more than they actually did, while females underestimated contributions. It is possible, however, that the effects observed in this study were due to a local social institution (*harambee*) and the increased activity of women in community groups compared to men (see section 2.1.2.5). In southwest China, males gave more in mixed-sex groups, while a male-biased sex ratio in the PGG groups was associated with smaller contributions (Wu et al. 2015).

The ethnic composition of groups can also affect contributions to public goods. PGGs conducted among multiple ethnic groups (castes) in India found that players cooperated conditionally, increasing their donations if others from the same caste also donated more (Waring & Bell 2013). Similarly, a survey study conducted in Indonesia found that individuals were more likely to take part in community groups if more people from their own ethnic group were also members (Muller & Vothknecht 2012). The relative social standing of different ethnicities in a group can also affect contributions. For example, cooperativeness was reduced when groups contained people from the servant (Dalit) caste along with higher-ranking castes (Waring & Bell 2013).

The bulk of field-based PGGs do not account for the relatedness of people

to their groups. This is predominantly because these studies do not derive their hypotheses from evolutionary theory and so tend not to account for theoretically important factors such as relatedness to community groups. As discussed in section 1.4.1, evolutionary theory predicts that more related groups would be more cooperative (Hamilton 1964; Rendueles et al. 2015), except where there is competition for limited resources (Wilson et al. 1992). In the rare cases where relatedness data are collected, they tend to be treated as a nuisance to be controlled for rather than an explanatory variable affecting cooperative behaviour (Waring & Bell 2013; Wu et al. 2015). Wu et al. (2015) found that the presence of close kin in the PGG group did not affect contributions.

For the purposes of this review, I re-analysed the PGG data published by Waring & Bell (2013) but using mean group relatedness as the predictor of interest, controlling for each participant's age, caste and experimental treatment and including each player as a random effect. Overall, higher mean relatedness to the group was associated with higher contributions to the PGG (Figure 2.1). The PGGs presented in Chapter 5 explicitly account for group-level relatedness and analyse its effect on public goods contributions.
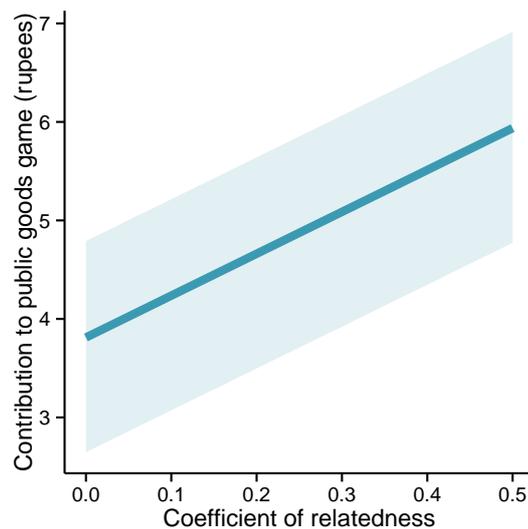
Figure 2.1: Predicted contributions to a public goods game by mean relatedness to a player's group. Data were re-analysed from Waring & Bell (2013). The multilevel model controls for age and caste, and includes each player as a random effect.

2.1.2.5 Context matters

The framing of a PGG can have mixed effects on cooperation. Some studies have found positive effects of framing; for example, PGGs framed in terms of local collective social institutions were associated with slightly lower donations when played among reindeer herders and salmon fishers in Kamchatka, eastern Russia (Gerkey 2013). Overall, donations were high, however, with nearly 80% of people contributing their full endowment and the mean donation was 89% of the endowment. Communities in post-civil war northern Liberia contributed more to a PGG when the winnings were funnelled into a community-driven reconstruction programme run by a non-governmental organisation (Fearon et al. 2009).

Others have found negative framing effects. Villagers in Sierra Leone donated 25% of their initial endowment to a PGG framed in terms of a community project, although they contributed 40% of their endowment to an abstract public good (Voors et al. 2012a). In rural India, framing had no effect on cooperation when comparing behaviour in a PGG framed around irrigation systems to an unframed PGG (Bouma et al. 2014).

Social institutions that prime or encourage particular behaviours can also shape cooperation. *Harambee* (Swahili for "let's pull together") is one such example. In Kenya, *harambee* refers to community projects and cooperative investments; participants contributed more to a PGG when they had equated the structure of the game with this social institution (Ensminger 2004). In Nairobi slums, women take part in more *harambee* activities than men, and were seen to contribute more to all-female groups compared to mixed-sex groups, which matches ethnographic evidence that women in these areas trust men less (Greig & Bohnet 2009). *Harambee* also creates an expectation that more affluent community members will contribute more to public projects (Ensminger 2004), although higher income was not associated with PGG donations (Greig & Bohnet 2009).

The perceived legitimacy of communal organisations has been posited to be an important factor in cooperation. Bouma et al. (2014) tested perceptions of legitimacy (in the sense of procedural justice, i.e. the implementation and

interpretation of rules) among farmers in rural Maharashtra, India. Their study found that although decentralised irrigation management organisations were seen as more legitimate, this did not translate into increased cooperation in PGGs. Other social organisations with high perceived legitimacy in the eyes of their members—namely, religions—may induce cooperation. For example, religious people living in a low-income urban neighbourhood in Texas, USA, gave more to religious causes (de Oliveira et al. 2012).

Beyond institutions, social networks are also likely to matter. In India, for example, the number of people invited to a harvest festival from surrounding villages—a proxy of social network size—was associated with increased contributions to a PGG (Lamba & Mace 2011).

Wider social, cultural and historical contexts matter as well. Previous exposure to violence, either individually or at the level of one's community, affects community cooperation. Conflicts can impede access to markets (Verpoorten 2009), thus potentially lowering cooperation, since better access to markets has been shown to increase collective action (Rustagi et al. 2010). Communities in Nepal exposed to violence through civil war were more likely to contribute to a PGG (Gilligan et al. 2014). Note, however, that in this case the PGG was structured such that nobody faced a trade-off between their own self-interest and the group's interest since they gained nothing through defecting; there was no social dilemma, so contributions are unsurprising.

Other studies (not utilising PGGs) have found that exposure to violence is associated with increased altruism to neighbours (Voors et al. 2012b). On the other hand, a survey of districts in Indonesia affected by violence after the 2007 Asian financial crash contributed less to real-life public goods (Muller & Vothknecht 2012).

In a similar vein, natural disasters can also have consequences on cooperation. African-American people who had been evacuated from Hurricane Katrina and had been unable to contact missing family members contributed less to a PGG (Whitt & Wilson 2007).

2.1.2.6 Sanctioning and punishment help cooperation

Monitoring and norm enforcement are needed, especially in larger and more heterogeneous groups, in order to maintain cooperation (Rustagi et al. 2010). Evolutionary scientists tend to define two kinds of mechanism: sanctions (a costless act, such as withholding investment) and punishment (an action that is costly to both the cheater and the cheated) (Raihani et al. 2012). Carpenter et al. (2004) found that Vietnamese communities responded to high variance in contributions (indicating the presence of free-riders as well as contributors) by sanctioning more; high contributors were not more likely to sanction than relative free-riders. Perhaps unsurprisingly, older people were also more likely to signal their disapproval in Thailand and Vietnam (Carpenter et al. 2004).

Groups in Ethiopia that contained more conditional co-operators also invested more time in monitoring the forest (Rustagi et al. 2010). Ugandan farmers tended to elect better-educated and wealthier local men as their group monitors, and their election was associated with higher PGG contributions (Baldassarri & Grossman 2011). In addition, donations to PGGs featuring a randomly chosen monitor were still higher than donations in a control PGG, even before the monitor had punished anyone (Baldassarri & Grossman 2011).

Sanctions do not have to be monetary. Low and high contributors were criticised in rural Zimbabwe; people adjusted their donations based on criticisms received by others who had behaved in a similar manner (Barr 2001). Shame, in a sense, selected out variation in behaviour. I will not make use of sanctioning or punishment mechanisms in the PGGs presented in Chapter 5. I do, however, investigate the role of withholding cooperation as a form of sanctioning in Chapter 8.

2.1.2.7 Communication and information increase contributions

Public discussion about contributions to a PGG was associated with an increased probability of selling coffee through producer organisations and attending general assemblies for Ugandan farmers (Baldassarri 2014). Information about the behaviour of others is also important. Ache people contributed more when they had information about how others had acted, even though

they did not know who else was in their group (Hill & Gurven 2004). A study of charitable giving (not making use of PGGs) also found that when people had more information about the donations of others, they donated more (Shang & Croson 2009).

Complete information does not always lead to socially optimal outcomes. Making people aware of the ethnic composition of their group, for example, has been shown to reduce cooperation among male agriculture workers in India (Waring & Bell 2013). The PGGs presented in Chapter 5 involve anonymous contributions and no information about group composition; however, participants know the pool of potential group members, since they belong to the same herding groups.

2.1.2.8 PGGs do not always predict real-world cooperation

There is equivocal evidence that cooperation in experimental games is related to real-world cooperative behaviours or outcomes. On the positive side, Ugandan farmers who contributed more to a PGG in which public discussion of strategies was allowed were also more likely to have sold their coffee through local producer organisations and attended general assemblies (Baldassarri 2014). Similarly, people from a low-income urban neighbourhood in Texas, USA, who donated more to the PGG were also more likely to donate to charity (de Oliveira et al. 2012).

Groups of forest users in Ethiopia that contained more conditional cooperators (measured through PGG behaviours) had more crop trees and invested more in monitoring the forest (Rustagi et al. 2010). However, in this case the PGGs were played with only two anonymous, randomly paired individuals, with a return rate that would lead rational players to be more willing to donate. In addition, Rustagi et al. (2010) did not link the behaviour in games to actual social behaviours that may have led to better outcomes, only to the outcomes themselves.

Other studies have found no link between game contributions and real-world behaviour. PGG donations were not associated with food sharing behaviours among the Ache, even when game participants had information about

other's contributions (Hill & Gurven 2004). Members of a non-profit village banking organisation in Ayacucho, Peru, who borrowed money from their peers were more likely to contribute to a PGG, although PGG donations did not predict whether or not people had repaid loans or saved more money one year later (Karlan 2005).

In this thesis, I will compare game behaviour to real-world outcomes as well as actual cooperative behaviour. Chapter 5 will analyse cooperation in PGGs alongside the productivity of herding groups. In Chapter 8, I compare cooperation in an experimental setting to measures of labour investment on farms.

2.2 Statistical analyses

This section will discuss model selection and model averaging approaches to testing hypotheses. I also outline the approaches taken to analyse the social networks emerging from my field experiments.

Traditionally, evolutionary scientists have drawn inferences from their data by using null hypothesis significance testing (NHST). This approach compares a hypothesis (normally formalised as a statistical model) with a null hypothesis in which no data-generating processes (variables or predictors) affect the observed outcome. While much of the work presented in this thesis eschews NHST in favour of an information theoretical approach (described below), I use NHST in Chapters 5 and 8 due to its simplicity and familiarity.

2.2.1 Model selection

Compared to NHST, model selection allows researchers to quantify the relative importance of a set of alternative hypotheses simultaneously, without necessarily being constrained by arbitrary significance thresholds (p-values). Model selection is an information theoretic approach that employs criteria to identify the 'best' model or set of models.

Like much in science, model selection relies on the principle of parsimony and entails a trade-off between simplicity (favouring models with fewer parameters but prone to under-fitting the data) and precision (favouring more

complex models but prone to over-fitting) (Burnham & Anderson 2004). The advantage of a model selection approach is that the relative support for competing hypotheses (i.e. a set of models) can be quantified, allowing robust inferences to be drawn based on estimates of parameters and uncertainty (Grueber et al. 2011).

2.2.1.1 Information theoretical approaches to hypothesis testing

Information theoretical (IT) approaches make no claim to the 'truth' of a model, in the sense that models can be nothing more than approximations of reality rather than an exact representation of full, noisy, ineffable reality (Burnham & Anderson 2004). Even the 'best' model from a set of candidates will be contingent on the available data and the precision of parameter estimates will depend on factors such as sample size. Large datasets contain more information and thus can be used to more accurately estimate smaller effects.

IT approaches are based on the concept that information, specifically the loss of information, can be quantified – in essence estimating the expected 'distance' between a model and reality (Burnham & Anderson 2002). Model selection is a formalised process for identifying which model (or models) loses the least amount of information, relative to competing models, about what processes (i.e. model predictors) generated the observed data (Efferson & Richerson 2006). Thus, we know nothing about how far each model is from the 'truth', only which is closer relative to the others. To co-opt the metaphor given by Efferson & Richerson (2006), if I stand next to Big Ben and my thesis examiners are standing three feet to my west, none of us know how far we are from Wales (where Wales represents truth in this example) by any absolute measure; we would only know that the examiners stand relatively closer to the truth: i.e. they have lost the least amount of information.

Information criteria, such as Akaike's Information Criterion and its nonparametric equivalent the quasi-likelihood under the independence model information criterion (AIC and QIC; both used in this thesis), estimate the information lost by a model, while penalising complexity in terms of a model's number of parameters. This allows a balance between reducing bias and re-

ducing variance, i.e. under-fitting and over-fitting (Efferson & Richerson 2006).

The best model is selected based on the minimum value(s) of information criteria calculated. Models with an AIC within a certain range of the least lossy model (typically $\Delta_i \leq 2$) are considered to have the most substantial support (Burnham & Anderson 2004). However, since this threshold captures the 95% set of top models (discarding the 5% 'worst' models), it is in practice little different to the arbitrary cut-off of $p = 0.05$ common in NHST. While NHST calculates the probability of observed data given the null hypothesis, IT approaches consider the strengths of competing hypotheses given the observed data (Garamszegi 2011). Of course, the best model will only be as good as the set of candidate models defined *a priori*.

2.2.1.2   Model averaging

When two or more models are highly and similarly ranked as being the 'best' models—the ones losing the least information—inferences can be drawn from a set of models using model averaging. This process, rather than simply taking a single top model despite others losing only slightly more information, can lead to more accurate parameter estimates – especially for weak effects (Grueber et al. 2011). Model averaging takes point estimates into account, as well as uncertainty estimates for model parameters, allowing inferences to be drawn from multiple well-fitting models according to the weighted support of each.

Following standard practice, I will use model averaging in cases where the model selection procedure reveals that either the 95% confidence set (in the case of AIC-based selection) or a set of models with $\Delta_i \leq 2$ (for QIC-based selection). All multimodel inferences will use the 'zero' method (Burnham & Anderson 2002; also known as the 'shrinkage' method). This means that a parameter estimate missing from particular models in the top set will be set to zero for those models and the estimate will be averaged across all models, reducing bias (Grueber et al. 2011).

2.2.2   Analysing social structure

Social interactions represent the structure of a population (Hinde 1976; Ilany et al. 2015) which can facilitate the evolution of cooperation through patterns

of relationships between individuals (Fehl et al. 2011; Nowak & May 1992). Individuals and their relationships can be modelled on a graph, a mathematical structure also known as a social network. Networks consist of nodes (also called vertices), representing individuals, and edges forming the ties between them.

Analysing individual-level behaviour on a network presents a challenge for classic statistical methods because data are clustered and thus violate the independence assumption of generalised linear models. For the purposes of the forthcoming chapters, the unit of analysis will be the dyad, i.e. a pair of individuals, where one is the 'ego' (e.g. a gift-giver) and the other is the 'alter' (e.g. a recipient). Many methods have been developed to draw statistical inferences from dyadic data, including generalised linear models with robust standard errors, multilevel (mixed-effect) models, exponential random graph models, social relations models, structural equation models, and actor-partner interdependence models (Kenny et al. 2006). For the research presented in this thesis, I make use of two: generalised estimating equations and quadratic assignment procedure, both of which I will describe below.

2.2.2.1   Generalised estimating equations

Generalised estimating equations (GEEs) are extensions of the generalised linear model (GLM) for dealing with correlated data (Hardin & Hilbe 2003). GEEs can account for multiple observations of each ego in dyadic social network data by clustering standard errors. Unlike multilevel models that explicitly account for subject-specific effects, GEEs are population-averaged models that average across all subjects; since I am interested in the effects of particular predictors rather than the differences between particular individuals, GEEs are the appropriate tool for modelling the network data presented here.

GEEs have become a popular method for analysing network data in the behavioural sciences, due in part to their relaxed assumptions compared to GLMs (e.g. GEEs can model non-normally correlated data with non-normal residuals; Ghisletta & Spini 2004). All GEEs presented in this thesis are logistic regressions across all possible dyads in each of the social networks, clustered

on each ego. For each model, I specified an exchangeable working correlation matrix, which models the dependence of observations within clusters; an independent specification did not improve model fits in any case. GEE does not use full likelihood estimates, so I computed and compared the quasi-likelihood under the independence model information criterion (QIC) for model selection (Pan 2001).

2.2.2.2 Quadratic assignment procedure

Measuring correlations between social networks—e.g. quantifying how gift-giving correlates with relatedness—also requires controlling for network structure. Quadratic assignment procedure (QAP; Krackhardt 1988) is a permutation test that first calculates Pearson's correlation coefficient between each dyad in any two networks. Next, the procedure permutes the networks to create multiple, random datasets. These 'scrambled' datasets represent the null hypothesis of no correlation, as well as its sampling distribution. If the majority (typically $> 95\%$) of these scrambled datasets do not result in a larger effect than the observed correlation, the relationship is unlikely to have occurred by chance.

To the best of my knowledge, this procedure has not been adopted for many anthropological social network studies, with the exception of Alvard (2003), Kasper & Borgerhoff Mulder (2015), Koster (2011), and Ziker & Schnegg (2005). Note that the first step of QAP algorithm described above calculates point estimates as if the data are independent, potentially leading to biased coefficients (Koster & Leckie 2014); for this reason, I use QAP only to calculate correlations and not to fit regression models.

2.2.3 Comparing relative effect sizes

Comparison of effect sizes is difficult when predictors are measured on different scales (e.g. comparing a binary predictor, such as whether or not a dyad belongs to the same social group, to a continuous one, such as the coefficient of relatedness) (Grueber et al. 2011). Following Gelman (2008) and Schielzeth (2010), I will standardise predictors to a mean of 0 and standard deviation of 0.5 in order to transform binary and continuous predictors to a common scale.

Since these parameter estimates are not biologically interpretable due to the scaling procedure (Schielzeth 2010), I will present them alongside the original, unstandardised estimates.

2.3   Software

All analyses were conducted in R 3.2.0 (R Core Team 2012) using the following packages:

- Model selection and averaging: `MuMIn` (Barton 2015) for GEE models and `AICcmodavg` (Mazerolle 2015) for generalised linear models

- Social network descriptive statistics: `iGraph` (Csardi & Nepusz 2006)

- QAP correlations: `sna` (Butts 2014), using a customised function for handling rectangular adjacency matrices (available from https://gist.github.com/matthewgthomas/728c53b7c7b99c12f1af)

- GEE analysis: `geepack` (Højsgaard et al. 2006)

- Tobit regressions (see Chapter 5): `VGAM` (Yee & Wild 1996)

- Cox regressions (see Chapter 8): `survival` (Therneau 2015)

- Zero-inflated Poisson regression (see Chapter 8): `pscl` (Jackman 2015)

- Standardisation of predictors: `arm` (Gelman & Su 2015), using a customised function to handle GEEs (available from https://gist.github.com/matthewgthomas/6e4ae7f55a339bd8c036)

- Data manipulation: `plyr` (Wickham 2011); `data.table` (Dowle et al. 2014); `reshape2` (Wickham 2007); `car` (Fox & Weisberg 2011)

- Plotting figures: `ggplot2` (Wickham 2009), with the `wesanderson` package (Ram & Wickham 2015) for colour schemes; `HH` (Heiberger 2015) for plotting Likert scales

Social network diagrams were drawn in Gephi 0.8.2.

Part I

Saami reindeer herders

Chapter 3

Overview of Saami reindeer husbandry and the study area

3.1 Introduction

This chapter will introduce Saami reindeer husbandry. I will provide an overview of the study area and the data collection methods, and present descriptive statistics from the sample.

The research presented in Part I was approved by the University College London research ethics committee.

3.2 Saami reindeer husbandry

The term 'Saami' describes a group of people indigenous to the areas that comprise northern Fennoscandia (Norway, Sweden and Finland), as well as the westernmost part of Russia. Today only a minority of Saami people subsist on reindeer pastoralism. As of 2013, there were 533 licensed reindeer herders (Norwegian: *siidaandeler*) living in Norway and 3,112 other Saami people connected to reindeer husbandry (Anonymous 2013); other Saami make a living as fishers, farmers, casual or skilled workers, with many migrating to large cities.

The *siida* is an important economic and cultural unit of cooperation and subsistence (Paine 1994). Membership is, for the most part, influenced by long-standing relationships between families, some of whom will be genealogically related. Traditionally, the siida was based on conjugal and sibling solidarity, which could be extended to include cousins and other affinal relatives of the

same generation (Bergman et al. 2008). Unmarried people and unrelated wage laborers may also join siidas on a facultative basis. Therefore, siidas can include both kin and non-kin.

People from different siidas can interact in a number of ways. With the adoption of snowmobiles and other vehicles as well as communication technologies, herders now live more sedentary lives: Members from several siidas live in the same towns for much of the year. In addition, herders from different siidas may help one another by splitting up mixed herds or finding lost reindeer. Conflicts may also arise, which has resulted in the destruction of fences separating the pasture areas of different siidas, among other issues.

In general, herders belong to two siidas: summer and winter. Summer siidas are large groups of households whose reindeer graze on the coastal pastures and islands of Norway. The summer siida became a legal entity in 2007 and can be thought of akin to a corporation with elected boards of leaders. Before the legal consolidation of siidas, membership was more flexible and could change over time; of the herders in my study sample (see section 3.4), only one person had moved summer siida within the past 15 years. Every year, summer siidas split into one or more smaller winter siidas whose herds graze in the interior of the country (Paine 1994). Summer siidas are grouped into administrative regions defined by the government, known as districts (Næss et al. 2009).

Households are likely to take on alternative sources of income as well as taking part in smaller-scale subsistence activities such as hunting and trapping, and catering to a burgeoning tourism trade. Fifty to sixty percent of income among herders in Finnmark is from meat production, and around 36% comes from government compensation and subsidy schemes; the remainder comes from additional labour and what are classified as 'incidental earnings' (e.g. hunting, fishing and foraging; Jernsletten & Klokov 2002). Livelihoods are supplemented by trade with more sedentary Saami farmers and fishers (the so-called 'Sea Saami'), as well as with non-Saami. Saami people recognise a special relationship with certain others outside of the husbandry business, with whom they reciprocally exchange goods and services. These people are called *verdde*

(a Saami word loosely translated as 'guest-friend').

Saami herders face occupational stresses from predators, weather conditions, financial pressures, changing land tenures, conflicts, and ethnic discrimination (Allard 2011; Bjerkli 2010; Hansen et al. 2010; Pape & Löffler 2012). A recent report found that the high levels of reindeer mortality observed in Finnmark might be due not to predation, as commonly believed, but rather overcrowding of reindeer and the poor condition of the animals (Tveraa et al. 2013). Conflicts can involve governments, industry (e.g. mineral extraction or logging companies), landowners, researchers, as well as other reindeer herders. Within the reindeer husbandry community, conflicts can arise over encroachment onto a rival siida's pasture, theft of reindeer, and destruction of fences, among other things (Paine 1970). Sanctions range from ridicule, to stemming the flow of information, and seizing or killing reindeer (Paine 1970; Sara 2002). Conflict is mediated through between-siida networks of reciprocity as well as shared collective action decision-making (Riseth & Vatn 2009).

Siidas are also loci for collective action. Siida group members work together on maintenance activities, run slaughterhouses, and gather herds into corrals so as to weigh and administer medicine to the animals, determine the number and quality of pregnant cows, and split herds by sex before seasonal migrations. Given the conflicts and cooperative behaviors described above, we would expect the siida to represent more than a decision-making body: rather, it would act as an important social unit. The focus of the work presented in Part I is the summer siida.

3.3   Study area

The research presented in Chapters 4 and 5 focusses on a single district in Finnmark County – the northernmost and largest reindeer herding area in Norway (Figure 3.1). Finnmark makes up over 15% of Norway's landmass and is the least densely populated county, with 73,787 people as of 2012.

My sample was formed of licensed herd owners within summer siidas. The Norwegian Government provides licenses to a subset of herders within each summer siida/district. These license owners are legally allowed to keep
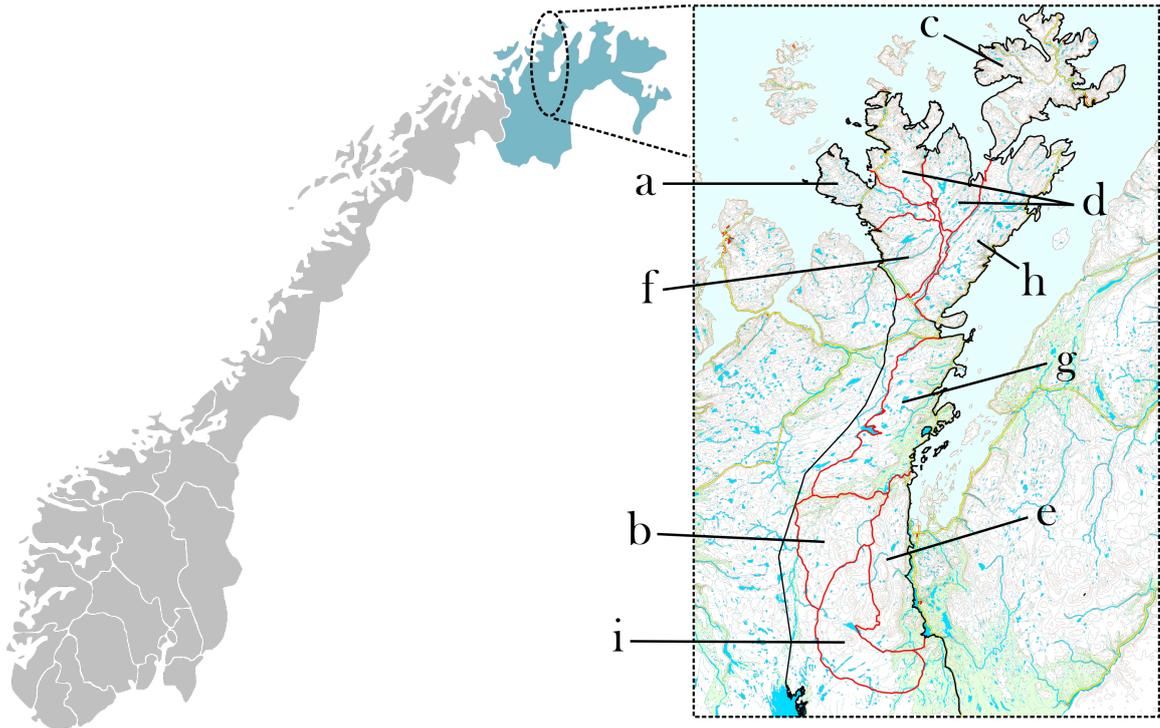
Figure 3.1: Location of the study site, situated in the county of Finnmark, Norway (shown in blue). The study site was a single district (dashed ellipse and inset). The inset map shows the study site, with the black outline representing the district border and red outlines representing summer siida pasture boundaries. Pastures are labelled with the siida code used in this study. Note that siida 'd' has two pastures since it was two siidas at the time the map was drawn; it is now considered a single siida. The map of Norway was created by Michal Jan Warecki and adapted by me. It is licensed under the Creative Commons Attribution-Share Alike 2.5 Generic license via Wikimedia Commons. The inset map was adapted from a map available on the study district's website.

reindeer and the Norwegian Agriculture Agency (*Landbruksdirektoratet*) tracks the productivity of their herds over time. As of 2013, there were 377 license owners in the county of Finnmark and 75 in the focal district (Anonymous 2013).

3.4 Data collection

In July and August 2013, I interviewed 30 licensed reindeer herders across all nine summer siidas in a single district in Finnmark, Norway (Figure 3.1) with the help of a Saami field assistant. My field assistant was the son of a local siida leader and we were also able to make use of his contacts in the community to arrange interviews. In addition, the names of siida leaders were published

on the district's website and telephone numbers were freely available via Norway's public online directory, *Gule Sider*. We also collected contact information through snowball sampling, whereby one participant suggested other potential participants.

All materials were translated into Norwegian by an independent person and back-translated by Marius Warg Næss. Næss and I agreed on the final translations. Information sheets, surveys and game scripts are reprinted in Appendix B.

Interviews were conducted either in Saami or Norwegian, depending on the respondent's preferred language. Informed consent was obtained from participants and interviews proceeded as follows:

1. District-level public goods game

2. Siida-level public goods game

3. Survey

4. Gift game

3.4.1 Surveys

Table 3.1 lists the categories and types of data collected from the survey, not necessarily in the order the questions were asked. Of the 30 interviews, most ($n = 22$) were conducted in the respondent's home, with the remainder taking place in local cafés or, in one case, at the summer corral. Some participants also engaged in unstructured interviews to further explore some of the topics raised once the formal data collection had finished; this sub-sample was gathered opportunistically.

3.4.2 Experimental games

After the survey, respondents played two public goods games (PGGs) and a gift game. The game scripts are included in Appendix B. The Norwegian-language instructions used in the field are available on request.

The currency for both games was petrol, measured in litres. I chose petrol because I wanted to investigate cooperative behaviour using a culturally salient

Table 3.1: Categories of questions asked during the interview process.

Variable	Details
Personal data	
Place of birth	
Year of birth	
Part of siida's leadership board	Yes/no
Marital status	From show cards
Post-marital residence (if ever married)	From show cards
Education	From show cards
Age at leaving education	
Measures of cooperation	
Within-siida labour sharing	8 item × 7 point Likert scale
Between-siida labour exchange	8 × 7 Likert scale
Vehicles, tools and other household items shared with siida	From show cards
Has *verdde* relationships	Yes/no
Trades with *verdde*?	Yes/no
Assortment	
Summer/winter siida membership history for past 15 years	Open answer
Reasons for leaving/joining siidas	Open answer
Wealth	
Types of income sources and main source	From show cards
Reindeer herd size	From show cards
Vehicles, tools and other household items owned	From show cards
Kinship	
Number of parents, siblings and children alive and living in the same household/siida (split by sex)	Numeric

currency: all herders require petrol to run snowmobiles, all-terrain vehicles and other modes of transport. Petrol becomes especially important during spring and autumn migrations, when they consume vast quantities over a two-week period.

Herders received vouchers for five litres of petrol in one litre denominations for each of the two PGGs. For the gift game, herders received three vouchers, each for five litres of petrol. At the time of the study, one litre of petrol cost NOK 15 (GBP 1.60; US$ 2.54). After I had completed all interviews, participants were paid their winnings plus a participation fee of NOK 150 (corresponding to 10 litres of petrol); people who did not take part in the interviews but who received petrol in the gift game were paid only their winnings. All payments were made in cash.

I will describe the gift game and public goods games procedures in more detail in Chapters 4 and 5 respectively.

3.4.3 Kinship data

Genealogical data were collected in May 2014 detailing how each license owner in the district ($n = 75$) was related to one another. I linked license owners to their previously assigned ID numbers and calculated a coefficient of relatedness (r_{ij}) for each pair of herders (i, j). This resulted in a full kinship network of licensed herd owners in the study district.

3.4.4 Herd productivity data

Herd sizes held by individual license owners were collected from data published by the Norwegian Broadcasting Corporation (*Norsk rikskringkasting AS*; Aslaksen 2014). I used the numbers of reindeer held by individuals in 2012 – the most recent data available. I was able to match herd sizes for 62 of the 75 people in our database, not achieving complete coverage due to changes in license owners between 2012 and the study period. Herd sizes were group-mean centred across the district.

3.5 Descriptive statistics

61 of the 75 herd owners in the district were male, with a median age of 53 (see Figure 3.2 for the age distribution and Table 3.2 for descriptive statistics). The median number of reindeer owned by herders in the district in 2012 was 456.5, ranging between 55 and 1,604 reindeer (Figure 3.3). Reindeer husbandry was the primary source of income for 23 of the 30 participants; four derived most of their income from other activities and three mainly lived on subsidies/benefits.

Table 3.2: Descriptive statistics about predictors from the questionnaire.

Variable	n (= 30)
Male	26
Siida leader	18
Marital status	
- Never married	10
- Married/cohabiting	17
- Other	3
Education	
- Primary/secondary	18
- Upper secondary	6
- High school/University	6

	Mean	Median	S.D.
Age	47.40	49	12.40
No. children	2.07	2	1.70
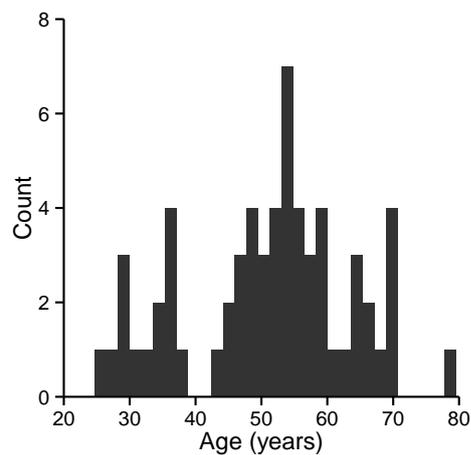
Figure 3.2: Distribution of herder ages within the study district.
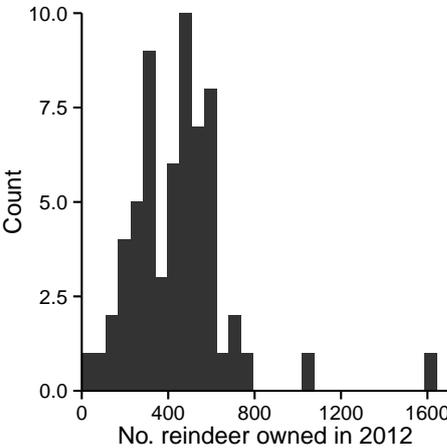
Figure 3.3: Distribution of reindeer owned by herders in 2012, according to figures published by the Norwegian Broadcasting Corporation (*Norsk rikskringkasting AS*). The mean herd size was 448.8 reindeer; the median was 456.5.

Chapter 4

Saami reindeer herders cooperate with social group members and genetic kin[1]

4.1 Introduction

Cooperation is prevalent in a wide range of taxa, including humans. Cooperative behaviours benefit other individuals, either at a cost to the cooperator or not; such behaviours can be favoured by selection due to their effects on others (West et al. 2007b). The most long-standing explanations of the evolution of cooperative behaviour are kin selection (Hamilton 1964) and reciprocal altruism (Trivers 1971), both of which are likely to play a role in human social interactions. A panoply of theoretical models of these and other effects have shown how the existence of cooperation is relatively easy to explain in evolutionary terms (Lehmann & Keller 2006; Nowak 2006; West et al. 2007b). Ultimately, cooperative behaviours will evolve if they increase the inclusive fitness of the individuals performing the behaviour. Exactly with whom one should cooperate, and to what extent, remains a contentious issue that is expected to depend on context.

Humans cooperate extensively in many regards. For example, cooperation is vital for survival and reproduction among humans following a pas-

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[1]Originally published as: Thomas, M. G., Næss, M. W., Bårdsen, B.-J., & Mace, R. (2015). Saami reindeer herders cooperate with social group members and genetic kin. *Behavioral Ecology, 26*, 1495–1501.

toralist way of life: a subsistence strategy involving a dependence on live-stock. Across the world, most pastoralist societies work in cooperative herd-ing groups formed from multiple families in multiple households (Næss 2012). Ariaal and Rendille pastoralists of East Africa herd in cooperative units typ-ically formed of siblings' families that, among the Ariaal at least, can fission from the wider settlement (Fratkin 1986). In Tibet, the *rukor* (or *ru skor*) is a co-operative group which tends to form for the summer and disband during win-ter (Nietupski 2012). Mongolian nomadic herders cluster into groups known as *Khot-Ail*, living and managing livestock as a socio-economic unit (Upton 2008). Saami pastoralists work in a cooperative institution known as the siida (Paine 1994).

Working in cooperative groups has many advantages, allowing herders to pool risk, defend herds from raiders or predators, protect pastureland, share knowledge and information, loan or gift animals to those in need, and ex-change labour (Aktipis et al. 2011; Dyson-Hudson & Dyson-Hudson 1980; Næss 2012; Paine 1994). These forms of cooperative behaviour may be a least-cost strategy compared to herding alone, allowing herding groups to achieve economies of scale, i.e. an increase in the percentage of output coupled with a reduction in the costs related to labour investment (Næss et al. 2009; Næss 2012).

Kin selection theory (Hamilton 1964) predicts that cooperative behaviours would evolve between genetic relatives as long as the fitness benefits, tempered by the degree of relatedness between them, outweigh the costs. Previous work on Saami reindeer pastoralists has shown that decisions to slaughter are medi-ated through kin relations (Næss et al. 2012) and that the presence of relatives, along with the availability of workers, had a positive effect on herd size (Næss et al. 2010). Such an effect is important for year-on-year household viability as well as during crisis periods; those with large pre-collapse herd sizes also had the largest post-collapse herds (Næss & Bårdsen 2010, 2013).

Group living can lead to a social dilemma where rational actors might choose not to contribute to a common enterprise (i.e. defect) but still try to reap the benefits of other's contributions, eventually leading to a breakdown

in cooperation. Avoidance of defectors can allow cooperators to assort together, either through mobility (Aktipis 2011), severing social links (Wang et al. 2012) or choosing partners (Stiff & Van Vugt 2008). The ability to choose from a 'marketplace' (Noë & Hammerstein 1994) of competing potential partners can lead individuals to act more cooperatively in relation to others, resulting in an escalation of 'competitive cooperation' (Barclay & Willer 2007). Individuals may direct cooperative behaviours to others based on their knowledge of the recipient's reputation (indirect reciprocity; Nowak 2006). In biological markets, being cooperative could act as an indicator of status, as can factors such as skill, prestige or experience.

Once partners have been chosen, rewards (such as gifts) and punishment may be important mechanisms for maintaining cooperation through partner control (Trivers 1971; West et al. 2007b). However, gift exchange might also function as a method of pooling risk in unpredictable environments in order to benefit all social group members. For pastoralists, exchanging gifts of livestock has been theoretically shown to boost long-term herd survival (Aktipis et al. 2011).

4.1.1 Predictions

Previous work on Saami pastoralists has looked at how relatedness and labour availability affect cooperation across districts, which are administrative clusters of herding groups (Næss et al. 2010, 2012). I extend this to investigate the relative effects of kinship and cooperative group membership on gift giving behaviour between individuals within a district. Saami pastoralists organise themselves into groups—composed of kin and non-kin—for the purposes of cooperative herding, their primary means of subsistence. Given the reliance on herding groups, I predict a strong cooperative bias towards fellow group members, regardless of whether or not the recipients are genealogical relatives.

However, this hypothesis does not imply that kinship will be unimportant. One manifestation of kin selection in humans may take the form of intergenerational resources flows from older to younger family members, especially from parents to children (Kaplan 1994). Thus, I predict that resources such

as gifts would be given preferentially to younger people when they are given within families.

I aim to quantify the relative effects of factors predicting cooperative behaviour by conducting a culturally salient experimental gift game among Saami reindeer herders living in Finnmark, Northern Norway. Participants could choose between one and three other reindeer herders to receive a gift of money. In order to ensure the game had contextual relevance to participants, I framed the gifts in terms of how much petrol they could be used to purchase, since petrol is a valuable commodity for Saami pastoralists.

4.2 Methods

4.2.1 Gift game

The 30 participants were endowed with vouchers (see below) and were then asked to give these as anonymous gifts to other licensed herd owners in their district. Respondents were presented with a list of license owners in the district (collected by a combination of publicly available contact information and snowball sampling, whereby one participant suggested other potential participants) coded with randomly generated ID numbers. Respondents read the ID numbers of their desired gift recipients to the field assistant. This procedure aimed to minimise experimenter bias, since the assistant was also a member of the district, although not a licensed herd owner.

I gave players 3 vouchers, each representing 5 litres of petrol. At the time, 1 litre of petrol cost approximately NOK 15 (US\$ 2.54). Players could choose to give the vouchers to $1-3$ other license owners – in multiples of 5 litres. They were not allowed to keep anything for themselves; they had to give the vouchers to at least 1 recipient. Players also gave reasons for their distribution of gifts. I coded these open answers into $1-3$ keywords, blind to the giver's name, siida and distribution of gifts (see below). At the end of the experimental period, all recipients were given their rewards in the form of cash, since the vouchers were created for the purposes of this study and were not legal tender, although all gift decisions were framed in terms of litres of petrol.

Communication was not allowed within the parameters of the experiment.

However, due to the vagaries of the herding lifestyle, I was unable to conduct all interviews within a sufficiently short time to rule out for the chance that herders did not communicate with one another.

I coded the open-response reasons for giving gifts using the following procedure:

1. Categorise the free-text reasons by whether or not each giver-receiver pair were related and/or members of the same siida.

2. Code each reason into categories closely matching the perceived intent behind the reason, but also fitting categories of theoretical interest (e.g. reciprocity, kinship, reputation, etc.).

3. Repeat (2) in an iterative manner to reduce the final number of categories.

Some participants gave one reason covering all of their gifts; others gave one reason per recipient. In cases of the former, I coded the same reason for each gift. Note this is why the "family" reason was applied to two non-kin, non-siida gifts (Table 4.8).

4.2.2 Statistical analysis

I fitted generalised estimating equation (GEE) models to all potential gift-giving dyads, where the egos were the 30 gift game participants and alters were the 75 licensed owners, giving $30 \times (75 - 1) = 2,220$ possible dyads. The binary response variable in all models was whether or not a gift was given within a dyad. I present unstandardised and standardised estimates, where in the latter case, binary factors were mean-centred and continuous variables were standardised over 2 standard deviations to allow estimates to be compared within models, following the recommendations of Gelman (2008) and Schielzeth (2010) (also see section 2.2.3). Note that I did not fit models containing the individual-level predictors gathered from the surveys since doing so would have dramatically reduced the number of dyads in the analysis.

Data are available from the Dryad Digital Repository:

http://dx.doi.org/10.5061/dryad.s3v63

Analysis code is available on GitHub:

4.3 Results

4.3.1 Description of the gift network

The 30 herders interviewed gave 71 gifts to 43 people (Figure 4.1a), some of whom were also participants. Of the 71 gifts, 45 (63.4%) were given to members of the same summer siida. A significantly higher proportion of gifts were given within siidas ($\chi_1^2 = 4.563,\ p = 0.033$). The majority of gifts (59) were for 5 litres of petrol and were given by 18 of the 30 people interviewed. Five gifts, given by 5 separate individuals, were worth 10 litres, while 7 gifts, given by 7 different people, were for 15 litres.
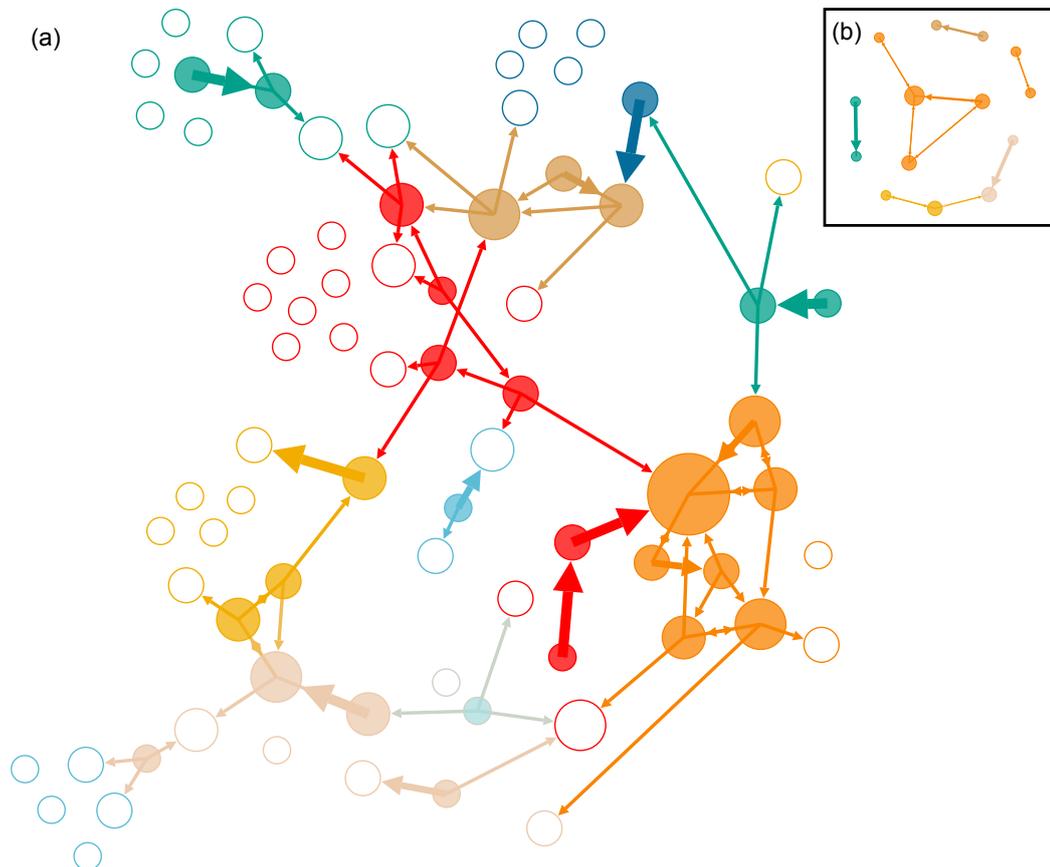
Figure 4.1: Gift networks showing license owners in the district (nodes) coloured by siida membership for (a) the entire district and (b) reciprocated gifts only. Filled circles represent the 30 license owners interviewed for this study. Edges are gifts, where edge thickness corresponds to gift size (5, 10 or 15 litres of petrol) and colour shows the siida from which the gift came.

The number of gifts received by individuals (in-degree) ranged from 0 to

Table 4.1: Number of gifts received (in-degrees) split by whether the herder is on their siida's leadership board or not.

Leader?	*n*	In-degree		
		Median	Mean	SD
Yes	18	1	1.28	1.02
No	12	1	1.75	1.91
Unknown	45	0	0.60	0.78

Table 4.2: Descriptive statistics for the gift network

No. components	26
Density	0.013
Reciprocity	0.282
Transitivity	0.17

7 (median = 1, mean = 0.95, standard deviation [SD] = 1.16). I do not report the number of gifts given (out-degree) or include it in the models since only the 30 people interviewed were able to give gifts. Gift givers received more gifts; that is, out-degree significantly correlated with in-degree (Pearson's product-moment correlation, $r = 0.415$, $p < 0.001$, 95% CI $[0.208, 0.587]$). One outlier received 7 gifts totaling 50 litres of petrol – twice as much as the second most popular herder. The reasons given for his gifts fell on a wide spectrum, from "Deserves it" and "Good reindeer herder" to "Always empty of fuel".

Ten gifts (28.2%) were reciprocated (Figure 4.1b), despite communication not featuring in the experiment. Of the reciprocated gifts, only 1 was given to a member of another siida. In this case, both were males living in the same town who clearly had a history of working together based on their stated reasons for giving the gifts. Table 4.2 shows descriptive statistics for the gift network.

Siida leaders did not receive more gifts than others (Table 4.1). There was a significant sex difference between number of gifts received where males on average received more (Mann-Whitney test, $W = 258.500$, $p = 0.015$), although the sample contains substantially fewer females (4 of the 43 herders who received gifts).

4.3.2 Relatedness in the district

The smallest two siidas ('a' and 'f' in Figure 4.2) were formed entirely of siblings and/or parents with children ($r_{ij} = 0.5$). These siidas contained, respec-

tively, 2 and 3 licensed owners. As the number of members increased, there was no discernible trend in relatedness across the nine siidas. The mean relatedness across the district was $r_{ij} = 0.02$ (i.e., between 2nd and 3rd cousins), whereas the grand mean of mean relatedness within siidas was $r_{ij} = 0.19$. Due to the small number of groups and their small sizes, I did not perform analyses grouped by individual siidas.
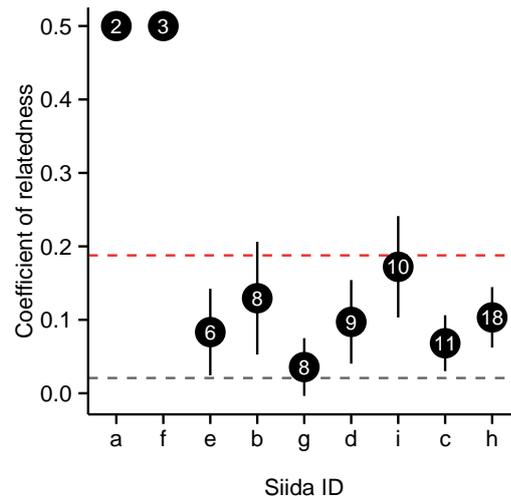
Figure 4.2: Relatedness within the nine siidas. Points are the mean coefficients of relatedness between licensed herd owners within each siida. Error bars show standard deviation. Data are ordered, from left to right, in increasing group sizes (also shown within the data points). The grey dotted line shows the mean relatedness in the entire district (i.e. across all siidas); the red dotted line shows the grand mean (i.e. mean of the mean within-siida relatedness coefficients).

4.3.3 Analysis of gift giving

Table 4.3 shows the distribution of gifts, split by whether recipients were genetically related to the giver and/or belonged to the same siida. I calculated correlation coefficients between the networks of gifts, relatedness and siida membership (Table 4.4). Summer siida membership correlated with genealogical relatedness ($r = 0.42$, $p \ll 0.01$, 95% CI $[0.38, 0.45]$). The coefficient of relatedness between givers and receivers correlated with receiving a gift ($r = 0.32$, $p \ll 0.01$, 95% CI $[0.29, 0.36]$).

In the best-fitting GEE model (Table 4.5), belonging to the same summer siida as the other person in a dyad was the strongest predictor of gift-giving

Table 4.3: Counts of people receiving a gift or not, split by whether they are genealogical relatives and/or members of the same summer siida, for all possible dyads in the district.

Same siida?	Related?	Received gift?		% receiving gift
		No	Yes	
Yes	Yes	74	30	28.8%
	No	153	15	8.9%
No	Yes	88	3	3.3%
	No	1,834	23	1.2%

Table 4.4: Pearson's correlation coefficients between the gift network, a network of close kin ($r_{ij} = 0.5$), a network of all kin ($r > 0$), and the siida membership network. Correlations were calculated using a quadratic assignment procedure (QAP; see section 2.2.2.2) to control for the non-independence of dyads in the networks.

	Gifts	All kin	Close kin
All kin	0.265	-	-
Close kin	0.344	0.703	-
Siida member	0.308	0.428	0.423

(standardised log odds = 1.875, S.E. = 0.447) compared to genealogical relatedness (standardised log odds = 0.691, S.E. = 0.187). Note that these estimates are only biologically interpretable in their unstandardised form (Table 4.5).

From the full set of candidate models, the model containing only a term for siida membership (Model 5 in Table 4.6) fitted the data better than the model containing only a term for relatedness (Model 6 in Table 4.6). Models with an interaction between relatedness and siida membership (Models 3 and 4 in Table 4.6) and models containing herd sizes for the potential giver and recipient (Models 2 and 4 in Table 4.6) did not provide a better fit compared to the model containing additive terms for relatedness and siida membership (Table 4.5; Model 1 in Table 4.6).

I hypothesised that gifts would preferentially be given to younger herders within families (where gifts to younger herders are scored as a negative age difference). Contrary to expectations, gifts were not preferentially given to younger kin ($\chi^2_1 = 0.05$, $p = 0.82$; Table 4.7). Age also had no significant effect on the number of gifts received (Spearman's rank correlation, $\rho = -0.140$, $p = 0.279$; Figure 4.3).

Table 4.5: Results from the best-fitting generalised estimating equation. Column 2 shows unstandardised log odds (S.E.); column 3 shows log odds (S.E.) standardised over 2 SD (Gelman 2008; Schielzeth 2010) so that the effect sizes can be directly compared. The predictors are the coefficient of relatedness, *r*, and a binary factor coding whether or not a dyad belongs to the same summer siida. The siida membership predictor most strongly predicts gift giving, although relatedness also has a positive effect. See Table 4.6 for a comparison of all candidate models.

Parameter	Log odds (S.E.)	Standardised log odds (S.E.)
Intercept	-4.178 (0.225)	-3.868 (0.184)
r	4.263 (1.152)	0.691 (0.187)
Same siida?	1.875 (0.447)	1.875 (0.447)

Table 4.6: Candidate set of generalised estimating equations. The full model contains an interaction between relatedness and siida membership as well as group-mean centred standardised herd sizes for the potential giver and recipient in each dyad. Model 1, the best fitting model, is also presented in the main text (Table 4.5).

Models	ΔQIC	Weight
1. kin + siida	0	0.651
2. kin + siida with herd sizes	2.5	0.187
3. kin, siida interaction	3.29	0.126
4. full model	5.79	0.036
5. siida only	19.33	0
6. kin only	22.58	0
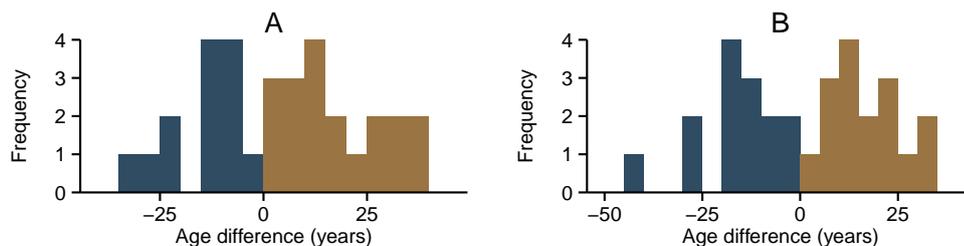
Figure 4.3: Age differences between givers and receivers of gifts where the pair are (a) kin or (b) non-kin. Positive values represent gifts given to older herders (brown bars) whereas negative values represent gifts to younger herders (blue bars). No gifts were given to herders of the same age.

Table 4.7: Number of gifts given to older or younger herders, split by whether or not the dyad were kin.

Gift to…	Older	Younger	Unknown
… kin	19	13	1
… non-kin	16	14	8

Table 4.8: Coded reasons for giving gifts, split by whether or not the recipient was a genealogical relative and/or belonged to the same summer siida.

Reason category	Kin in same siida	Non-kin in same siida	Kin in another siida	Non-kin another siida	Total
Good herders	3	2		8	13
Young/new owners	1	1		5	7
Current or future reciprocity	12	9	1	2	24
Old friend				1	1
Need help		1		1	2
Deserving	2	1			3
Lazy				3	3
Selfish	1				1
Family	7		2	2	11
No reason given	4	1		1	6
Total	30	15	3	23	71

4.3.4 Why give?

Table 4.8 lists the coded translations of all reasons for giving gifts (Table 4.9 provides the full text). The most common category ($n = 24$) for giving a gift, regardless of kinship and siida membership, was current or future reciprocity. Thirteen gifts were given to recipients with good reputations.

An interesting case is the gifts given to non-kin belonging to other siidas. Over half of these gifts were split between those with reputations of being a 'good herder' and young license owners who were newly established in reindeer husbandry.

4.4 Discussion

Summer siidas are stable cooperative groups. Only 1 person of 30 interviewed had moved between summer siidas within the last 15 years. Belonging to the same summer siida was the stronger predictor for gift-giving compared to being genetically related (Table 4.5). Interactions between relatedness and siida membership (Models 3 and 4 in Table 4.6) did not provide a better fit to the data. Similarly, including the herd sizes for the potential gift giver and recipient did not improve the fit (Models 2 and 4 in Table 4.6). Siida membership may be important for this population if strategies that benefit direct fitness are optimal compared to those increasing indirect fitness. Alternatively, herders might receive inclusive fitness benefits by virtue of assorting into the same groups as

Table 4.9: English translations of herders' stated reasons for giving gifts, along with keywords coded *ex post facto*. Each row corresponds to one of the $n = 30$ herders interviewed. Reasons coded as 'reciprocity' refer to both current and potential future relationships.

Reason for gift(s)	No. gifts	Reason for gift 1	Reason for gift 2	Reason for gift 3
They deserve it	2	Deserving	Deserving	
Siida working together	3	Reciprocity	Reciprocity	Reciprocity
My job becomes less. Extra holiday days	3	No reason given	No reason given	No reason given
Always empty of fuel	1	Selfish		
Old friend, hero; young owner; brother	3	Old friend	Young/new owners	Family
68 good worker and good memory. 2 and 100 young guys	3	Good herders	Young/new owners	Young/new owners
Brothers	3	Family	Family	Family
Good to help people and necessary to have helpers	3	Reciprocity	Reciprocity	Reciprocity
1. So they can do some work. 2. Gets more fuel because he does more of the work than others	2	Need help	Deserving	
It's the most reasonable (decision) for my future (because he just started)	3	Young/new owners	Reciprocity	Reciprocity
They aren't seen so often at the mountains. Maybe they will join the work now.	3	Lazy	Lazy	Lazy
34 is newly established so that's why he receives more than 35	2	Young/new owners	No reason given	
More help (giving help without expecting any back) for me and good contact with each other	3	Reciprocity	Reciprocity	Reciprocity
They are helpful and observant (e.g. helping with wandering reindeer)	3	Good herders	Good herders	Good herders
Young participant and good driver	1	Young/new owners		
These are people who are helpful and good use for me	3	Good herders	Good herders	Good herders
Is my son	1	Family		
Trust. I work for each other	2	Reciprocity	Reciprocity	
Good reindeer herders	3	Good herders	Good herders	Good herders
People who are closest (family) to me	3	Family	Family	Family
I work together	2	Reciprocity	No reason given	
Because he drives our siida	1	Good herders		
These are who I work with	3	Reciprocity	Reciprocity	Reciprocity
Gets a lot of help in return	3	Reciprocity	Reciprocity	Reciprocity
49 is good and eager helper. 93 is newly established, needs this support. 27 needs support.	3	Good herders	Young/new owners	Reciprocity
Helps to drive and drives for me if I don't have time	1	Reciprocity		
They are closest family	3	Family	Family	Family
64 winner siida neighbour, watches over the herd. 35 same but summer place. 8 summer siida friend and a good driver	3	Reciprocity	Reciprocity	Good herders

kin, whereas cooperation with non-kin might need to be maintained via reward mechanisms such as gift giving.

There was no preference for giving gifts to younger herders within families (Table 4.7 and Figure 4.3), contrary to the prediction derived from parental investment theory regarding the flow of resources down generations within families. The absence of this pattern is likely due to participants not viewing the gifts as resources to be invested in younger relatives. It should be noted that some close relatives (such as a son and heir) might be jointly herding with the herd owner and therefore not eligible to receive a gift as they are not yet a licensed herd owner themselves.

Twenty-four of the 71 gifts (33.8%) were given for reasons related to existing reciprocal relationships or developing future relationships (Table 4.8 and 4.9). In addition, 10 gifts (28.2%) were reciprocated although the experimental setup did not allow communication between participants (Figure 4.1b). This form of direct reciprocity has been conceptualized as an important mechanism behind the evolution of cooperation (Nowak 2006; Trivers 1971). The experiment did not explicitly account for either indirect (reputational) or direct reciprocity as mechanisms underlying cooperation; rather, I investigated the relative importance of kinship and social group membership in predicting gift giving. Membership of the same siida may imply multiple opportunities for reciprocation.

While the stated reasons for why participants gave particular gifts were *ad hoc*, I argue they provide valuable insight into behaviour in the games. Thirteen of the 71 gifts (18.3%) were given to those with the reputation of being a 'good herder' (Table 4.8), something important to Saami pastoralists (Paine 1970). Gifts were not given preferentially to siida leaders (Table 4.1). In this study, I was not able to control for potential confounds such as prestige, skills, experience, etc. that may have biased gift giving behaviours, although I did control for herd size as a proxy of wealth. Given this indication that cultural factors such as reputation may be important mediators of cooperative behaviour for Saami reindeer herders, future work could attempt to define measures of reputation and prestige that are meaningful to this population. One approach

would be to ask herders, preferably in group interviews, to rank others by their experience, skill, history of good decisions, etc. These culturally derived measures could then be linked to quantitative measures of wealth and used to predict gift giving.

Gifts in this study were small and anonymous, and communication between participants was not allowed. This makes it unlikely that costly signals, reputation or competitive altruism were driving the observed behaviours, although I was unable to test this formally. However, indirect reciprocity and competitive cooperation play important roles in human social groups, especially when cooperative behaviours are public (Barclay 2013; Sylwester & Roberts 2013). This chapter investigated the factors underlying partner choice but did not look at mechanisms of partner control that might enforce or maintain cooperation. Future work should attempt to understand the relative importance of partner control compared with partner choice as well as the roles of indirect reciprocity, partner choice and direct reciprocity (especially reciprocity based on reputation, i.e., competitive cooperation) in real-world contexts.

4.5 Conclusion

This work represents a first step towards quantifying the forms and diversity of cooperative strategies among Saami people. Saami pastoralists face many social and ecological challenges. Competition for access to winter pastures may explain herd accumulation as the only viable risk-reducing strategy, although the efficacy of this strategy may be limited by quotas on maximum herd size (Næss & Bårdsen 2010). This suggests the future of reindeer husbandry presents a collective action problem for the herders: one that may be solved from within the community without necessitating the privatisation of pastures (Bjørklund 1990; Hausner et al. 2012; Marin 2006). At present, management policies seem to be designed to attain sustainability by targeting only individual reindeer owners (e.g. providing subsidies to increase slaughter rates), while disregarding the cooperative nature of reindeer pastoralism (Næss et al. 2012). Understanding the mechanisms of cooperation in this population will be an important task for its future viability.

Chapter 5

Solving Saami social dilemmas

5.1 Introduction

Group living often entails a balance between individual self-interest and benefits to the group as a whole. When these interests are not aligned, individuals may act selfishly to the detriment of all in the group, including themselves. Such situations, where an individual's vested interests conflict with collective interests, are known as social dilemmas (Kollock 1998). Countless social dilemmas have been described and analysed, all tending to be variants of the Prisoner's Dilemma (PD; see section 1.4.2.1), the problem of provisioning public goods, or the tragedy of the (unmanaged) commons; the latter two being, in essence, multiplayer extensions of the PD (Hardin 1968, 1994; Kollock 1998; Samuelson 1954).

In this chapter, I investigate how Saami reindeer herders respond to social dilemmas by employing an experimental economic game, namely a public goods game. Saami pastoralists work in cooperative groups formed of kin and non-kin, and these groups cooperate and conflict to varying extents. Social dilemmas pervade this way of life and individual herders must balance their own interests—generating income, managing the risks inherent in pastoralism—with the interests of their herding group and the wider community in which others face similar quandaries. Understanding how Saami people solve their social dilemmas might have implications for the future of reindeer husbandry in this area, especially given a background of shifting land tenure regimes, overcrowding of reindeer and climate change.

From an evolutionary point of view, social dilemmas are solved when access to a good increases inclusive fitness, i.e. when fitness is at stake, public goods are more likely to be provisioned or commons will not become over-exploited. This might occur, for example, if reciprocal cooperation increases the direct fitness of individuals within a group, when groups are formed of genetic relatives (thus affecting indirect fitness) or when groups also contain affinal kin with shared reproductive interests in future generations (Hamilton 1964; Hughes 1988; Trivers 1971).

A common tool for understanding the dynamics of cooperative behaviours in groups is the public goods game (PGG). PGGs involve a group of players individually deciding how much of an endowment to contribute towards a public account. Donations to the group are multiplied, in this case by a constant factor. The increased sum is then shared equally among all group members regardless of their initial contributions. When the multiplier is less than the group size, contributors receive less in return than they contributed. The ratio of multiplier to group size is known as the marginal per-capita return rate (MPCR; Ledyard 1995). Donations when MPCR < 1 do not maximise utility and are either interpreted as acts of prosociality (Camerer 2013) or mistakes (Burton-Chellew & West 2013).

When the public good multiplier is held constant, group size becomes an important factor in an individual's cooperative calculus. MPCR shrinks as group size increases, making donations less individually optimal (Ledyard 1995). A meta-analysis of laboratory-based public goods games found that higher MPCR (range $0.003 - 0.8$) was associated with larger contributions to the group (Zelmer 2003). Other laboratory experiments attempting to mirror the small MPCRs expected in real-world public goods dilemmas have shown that MPCR, but not necessarily absolute group size, has a strong effect on cooperation (Weimann et al. 2012).

As discussed in section 2.1.2.2, larger groups can be more (Zhang & Zhu 2011) or less cooperative (Soetevent 2005), and this effect may not be linear (Yang et al. 2013). Laboratory evidence suggests that intermediate group sizes are favourable when the output from a public good means that benefits quickly

accrue for early cooperators compared to those contributing later when groups have become larger (Barcelo & Capraro 2015). In addition, factors such as participants' ages, group composition, and social context are likely to affect cooperation (see section 2.1.2).

Typically, MPCR $\approx$ 0.5 in field-based experiments, due to standard group sizes of $\sim$4 people (Gerkey 2013; Henrich et al. 2005). Regressing donation size on MPCR for the field-based PGGs reported in (Gerkey 2013; Table 1), the return rate has a positive but not statistically significant effect ($B = 152.44$, $p = 0.128$, $R^2 = 0.183$). In a meta-analysis of the effects of punishment on cooperation reported across 18 countries, group size (and thus MPCR) did not have a statistically significant effect (Balliet & Lange 2013). A review of field-based public goods games played with non-students (Cárdenas & Carpenter 2008) found that the average donation was 51% of the initial endowment (range: $23\% - 81\%$).

My study takes advantage of natural variation in group size within a single population, where the groups are important hubs of cooperation. Given the evidence discussed above that group size affects levels of cooperation, I aim to investigate how decisions to provision a public good are affected as the perceived marginal per-capita return rates vary due to participants' knowledge of their herding group and, thus, potential PGG group members.

This study thus departs from the usual structure of public goods games in that I did not artificially limit the number of participants in the groups but rather used real-world group sizes. Quantifying how the size of meaningful social groups affects cooperative behaviours could potentially have implications beyond lab-in-the-field experiments or pastoralism *per se*; our ability to respond to large-scale collective action problems such as climate change might be affected if increasing group size deters (or, in some cases, promotes) cooperation.

5.1.1 Saami social dilemmas

Researchers have identified various mutually inclusive routes to solving social dilemmas, including assorting with kin and/or cooperative individuals,

communication, coordination, exclusion, institutions, leadership, legislation, mobility, monitoring, parcelling out cooperation or access to resources, partner choice, partner control, policing, repeated reciprocal interactions, rewards, sanctioning, and social norms (Levin 2014; Raihani & Bshary 2015; Trivers 2005; West et al. 2007b; see section 1.4). In this section, I discuss individual and collective strategies for how pastoralists, especially Saami reindeer herders, solve real-world social dilemmas.

Much theoretical and experimental work has shown that people have strong preferences for cooperating with members of an 'in-group' (e.g. their family, neighbourhood, school, office, herding group) to the exclusion—and sometimes the detriment—of 'out-groups' (Hewstone et al. 2002; Silva & Mace 2014). Saami pastoralists organise themselves into cooperative herding groups known as siidas and, as shown in the previous chapter, herders exhibited a preference towards cooperating with members of their siida.

The siida is a collective action group tied to an area of pastureland. Cooperation within siidas takes many forms and fulfils many purposes. The forms of cooperative behaviours can broadly be categorised into those that provision public goods and those that exploit common-pool resources, both of which can lead to tensions between individual self-interest and collective interests.

Cooperative decisions in the form of labour investment can be understood as akin to provisioning public goods. Everybody benefits from the labour of those who help with herding tasks such as gathering reindeer for spring corrals. The benefits of cooperative acts can extend beyond the siida. For example, somebody might maintain a fence along the borders of their pasture to help themselves and their fellow siida members but neighbouring siidas happen to benefit as a by-product. In the case of shared borders, neighbouring siidas would each have an incentive not to invest (i.e. to free-ride) if the other siida is likely to provision the good and they can reap the benefits without expending effort.

Some pastoralist societies have developed systems of livestock and labour exchange, which theoretically allows groups of herders to pool risk (i.e. partially transfer risk in order to decrease the severity of individual herd losses),

boosting long-term herd survival (Aktipis et al. 2011). These are not systems of reciprocal exchange *per se* (see Woodburn 1998); rather gifts are given only when requested by those in need, if the giver is able to do so, as exemplified by the Maasai tradition of *osotua*, which follows a norm of 'from each according to their abilities, to each according to their needs', prizing restraint, responsibility and respect (Cronk 2007). This form of collectivism might function as a normative cultural solution to a social dilemma, whereby members of the cultural group are obliged to behave cooperatively.

Saami reindeer herders have an analogous needs-based social arrangement with people outside the husbandry known as *verdde* (loosely translated as 'guest-friend'; Paine 1994). *Verdde* may be neighbours, friends from childhood and non-herder relatives, possibly representing long-standing family relationships stretching back generations. The presence of *verdde* depends on local conditions – e.g. non-Saami *verdde* are less likely to live on the tundra, whereas herders with coastal pastures may have *verdde* relationships with fishers. Herders might provide *verdde* with dried or smoked meat, perhaps receiving fish at some point in the future. One family in the study district received bales of hay from a farmer *verdde*. As with the example of *osotua* described above, *verdde* relationships are not explicitly systems of reciprocal exchange (one informant described them as "natural favours"). Such relationships may function as a way of pooling risk for Saami pastoralists, although this hypothesis is yet to be explored.

Explicit cooperation also occurs between siidas. Borders to winter pastures can overlap and are permeable to a certain extent, depending on the needs of the reindeer – grazing rights in these patchy areas can shift to match herd size, for example, so siidas might tolerate a modicum of encroachment, especially in 'emergency' situations such as during bad winters (Marin & Bjørklund 2015). Herders are also sensitive to situations in which encroachment becomes a 'shameful' (Saami: *hæppat*) act of trespassing (Paine 1994). Herders will cooperate in a contingent and reciprocal manner, working with neighbouring siidas to separate herds when they become mixed, and ensuring against the degradation of lichen along shared migration corridors (Marin 2006).

Ties to the land were once formed around customary access rights operating in a system of sequential usufruct (Reinert 2006). In recent years, land has been steadily privatised across many herding areas in Norway, especially in the county of Finnmark – the location of this study. This has been due, in part, to assumptions of a tragedy of the commons. Contrary to expectations from a purely game theoretical treatment of common-pool resources (Hardin 1968), it is not uncommon that limited resources are managed by communities in a sustainable manner (Lansing 1991; Ostrom 1990).

A recent report by the Norwegian Institute for Nature Research (Tveraa et al. 2013) found that the high levels of reindeer mortality observed in Finnmark might be due not to predation, as commonly believed, but rather overcrowding of reindeer and the poor condition of the animals. Overcrowding does not necessarily imply overgrazing, however. Evidence for a tragedy of the commons in this area is equivocal. There is a negative density dependence effect where increased reindeer density in a district was associated with decreased future herd size (Næss & Bårdsen 2010) and lower reindeer body mass (Bårdsen et al. 2014), both of which are linked to higher rates of mortality (Tveraa et al. 2013). However, a tragedy of the commons would also predict a negative relationship between slaughter undertaken by neighbouring herders and an individual's own slaughter decisions, whereas the observed relationship was positive (Næss et al. 2012).

The high reindeer numbers in Finnmark could be a product of the intensive commercialisation of reindeer husbandry into a market-oriented industry, beginning in 1976, which incentivises herders to maximise meat production and thus their income (Hausner et al. 2011), whereas Saami pastoralists balance economic gains with the need to manage risk through increasing their herd sizes (Næss & Bårdsen 2015). An enforced shift away from customary land tenure towards 'common' or 'open' pastures—and, increasingly, privatised pastures—may be partly responsible for any apparent tragedies in this area (Marin & Bjørklund 2015).

As discussed in this section, pastoralists face social dilemmas at many turns. In order to manage these situations, herders deploy a range of flexi-

ble cooperative strategies, both on an individual level as well as a collective level. The next section will outline the hypotheses I will test regarding social dilemmas relevant to Saami reindeer herders. The remainder of this chapter will analyse data collected from field experiments and discuss the results in the light of theoretical and ethnographic studies of collective action.

5.1.2 Predictions

Following the theoretical models of how marginal incentives affect cooperation (Ledyard 1995), I predict that donations will increase as MPCR increases. Unlike theoretical models, but in keeping with observed behaviour in the laboratory and in the field, I also predict that the majority of participants will donate non-zero amounts even though, by design, MPCR will always be less than one, thus creating a social dilemma.

These two hypotheses will be tested via two one-shot PGGs, both framed in terms of petrol that can be donated to a group pot. In the first game, participants can donate petrol to a group account that will be shared across the entire district; the second game frames decisions in terms of their summer siida. MPCR will be calculated based on the number of people in each participant's summer siida – a quantity that reflects perceived return rates and should factor into strategic decision-making (provided participants understand the structure of the game). Players did not know at the point of participating how many other people in their siida would be taking part, beyond their own insights into who might be likely to participate given their past experiences of working with these people. While the final group size was not necessarily known to each player at the time of the experiments, I hypothesise that players would expect a certain number of participants—and, hence, perceive a certain return rate—given their knowledge of and history with their siida. The variations in group size within our study site will act as a form of natural experiment in which 'expected MPCR' varies by siida.

Whereas herders work with members of their siida on a regular basis, between-siida cooperation is more facultative. District-level cooperation is likely to be lower compared to within-siida cooperation, since the district is a

large administrative area rather than a salient cooperative unit. (Note that this pattern of multiple siidas within a district is specific to my study site. In other parts of Norway, most districts contain only one summer siida.) Therefore, I expect donations to the siida PGG to be substantially larger than donations to the district PGG. Similarly, from kin selection theory, I predict that members of more closely related siidas will donate more compared to less-related siidas.

5.2 Methods

In July and August 2013, I interviewed 30 licensed herd owners belonging to all nine siidas in a single district of Finnmark, Norway (see Chapter 3 for details of the field site and sample).

5.2.1 Public goods games

Participants played two one-shot public goods games (PGGs), deciding how much of their endowment to donate to the public good and how much to keep for themselves. Before each PGG, herders received vouchers for five litres of petrol in one-litre denominations. They could choose to donate any amount to the group pot or keep as much as they wanted for themselves.

The first PGG was conducted with all participants in one large district-level group with donations to the public good eventually distributed equally among all 30 people who eventually took part in the study (42.3% of all licensed herd owners in this district). Participants were originally told they would be split into randomly-formed groups of six (see Appendix B). For logistical reasons, I changed the protocol so that there was only one district-level group. Based on participants' stated reasons for donating the amounts they donated, they understood the district-level PGG as if it would be one large group anyway. After participants made their donation decision in the district-level PGG, they played a second PGG. This group in the second PGG was formed of only the members of the participant's summer siida; this game followed the same protocol as the first but without limitations on group size.

At the time of interview, respondents did not necessarily know exactly who else would be participating in the study. The games, therefore, were

pseudo-anonymous in the sense that players had no knowledge of exactly who would be in their PGG groups, although players were told their groups would be formed of license owners from the district (for the first game) and license owners belonging to their summer siida (for the second game).

The total amounts donated in each PGG were multiplied by a factor of 1.5. This number was chosen because for some siidas, especially the smallest ($n = 2$), I could not guarantee in advance I would be able to interview more than two herders: the minimum number required for a social dilemma to exist. I was only able to interview one person for three of the nine siidas. In these one-player cases, the dominant strategy would become the Pareto optimal strategy of donating the entire endowment since no social dilemma exists. However, the respondents (and the experimenter) would not have been aware of this fact at the time. MPCR varied for different participants since siida group sizes differed.

After both donation decisions, I asked respondents why they chose to give particular amounts. Reasons were given verbally in either Saami or Norwegian (in whichever language the interview was conducted), recorded in Norwegian by the field assistant and translated into English by the field assistant and me.

5.2.2 Siida productivity data

I use the following siida-level measures (see section 3.4) in the analyses presented here: total herd size in 2012; number of reindeer per herder (not limited to license owners); average calf slaughter weight in 2012 (kg); average adult slaughter weight in 2012 (kg). (Reindeer aged $0 - 1$ years are classified as calves.)

5.2.3 Statistical analysis

Because the amount an individual contributes to the PGGs can be no larger than five litres of petrol, I use Tobit regressions to account for this right-censoring (Tobin 1958). Table 5.1 lists the Tobit models fitted in this chapter; all models control for participants' age, sex, education and number of reindeer owned in 2012. Parameter estimates are interpreted in the same manner as a standard linear regression.

Table 5.1: Tobit regressions predicting contributions to either the siida or district public goods games (PGGs). All models control for age, sex, education and number of reindeer owned in 2012. Models are listed in the order they appear in the main text.

Model	Response variable	Predictor of interest
1	Donation to siida PGG	Self-reported within-siida cooperation
2	Donation to district PGG	Self-reported between-siida cooperation
3	Donation to siida PGG	Mean relatedness within siidas
4	Donation to siida PGG	Marginal per-capita return rate

5.3 Results

5.3.1 People cooperate more with their herding group

Participants donated more to their siida pot (median = 3 litres of petrol) than to the district pot (median = 0 litres; Figure 5.1). Donations to the siida pot were significantly larger than donations to the district pot (two-tailed paired Wilcoxon test, $V = 246$, $p < 0.001$, 95% CI $[2.0, 4.0]$). Eight people gave equal amounts to the district and their siida, while one person gave more to the district than to the siida.

Eighteen people gave nothing to the district and three people gave nothing to their siida. The same three people also donated nothing to the district. Five people donated 4 or more litres of petrol to the district pot. Of these, four donated all 5 litres to their siida (the fifth donated 3 litres). Of the four people donating all 5 litres, the primary source of income for two of them was through reindeer sold, the other people's income came from outside the reindeer husbandry.

Herders reported taking part in cooperative activities more frequently within their own summer siida compared to the frequency of doing those activities for other siidas (Figure 5.2). For most questions, the majority of people interviewed reported never taking part in the list of activities for other siidas. Ranking herders by cooperation scores did not predict larger donations to the siida from higher-ranked individuals ($B = 0.056$, S.E. $= 0.354$, $p = 0.873$; Table 5.2). Similarly, ranking herders by their cooperativeness to other siidas did not predict donations to the district PGG ($B = -0.325$, S.E. $= 0.361$, $p = 0.367$; Table 5.3).
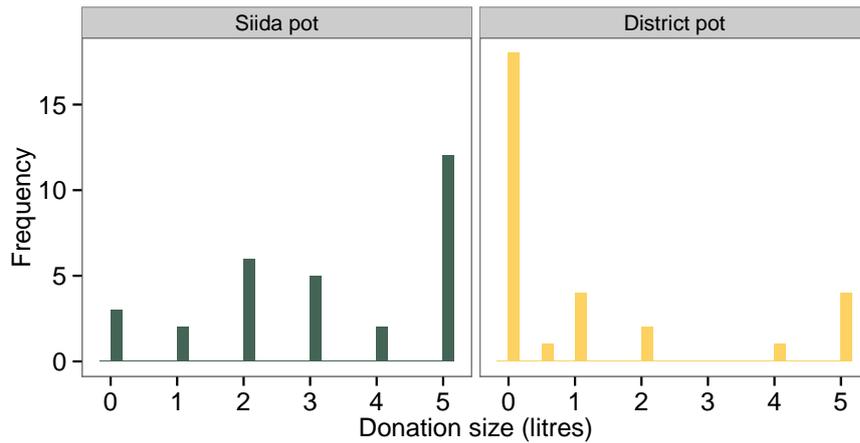
Figure 5.1: Distribution of donations in the district (yellow) and siida (green) public goods games. The median donation size in the district game was 0 litres of petrol; the median donation in the siida game was 3 litres.

Table 5.2: Effects of (1) relatedness, (2) marginal per-capita return rate and (3) self-reported cooperation on contributions to the siida public goods game. Parameter estimates are from Tobit regressions predicting size of contribution (0 − 5 litres of petrol). Statistically significant effects are in bold. ΔAIC represents differences compared to the best-fitting model (Model 2).

Parameter	Model 1			Model 2			Model 3		
	B	**S.E.**	**p**	**B**	**S.E.**	**p**	**B**	**S.E.**	**p**
Mean relatedness	3.184	4.291	0.458						
MPCR				**67.775**	**33.442**	**0.043**			
Cooperation rank							0.056	0.354	0.873
Age	-0.008	0.053	0.873	0.013	0.051	0.795	-0.015	0.055	0.786
Sex (ref: male)	0.830	2.762	0.764	1.069	2.494	0.668	0.641	2.700	0.813
Education (years)	-0.098	0.080	0.221	-0.072	0.073	0.323	-0.102	0.081	0.209
Siida leader?	1.083	1.330	0.415	0.420	1.175	0.721	1.390	1.261	0.270
Herd size in 2012	-0.003	0.004	0.432	-0.003	0.004	0.531	-0.004	0.004	0.373
(Intercept)	6.942	3.952	0.079	3.082	3.870	0.426	**7.589**	**3.739**	**0.042**
Log-likelihood	-44.286			-41.577			-44.461		
ΔAIC	5.236			0.000			5.550		

Siida size did not affect self-reported cooperation, either within or between siidas (Figure 5.3). A participant's mean relatedness to their siida did not predict contribution size ($B = 3.184$, S.E. $= 4.291$, $p = 0.458$).

Combining with the gift game data reported in the previous chapter, herders with higher self-reported cooperative scores towards their own siida did not preferentially give gifts to other cooperators within their siida ($B = -0.002$, S.E. $= 0.162$, $p = 0.992$, $R^2 \ll 0.001$). Similarly, herders reporting more frequent cooperation with other siidas did not give more gifts to other co-

Table 5.3: Effect of self-reported cooperation on contributions to the district public goods game. Parameter estimates are from a Tobit regression predicting the size of contributions ($0 - 5$ litres of petrol). Statistically significant effects are in bold.

Parameter	*B*	S.E.	*p*
Cooperation rank	-0.325	0.361	0.367
Age	-0.018	0.052	0.736
Sex (ref: male)	1.117	2.784	0.688
Education (years)	-0.096	0.081	0.236
Siida leader?	1.265	1.242	0.309
Herd size in 2012	-0.003	0.004	0.490
(Intercept)	**8.329**	**3.850**	**0.031**
Log-likelihood	-44.039		

operators ($B = -0.320$, S.E. $= 0.321$, $p = 0.342$, $R^2 = 0.091$). Overall, people reporting higher within-siida cooperation did not receive more gifts from people in their siida ($B = 0.021$, S.E. $= 0.047$, $p = 0.652$, $R^2 = 0.008$) whereas those who behaved cooperatively by donating more to their siida's public good received more gifts from fellow siida members, although the effect was borderline statistically significant ($B = 0.219$, S.E. $= 0.112$, $p = 0.061$, $R^2 = 0.133$). Similarly, participants who donated more in the siida PGG did not give gifts to one another ($B = -0.055$, S.E. $= 0.167$, $p = 0.746$, $R^2 = 0.004$).

5.3.2 Marginal incentives matter

Despite the district PGG's marginal per-capita return rate being very low (0.004), 12 people (40%) donated at least one litre of petrol to the district.

Expected MPCR—the return rate herders might calculate or perceive—depends on the number of herders in each siida. This ranged from 0.0197 in the largest siida ($n = 76$ people) to 0.107 in the smallest ($n = 14$ people). Increasing MPCR predicted larger donations to the siida ($B = 67.775$, S.E. $= 33.442$, $p = 0.043$; Table 5.2 and Figure 5.4).

As shown in Figure 5.4, the three people from the smallest siida seem to be driving the positive effect of MPCR. Removing these three people from the model reduced the effect and caused the parameter estimate to no longer be statistically significant ($B = 44.324$, S.E. $= 46.534$, $p = 0.341$).

Group size had a linear rather than curvilinear effect on PGG contributions (Table 5.4). For every additional person in the siida, there was an expected
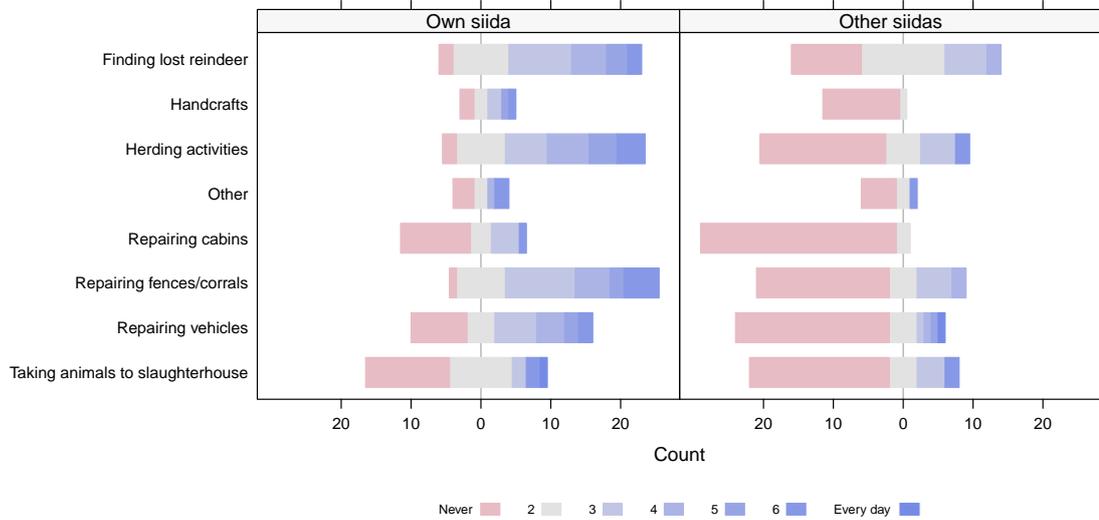
Figure 5.2: Self-reported frequencies for a range of cooperative activities that individuals took part in on behalf of their own summer siida (left panel) and for other siidas (right panel). Study participants were asked to report how often they had performed each activity on a scale of 1 (never) to 7 (every day) over the previous year. Red bars show the number of people who answered 'never'; darkening blue bars show increasing frequencies of activity.
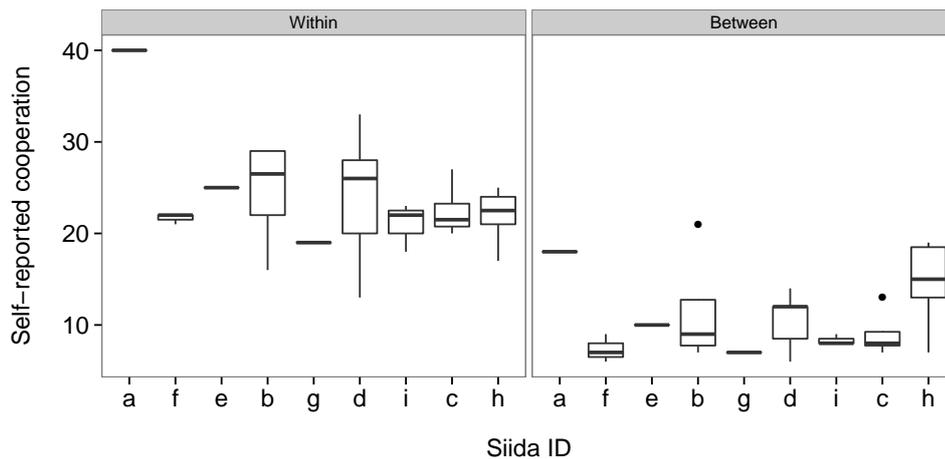
Figure 5.3: Total self-reported cooperation for each participant, aggregated into siidas and split by whether cooperation was directed towards the participant's own siida (left panel) or to other siidas (right panel). Siidas are ordered, left to right, in ascending order of size, based on number of license owners.
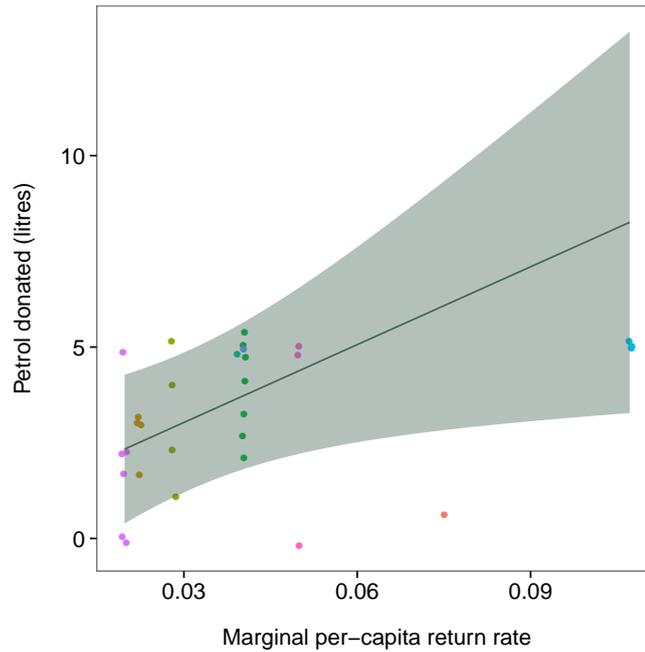
Figure 5.4: Marginal per-capita return rate predicts the size of donations to the summer siida public goods game (Model 2 in Table 5.2). Points show individual donations coloured by the summer siida of each herder. The line shows the fitted Tobit regression with 95% confidence interval.

Table 5.4: Linear and curvilinear effects of group size on contributions to the siida public goods game. Parameter estimates are from Tobit regressions predicting size of contribution $(0 - 5$ litres of petrol). Statistically significant effects are in bold. ΔAIC represents differences compared to the best-fitting model ('Linear').

Parameter	Linear			Quadratic		
	B	**S.E.**	**p**	**B**	**S.E.**	**p**
Group size	**-0.082**	**0.030**	**0.006**	0.006	0.146	0.965
Group size^2				-0.001	0.001	0.543
Age	0.017	0.047	0.723	0.016	0.046	0.730
Sex (ref: male)	0.366	2.296	0.874	0.132	2.398	0.956
Education (years)	-0.049	0.069	0.478	-0.049	0.070	0.487
Siida leader?	0.595	1.075	0.580	0.756	1.114	0.498
Herd size in 2012	-0.004	0.004	0.298	-0.005	0.004	0.234
(Intercept)	**9.605**	**3.371**	**0.004**	**8.018**	**4.155**	**0.054**
Log-likelihood	-40.425			-40.261		
ΔAIC	0.000			1.670		

decrease in contributions of 0.082 litres of petrol. Restricting group size to include only license owners did not significantly predict donation size (results not shown).

Table 5.5: Reasons for donating to the district public goods game (or not) and donation size (litres). Reasons were translated from the participants' Norwegian or Saami responses.

ID	Donation reason	Donation
1	So reindeer herders keep the work going	5
2	Supporting the district	5
60	Can't do much with 5L	5
73	People I know	5
36	Those siidas who receive should keep their own animals at their own place to avoid herds mixing	4
16	If district asks he'll give but if not, won't give. Depends on situation.	2
85	It depends on the time of year. It can be used for everything	2
5	For good conscience	1
26	It's necessary for people to drive	1
27	For herding my reindeer	1
49	To show manners. If they really need it	1
3	A symbol of sharing	0.5
9	Has worked enough for free. [District] gets paid by the state. Have no relationship	0
18	Not herder's choice to have one big district. Giving nothing	0
19	Give nothing back. Needs it himself	0
34	Don't get anything back	0
35	They don't need it	0
40	Doesn't give any fuel because district are not doing anything useful for him	0
46	They are such a small siida it will have no influence	0
64	Gets nothing and gives nothing	0
70	They don't need it and they don't drive for me. They get money from the state	0
72	Doesn't want to share	0
74	Because so many sharing the litres and challenging for a few litres	0
75	Not sharing with the district	0
76	Don't know	0
77	District doesn't have any responsibility for driving. It is given to each siida	0
82	Doesn't give for no reason	0
86	I need it myself. District is too big for sharing	0
97	Needs it himself	0
100	Why give when I won't get anything back	0

5.3.3 Reasons for provisioning the public good

Tables 5.5 and 5.6 show, respectively, the stated reasons for donating to the district and siida public goods games. Reasons in both tables are listed with herders' IDs so can be compared across tables. Three people gave the same reason for their siida donation as for their district donation (IDs 9, 16 and 82).

Three of the four people donating all 5 litres of petrol to the district did so because they knew the other people and wanted to support the district and/or reindeer husbandry. The fourth (herder 60) donated his entire endowment of petrol because he "can't do much with 5 litres". Two people (herders 3 and 5) donated as a symbolic or normative gesture. Of the 18 people who donated

Table 5.6: Reasons for donating to the siida public goods game (or not) and donation size (litres). Reasons were translated from the participants' Norwegian or Saami responses.

ID	Donation reason	Donation
2	Giving to siida. Working together	5
3	Close family and they will have good use of it	5
18	We have the same job	5
34	It will be used for the purpose that I have needs for	5
35	It will come to good use for everybody in the siida	5
36	We are only 3. We have a good infrastructure. We are using the petrol together after a meeting about scheduling work.	5
49	It's demanding to drive, so giving to younger herders because they have good health and agility	5
60	Someone in summer siida does something for me and I do something for them	5
64	Gets it back anyway	5
70	If I'm not there myself, the others can use it	5
73	I also have a use for this	5
76	Work together anyway	5
27	Wants cooperation	4
77	We are often 5 who are driving	4
1	They have the same herd and the same work	3
26	Everyone should participate	3
46	When we see all of the work for example in autumn is a lot of work	3
74	Keeping work together (cooperating)	3
75	We work together	3
5	For the young people, for better yield	2
16	If district asks he'll give but if not, won't give. Depends on situation.	2
40	For cooperating and working against the predators	2
72	Even/equal sharing	2
85	If I take everything for myself it'll be used for driving the herd. If I give everything, will they give back?	2
100	It comes to good use for everyone	2
86	So the job will be done	1
97	We are 2. Need it ourselves	1
9	Has worked enough for free. [District] gets paid by the state. Have no relationship	0
19	Little cooperation in summer siida. We (the family) drive for the most part	0
82	Doesn't give for no reason	0

nothing in the district PGG, 13 reasoned that they had no relationship with the district as a whole and would be unlikely to receive anything in return.

Overall, 21 people reported donating to their siida for reasons relating to cooperation, shared work and reciprocity. Two people donated in order to help younger herders. Herder 19 reported little cooperation in his summer siida, while herder 85 seemed to worry about whether other members of his siida would contribute to the PGG.

There seemed to be some misunderstanding of the PGG. For example, herder 36's response (Table 5.5) implied that he thought particular siidas would

Table 5.7: Estimates from four separate linear regressions, each with a single siida-level predictor. The response variable in all four models was the size of donations in the siida public goods game. Average calf slaughter weight (Model 3) was a borderline statistically significant predictor of donation size and, comparing AICs, that model best fitted the data.

Model	Predictor	B	S.E.	p	R^2	AIC
1	Reindeer per capita	0.021	0.017	0.279	0.164	35.485
2	Total herd size in 2012	0.000	0.000	0.709	0.021	36.905
3	Calf slaughter weight in 2012	0.602	0.262	0.055	0.430	32.042
4	Adult slaughter weight in 2012	0.140	0.202	0.511	0.064	36.502

receive petrol from the PGG, as opposed to everybody receiving a share. Similarly, herder 97 only donated 1 litre to his siida (Table 5.6), claiming that he and the only other license owner in the siida needed the petrol for themselves, perhaps without realising they would be the ones receiving the pot ("Need it ourselves") since they were the only eligible participants.

5.3.4 Herd size and slaughter weights do not predict siida donations

Individual donations to the siida were not predicted by number of reindeer owned in 2012 or by the mean number of reindeer owned between 2008 and 2012 (results not shown). Table 5.7 shows estimates from four linear regressions on PGG donations aggregated by siida. Note that these are standard linear regressions rather than Tobit regressions because aggregated PGG contributions are not right-censored. Each model contains a single siida-level predictor relating to herds. None of the predictors produced a statistically significant effect, although the calf slaughter weight in 2012 had a borderline significant effect size and explained 43% of the variation in donation size (Model 3 in Table 5.7); higher average slaughter weight in the previous year predicted larger donations to the siida PGG. Siidas required to reduce their herd sizes did not receive more gifts (two-tailed Wilcoxon test, $W = 2$, 95% CI $[-20, 4]$, $p = 0.186$). Lack of statistical significance in these cases is likely due to the small number of siidas in the district (n = 9).

Self-reported measures of cooperation within and between siidas (Figure 5.2) did not correlate with the four measures of siida herd productivity

Table 5.8: Pearson's correlation coefficients between four measures of siida productivity and self-reported measures of within-siida and between-siida cooperation (see Figure 5.2). For each correlation, $p \gg 0.05$.

Productivity measure	Within-siida cooperation	Between-siida cooperation
Reindeer per capita	-0.049	0.005
Total herd size in 2012	0.363	0.571
Calf slaughter weight in 2012	-0.433	-0.516
Adult slaughter weight in 2012	-0.037	-0.074

(Table 5.8).

5.4 Discussion

Herders donated larger amounts of petrol to their summer siida's group pot than to the district's pot (Figure 5.1). Participants also reported more frequent cooperative interactions with their own siida compared to how often they helped other siidas (Figure 5.2). These patterns support the idea that the siida is an important locus for collective action. Participants who were, on average, more related to their siida did not contribute more to the siida PGG (Model 1 in Table 5.2).

Most field experiments using PGGs tend either to ignore relatedness or control for it, rather than treating it as an interesting explanatory variable (see section 2.1.2). Unlike in previous lab-in-the-field public goods games, I find no support for effects of age, sex, education (years of education), or wealth (measured as herd size) on size of contributions. Future studies should investigate whether this pattern holds in a larger sample including other herding districts.

Self-reported cooperation, measured as the frequency that participants engaged in cooperative activities on behalf of their own as well as for other siidas, was not associated with donations to the siida's public good (Model 3 in Table 5.2) or with the number of gifts received in the gift game. The lack of relationship implies that self-reporting was not a useful measure of real-world cooperative behaviour. The Likert scales employed here also have a particular shortcoming, namely they cannot capture rare events where herders turn up every time: these instances would be reported as a low Likert score. These issues may have ramifications for future field studies of cooperation that rely

on survey methods and self-reports. In order to better understand social be-
haviours relevant to real-world situations, researchers should seek to combine
these sociological methods with observational data and longer-term ethnogra-
phy.

There was a positive and borderline statistically significant association be-
tween the size of a participant's donation to their siida PGG and the number
of gifts they received. This suggests that the PGG might be providing a better
measure of cooperation compared to self-reports, and that more cooperative
herders are themselves likelier targets of cooperative behaviours (here, in the
form of gifts) or, simply, are more popular. However, people who donated more
in the siida PGG did not give gifts to one another. In future work, I intend to
explore the extent to which more cooperative herders have better reputations
and engage in directly reciprocal cooperation.

Group size had a linear, rather than curvilinear, effect on PGG contribu-
tions (Table 5.4). Different siida sizes allowed me to explore natural variation
in marginal per-capita return rates (MPCR). If people understood the PGG and
behaved as theoretically predicted, larger perceived returns (as a function of
smaller group size) would lead to people donating more to their siida pot.
This pattern emerged from the data, although the magnitude of the effect was
mostly driven by the three members of a single, small siida (Model 2 in Ta-
ble 5.2 and Figure 5.4). Removing this siida from the analysis caused the effect
to lose statistical significance, although the magnitude and direction remained
comparable.

Two limitations restrict my interpretation of this result. First, by keeping
the pot multiplier constant at 1.5 for all groups, I was unable to test whether
MPCR > 1 would have led all players to donate their full endowment to the
public good, as predicted by theory. Second, I did not investigate whether
players thought strategically in terms of maximising their returns based on the
MPCR. From the *ex post facto* reasons given by participants for their donation
decisions (Table 5.6), the majority donated for reasons pertaining to collective
action (e.g. "We have the same job", "It will come to good use for everybody
in the siida", "We work together"), including a normative approach to cooper-

ation ("Everyone should participate"). Others reported reciprocity ("Someone in summer siida does something for me and I do something for them"). Conversely, those who donated nothing to their siida pot reported little cooperation in their siida or declared they needed reason to donate.

Since these reasons are likely to be *post hoc* rationalisations of behaviour, I caution against over-interpretation of these results as giving insights into the decision-making process. Regardless, participants donated to their siida pot even though MPCR < 1, which is not the predicted behaviour of economically self-interested rational actors. My findings mirror those of other field-based public goods games (Gerkey 2013; Henrich et al. 2005; Lamba & Mace 2011).

People on the whole donated little to nothing to the district PGG (Figure 5.1). Only four people (13.3%) gave their full endowment, whereas 18 (60%) donated nothing. Two people who donated their full endowments to the district seemed to reason in terms of large-scale collective action ("So reindeer herders keep the work going"; "Supporting [the district]"); another approached the dilemma in a more cautious, contingent manner ("If district asks he'll give but if not, won't give. Depends on situation"). Three participants (10%) donated 0.5 - 1 litres as a form of normative signal of cooperation ("For good conscience"; "To show manners..."; "A symbol of sharing"). One person stated that the endowment was too small ("Can't do much with 5 [litres]"; all quotes from Table 5.5). Future work could involve more significant amounts of petrol/money, although the expensive nature of this field site might further limit the sample size attained. There were also hints towards demand sharing regarding the district PGG ("If district asks he'll give but if not, won't give"; "Doesn't give for no reason"; Table 5.5). One participant stated after the interview that donation decisions may depend on the time of year; herders may need more petrol for themselves during summer, no matter how cooperative the siida.

The productivity of siidas—measured as herd size in 2012, number of reindeer per capita, and average slaughter weights of adults and calves in 2012—did not predict donations to the siida PGG (Table 5.7) and did not correlate with the self-reported measures of within-siida and between-siida cooperation

(Table 5.8). We might expect that larger herds would encourage more cooperation as much as they result from efficient cooperation, since siidas with more animals can potentially capture better-quality land (Paine, 1994). However, with the increasing privatisation of pastures, this may soon not be possible. On the other hand, more reindeer held by a siida might lead to more conflicts rather than cooperation because of the increased risk of reindeer mortality and worsening quality of reindeer as the overall number of animals in Finnmark has increased – a trend not simply due to climate change (Bårdsen et al. 2014; Tveraa et al. 2013).

An unexpected outcome was that average calf slaughter weight had a borderline statistically significant effect size and explained 43% of the variation in donations to the siida (Table 5.7). Calf slaughter weight may therefore function as an indicator of how well a siida cooperates, given the importance of good-quality calves for pastoralists. Alternatively, high slaughter weight might signal that the siida had a good year previously and its members were well-disposed to one another at the time of our study. Regardless, the small number of siidas in this district ($n = 9$) means that siida-level analyses cannot attain statistical power in order to be confident in the parameter estimates.

The cooperative activities used in my survey (Figure 5.2) only represent a small portion of Saami pastoralist life. Several participants criticised the choice of activities as being biased towards males, with one stating that women "are the forgotten part of the Saami story." With the advent of compulsory schooling, closure of boarding schools and the increased use of heavy machinery, women were "pushed out of daily work" and now work less in the fields. The pastoralist lifestyle requires herders to be available to tend to their herds 24 hours a day. As well as looking after children (grandparents also work so can only provide limited care for grandchildren), mothers are also "doing the invisible work" within households: according to one informant, women are "working to keep the family running." Another informant lamented that Saami people "lost part of our culture" when women could no longer take part in herding.

Table 5.9: Typology of economics goods based on whether or not they are excludable and subtractable.

	Non- excludable	Excludable
Non-subtractable	Public (streetlights, National Health Service)	Club (religions, European Union)
Subtractable	Common (pastures, planets)	Private (clothes, cars)

5.4.1 The efficacy of public goods games

The results presented in this chapter suggest that public goods games might not provide the best model for at least some of the major social dilemmas facing this population. Some of the stated reasons for donating to the siida public good suggest that some participants may have misunderstood the structure of the game (Tables 5.5 and 5.6). Other researchers have questioned the utility of the public goods game as a model of real-world behaviour. Laboratory experiments suggest that participants do not immediately understand the game's payoff structure but rather learn it over repeated rounds, all the while acting to maximise their own incomes (Burton-Chellew & West 2013; Burton-Chellew et al. 2015), although some researchers go so far as to argue that inexperienced or poorly incentivised players "cannot usefully be modeled as optimizers of anything at all," (Binmore & Shaked 2010: 88). Due to logistical constraints, the PGGs were one-shot and so I was not able to investigate these issues.

It is worth mentioning that economists distinguish four types of good (I use the term 'good' in its broadest sense to refer to goods, resources, services) based on whether or not they are excludable and/or subtractable (Table 5.9). Potential users cannot be excluded from accessing public goods or common-pool resources; however, the difference between the two is that common-pool resources are finite and through using them, they become depleted (i.e. they are subtractable or rivalrous).

Public goods and common-pool resources (CPR) are typically conflated since both are non-excludable (and so are vulnerable to free-riders) and can be reduced to a Prisoner's Dilemma (Ledyard 1995). However, the two social dilemmas are distinct. Although the two games have the same Pareto optimum, they have different Nash equilibria (Apesteguia & Maier-Rigaud 2006).

The Pareto optimal (welfare-maximising) outcome in both games is for everybody to donate their full endowment to the group pot. The Nash equilibrium strategy in the PGG is for everyone to hold on to their endowments, whereas everybody should cooperate in the CPR game (Apesteguia & Maier-Rigaud 2006). Therefore, rivalry is important – that is, whether or not a good is finite and subtractable will affect the behaviours of individuals in a group (Dionisio & Gordo 2006).

Unlike laboratory games, my study investigated cooperative behaviour in real-world groups (siidas and the district) using a currency important to the reindeer herding lifestyle (petrol). However, I argue a similar point to Burton-Chellew and colleagues (Burton-Chellew & West 2013; Burton-Chellew et al. 2015), namely that PGGs may not be the best approach to modelling social dilemmas in real-world groups. In the case of pastoralists such as the Saami, the most important social dilemmas to solve (e.g. use of common pastures) might better be modelled as a tragedy of the commons game involving resources that diminish in a density-dependent manner. Even what seem on the surface like public goods (e.g. fences or corrals) are in reality more like club goods, in the sense that others can be excluded from their benefits (Table 5.9). Future experimental work could attempt to tease apart the cooperative dynamics of herders when faced with different types of goods and a need to balance their own interests with those of their fellow siida members, for example by playing games in which participants must individually choose to extract 'resources' from a common pool (Cárdenas 2003).

In the experiments presented here, provisioning the public good was costly to participants in the sense that most herders—especially in the siida PGG—were not maximising their returns. This might be the case for several (not mutually exclusive) reasons: (i) participants did not understand the game[1], as was evident from at least one player; (ii) relatedly, participants may have learned to maximise their personal incomes over repeated rounds (Burton-Chellew et al. 2015); (iii) participants did not have the incentive to maximise their income

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[1]Due to my field assistant's dyslexia, many participants preferred reading the game instructions themselves. Unfortunately this meant we were often unable to test whether participants understood the PGG instructions.

(Binmore & Shaked 2010); (iv) there are social factors affecting decisions to donate. The latter has some support from the reasons people gave for their donations (Tables 5.5 and 5.6), which included ideas of obligation, reciprocity and collective action.

Experiments involving explicit costs as well as benefits are likely to alter the resulting behaviours. Thus, while abstract PGGs serve some utility in, e.g., comparative studies, future research may benefit from considering games whose structure more closely models the costs and benefits as well as the excludability and subtractability of real-world contexts.

Siidas fulfil many roles. For example, cooperative herding can prevent land-grabs from competing groups. Although this is less of a worry given the current shift towards privatised and fenced land, pastoralists still face the task of preventing unwanted encroachment. Similarly, herders must work together to protect their livestock from predators, not all of which can be legally hunted (this is especially relevant for the siida whose summer pasture is located in a national park). Contribution problems such as provisioning public goods (e.g. deciding whether to invest time and energy in labour, herd protection, fence repair, etc.) are likely to exist in concert with consumption problems regarding how to best use common-pool resources. Thus, I recommend that researchers should consider the interplay between public goods (e.g. in the form of cooperative labour investment) and common-pool resources, perhaps playing both types of game in the field.

This chapter investigated cooperative behaviour within context-laden experimental games and linked cooperation with real-world outcomes. Future work on Saami reindeer husbandry should investigate other arenas in which social dilemmas might occur. For example, while the majority of herders must sell their reindeer on the hoof to a purchasing oligopoly (oligopsony) of Norwegian-owned slaughterhouses, approximately 20% of herders in Norway operate their own slaughterhouses (Reinert 2006). The latter have greater economic freedom although they face opportunity costs in the sense that time and labour spent on their slaughterhouses diverts from their herding and husbandry tasks, and introduces additional social dilemmas brought about by run-

ning a business.

5.5 Conclusion

This chapter investigated how cooperative behaviour within and between groups can solve social dilemmas. To do so, I played two public goods games (PGGs) – one where participants could choose to donate petrol to their summer siida and another where they were grouped with the entire district. Contrary to expectations, increasing mean relatedness had no effect on the number of gifts given within siidas. Participants donated larger amounts of petrol to their siida's group pot than to the district, supporting the idea that the summer siida is an important locus of collective action. The natural variation in group size across siidas allowed us to investigate the effect of changing marginal per-capita return rate (MPCR) on PGG donations. Increasing MPCR—a feature of smaller groups—predicted an increase in donation size.

Participants donated to their group pots despite the return rate being less than one. Theoretically, individuals playing a pure strategy of self-interested utility-maximisation would donate nothing in this situation. These results – in line with a number of laboratory and field studies – found that players donated regardless, suggesting that mechanisms such as reciprocity, social norms and aligned interests help siidas solve their social dilemmas.

Cooperation need not always be tangible. Saami people also share traditional knowledge (TK: "a systematic way of thinking applied to phenomena across biological, physical, cultural and spiritual systems;" Inuit Circumpolar Council 2013) about herding and husbandry (including ways of understanding the quality of herds and individual reindeer), weather conditions (famously relating to snow and ice), navigation and social norms or conventions. Older herders are commonly sources of TK. One informant described grandparents as "psychologists and teachers and providers of clothes and knowledge," especially, in the case of TK, relating to herding decisions and names for antlers, pelt and snow. Coordination via common knowledge is one method of achieving cooperation (Cronk & Leech (2013) but see Binmore (2008)), and researchers are beginning to explore how TK interacts with observed behaviours (Ziker et al.

2015). A tantalising possibility is that shared knowledge could be considered a good with its own provisioning problem, whereby some people might strategically withhold or manipulate what and with whom they share.

Flexibility has been an important aspect of Saami cooperation. Nowhere is this more apparent that in the movement of individuals between winter siidas. The ability to walk away from uncooperative others has been theoretically shown to maintain cooperation through the positive assortment of cooperators (Aktipis 2004; Lewis et al. 2014). Similarly, Apicella et al. (2012) found that co-operative people assorted together in Hadza public goods games. My public goods games, self-reported measures of cooperation and gift network did not lend support to the idea that cooperative people prefer to interact with one another and cluster in social networks. However, I urge caution in interpreting the lack of evidence for cooperative assortment; my analyses are based on a small sample from a single district and so suffer from low statistical power.

Despite the many theoretical and empirical avenues towards cooperation discussed in this chapter, Saami herders have reported that trust and cooperation are lacking in Finnmark, especially on winter siidas (Hausner et al. 2012). This mistrust may be borne of herders' responses to Finnmark's particular ecology, resulting in overstocking of reindeer compared to the good levels of coordination found among reindeer herders further south (Riseth & Vatn 2009). While this study focussed on cooperation within and between summer siidas, future work could investigate cooperative and competitive behaviours in winter siidas, where land tenure changes may create barriers to mobility and so potentially prove detrimental to cooperative reindeer husbandry.

Part II

Mosuo farmers

Chapter 6

Overview of Mosuo society and the study area

6.1 Introduction

This chapter will introduce the Mosuo way of life as well as the study area for Chapters 7 and 8. The research presented in Part II was approved by the University College London research ethics committee and by the Chinese Academy of Sciences, Beijing.

6.2 Study area

'Mosuo' refers to an ethnic group in rural southwest China, located around Lugu Lake on the border of Sichuan and Yunnan provinces. Mosuo (also known as Na) social life is typically organised around matrilineal households in which family members spend most if not all of their lives.

Agriculture is a primary means of subsistence in this area, although suitable land is constrained by steep, forested hills. Likewise, diet is constrained by depleted wildlife resources and an increasingly polluted lake. Members of different households come together to help one another during planting and harvesting seasons; everybody works the fields during this time, regardless of gender or age. Households also cooperate in the construction of new houses, share funeral costs if the deceased's household cannot afford the ceremony, and jointly invest in economic ventures (Shih 2009).

The area has become an increasingly popular tourist spot, which has led to

a number of Mosuo households deviating from matrilineal norms due to a mixture of cultural diffusion and economic motivations (Mattison 2010). Households in Sichuan province, the site of this study, follow the traditional Mosuo way of life, although encroaching tourism and more intermarriage with Han people are causing this to shift (Ji et al. forthcoming).

Within the matrilineal families, all residents share the fruits of household labour. Sisters reproduce communally. Older sisters invest more time in farm work and have correspondingly higher reproductive success compared to their younger sisters (Ji et al. 2013). (Note that unlike the Han and others in China, rural ethnic minorities like the Mosuo people have been allowed 2-3 children since the 1979 fertility policy.)

In traditional Mosuo life, "marriage is rejected as an institution that disrupts household harmony," (Blumenfield 2003: 487). Harmonious relationships are the ideal between household members (Shih 2009) and grandmothers tend to be the heads of houses. Family members will eat and farm together, pool money and care for children communally. Big families are preferred but households can fission if they become too large or if relationships are riven by conflict (Mattison 2010); however, fissions are seen as shameful and to be avoided (Shih & Jenike 2002).

The most famous aspect of Mosuo culture is *sese* (or *tisese*: 'walking marriage'). A man in a walking marriage will visit his partner's house during the night and return to his natal household at daybreak (Cai 2001). Once a union is publicly recognised, the male may eat with or give gifts to his partner's family (Shih 2009). *Sese* does not prescribe how individuals should behave sexually; it is fine to want many (potentially simultaneous), one or no partners. However, since the 1980s, formal marriage has been a requirement for reproduction throughout China as part of the government's family planning policy, so the idea of conjugal partners has become more similar to the Han norm if a child is involved, even when partners live apart. For simplicity, I use the terms 'husband' and 'wife' to refer to male and female *sese* and/or marriage partners identified as such in the household surveys.

6.3   Data collection

All data collection was carried out by Jiajia Wu, Qiao-Qiao He and Ting Ji. Demographic surveys were conducted in five villages in Sichuan province around Lugu Lake during 2012. One adult was interviewed on behalf of all household members about details including name, age, sex, ethnic group, names of spouses and parents. GPS locations were also captured for households. Pedigrees were created by linking every person in the census to their mother and father.

In 2013, participants played two gift games: one in which they gave gifts to individuals (the "individual game") and another in which they could give cash to the heads of households, who would then share the gifts among co-residents (the "household game"). In both games, participants were endowed with 15 yuan, which they could give—in five yuan denominations—to between one and three recipients. Here I will only analyse gift-giving in the individual game.

Spot observations of people working on farms were conducted during the planting seasons of 2011 and 2012 and the harvest season of 2012. Locations were randomly sampled within the study villages, giving unbiased, although incomplete, coverage. Workers were linked to their records in the demographic database.

Wealth ranking of households was conducted by 1-3 people in each village. The fieldworkers presented them with cards representing the heads of each household; they then divided the cards into three piles: rich, medium, and poor. The villagers further divided 'medium' into another four piles, leaving a total of 6 piles of households: very rich (1) to very poor (6). The people who did the wealth ranking were usually heads of that village who were familiar with every household. Note that wealth ranks can only be interpreted within the context of each village – e.g. a household ranked 3 in village 1 does not necessarily have equivalent wealth to a household ranked 3 in village 5.

All analyses in Part II will be conducted on Mosuo and Han people only.

6.4 Descriptive statistics

6.4.1 Individual demographics

In total, there were 3,795 people aged 15 or older, and 960 children aged < 15; 4,618 people were Mosuo and 137 were Han. There were 12 more males than females in the sample (sex ratio = 1.005). Figure 6.1 shows the age distribution of the sample split by sex and ethnicity.
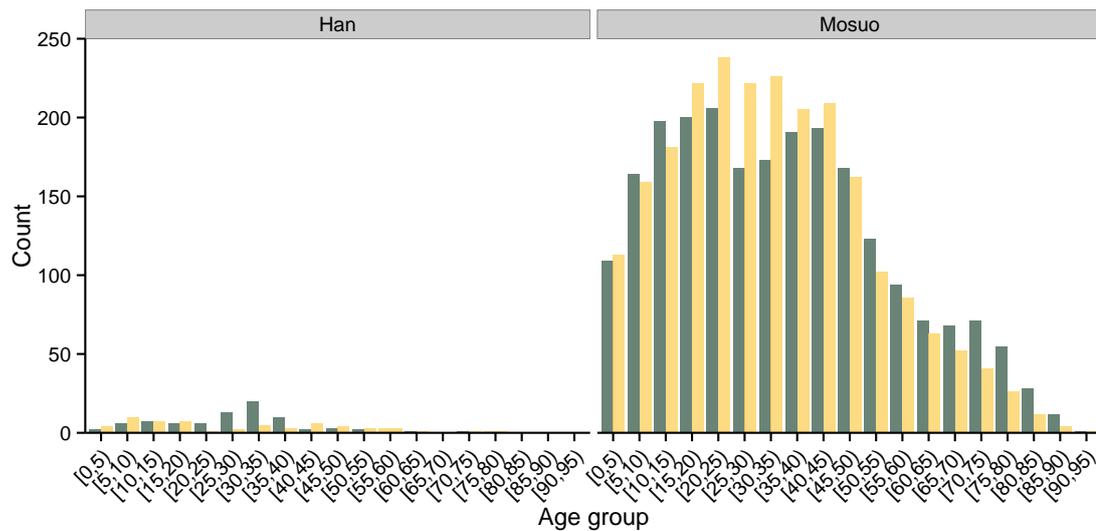
Figure 6.1: Age distribution of each ethnic group in the sample, split by female (green) and male (yellow).

There were 953 couples in the study area. The majority of couples (51.8%) lived in the same house. Only 12 people had more than one partner (i.e. opposite-sex person with whom they had a child). In relationships where both partners were Mosuo, slightly more lived in separate households (Table 6.1), although the proportional difference compared to numbers living together was not statistically significant (proportion test $P = 0.526$, 95% CI $[0.493, 0.560]$, $\chi^2_1 = 2.328$, $p = 0.127$).

6.4.2 Household demographics

Across all five villages in the study area, there were 780 households headed by Mosuo people. 373 household heads (47.8%) were female. Members of 200 households had wives living in another house ($n = 258$ dyads) and 209 households had husbands in other houses ($n = 257$ dyads). Four households

Table 6.1: Number of couples living together or apart, split by ethnicity of both partners.

Ethnicity of partners	Live in same house?	
(male-female)	No	Yes
Han-Han	0	1
Han-Mosuo	1	8
Mosuo-Han	0	73
Mosuo-Mosuo	458	412

Table 6.2: Median distance (km) between households and number of households in each of the five study villages.

Village ID	Median distance (km)	No. households
A	0.601	120
B	0.812	120
C	1.209	132
D	1.222	250
E	0.521	158

had both wives and husbands living in another household.

Table 6.2 shows the distances between all household dyads in each of the five study villages. The largest distance between any two houses was 7.1 km (in village D) and villages contained 120-250 households headed by Mosuo people. Household size, including adults and children, ranged from 1 to 18 people (median = 5).

Figure 6.2 shows the mean relatedness of individual between and within households in each village. Related households tended to be geographically nearer one another (Pearson's product-moment correlation, $r = -0.102$, 95% CI $[-0.110, -0.094]$, $p \ll 0.001$; Figure 6.3). The grand mean coefficient of relatedness across all villages was $r = 0.003$.

The majority of households (94.1%) were not related on average but, of those where $r > 0$, most were related at $r \in [0.031, 0.063)$. Households were more closely related to themselves than to other households, since people live with close family (Figure 6.2); note, however, that 33 pairs of households were related to one another at the level of grandparents, uncles, aunts, nephews and nieces ($r \in [0.25, 0.5)$). Residents were not related to one another in four households.
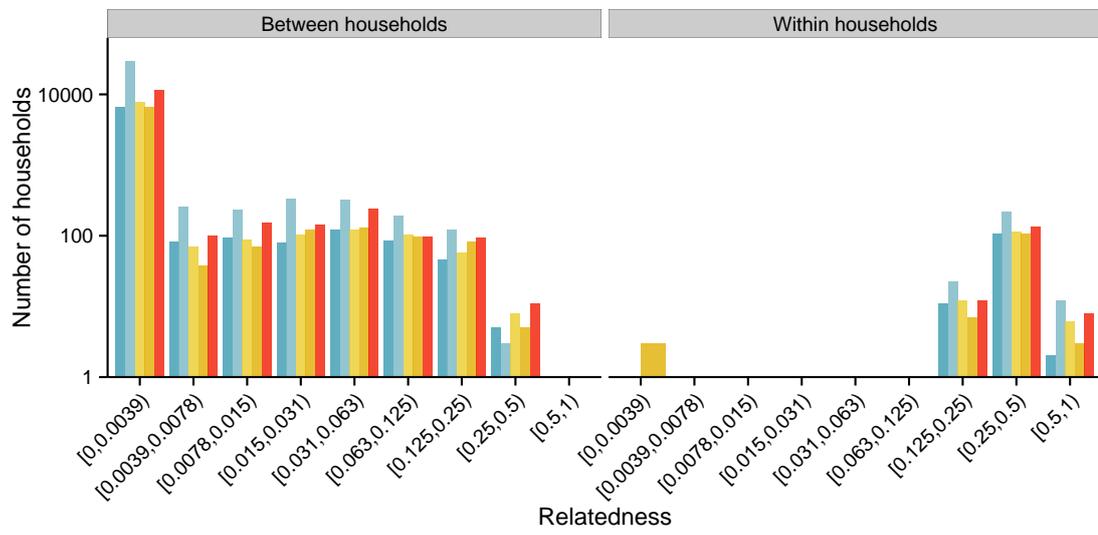
Figure 6.2: Relatedness between and within households, coloured by village.
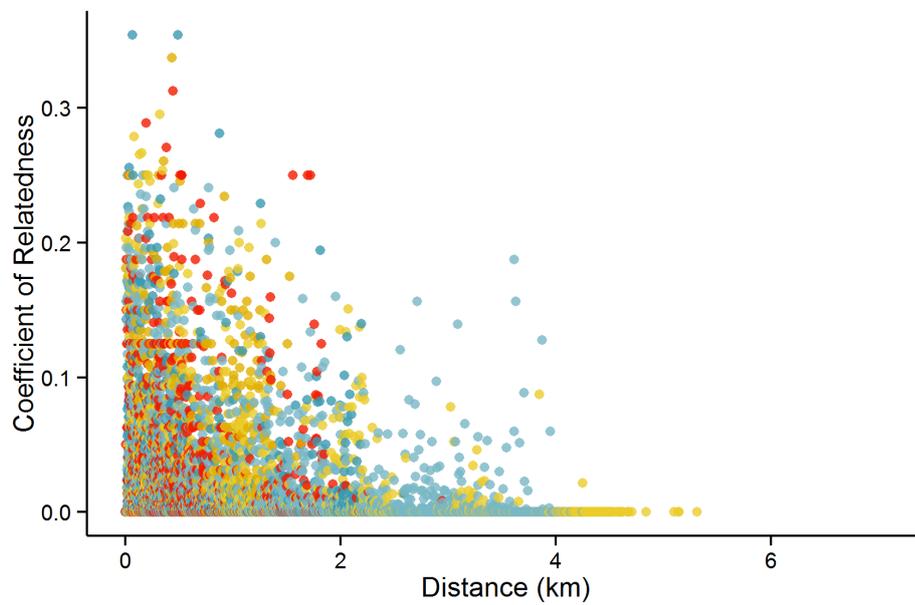
Figure 6.3: Mean relatedness between households as a function of distance in kilometres. Points are coloured by village.

6.4.2.1 Wealth ranks of households

The relative ranking of households by wealth varied greatly across villages (Figure 6.4; a rank of 1 means the wealthiest in the village; note that wealth ranks are only comparable within villages). The majority of households in village B were ranked 1 or 2, whereas in village C, most households were towards the bottom end of the scale. In the remaining villages, most households were ranked 3. Larger households were slightly wealthier (Pearson's $r = -0.210$, 95% CI $[-0.277, -0.142]$, $p \ll 0.001$).
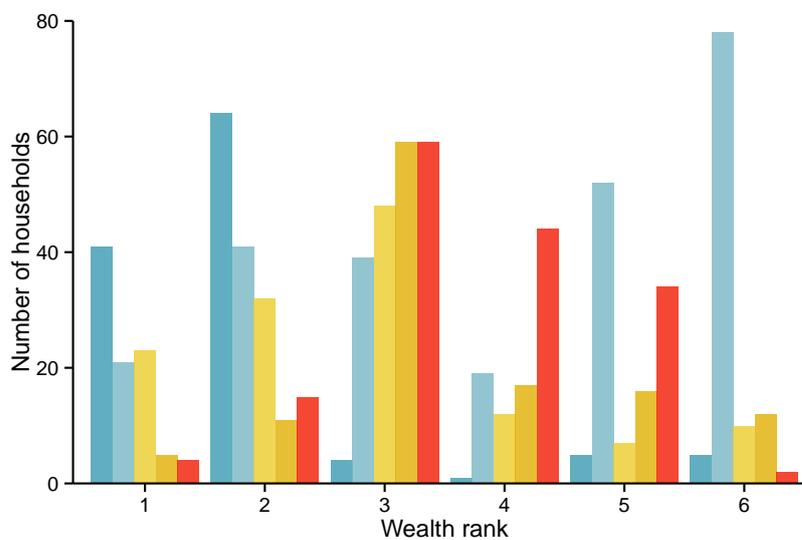
Figure 6.4: Households' wealth ranks, split by village (coloured bars). Note that wealth ranks are only comparable within villages. A rank of 1 means the wealthiest households in the village.

Chapter 7

Affinal links encourage cooperation between Mosuo households

7.1 Introduction

Households are hubs for our social relationships. Within them, biological and affinal kin, friends and neighbours eat, sleep and perpetuate their genes. Households work together in communities on common enterprises such as farming, herding and neighbourhood watches. The household in essence reflects our common willingness to cooperate with non-kin as well as kin.

This chapter will investigate the factors affecting cooperation between households. I will use a real-world measure of cooperation—labouring on farms—and a gift game, to understand the dynamics of cooperation in a multi-ethnic population of rural farmers living in southwest China.

7.1.1 Networks of household cooperation

No human is an island; we live in groups composed, variably, of family and non-kin. In many contexts, the household is a seemingly intuitive concept but is difficult to define in practice (Randall et al. 2011). 'Household' here will refer to a physical building, usually around a gated courtyard, in which multiple generations of a single family live alongside livestock, sharing all food and resources from their communal business, which is usually a farm. Occasionally marriage partners join the household, but often only when there is an imbalance in the sexes.

Cooperation within a household is no surprise. The combination of higher relatedness and the chance for repeated interactions sets up a context for reciprocal cooperation with kin. However, cooperation between households is commonly observed worldwide, despite relatedness being concentrated within houses. Dispersal (e.g. through the exchange of marriage partners) increases the average relatedness between households, potentially nurturing a context for cooperation through kin selection (Wu et al. 2015). This can in turn lead to the creation of reciprocal helping between non-relatives in these households. In addition to bolstering reciprocal relationships, individuals might choose to help others in order to signal their quality as a potential mate. Where parents and affinal kin do not live with all their offspring, different households may share reproductive interests and so helping may act as a form of parental or grandparental investment.

Households cooperate in many ways, from farming, hunting and sharing food, through to policing their communities and arranging marriages. Reciprocal relationships between households might mitigate the risks of living in variable environments, for example, if crops fail in bad years. Labour investment, such as through working on the farms of other households, might help create economies of scale, where investment costs are reduced while output increases (Næss 2012).

Sharing food is a particularly well-studied form of cooperation and the factors that affect sharing vary from place to place. Among north Siberian reindeer herders, kinship was the strongest predictor of food-sharing between households of nuclear families (Ziker & Schnegg 2005). A combination of relatedness, geographical proximity and an index of association measuring the time members of households spend together explained food sharing among horticulturalists in Nicaragua (Koster & Leckie 2014), although non-kin relations were more important for horticulturalists in Venezuela (Koster et al. 2015). Reciprocity also explains food transfers among Ache people, more so than kin selection (Allen-Arave et al. 2008). A meta-analysis of food sharing across human and non-human primates found that reciprocity had a relatively (although not statistically significantly) stronger effect than kinship (Jaeggi &

Gurven 2013).

Non-kin relations are also important in domains beyond food sharing. Membership of a cooperative herding group was the strongest predictor of gift-giving among Saami pastoralists in Norway (Thomas et al. 2015; see Chapter 4), although close kin were also important. Similarly, lineage membership explained cooperative hunting alliances for whale hunters in Indonesia, more so than relatedness (Alvard 2003).

7.1.2 Predictions

Mosuo people, the focus of this chapter, do not traditionally reckon kinship through the patriline (Cai 2001; Shih 2009). Matrilineal kin are also likely to be seen working on each other's farms (Wu et al., 2013). Therefore I predict patrilineal relationships to be less important compared to matrilineal relatedness in explaining occurrences of help on other households' farms. Although kinship is not reckoned through the patriline and men tend not to live with their offspring, fathers do invest with direct care and money (Mattison et al. 2014). Therefore, I expect a household will be more likely to work on another's farm when members of the former have children living in the latter.

The unique form of marriage institution found in the study population (see Chapter 6) can forge cooperative bonds between households (Shih 2009). Thus I predict that the presence of partners in another household will be associated with labouring on their farm. Wu et al. (2013) found that duolocal females worked on their natal farms as well as farms belonging to matrilineal kin, while males preferred to help on their natal households' farms as their number of communally breeding sisters increased. In this chapter I will analyse cooperation on the household level, so the labour patterns of individual females and males will be aggregated; however, I will include matrilineal kin and numbers of reproductive-age females as predictors.

Following previous studies of household cooperation (e.g. Koster & Leckie 2014; Koster et al. 2015), I also expect help to be more likely on the farms of closer neighbours compared to more distant households. According to Shih (2009: 208): "the prosperity of a [Mosuo] household was usually a function

of its size." Land was allocated to households on the basis of household size shortly after the establishment of the People's Republic of China in 1949. Therefore, larger households and those identified as wealthier will be more likely to receive help on their farms.

I analyse behaviour in a gift game to gain insights into the relationships between households; participants could give gifts to specific others of their choosing (see section 6.3). Therefore, I predict that gifts will preferentially be given to households in which the giver's partners or children reside, and thus will be associated with patterns of labour on other households' farms, where affinal links exist.

7.2 Methods

7.2.1 Data preparation

Relatedness between each pair of individuals was calculated from the pedigree data using a modified version of PyPedal (Cole 2012). Relatedness between households was calculated as the mean relatedness between each pair of individuals in the ego and alter households (Allen-Arave et al. 2008; Hames 1987; Koster & Leckie 2014). Matrilineal and patrilineal kinship was calculated as the coefficient of relatedness between one individual to the mother and father (respectively) of another. Means were calculated for matrilineal and patrilineal relatedness, in the same manner as mean between-household relatedness. The numbers of co-resident reproductive-aged females was calculated for each household.

Distance in kilometres between households within the same village was calculated from the longitude and latitude GPS coordinates. Household size was calculated as the total number of people living there at the time of the census. The three seasons of farm observations were aggregated by household. Relative wealth ranking was calculated by subtracting ego's rank from alter's; positive relative rank means the household receiving help was ranked lower than the helping house (i.e. alter's wealth rank number > ego's rank). Larger differences in rank indicate greater wealth disparity.

Household dyads were limited to include only those headed by Mosuo

people. Binary predictors were coded as 1 for each household dyad if any member of one household:

- was ever observed helping on the farm of another household

- ever gave a gift to any member of another household

- had any children (of any age) in another household

- had a partner in another household

7.2.2 Statistical analysis

As in many human societies, I expect cooperation to be variable and facultative, with no single 'silver bullet' neatly predicting interactions. Thus, I will use a model selection and model averaging approach (see section 2.2.1) to examine which factors predict farm work and estimate their relative importance within the best-fitting model via standardisation of predictors.

I used quadratic assignment procedure (QAP) to calculate correlation coefficients between the farm labour and gift game networks. QAP controls for social network structure because dyads are not independent (Krackhardt 1988; see section 2.2.2.2). I also calculated asssortativity coefficients to measure the correlation between pairs of connected nodes on variables of interest (Newman 2002). I calculated whether households within the farm-work and gift networks assort on the amount of help or gifts they received (in-degree).

Generalised estimating equations (GEEs) were fitted to investigate which household dyadic covariates predicted whether any residents of ego ever worked on an alter household's farm. In order to allow comparison of coefficients within models, I standardised continuous parameter estimates over 2 standard deviations and mean-centred binary estimates (see section 2.2.3). Note that all reported coefficients are standardised log odds unless otherwise stated. To select the best models, I compared the quasi-likelihood under the independence model information criteria (Pan 2001).

Table 7.1: Attributes for networks of observed work on other households' farms in each of the five study villages. Here, *n* is the number of household dyads observed helping one another rather than the total number of instances of help observed. See Table 6.2 for the number of households in each village. 'Assortativity' refers to assortativity on in-degree.

Village ID	*n*	Clusters	Reciprocity	Density	Transitivity	Assortativity
A	29	91	0.000	0.002	0.000	-0.320
B	78	55	0.205	0.005	0.106	-0.146
C	132	34	0.258	0.008	0.146	-0.086
D	154	117	0.078	0.002	0.065	-0.058
E	165	48	0.194	0.007	0.165	-0.082

7.3 Results

I limited the analyses to Mosuo and Han people living in households whose heads were ethnically Mosuo. See section 6.4 for a description of individual and household demographics in the sample.

7.3.1 Working on farms

A total of 952 Mosuo and Han people from 565 (out of 780) households were observed working on the farms of 310 other households over three seasons.

Assortativity in networks indicates a bias whereby households connect to other households with similar properties. The assortativity on in-degree was negative in all villages, suggesting households receiving a lot of help themselves tended not to help others that received a lot of help, but rather helped households with lower in-degrees, if they helped anyone (Table 7.1). The negative assortativity coefficients were particularly strong in villages A and B. In village A, for example, three households had an in-degree of 10 (i.e. received help from members of 10 other households), did not help other households, and received all their help from households who were not helped themselves (in-degree = 0).

Across all villages, there were 345 clusters. Reciprocity was 0.168, transitivity was 0.113 and the network's density was 0.001. There was a slight disassortment on help received (assortativity on in-degree = -0.098); the small negative coefficient suggests that households receiving more help (higher in-degree) slightly preferred helping other households that, overall, received less help (lower in-degree).

Table 7.2: Social network attributes for the gift game, split by village. 'Assortativity' refers to assortativity on in-degree.

Village ID	*n* gifts	Clusters	Reciprocity	Density	Transitivity	Assortativity
A	84	59	0.262	0.006	0.263	0.340
B	90	53	0.311	0.006	0.262	0.015
C	58	82	0.207	0.003	0.044	0.068
D	116	156	0.276	0.002	0.084	0.231
E	138	66	0.217	0.006	0.132	0.211

7.3.2 Gift games

Residents of 285 Mosuo-headed households took part in a gift game, giving a total of 522 gifts to people in 319 other households. Most households (87.4%) received one gift from another household, although 24 households received two gifts from a single household and 6 households received three gifts. See Figure 8.5 in the next chapter for gift networks.

Across all villages, there were 416 clusters. Reciprocity was 0.255, transitivity was 0.153 and the network's density was 0.001. Assortativity on in-degree was 0.222, suggesting that households who gave more gifts also received more gifts. Table 7.2 shows the social network attributes for each village.

7.3.3 Cooperation between households

Correlations between the gift game and observed farm work were in the range $0.052 - 0.174$ (Table 7.3). The presence of partners in another household was positively correlated with gift-giving in all villages (range $0.029 - 0.098$). Presence of children in other households was negatively (albeit weakly) correlated with gifts in villages B and C, but positively correlated in the other three villages. The presence of partners and children in other households was positively correlated with observations of help on those household's farms as well with gift-giving. As expected, the partners and children networks were positively correlated with one another. Overall, the presence of children (of any age) living in a household were most strongly correlated with instances of help and gift giving.

I fitted GEE regressions to analyse which factors best predicted observations of working on other households' farms ($n = 55,780$ dyads, including only complete cases from 507 households). The response variable was whether

Table 7.3: Pearsons' correlation coefficients between adjacency matrices for gifts, observed instances of working on another household's farm, partners living in other households and children (of any age) living in other households. All matrices were split into within-village household dyads and all households were included regardless of whether or not they participated in the gift game or were observed to have worked on farms. Coefficients were calculated using quadratic assignment procedure (QAP) to control for the non-independence of ego and alter households within social networks.

	Gift	Help	Partner	Gift	Help	Partner
	Village A			**Village B**		
Help	0.078	–	–	0.066	–	–
Partner	0.093	0.080	–	0.029	0.156	–
Children	0.195	0.097	0.347	0.096	0.212	0.585
	Village C			**Village D**		
Help	0.052	–	–	0.073	–	–
Partner	0.035	0.185	–	0.076	0.182	–
Children	0.045	0.201	0.497	0.117	0.144	0.514
	Village E					
Help	0.174	–	–			
Partner	0.098	0.158	–			
Children	0.232	0.159	0.275			

or not any member of the ego household was observed working on the alter household's farm. Table 7.4 shows the unconditional averaged estimates from the best-fitting models where ΔQIC < 2 (see Table 7.5 for the full set of candidate models). For ease of comparison between effect sizes, I will discuss standardised odds ratios with 95% confidence intervals.

By far the strongest predictor of helping on another household's farm was the presence of male partners ('husbands') in that household (Odds ratio [OR] $= 7.423$, 95% CI $[4.033, 13.663]$; Table 7.4). The next strongest predictor was the presence of female partners ('wives') in the landowning house (OR $= 5.429$, 95% CI $[2.035, 14.479]$).

Households more closely related were more likely to work on each other's farms (OR $= 2.822$, 95% CI $[2.497, 3.19]$). Help was given to closer neighbours (i.e. distance had a strong negative effect: OR $= 0.293$, 95% CI $[0.162, 0.529]$). The interaction between distance and relatedness had a positive effect (OR $= 1.528$, 95% CI $[1.226, 1.906]$), meaning the people were willing to travel further to help a highly related household.

Households were more likely to help one another if children (of any age, not just < 15 years) sired by any member of one household resided in the other (OR = 4.689, 95% CI [1.227, 17.917]). However, the negative interaction between child presence and mean between-household relatedness (OR = 0.624, 95% CI [0.481, 0.81]) suggests that help was less likely as relatedness increased when children lived in the landowning households (Figure 7.1). Therefore, farm labour might act as a form of parental investment when children do not live with other people who are related to the helper(s).
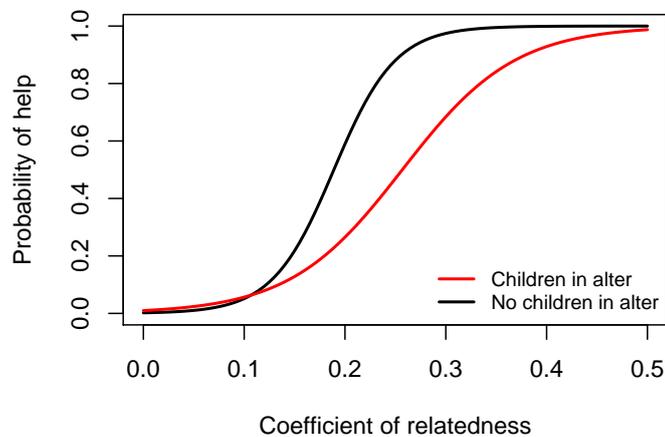
Figure 7.1: Predicted probability of observed farm work as a function of relatedness when members of a potentially helping household have children living in the landowning household (red line) or not (black line). See Table 7.4 for parameter estimates.

Matrilineal and patrilineal relatedness did not appear in the best-fitting models. Comparing the subset of models containing only predictors for relatedness, matrilineal relatedness provided a better fit to the observed data compared to patrilineal relatedness (Table 7.6), as expected, due to the emphasis traditionally placed on matrilines in this population.

In addition, larger households were more likely to receive help (OR = 1.584, 95% CI [1.237, 2.028]) and give help (OR = 1.557, 95% CI [1.211, 2.001]). Differences in the wealth ranks of the two households were not associated with instances of help.

Gift-giving appeared in the best-fitting models, suggesting it was an im-

Table 7.4: Model-averaged parameter estimates for the best-fitting GEE predicting whether instances of farm working were observed on behalf of other households. Ego refers to the household providing help; alter is the landowning household. Predictors are presented in descending order of absolute standardised effect size (column 3). See Table 7.5 for the full set of candidate models.

Parameter	Unstandardised log odds (S.E.)	Standardised log odds (S.E.)
(Intercept)	-6.565 (0.275)	-6.092 (0.104)
Any husbands in alter?	2.005 (0.311)	2.005 (0.311)
Any wives in alter?	1.692 (0.501)	1.692 (0.501)
Any children in alter?	1.587 (0.694)	1.545 (0.684)
Distance (km)	-0.696 (0.168)	-1.228 (0.302)
r	24.29 (1.623)	1.038 (0.063)
Any children in alter? $\times r$	-14.84 (4.191)	-0.471 (0.133)
Size of landowner household (alter)	0.083 (0.023)	0.46 (0.126)
Size of helper household (ego)	0.079 (0.023)	0.443 (0.128)
Distance $\times r$	7.344 (1.949)	0.424 (0.113)
Relative wealth rank	-0.058 (0.033)	-0.245 (0.138)
Gift given from ego to alter?	0.137 (0.273)	0.137 (0.273)

portant predictor of farm help, although it had a small, imprecise effect size (OR $= 1.147$, 95% CI $[0.672, 1.957]$). The number of reproductive-age females in helper and landowning households did not appear in the best models.

7.3.4 Close neighbours, relatedness and child presence predict gifts

I re-ran the GEE analysis with a similar set of candidate models but with the response variable as whether or not a gift was given from anybody in the ego household to anyone in the alter household. In the average over the best-fitting models where ΔQIC < 2 (Table 7.7; see Table 7.8 for the full set of candidate models), by far the strongest predictor of a gift given between households was geographical proximity (i.e. spatially nearer neighbours were more likely to receive gifts; odds ratio [OR] $= 0.007$, 95% CI $[0.001, 0.034]$).

Relatedness was also important in gift-giving: closer relatives were more likely to receive gifts (OR $= 3.646$, 95% CI $[3.108, 4.28]$) even if they lived further away (Distance $\times r$; OR $= 2.46$, 95% CI $[1.761, 3.44]$). More people in the household receiving gifts also increased the likelihood of gift-giving (OR $= 1.442$, 95% CI $[1.06, 1.96]$).

Children present in the household receiving gifts led to more instances of

Table 7.5: Full set of candidate models predicting labour investment on farms from one household (ego) to another (alter). The averaged best models (ΔQIC < 2, highlighted in bold below) are detailed in Table 7.4. The control model includes: distance between households + relative wealth rank of the two households + no. people in ego + no. people in alter. 'Partners' refers to whether or not any members of ego have a 'husband' or 'wife' living in alter. Similarly, 'Children' refers to whether or not any members of ego have children (of any age) living in alter. 'No. reproductive females' refers to total numbers of females aged between 15 and 50 years living in ego and in alter at the time of the census. 'Gift' refers to whether or not any member of the ego household gave a gift to any member of the alter household.

Model	qLik	ΔQIC
Control + Partners + Children + $r\times$ Distance + $r\times$ Children	**-1255**	**0.00**
Control + Gift + Partners + Children + $r\times$ Distance + $r\times$ Children	**-1254**	**1.33**
Control + Partners + Children + $r\times$ Distance	-1262.39	12.66
Control + Gift + Partners + Children + $r\times$ Distance	-1261.38	14.17
Control + Partners + $r\times$ Distance	-1265.77	16.08
Control + Gift + Partners + $r\times$ Distance	-1264.67	17.36
Control + Partners + Children + $r\times$ Distance + No. reproductive females	-1262.20	17.58
Control + Gift + Partners + Children + $r\times$ Distance + No. reproductive females	-1261.17	18.99
Control + $r\times$ Distance	-1315.97	111.98
Control + Gift + $r\times$ Distance	-1315.15	113.92
Control + r	-1333.22	141.56
Control + Gift + r	-1332.85	145.04
Control + Gift + Partners + Children	-1413.73	310.45
Control + Gift + Matrilineal r	-1419.47	317.28
Control + Matrilineal r	-1423.29	320.35
Control + Partners + Children	-1436.67	351.52
Control + Gift + Patrilineal r	-1453.79	384.79
Control + Gift + Children	-1460.03	394.98
Control + Patrilineal r	-1474.47	421.67
Control + Children	-1481.08	433.01
Control + Gift	-1534.49	538.62
Control + Gift + No. reproductive females	-1534.31	542.34
Control model	-1581.77	630.20
Control + No. reproductive females	-1581.66	633.64
Null model	-1639.09	736.51

Table 7.6: Subset of candidate models predicting observed farm work (see Table 7.5) containing only terms for relatedness in order to rank the importance of each relatedness predictor. Mean relatedness between households (top row) best predicts helping on farms. The model containing matrilineal relatedness outranks the model containing patrilineal relatedness. The control model includes: distance between households + relative wealth rank of the two households + no. people in ego + no. people in alter.

Model	qLik	ΔQIC
Control + r	-1333.22	0.00
Control + Matrilineal r	-1423.29	178.79
Control + Patrilineal r	-1474.47	280.10
Control + Children	-1481.08	291.45
Control model	-1581.77	488.64
Null model	-1639.09	594.95

Table 7.7: Model-averaged parameter estimates for the best-fitting GEE model predicting whether gifts were given from one household (ego) to another (alter). Estimates are sorted in descending order of absolute standardised log odds.

Parameter	Unstandardised log odds (S.E.)	Standardised log odds (S.E.)
(Intercept)	-5.509 (0.364)	-7.703 (0.357)
Distance (km)	-2.785 (0.454)	-4.989 (0.813)
Any children in alter?	1.817 (0.661)	1.779 (0.652)
r	22.841 (1.716)	1.294 (0.082)
Distance $\times r$	15.585 (2.956)	0.9 (0.171)
Any children in alter? $\times r$	-13.43 (3.859)	-0.426 (0.123)
Size of recipient household (alter)	0.066 (0.028)	0.366 (0.157)
Any wives in alter?	0.361 (0.528)	0.361 (0.528)
Size of giving household (ego)	0.059 (0.033)	0.326 (0.186)
Relative wealth rank	0.062 (0.045)	0.26 (0.188)
Ego helped on alter's farm?	0.226 (0.341)	0.226 (0.341)
Any husbands in alter?	-0.044 (0.562)	-0.044 (0.562)

gift-giving (OR $= 5.924$, 95% CI $[1.652, 21.2]$). As with farm labour, there was a negative interaction between child presence and between-household relatedness (OR $= 0.653$, 95% CI $[0.514, 0.83]$), suggesting that people preferred giving gifts to households in which their children did not live with other relatives of the giver.

Observations of help on the recipient households' farms appeared in the best-fitting models but the effect size was weak and imprecise; similarly, gifts were not given preferentially to wealthier or poorer households. Predictors for the presence of wives or husbands in the household potentially receiving gifts also appeared in the best-fitting models but did not have any inferential power.

Table 7.8: Full set of candidate models predicting gifts given from one household (ego) to another (alter). The best models (ΔQIC $<$ 2, highlighted in bold below) are detailed in Table 7.7. The control model includes: distance between households + relative wealth rank of the two households + no. people in ego + no. people in alter. 'Partners' refers to whether or not any members of ego have a 'husband' or 'wife' living in alter. Similarly, 'Children' refers to whether or not any members of ego have children (of any age) living in alter. 'No. reproductive females' refers to total numbers of females aged between 15 and 50 years living in ego and in alter at the time of the census. 'Help' refers to whether or not any members of the ego household were observed helping on the alter household's farm.

Model	qLik	ΔQIC
Control + Partners + Children + $r\times$ Distance + $r\times$ Children	**-972.00**	**0.00**
Control + Help + Partners + Children + $r\times$ Distance + $r\times$ Children	**-970.00**	**0.94**
Control + $r\times$ Distance	-983.41	3.64
Control + Help + r x Distance	-980.64	4.05
Control + Partners + Children + $r\times$ Distance	-977.65	5.61
Control + Partners + Children + $r\times$ Distance + No. reproductive females	-975.93	5.84
Control + Partners + $r\times$ Distance	-978.71	6.16
Control + Help + Partners + $r\times$ Distance	-976.39	7.69
Control + Help + Partners + Children + $r\times$ Distance	-975.52	7.91
Control + Help + Partners + Children + $r\times$ Distance + No. reproductive females	-973.66	8.59
Control + r	-1002.58	50.18
Control + Help + r	-999.99	53.57
Control + Help + Matrilineal r	-1054.43	160.93
Control + Matrilineal r	-1063.00	166.28
Control + Help + Patrilineal r	-1145.61	337.82
Control + Help + Partners + Children	-1151.83	358.13
Control + Help + Children	-1154.89	358.99
Control + Patrilineal r	-1165.11	363.20
Control + Partners + Children	-1174.16	394.21
Control + Children	-1176.68	395.34
Control + Help + No. reproductive females	-1212.00	470.57
Control + Help	-1214.45	471.13
Control + No. reproductive females	-1254.55	540.65
Control model	-1256.65	544.10
Null model	-1409.94	850.75

7.4 Discussion

The strongest predictor of cooperation between households in the best-fitting model was whether or not anyone in the helping household had a male partner ('husband') in the landowning household (Table 7.4); the presence of a female partner ('wife') also predicted help, although it had a smaller effect. Despite this, very few gifts were given by males directly to their partners and no gifts were given to partners by females. Therefore, although conjugal relations were not necessarily important predictors of help on an individual-to-individual scale, they might forge links between households. Affinal networks may be important sources of cooperation between women in Mosuo households, as observed ethnographically (Shih 2009). These patterns suggest that individuals might be seeking to invest in their partners when neither resides in the same household.

The presence of children (of any age, not just those younger than 15 years) in one household belonging to members of another was associated with a higher likelihood of helping on the farm where the children reside (Table 7.4), but only when the child did not live with other relatives of the parent (Figure 7.1). Only 7.1% of males who were observed working on the farms of other households did so where their children lived in those households. These results seem at odds with evidence that Mosuo fathers living in the agricultural areas on the other side of Lugu Lake had a positive effect on their children's educational attainment and decreased their age at first reproduction (Mattison et al. 2014). However, Mattison et al. (2014) found that fathers residing with their children were important, while I focussed solely on between-household cooperation when children lived elsewhere. Farm labour might only function as a form of paternal investment in this population when children live with fewer other relatives.

Households were more likely to help on other farms as between-household relatedness increased; geographically closer neighbours tended to be more related (Figure 6.3) and received more help (Table 7.4). Households located further away were less likely to receive help. Mean relatedness within households was $r = 0.354$, an order of magnitude higher than household relatedness re-

ported in other studies. For example, mean $r = 0.06$ among horticulturalists living in Venezuela (Koster et al. 2015) and $r = 0.03$ among horticulturalists in Nicaragua (Koster 2011), while $r = 0.02$ within Ache households (Allen-Arave et al. 2008). Larger Mosuo households were more likely to receive and give help. Although larger households were slightly wealthier, the difference in wealth rank between pairs of households did not predict labour investment.

Relatedness through the matriline or patriline was not important compared to mean relatedness between households and did not appear in the best-fitting models (Tables 7.5 and 7.6); this is most likely because matrilineal relatedness tends to cluster within Mosuo households, while patrilines are not traditionally important in this area (Cai 2001; Shih 2009; Wu et al. 2013). Matrilineal relatedness was a better predictor of farm help compared to patrilineal relatedness (Table 7.6). Wu et al. (2013) found that Mosuo women helped on the farms of households to whom they were related through the matriline; in this chapter (using the same dataset), I found that when farm help was aggregated at the household level, this sex-specific pattern did not hold.

Gifts were given to geographically closer neighbours and to closer relatives (Table 7.7). The presence of conjugal partners had no effect on gift-giving. People gave gifts to households where their children resided but not when those children lived with other relatives. Thus, gift-giving may have been considered a form of parental investment in cases where children might receive less provisioning from other relatives since the smallest gift (5 yuan) was equivalent to, at most, ~8% of a day's unskilled labour ($60 - 80$ yuan in 2014), while the largest gift (15 yuan) formed at most 25% of daily wages.

Observations of help on another household's farm did not predict gift giving between households, although it did appear as a predictor in the best-fitting models. Similarly, the odds of working on other households' farms did not increase when members of the helping house also gave gifts; although the parameter estimate appeared in the best-fitting model, its effect was statistically indistinguishable from zero (Table 7.4). The gift game did not strongly correlate with farm work either (Table 7.3).

These results suggest that although gift games are useful tools for investi-

gating social relationships (Apicella et al. 2012; Chaudhary et al. 2015; Thomas et al. 2015; Chapter 4), gift relationships in this case provided only equivocal insights into the patterns of labour investment. Given that real-world cooperation heavily depends on context (Gerkey 2013), researchers should design experimental games with this in mind and attempt to make games reflect particular salient forms of cooperation rather than study 'generic' cooperativeness. I will discuss these issues further in Chapter 9.

It is hard to make causal claims from observational data and disentangle cases where household members fulfil multiple roles, e.g. being related on average yet also having partners and children present in other locations. Through mean-centering and standardising regression coefficients (Gelman 2008; Schielzeth 2010), I was able to contrast effect sizes within the best-fitting models (Table 7.4 and Table 7.7). The strongest predictors of observed farm labour were the presence of marital partners and/or children of someone in the helping household residing in the household being helped (predominantly 'husbands') and closer spatial proximity to the households providing help. These results match studies of food sharing networks, which similarly found that proximity, genealogical relatedness and affinal links were predictors of cooperative behaviour (Koster & Leckie 2014; Koster et al. 2015).

7.5 Conclusion

I have shown that households are more likely to cooperate through labouring on one another's farms when there are genetic and/or affinal links between the households, as well as when the households are geographically closer to one another. Links between households due to the presence of partners were the strongest predictors of farm work. This reflects and quantifies ethnographic observations from Mosuo villages whereby affinal associations between households promote cooperation (Shih 2009).

The traditional Mosuo lifestyle has been and continues to change with increased tourism, media attention and shifting economic opportunities (Mattison 2010). Households in the study area help one another by investing labour into each other's farms. This chapter has shown that relatedness, shared repro-

ductive interests and affinal kinship are important predictors for this form of cooperation. It remains to be seen whether these evolutionarily salient factors continue to be important as Mosuo culture transitions.

Chapter 8

People accused of witchcraft are isolated but not helpless in Mosuo communities

8.1 Introduction

Cooperation that is based on reputation seems fundamentally important to human social dynamics (Roberts 2015a). As with all social behaviour, in order for reputation-based cooperation to evolve, the helpful individual must be increasing their lifetime inclusive fitness (West et al. 2007b). Indirect reciprocity explains cooperation in cases where individuals might not necessarily be related or have direct experience of interacting with one another; rather, cooperation becomes contingent upon the reputations of others, which in turn are affected by their own past social behaviours (Nowak 2012a).

Field studies of reputation-based cooperation tend to focus on the importance of building a good reputation in order to accrue benefits or gain access to cooperative partners (Alvard & Gillespie 2004; Lyle & Smith 2014; Price 2006; Sylwester & Roberts 2013). In this chapter, I focus on the opposite situation to investigate whether having a poor reputation negatively affects cooperative interactions and has detrimental effects on reproductive success.

While much existing work—including the previous three chapters of this thesis—focusses on the positive side of cooperation, a large body of literature exists detailing how mechanisms such as punishment can also promote coop-

eration. Punishment can either be direct and costly to the punisher, or indirect and costless (Raihani et al. 2012). Indirect punishment (also known as sanctioning) is a key assumption of indirect reciprocity (Balafoutas et al. 2014; Nowak & Sigmund 1998; Panchanathan & Boyd 2003); an example would be refusing to help people with bad reputations.

Theoretical and field studies suggest that indirect punishment—costless punishment such as the withholding of help or rewards—is preferable to direct, costly punishment as a means of maintaining cooperation via indirect reciprocity (Balafoutas et al. 2014; Ohtsuki et al. 2009). For populations who rely on agriculture, help with farming can provide very real boons to survival and reproduction (see previous chapter). On the other hand, withholding help might have long-term repercussions, leading to harmful effects on fitness for people held in poor standing.

Publicity is the key to reputation systems, both in terms of public behaviours (e.g. conspicuously helping) and public knowledge (e.g. of who to trust). Reputation systems require image scoring, some form of coordination (everyone must agree, to an extent, on what constitutes a good or bad reputation), and social networks through which reputations become known. Such systems can also lead to reputation-based exclusion: the selective admission of co-operators into beneficial interactions alongside the isolation of others.

Reputations change and spread based on direct observation of social interactions as well as the communication of information about individuals (Sommerfeld et al. 2007). Up to 70% of conversation time relates to social matters, at least in Western samples, although a smaller proportion of chat tends to be about absent third-parties, and negative gossip forms a smaller proportion still: 14% of conversation time according to estimates from one workplace (Foster 2004).

Gossip networks can spread information about the past behaviour of others in order to protect against free-riders (Enquist & Leimar 1993). Gossip allows the spread of reputations not just as a means of identifying others as good or bad social partners but also potentially to advance the interests of the gossiper by painting others in a certain light, regardless of their actual behaviour

(Paine 1967). As such, forms of negative gossip (e.g. slander, denigration, ridicule, rumours) might also be dishonest signals because they further the interest of the gossip-spreader to the detriment of the gossiped-about. This creates a second-order (and beyond) problem of reputation, where individuals must take into account not only the gossip but also the reputation of the gossiper.

While the mechanisms by which reputations spread and change, such as gossip, are beyond the scope of this chapter, it is informative to bear in mind the potentially self-interested reasons that somebody might try to damage the reputation of another. Tarnishing or manipulating reputations can also act as a mechanism for punishing individuals; for example, a Saami pastoralist with a poor reputation might lose the help of others, who disassociate their herds from his (Paine 1970; gendered pronoun intentional).

Reputations can also translate into reproductive success. For example, successful Meriam turtle hunters in Australia had greater reproductive success due to the reputational benefits of their prowess (Smith et al. 2003). In a Peruvian village, people and households with good reputations due to their contributions to collective projects had larger support networks and better health outcomes: important proxies of fitness (Lyle & Smith 2014). It follows that the converse may be true: people with poor reputations may receive fewer benefits (Price 2006), which in turn may negatively affect reproductive success.

In this chapter, I will investigate how a poor reputation—associated with accusations of food poisoning—affects a household's cooperative relationships with others in their villages. I also analyse how living in a house shrouded by this reputation affects the reproductive success of its residents. As such, I aim to further our understanding of the consequences of poor esteem in a real-world reputation system. The reputation system in question is based around taboos and beliefs outside of what we in a Western scientific context would consider 'natural', and so shares commonalities with witchcraft. Thus I will begin with an overview of witchcraft, as studied by anthropologists.

8.1.1 Witchcraft in anthropology

Swanson (1960: 151) wrote that "witchcraft tends to be prevalent when people must interact with one another on important matters in the absence of legitimated controls and arrangements." Accusing people of witchcraft could therefore function as a form of social sanctioning in places where no formal institutions exist to act as third-party punishers. Witchcraft, then, can been seen as a strategy of social exclusion or rejection (Douglas 1991), strongly linked to conflicts within communities (Levine 1982), emerging as a response to inequalities in production (e.g. poor harvests) and reproduction (e.g. infertility). Furthermore, witchcraft can be a dynamic cultural trait, becoming dormant during times of growth or lessened competition (Douglas 1970).

Witchcraft refers to a worldview, a system of knowledge and an entwined set of social institutions involving not only witches (in the pejorative sense) but that can also include healers (witchdoctors), diviners (who detect witches) and witch-cleansers. Far from being a primitive or supernatural belief, witchcraft regulates social relations, forms an agentive way of explaining cause and effect, and has been linked to economic reforms (Evans-Pritchard 1977; Geschiere 1997). As a 'natural philosophy', witchcraft can explain inequality in misfortune: why a bad event befalls one person in particular but not all people equally (Evans-Pritchard 1977). In some societies, witches are understood to gain wealth at the expense of others losing material goods or even their lives; magic, in an 'occult economy', acts as a means of conjuring wealth without production (Comaroff & Comaroff 1999).

Witchcraft is often embodied as a physical, heritable substance. Among the Tibetan Nyinba, the most common pattern of inheritance is from mothers to daughters (Levine 1982). Witches are often well known, even related, to the people suffering misfortunes (Mesaki 2009). In a study of Ghanaian witchcraft, (Bleek 1976) found that, of 71 witch accusations, 27 occurred between close relatives (mothers, siblings, grandparents, uncles and aunts), while 40 were between more distant relatives and 4 between affines. The majority of accusations (56) were cases of younger people accusing older people; 66 accusations were directed at women (31 of which also came from women).

Witchcraft accusations may be a way to air grievances as a form of 'covert aggression' (Nash 1973) while still maintaining relationships. Accusations might also sever social relations, allowing individuals to disassociate with uncooperative people, a mechanism that has been shown to promote cooperation and increase individual payoffs (Wang et al. 2012). Accusations may also allow for publicly sanctioned harm on particular groups of people. Older women are vulnerable to accusations of witchcraft and their consequences, including death, although a non-trivial number of men may also suffer the same fate (Mesaki 2009).

The reputation system present among the Mosuo is similar to witchcraft in the sense that a person's poor standing is widely known in their community, appears to be heritable, and involves notions of harm and taboo. Taking an evolutionary perspective, I will analyse this Mosuo reputation system in terms of its functional relationship to an individual's inclusive fitness. I use an emic definition of poor standing, as employed by the Mosuo (see section 8.2). This chapter will therefore focus on the social outcomes of being held in poor regard within one's community and whether this reputation is associated with indirect punishment in the form of withheld help during planting or harvesting seasons, as well as lowered reproductive success.

8.1.2 Mosuo food taboos

People whose reputations are damaged through accusations of poisoning others who eat in their houses are known as *zhubo*. For the Mosuo, these accusations cast a cloud over an entire household. Little is known ethnographically about the beliefs and practices associated with the food taboos in the areas surrounding Lugu Lake. Based on observations in the field (see section 6.3), *zhubo* can marry one another as well as marry people from other ethnic groups. This pattern of behaviour is similar to the qualms over food purity seen among Tibetan Nyinba (Levine 1982). However, Mosuo *zhubo* can labour on the farms of *zhubo* and non-*zhubo* alike, receiving food in return. The presence of *zhubo* seems to be tolerated within Mosuo villages. In other parts of the world, people with similarly accursed reputations may be exiled or even killed. To the best of

my knowledge, such practices do not occur around Lugu Lake.

8.1.3 Predictions

If accusations of poisoning function as a form of punishment, households containing *zhubo* will receive less help on their farms as well as fewer gifts, especially from non-*zhubo* houses. Since there appears to be no taboo against *zhubo* eating in non-*zhubo* households, I expect *zhubo* households to help all households equally, regardless of reputation. If *zhubo* are marginalised within villages, residents of non-*zhubo* households will rarely have partners or children living in *zhubo* households. In cases where non-*zhubo* do have partners/children in *zhubo* households, I predict members of the non-*zhubo* household will help on the *zhubo* farm.

People with 'dangerous' reputations need not be uncommon within a community, even where accusations leading to such a reputation act as a form of punishment (Evans-Pritchard 1977). One might therefore expect those accused of poisoning to interact preferentially with each other as a form of resilience against sanctions that might otherwise harm their lifetime reproductive success. Thus, I predict that members of *zhubo* households will cluster on cooperative behaviours such as exchange of farm labour and gift-giving. I also predict that where such clustering occurs, *zhubo* will not suffer a decrease in their fitness compared to members of non-*zhubo* households.

If poor reputations negatively affect reproductive success (measured as number of living children) or age at first birth, models containing a predictor for *zhubo* will appear in the 95% confidence set of selected models (see section 8.2.2 and Tables 8.1 and 8.2). I predict that *zhubo* and people living in *zhubo* houses will have fewer children compared to non-*zhubo* and also experience later age at first birth. One possibility for escaping the detrimental effects of poor reputations would be through neolocality (i.e. where both partners have dispersed from their natal households). Therefore, I predict that people in neolocal relationships who are *zhubo* will have higher reproductive success compared to *zhubo* in other kinds of relationship.

8.2 Methods

An informant identified households containing *zhubo*, some of which were corroborated by behavioural observations of whether or not people would eat in certain houses. To the best of my knowledge, household heads are the ones identified as *zhubo*, although the accusation casts a shadow over all residents of the household. A poor reputation, for the purposes of this chapter, is thus a household-level phenomenon, except where applied to household heads.

8.2.1 Data preparation

8.2.1.1 Number of reproductive-age siblings

I counted each person's number of brothers and sisters (aged ≥ 15 years) living in the same household. Siblings were defined as individuals related $r \geq 0.5$ who shared at least one parent.

8.2.1.2 Number of children

For the purposes of household-level cooperation, measured as labour investment on farms (see previous chapter), the number of children belonging to members of one household but living in another was calculated regardless of age; 'children' might be adults in some cases.

8.2.1.3 Partnership types

For each person in the census, we know their natal household as well as where they lived in 2012. If these two households differed, I flagged the person as having dispersed. A couple's partnership type was coded as 'neolocal' if both partners had dispersed, 'duolocal' if neither dispersed, 'patrilocal' if only the female dispersed, or 'matrilocal' if only the male dispersed; people not in relationships at the time of the census were coded as 'single'.

8.2.2 Statistical analysis

Analyses of reproductive success were limited to Mosuo people (because they believe in *zhubo*), whereas all other analyses were conducted on all Mosuo and Han people. I used Poisson regressions to analyse the relationship between reputation and reproductive success, measured as number of living children, and Cox regressions to determine the effect of being known as a *zhubo* on age

Table 8.1: Full set of candidate models for estimating number of living children for Mosuo females and males. Control includes age + age^2 + no. adult sisters + no. adult brothers + age × no. brothers + age × no. sisters + years of education + income from tourism in 2012 (yes/no) + no. livestock in 2012. 'Partnership type' refers to people living neolocally with a partner (i.e. both dispersed from their natal households), in a duolocal relationship (i.e. neither dispersed), or people not in relationships (the reference category).

Candidate models
Null model
Control
Control + *Zhubo*
Control + Partnership type
Control + Partnership type + *Zhubo*
Control + Partnership type × *Zhubo*

Table 8.2: Full set of candidate models for estimating age at first birth for Mosuo females and males. Control includes age cohort (categorical variable with three levels: born before 1941, between 1941 and 1972, and born after 1972) + no. adult sisters + no. adult brothers + years of education + income from tourism in 2012 (yes/no) + no. livestock in 2012.

Candidate models
Null
Control
Control + *Zhubo*

at first birth. For both analyses, I used a model selection approach on sets of a priori candidate models (Tables 8.1 and 8.2) fitted separately for Mosuo females and males; both samples contained adults aged 15 years or older. Note that I fitted single-level models since a multilevel null model accounted for a statistically insignificant amount of variance at the household level compared to a one-level null model (likelihood ratio test, $\chi_1^2 \ll 0.001$, $p \approx 1$).

I used Zero-inflated Poisson (ZIP) regressions to model how being known as a *zhubo* house affected the instances of help observed on a household's farm and the number of gifts received from other households (both measures of in-degree). ZIP models account for overdispersion—in this case, an 'excessive' number of households with in-degree of zero—by assuming there are two 'types' of household: households whose in-degree is generated by a Poisson process, and households with a zero probability of having in-degree > 0 (i.e. households for which no farm work was observed due to the random sampling of households). ZIP models thus estimate a Poisson model for the count

Table 8.3: Candidate set of models for estimating the number of observations of farm labour and gifts received for each household (both measures of in-degree). Control model includes household size + wealth rank + sex of household head + dummy variables for villages.

Candidate models
Null
Control
Control + *Zhubo*

data alongside a logistic regression predicting the log odds that a household had in-degree = 0; both are interpreted in the standard manner.

The ZIP models controlled for household size, wealth rank and sex of the household head, and included village as a dummy variable (Table 8.3). This analysis did not include village A because the fewest farm observations were made there and none included helping on *zhubo* farms – most likely due to chance rather than prejudice. This left $n = 660$ households.

I used 'join count' statistics to examine whether or not *zhubo* houses were physically clustered in the study villages. Join counts test the extent to which the occurrence of *zhubo* households at spatially adjacent locations was due to chance (Fortin & Dale 2005). In cases where there were more observations of *zhubo*/non-*zhubo* 'joins' than expected, there was negative spatial autocorrelation, meaning that *zhubo* households were dispersed throughout their villages. Where there was positive spatial autocorrelation, *zhubo* households clustered together. If the test statistic was not statistically significant then *zhubo* households were randomly distributed within villages (no spatial autocorrelation).

8.3 Results

As in Chapter 7, I limited analyses to Han and Mosuo people living in households headed by Mosuo people. 107 of the 780 households (13.7%) in the sample were identified as being home to *zhubo*.

8.3.1 Household composition

Zhubo and non-*zhubo* households did not differ in age or sex composition (Figure 8.1; note that the sample contained people for whom I do not know age, sex or whether or not *zhubo* reside in their homes). There were no significant

differences in the numbers of Han and Mosuo people in *zhubo* and non-*zhubo* houses. In total, 64 females and 43 males (all Mosuo) were heads of *zhubo* households, compared to 307 females and 363 males heading non-*zhubo* households. Among the household heads, older women were not more liable to be accused of being *zhubo* (Table 8.4).

Proportionally, 39.3% of *zhubo* households were in the top two wealth ranks, compared to 31.9% of non-*zhubo* households. While 15.3% of non-*zhubo* households were ranked least wealthy, only 3.7% of *zhubo* households fell into this bracket. Overall, *zhubo* houses were ranked towards the wealthier end of the community (Figure 8.2).
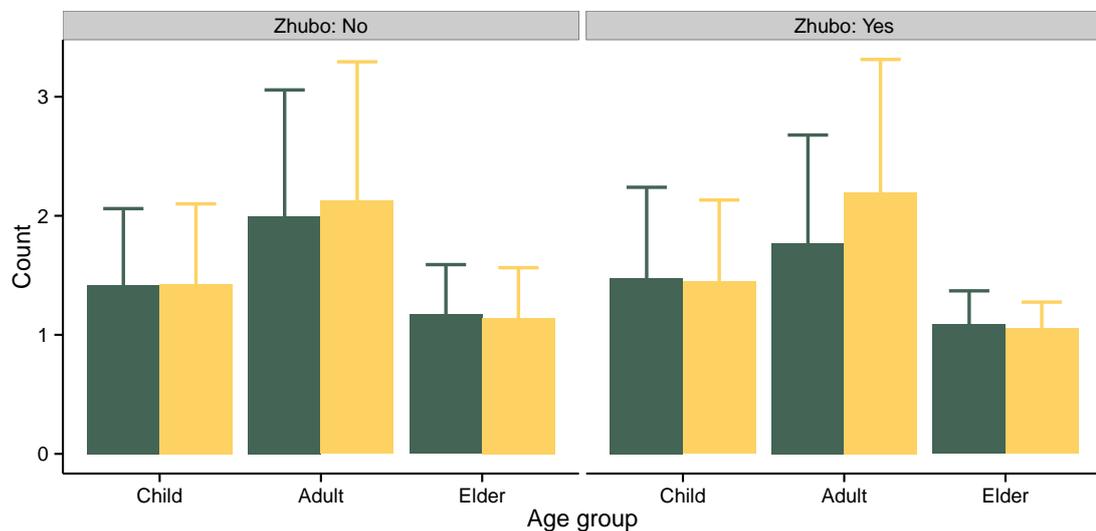
Figure 8.1: Household composition for households containing *zhubo* (right panel) or not (left panel). Bars show the mean number of females (green) and males (yellow) in each type of house, categorised by age. Child refers to people aged < 15, 'adult' means aged 15 to 50 and 'elder' is 50 or older.

8.3.2   Partners, children and post-marital residence of *zhubo*

Table 8.5 and Figure 8.5 show links between households (containing *zhubo* or not) where members of one had a partner or a child (aged < 15 years) in another household. Fifteen non-*zhubo* households had partners living in *zhubo* households (Table 8.5a). Only one of these non-*zhubo* households gave gifts to two different *zhubo* houses; members of this same non-*zhubo* house were also observed working on the farms of the two *zhubo* households. One other household was observed helping on the farm of a *zhubo* household (giving a total of
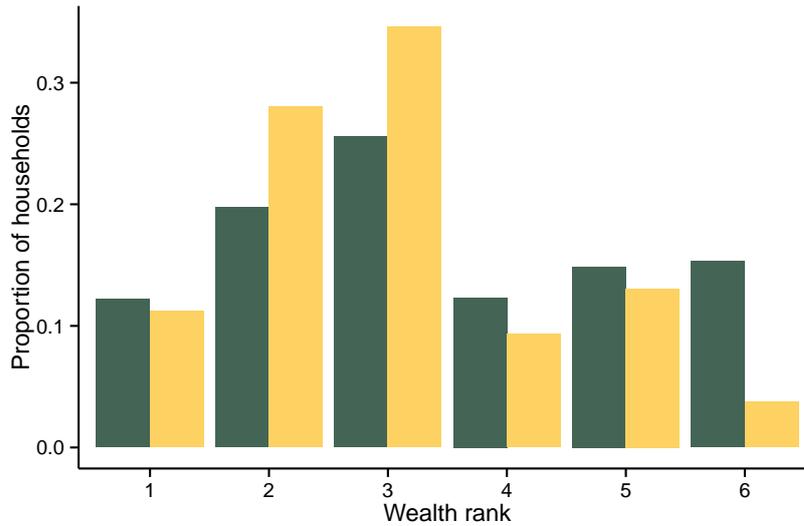
Figure 8.2: Wealth rankings of *zhubo* (yellow) and non-*zhubo* (green) households. Bars show the proportions of households in each rank compared to the total numbers of *zhubo* and non-*zhubo* households.

Table 8.4: Demographics of Mosuo household heads and all people in the sample, split by sex and whether or not they are *zhubo*.

	Sex	*Zhubo?*	*n*	Age (mean ± SD)	Age at first birth (mean ± SD)
Household heads	♀	No	307	50.7 ± 12.1	21.8 ± 3.4
	♀	Yes	64	50.8 ± 12.4	22.3 ± 3.6
	♂	No	362	47.7 ± 12	25.8 ± 4.2
	♂	Yes	43	47.3 ± 10.8	25.7 ± 3.9
All Mosuo/Han people	♀	No	1,647	40.6 ± 17.8	22.4 ± 3.6
	♀	Yes	240	41 ± 17.2	22.6 ± 3.8
	♂	No	1,643	37.6 ± 15.9	26 ± 3.9
	♂	Yes	265	36.9 ± 15.3	26.1 ± 4

three instances where non-*zhubo* were observed helping *zhubo* when partners were present in the *zhubo* households).

There were more non-*zhubo*/non-*zhubo* partnerships ($n = 455$) than expected ($n = 432.3$) under the null hypothesis that poor reputation has no effect on marriage patterns ($\chi^2_1 = 177.26$, $p \ll 0.001$). Similarly, there were also more *zhubo*/*zhubo* partnerships ($n = 26$) than expected ($n = 3.3$), while there were fewer *zhubo*/non-*zhubo* partnerships ($n = 15$) than expected ($n = 37.7$).

There were more cases of non-*zhubo* children living in non-*zhubo* households ($n = 489$; Table 8.5b) than expected ($n = 450.8$) and more *zhubo* children living in *zhubo* households ($n = 45$) than expected ($n = 6.8$) under the null hy-

Table 8.5: Counts of whether or not households containing *zhubo* (a) have partners living in, or (b) have children living in other households containing *zhubo* (or not). Note that 'children' refers to all offspring, regardless of age.

(a)		Households containing partners	
		Non-*zhubo* house	***Zhubo* house**
Households with	**Non-*zhubo* house**	455	15
partners elsewhere	***Zhubo* house**	15	26

(b)		Households containing children	
		Non-*zhubo* house	***Zhubo* house**
Households with	**Non-*zhubo* house**	489	24
children elsewhere	***Zhubo* house**	11	45

Table 8.6: Post-marital residence patterns of couples, partitioned by whether both, one or neither are *zhubo*. Numbers are raw counts of observed couples; percentages show proportions of residence strategies relative to the rest of that row (e.g. 44.6% of all *zhubo-zhubo* couples were neolocal).

	Neolocal	**Duolocal**	**Matrilocal**	**Patrilocal**	**Row totals**
Neither *zhubo*	295 (36.3%)	243 (29.9%)	115 (14.2%)	159 (19.6%)	812 (100%)
One *zhubo*, one not	5 (20.0%)	10 (40.0%)	5 (20.0%)	5 (20.0%)	25 (100%)
Both *zhubo*	50 (44.6%)	19 (17.0%)	23 (20.5%)	20 (17.9%)	112 (100%)

pothesis that poor reputation has no effect on child residence ($\chi_1^2 = 264.31$, $p \ll 0.001$). There were fewer children of non-*zhubo* people living in *zhubo* houses ($n = 24$) than expected ($n = 62.2$), as well as fewer children of *zhubo* people living in non-*zhubo* housesholds ($n = 11$) than expected ($n = 49.2$).

Table 8.6 shows the numbers and proportions of post-marital residence strategies for couples where one, both or neither of the partners lived in *zhubo* houses. A greater proportion of *zhubo-zhubo* couples were neolocal compared to the proportion of non-*zhubo* couples; the latter had more instances of duolocality. Note that the higher proportion of patrilocal relationships described here compared to earlier work (Wu et al. 2013) is due to defining relationship type as a property of the couple, whereas previously it was a property of a household.

8.3.3   Reproductive success of *zhubo*

8.3.3.1   Age at first birth

The earliest ages at first birth were 16 years for female *zhubo* and 15 years for female non-*zhubo*, 17 years for male *zhubo* and 15 years for male non-*zhubo*.

Table 8.7: Hazard ratios [95% confidence intervals] predicting age at first birth estimated from Cox regressions and averaged over the 95% confidence set of models (Table 8.8). Models were fitted separately for all Mosuo females ($n = 1,667$) and males ($n = 1,691$) aged 15 years and over.

	Hazard ratio [95% CI]	
Parameter	Females	Males
Zhubo		
No	1	1
Yes	0.923 [0.781, 1.092]	0.973 [0.805, 1.176]
No. sisters	0.76 [0.688, 0.841]	0.939 [0.859, 1.027]
No. brothers	0.866 [0.808, 0.929]	0.895 [0.83, 0.964]
Education (years)	0.972 [0.95, 0.994]	1.001 [0.985, 1.017]
Tourist income	1.024 [0.91, 1.153]	1.063 [0.929, 1.216]
No. livestock	1.008 [1.001, 1.014]	0.998 [0.993, 1.004]
Cohort		
Before 1941	1	1
1941 to 1972	1.915 [1.566, 2.341]	1.493 [1.117, 1.997]
After 1972	2.07 [1.657, 2.586]	1.605 [1.179, 2.185]

Table 8.4 summarises the ages at first birth for female and male *zhubo* and non-*zhubo*.

To analyse whether an association with witchcraft was also associated with delayed age at first reproduction, I fitted Cox regression models, accounting for censored cases in which some individuals may not yet have given birth or may never have reproduced. The sample was restricted to all Mosuo people aged 15 years or older ($n = 1,667$ females and $1,691$ males); females and males were analysed separately. Parameter estimates averaged over the 95% confidence set of models are shown in Table 8.7, summaries of the models are in Table 8.8 and the complete set of candidate models is presented in Table 8.2.

Poor reputation did not have an effect on age at first birth for females or males (confidence intervals overlapped with zero; Table 8.7). The number of co-resident adult sisters was associated with later age at first reproduction for females (hazard ratio [HR] = 0.76) and but there was no discernible trend for males. A larger number of adult brothers was also associated with later age at first birth for females (HR = 0.866) and for males (HR = 0.895). Larger herd sizes were linked to a slightly earlier age at first birth for females (HR = 1.008) but not for males, while more time spent in education was associated with a later age at first birth for females (HR = 0.972). In Figure 8.3, *zhubo* have a slightly

Table 8.8: 95% confidence set of models for Cox regressions on age at first birth, including number of parameters (*K*), differences in AICc relative to the minimum in the set (ΔAICc), Akaike weights (*ω_i*) and the log-likelihood of each model (LL). Control includes age cohort (categorical variable with three levels: born before 1941, between 1941 and 1972, and born after 1972) + no. adult sisters + no. adult brothers + years of education + income from tourism in 2012 (yes/no) + no. livestock in 2012. Model-averaged estimates are shown in Table 8.7.

Sample	Models	K	ΔAICc	ω_i	LL
♀	Control	7	0.00	0.64	-7822.04
	Control + *Zhubo*	8	1.13	0.36	-7821.59
♂	Control	7	0.00	0.73	-5639.55
	Control + *Zhubo*	8	1.94	0.27	-5639.51

later age at first birth compared to non-*zhubo*, although the confidence intervals overlap (not plotted for additional clarity).
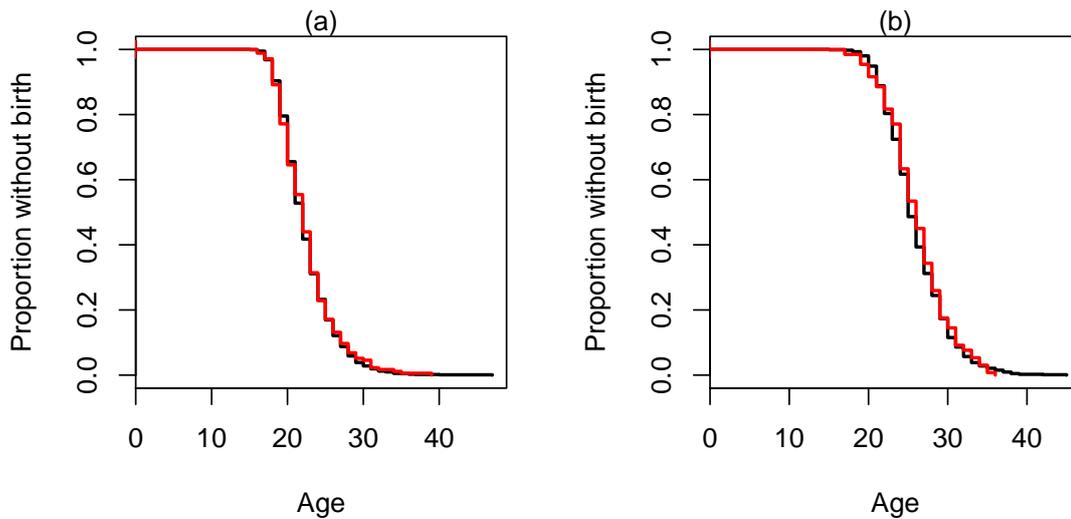
Figure 8.3: Kaplan-Meier survival curves showing progression to first birth for (a) female and (b) male non-*zhubo* (black line) and *zhubo* (red line). Confidence intervals have not been plotted for greater clarity.

8.3.3.2   Number of living children

I fitted Poisson regressions to analyse the effect of poor reputation on reproductive success, measured as number of living children, controlling for factors such as age, age^2, education, wealth, and reproductive competition (numbers of co-resident reproductive-age brothers and sisters, as well as interactions be-

tween these terms and age). Model-averaged parameter estimates are shown in Figure 8.4, with 95% confidence sets of candidate models in Tables 8.9 to 8.12 and the full set of models in Table 8.1.
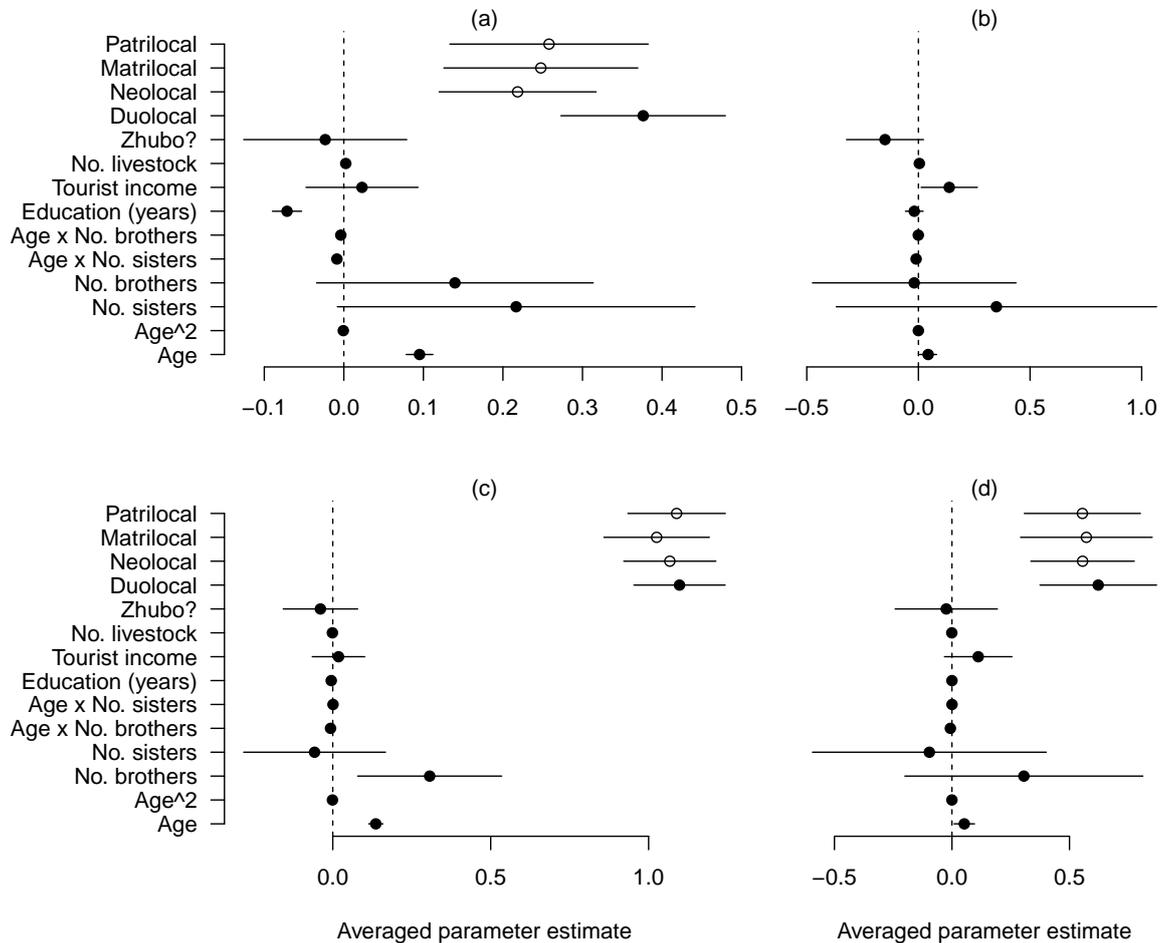
Figure 8.4: Model-averaged parameter estimates with unconditional 95% confidence intervals predicting number of living children for Mosuo adults aged 15 and over, including (a) all females ($n = 1,667$), (b) female heads of households ($n = 363$), (c) all males ($n = 1,691$), (d) male heads of households ($n = 394$). In all cases, the response variable was number of living children at the time of census.

Poor reputations were associated with fewer living children for female household heads, although the confidence intervals slightly overlapped with zero (Figure 8.4b; $\beta = -0.15$, 95% CI $[-0.322, 0.023]$). Living in a *zhubo* household was associated with lower fertility for the remaining subsamples, although there was greater uncertainty in the estimates (Figure 8.4; females: $\beta = -0.023$, 95% CI $[-0.126, 0.079]$; males: $\beta = -0.039$, 95% CI $[-0.157, 0.079]$; male household heads: $\beta = -0.024$, 95% CI $[-0.242, 0.193]$).

Table 8.9: Summary of the best 95% a priori models predicting number of living children for all Mosuo female adults, including number of parameters (*K*), differences in AICc relative to the minimum in the set (ΔAICc), Akaike weights (ω_i) and the log-likelihood of each model (LL). Control includes age + age^2 + no. adult sisters + no. adult brothers + age × no. brothers + age × no. sisters + years of education + income from tourism in 2012 (yes/no) + no. livestock in 2012. 'Partnership type' refers to people living neolocally with a partner (i.e. both dispersed from their natal households), in a duolocal relationship (i.e. neither dispersed), in a matrilocal or patrilocal relationship (i.e. male or female dispersal, respective), or people not in relationships (the reference category).

Models	K	ΔAICc	ω_i	LL
Control + Partnership type	14	0.00	0.71	-2338.66
Control + Partnership type + *Zhubo*	15	1.84	0.28	-2338.56

Table 8.10: Summary of the best 95% a priori models predicting number of living children for all Mosuo female household heads, including number of parameters (*K*), differences in AICc relative to the minimum in the set (ΔAICc), Akaike weights (ω_i) and the log-likelihood of each model (LL). Control includes age + age^2 + no. adult sisters + no. adult brothers + age × no. brothers + age × no. sisters + years of education + income from tourism in 2012 (yes/no) + no. livestock in 2012.

Models	K	ΔAICc	ω_i	LL
Control + *Zhubo*	11	0.00	0.59	-577.75
Control	10	0.86	0.38	-579.25

Type of partnership—being in a duolocal, neolocal, matrilocal or patrilocal relationship—had positive effects on number of children from Mosuo females (but not the subset of female household heads) as well as all males; this is unsurprising since fewer people not in relationships at the time of the census had reproduced (642 Mosuo people had children but were not in partnerships). Interactions between partnership types and poor reputation did not appear in any of the best-fitting models, contrary to predictions.

8.3.4 Working on *zhubo* farms

There were 34 observations of people from non-*zhubo* households working on the farms of *zhubo* households and 35 instances where *zhubo* houses worked on non-*zhubo* farms (Table 8.13a). Of the 35 instances where *zhubo* households helped on non-*zhubo* farms, nine were directly reciprocated by non-*zhubo* people. There were more observations of help between pairs of non-*zhubo* house-

Table 8.11: Summary of the best 95% a priori models predicting number of living children for all Mosuo male adults, including number of parameters (K), differences in AICc relative to the minimum in the set (ΔAICc), Akaike weights (ω_i) and the log-likelihood of each model (LL). Control includes age + age^2 + no. adult sisters + no. adult brothers + age $\times$ no. brothers + age $\times$ no. sisters + years of education + income from tourism in 2012 (yes/no) + no. livestock in 2012. 'Partnership type' refers to people living neolocally with a partner (i.e. both dispersed from their natal households), in a duolocal relationship (i.e. neither dispersed), in a matrilocal or patrilocal relationship (i.e. male or female dispersal, respective), or people not in relationships (the reference category).

Models	K	ΔAICc	ω_i	LL
Control + Partnership type	14	0.00	0.67	-1879.16
Control + Partnership type + *Zhubo*	15	1.61	0.30	-1878.95

Table 8.12: Summary of the best 95% a priori models predicting number of living children for all duolocal/neolocal Mosuo male household heads, including number of parameters (K), differences in AICc relative to the minimum in the set (ΔAICc), Akaike weights (ω_i) and the log-likelihood of each model (LL). Control includes age + age^2 + no. adult sisters + no. adult brothers + age $\times$ no. brothers + age $\times$ no. sisters + years of education + income from tourism in 2012 (yes/no) + no. livestock in 2012. 'Partnership type' refers to people living neolocally with a partner (i.e. both dispersed from their natal households), in a duolocal relationship (i.e. neither dispersed), in a matrilocal or patrilocal relationship (i.e. male or female dispersal, respective), or people not in relationships (the reference category).

Models	K	ΔAICc	ω_i	LL
Control + Partnership type	14	0.00	0.73	-590.40
Control + Partnership type + *Zhubo*	15	2.12	0.25	-590.37

holds ($n = 443$) than expected ($n = 408.6$) under the null hypothesis that poor reputations do not bias labour investment ($\chi^2_1 = 135.04$, $p \ll 0.001$; Table 8.13a). Similarly, there were more observations of help given between pairs of *zhubo* households ($n = 46$) than expected ($n = 11.6$), while there were fewer observations of non-*zhubo* houses helping *zhubo* ($n = 34$) than expected ($n = 68.4$) as well as fewer *zhubo* households helping non-*zhubo* ($n = 35$) than expected ($n = 69.4$).

When both the helping and landowning households contained *zhubo*, affinal kinship accounted for 53.4% of relationships, while 12.9% of helpers were related through the matriline and 2.6% were related through the patriline (Table 8.14). 13.8% of helper relationships were siblings. Where *zhubo* households helped on non-*zhubo* farms, only 32.3% of relationships were affinal, whereas

Table 8.13: Counts of whether or not households containing *zhubo* (a) help on the farms of or (b) gave individual gifts to other households containing *zhubo* (or not).

(a)		Households receiving help on farms	
		Non-*zhubo* house	***Zhubo* house**
Households helping on other farms	**Non-*zhubo* house**	443	34
	***Zhubo* house**	35	46

(b)		Households receiving gifts	
		Non-*zhubo* house	***Zhubo* house**
Households giving gifts to others	**Non-*zhubo* house**	382	34
	***Zhubo* house**	29	41

Table 8.14: Relationship frequencies of observed help split by whether *zhubo* reside in the helping or landowning households.

Relationship	Ego *zhubo*, alter not	Alter *zhubo*, ego not	Both *zhubo*
Affine	8	9	21
Grandchildren	1	0	1
In same village	6	8	2
Maternal kin	9	10	15
Neighbour	4	2	0
Other	6	16	4
Other kin of partner	0	0	1
Others in partner's house	0	0	2
Owner	1	4	9
Parents and children	4	6	4
Paternal kin	4	1	3
Siblings	9	14	16
Partner	4	4	19
Partner of close kin	7	9	19
Partner of kin	2	0	0
Totals	**65**	**83**	**116**

41.5% of relationships were genealogical relatives. In instances where non-*zhubo* helped on *zhubo* farms, 26.5% of relationships were affinal but 37.3% of relationships were genealogical; the remainder were neighbours and others in the same village, landowners themselves, or were unclassified relationships.

8.3.5 Accusations of wrongdoing do not strongly predict less farm work or fewer gifts

The number of gifts received and number of farm help observations for each household—both measures of in-degree on social networks—were analysed using Zero-inflated Poisson (ZIP) regressions on a set of candidate models (Table 8.3; results from the 95% confidence set of models are shown in Table 8.16).

Table 8.15 shows the model-averaged parameter estimates for the best-fitting models. For ease of interpretability, below I will discuss the incidence rate ratios (IRRs) for the count (Poisson) portion of the ZIP models and odds ratios (ORs) for the zero-inflation (logistic) portion along with 95% confidence intervals (CIs). In the zero-inflation model, if OR > 1, the household has higher odds of not receiving help or gifts (i.e. in-degree is more likely to be zero).

Being a *zhubo* house was associated with small in-degrees in both models, i.e. receiving fewer instances of help on their farms (IRR = 0.886, 95% CI [0.631, 1.243]) and fewer gifts (IRR = 0.813, 95% CI [0.545, 1.213]) compared to non-*zhubo* households. Note that both parameter estimates were imprecise and the confidence intervals overlap with zero.

Households headed by Mosuo men had increased odds of receiving no help on their farms (OR = 1.642, 95% CI [1.099, 2.453]). However, the male-headed households that did receive help were predicted to receive more instances of help compared to female-headed households (IRR = 1.269, 95% CI [1.027, 1.567]). Larger households were also associated with more observations of help on their farms (IRR = 1.049, 95% CI [1.005, 1.094]). In addition, larger households were more likely to receive any help at all compared to smaller households (OR = 0.846, 95% CI [0.78, 0.917]; zero-inflation model in Table 8.15). Household size or having a male head did not predict receiving more or fewer gifts.

8.3.6 *Zhubo* households cluster together on social networks but not spatially

Zhubo houses positively assort on farm help, gift giving, and the presence of partners and children in other *zhubo* houses (Table 8.17). *Zhubo* houses are spatially dispersed throughout villages B and C ($p = 0.001$ and $p \ll 0.001$, respectively). In villages A, D and E, *zhubo* and non-*zhubo* households are randomly distributed (i.e. no spatial autocorrelation; $p = 0.326$, $p = 0.352$ and $p = 0.279$ respectively).

Table 8.15: Model-averaged parameter estimates from the best-fitting Zero-inflated Poisson (ZIP) regressions predicting in-degree (i.e. number of observations) for (i) observed farm help and (ii) gifts received by households. Each ZIP regression fits a Poisson model ('count model'), as well as a logistic model predicting whether or not a household has Pr = 0 of in-degree > 0 ('zero-inflation model').

	Farm help		Gifts	
Count model:	**B**	**S.E.**	**B**	**S.E.**
Zhubo house (ref: no)	-0.121	0.173	-0.207	0.204
Household size	0.047	0.022	0.030	0.029
Wealth rank	-0.023	0.044	0.085	0.057
Head's sex (ref: female)	0.238	0.108	0.039	0.168
Village (ref: B)				
Village C	0.202	0.192	-0.312	0.368
Village D	0.365	0.201	-0.552	0.273
Village E	0.816	0.190	0.434	0.236
(Intercept)	-0.012	0.281	-0.566	0.360
Zero-inflation model:				
Zhubo house (ref: no)	-0.116	0.234	-1.464	1.633
Household size	-0.167	0.041	-0.033	0.123
Wealth rank	-0.014	0.075	-0.339	0.213
Head's sex (ref: female)	0.496	0.205	1.024	0.716
Village (ref: B)				
Village C	-0.520	0.373	2.407	8.646
Village D	0.664	0.354	1.942	8.458
Village E	0.008	0.347	2.788	8.529
(Intercept)	1.245	0.466	-2.354	8.759

Table 8.16: 95% confidence set of models for Zero-inflated Poisson regressions on in-degree for households in the farm labour and gift networks. Columns report number of parameters (K), differences in AICc relative to the minimum in the set (ΔAICc), Akaike weights (ω_i) and the log-likelihood of each model (LL). Control model includes household size + wealth rank + sex of household head + dummy variables for each village (ref: village b).

	Model	K	Δ**AICc**	ω_i	**LL**
Farm help	Control	14	0.000	0.569	-756.880
	Control + *Zhubo*	16	0.555	0.431	-755.060
Gifts	Control + *Zhubo*	16	0.000	0.685	-677.589
	Control	14	1.553	0.315	-680.463

Table 8.17: Coefficients for assortativity on whether households contain *zhubo* for the four social networks.

Social network	Assortativity coefficient
Farm help	0.499
Gifts	0.489
Presence of partners	0.602
Presence of children	0.686
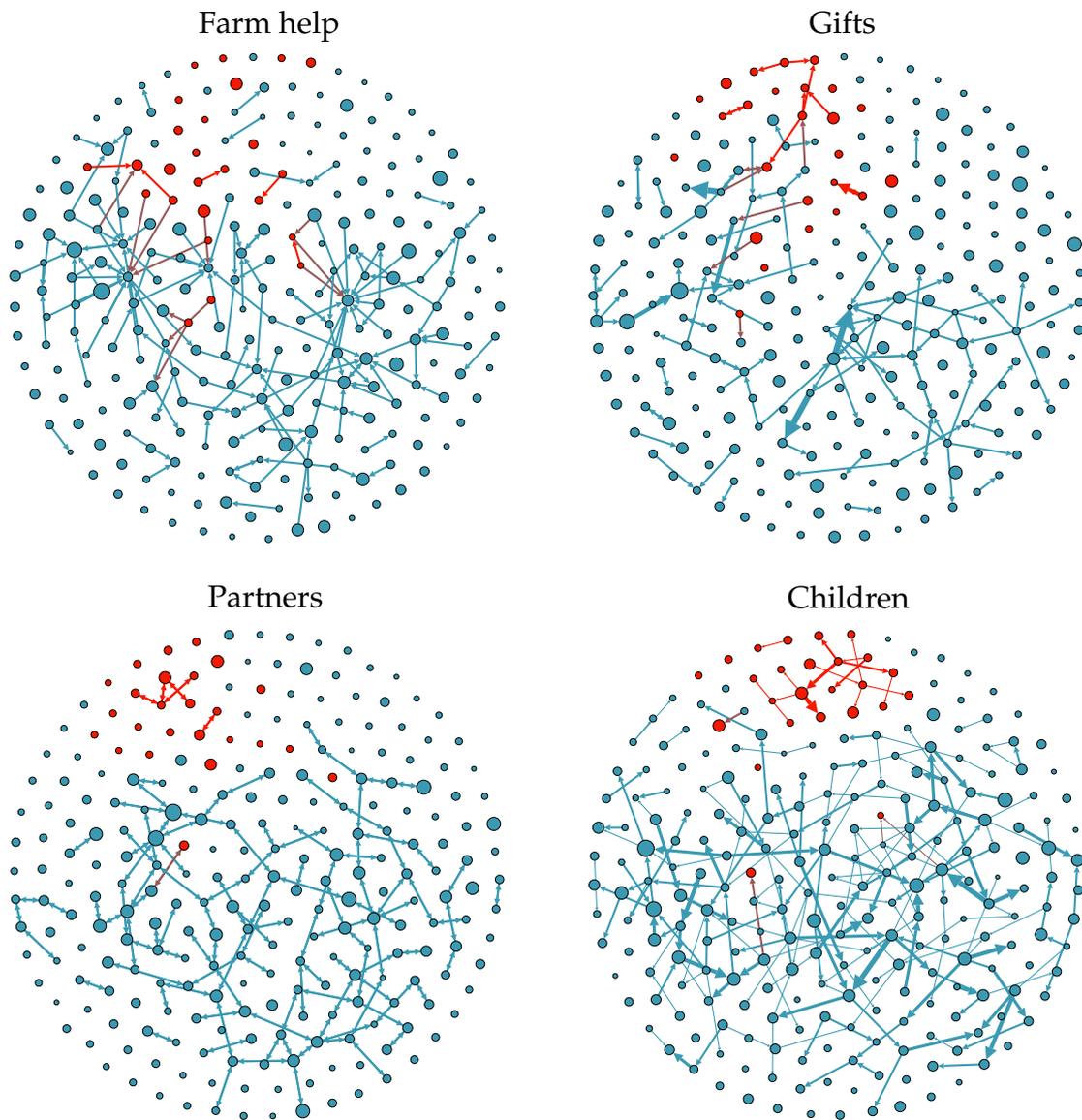
Figure 8.5: Networks of observed farm work, gifts, and partners and children living in other households for one of the study villages. Circles show households, coloured by whether it is a house accused of witchcraft (*zhubo*; red) or not (blue). Circle size represents the number of people living in the household at the time of the census. Arrows show links between household for each of the four networks. Arrow thickness in the partners and children networks indicates numbers of each living in other households. Instances of farm help depended on the amount of fieldwork conducted per village and gift-giving depended on whether households chose to participate in the games. The absence of either should not be taken as absence of cooperation.

8.4 Discussion

8.4.1 Reproductive success of people accused of wrongdoing

Female heads of households who had been accused of poisoning food (*zhubo*) suffered slightly lower fertility compared to male household heads with poor reputations, other females and males with poor reputations, and everybody else (Figure 8.4). Fertility, measured as number of living children, was not affected by poor reputations for other people living in a *zhubo* household (Figure 8.4a, c and d). Poor reputation did not decrease or increase age at first birth for Mosuo females or males compared to non-*zhubo* (Table 8.7 and Figure 8.3); one plausible explanation is that people's standing in their village fell after they had already given birth for the first time.

These results suggest that the majority of females and males living in *zhubo* households might not especially have to buttress themselves against their poor reputation compared to female household heads. *Zhubo* households were more likely to contain neolocal couples than households without a reputation for food poisoning (Table 8.6).

The analyses of reproductive success (Figure 8.4) used the best-fitting model structure reported by Ji et al. (2013) in order to control for factors known to affect reproductive success, including age, numbers of siblings, education, and measures of wealth. Reputation and partnership type (neolocal, duolocal, matrilocal, patrilocal, or un-partnered) variables appeared in all best-fitting models, and models including reputation had marginally improved fit compared to models without, as evidenced by the slight decrease in log-likelihoods (Tables 8.9 to 8.12).

The number of co-resident adult brothers had a positive effect on number of living offspring for Mosuo males, regardless of their reputational status, although more brothers had a negative effect for older generations (Figure 8.4c). The number of co-resident adult sisters was associated with higher fertility and later age at first birth for females, contrary to patterns reported by Ji et al. (2013), although the parameter estimate for fertility was imprecise and so we cannot say there is a definite trend in this case. Note that I used a different, larger sam-

ple of Mosuo people and did not account for size of farmland or the presence of female/male kin beyond siblings. In addition, I defined 'types' of partnership in a more bottom-up way as a property of couples and included neolocal, duolocal, matrilocal and patrilocal couples along with people not in relationships; Ji et al. (2013) defined residence as a property of households, analysing only duolocal and 'mixed' residence types.

People from *zhubo* households tended to be in relationships with one another rather than with people living in non-*zhubo* households. Similarly, non-*zhubo* households tended to have partners and children in other non-*zhubo* households rather than in *zhubo* households (Table 8.5a). Households containing *zhubo* assorted together in terms of farm labour, gift-giving, affinal relations and child residence (Tables 8.5, 8.13 and 8.17). There were more female heads of *zhubo* houses compared to male heads (63 female, 45 male); the pattern was reversed in other houses (310 female, 375 male). Head of household in our census refers to the person registered with the Chinese government as the head and might be a younger, more educated person compared to the person who would fulfil that role in 'traditional' domestic arrangements.

Households identified as containing food poisoners did not differ in size or composition (by age, sex or ethnic groups; Figure 8.1) compared to other households, and they were no more or less related to one another or themselves (result not shown). More *zhubo* households were ranked towards the wealthier end of the spectrum compared to the wealth distribution of other households, and proportionally fewer *zhubo* households were in the bottom wealth rank compared to other households (Figure 8.2). This form of poor reputation in Mosuo villages might thus act as a response to inequalities, in a similar manner to patterns of witchcraft accusations elsewhere (Geschiere 1997; Smith 2001).

8.4.2 Labour investment on the farms of people with poor reputations

The majority of relationships between *zhubo* helping on non-*zhubo* farms were reckoned through genetic kinship and affinal kinship (Table 8.14). The same pattern held when roles were reversed. If both households contained *zhubo*,

the majority of helper relationships were affinal rather than genetic.

A greater proportion of non-*zhubo* households did not receive any help on their farms compared to *zhubo* households, although this pattern might simply be due to the random sampling of farms via spot observations. Houses containing *zhubo* preferred to help other *zhubo* over and above non-*zhubo* (Table 8.13). People believed to poison food can nevertheless obtain food from households on whose farms they work; the only taboo is against eating in *zhubo* households, although I can only speculate whether *zhubo* observe the taboo themselves when in the houses of other people accused of poisoning food.

I fitted a Zero-inflated Poisson model to estimate the factors predicting two measures of in-degree: instances of observed farm work and number of gifts received (Table 8.15). *Zhubo* households received slightly less help on their farms and slightly fewer gifts, although the parameter estimates were uncertain. Larger households received more instances of help on their farms. Households headed by Mosuo men were less likely to receive help on their farms, although those that did were observed to have more instances of help compared to female-headed households (Table 8.15).

Despite a taboo against eating where *zhubo* live, some *zhubo* households received help from non-*zhubo* (Table 8.13a; farm work is rewarded with food prepared by the household receiving help). Only two of these non-*zhubo* households had partners living in three of the *zhubo* houses. All three of these partners were females who resided with the children of the non-*zhubo*. Thus, affinal links alone cannot explain the observed cooperation between *zhubo* and non-*zhubo* households.

Households containing *zhubo* tended to cluster together (Figure 8.5), although they were not geographically isolated or marginalised within their villages. Coefficients of assortativity in the networks of farm help and gift-giving were 0.499 and 0.489 respectively, suggesting that non-*zhubo* households tended to work on each other's farms and give each other gifts rather than work for or give gifts to *zhubo* houses; similarly, *zhubo* households assorted together rather than with non-*zhubo* houses. Similarly, *zhubo* households strongly assorted in terms of partners and children living in one another's households

(Table 8.5 and Table 8.17). These high assortativity coefficients may not only reflect social norms and reputations but also serve to reinforce them within the communities (Apicella et al. 2012).

The analyses presented in this chapter suggest that people with poor reputations clustered together to help one another and, although the majority of *zhubo* households were isolated in the sense that they did not receive help from non-*zhubo*, help was not completely withdrawn from houses with bad reputations. In addition, instances of help were not entirely due to affinal links or parenthood. *Zhubo-zhubo* couples were more likely to live neolocally (i.e. both partners dispersed from their natal homes; Table 8.6). Perhaps due to these clustering and residence strategies, the majority of people with poor reputations did not suffer lower fertility or delayed age at first birth compared to others (Figure 8.3, Figure 8.4 and Table 8.7).

8.4.3 Limitations and future directions

Much remains unknown about this Mosuo reputation system. We currently have no ethnographic insights into why certain people come to be accused of poisoning food, if the reputation is heritable or gendered (although our results suggest no gender bias; Table 8.4), or how rumours and accusations spread. In the latter case, it would be interesting to find out whether the fields are as much a place for cultivating gossip as they are for crops (Gilmore 1978).

This chapter also suffers from a handful of limitations. We only know whether households contain *zhubo* or whether heads of households are *zhubo*, but not whether particular individuals are considered *zhubo* (although our current ethnographic understanding is that everybody living in a household headed by a *zhubo* might also be considered a *zhubo*, or at least affected by the reputation of their household's head). The analyses of reproductive success presented here suggest that poor reputations bring no long-term detrimental effects on fitness for most people; however, female heads of *zhubo* households suffered lower reproductive success compared to other household heads. Given our data, we cannot currently gain a sense of the dynamics of reputational accusations or their short-term or long-term effects (e.g. freshly accused

people might immediately lose out on farm labour while 'established' *zhubo* might have a chance to build up directly reciprocal relationships over time).

Although there was a bias against *zhubo* helping on non-*zhubo* farms, where this did occur, the non-*zhubo* households reciprocated approximately one quarter of the 35 instances of help. These reciprocated instances of help might also represent cases where *zhubo* are withholding help from non-*zhubo* in order to ally with other accused people. On the other hand, some people with poor reputations might strategically cooperate with others as an attempt to shift their reputation or compensate for it, or to start directly reciprocal relationships. This chimes with laboratory evidence that ostracised individuals cooperate once they are allowed back into the social arena (Feinberg et al. 2014). Laboratory studies have also shown that when potential social partners have poor reputations, individuals will decide to help based on their past personal experiences with the recipient (Molleman et al. 2013).

Thus, future studies of reputation and cooperation in the field should take into account the effects of direct as well as indirect reciprocity. Similarly, I only looked at indirect punishment (withholding help), whereas direct punishment of defectors might also be important (Raihani et al. 2012), even in small-scale societies (Mathew & Boyd 2011). Future work should investigate whether there is any costly punishment towards people with poor reputations and whether this has detrimental effects on their reproductive success, e.g. through increased risk of death.

One major drawback to studying indirect, costless punishment such as withholding labour in real-world systems is that one cannot easily gather evidence of a deliberate absence of cooperation. Alongside a deeper ethnographic study, future work could also attempt experiments such as trust games (as employed by, e.g. Cronk 2007) framed around the local reputation system in order to gain an understanding of whether or not (or to what extent) reputational aspersions function as a form of punishment in Mosuo society.

This chapter looked at observations of cooperative behaviour on farms. The data covered randomly sampled farms over two planting seasons and one harvest. While this sampling strategy only allowed direct comparison of *zhubo*

and non-*zhubo* households in a quasi-experimental fashion, it does give greater confidence that the results presented here are unbiased. Future studies might also account for ecological factors such as the productivity of *zhubo* farms compared to others. Depending on such factors, indirect punishment such as withholding labour might not necessarily have negative long-term effects.

8.5 Conclusion

This is the first evolutionary study to quantify the effects of a poor reputation based around supernatural beliefs on social behaviour and reproductive success, to the best of my knowledge. In this chapter, I have sought a functional explanation for how witchcraft accusations affect cooperation among Mosuo farmers. I predicted that those accused of poisoning food (known as *zhubo*) might be indirectly punished through the withholding of labour investment on their farms during planting and harvesting seasons. The analyses presented here suggest that *zhubo* are isolated to an extent, although any boundaries between *zhubo* and others are permeable.

The high number of *zhubo* households in the sample (13.7% of all households) suggests that accusations are not a rare event and many people might face accusations at some point during their lives. *Zhubo* clustered together, especially as regards labour investment. Female *zhubo* who were heads of households experienced slightly lower reproductive success compared to other female heads of households. Poor reputations did not affect the fitness of male household heads, or females or males more generally. Thus, people with poor reputations may have developed mechanisms in order to become resilient to potential damaging effects.

As discussed in Part I, reputational concerns can be important mediators of cooperation through indirect reciprocity. Ohtsuki & Iwasa (2006) argue that indirect reciprocity can maintain cooperation if individuals are, among other attributes, apologetic and forgiving. On the other hand, reputational aspersions can allow gossip to become weaponised. Future ethnographic work might investigate how people in this area accuse and respond to being accused over a longer time period.

Mosuo lifestyle is changing and, as in other places in the world (e.g. Bleek 1976), the prevalence of reputation systems based on the supernatural might decline with increased tourism or emigration (e.g. people moving to cities for work or intermarriage with other groups who do not believe in witchcraft). However, reputation systems such as witchcraft can also be understood as a re-actions to inequalities borne of encroaching modernity, especially alongside the emergence or enforcement of economic reforms (Comaroff & Comaroff 1999; Geschiere 1997); such institutions may not die out so readily.

Part III

Conclusion

Chapter 9

Conclusion

This thesis furthers our empirical understanding of how the evolutionary forces of kin selection (Hamilton 1964), reciprocal altruism (Trivers 1971) and indirect reciprocity (Nowak & Sigmund 1998) interact to influence patterns of cooperation. In doing so, I have explored the flexible cooperative strategies employed by two populations broadly following their traditional ways of life: Saami reindeer herders in Norway and Mosuo farmers in China.

While the two populations studied in this thesis are very different in terms of their ecology and environment, their modes of subsistence, social systems, mobility (or lack thereof), land tenure, histories, etc., they also share much in common (beyond the fact that both countries border Russia). They are both marginalised ethnic minorities; both, in part, cater to an ethno-tourism trade as a means of supplementing their traditional forms of subsistence and income which, for the Mosuo at least, is changing their social system (Mattison 2010); and both populations face the collective action problem of adapting their ways of life to changing political and environmental circumstances.

This concluding chapter will first summarise the main findings from the research presented in preceding chapters. I will then offer suggestions for how researchers can better study cooperation in human societies and close by considering my work's implications for social evolution research.

9.1 Overview of findings

Part I conducted the first quantitative, experimental study of cooperation among Saami reindeer herders living in northernmost Norway. In Chapter 4,

I compared the relative importance of kinship and membership of herding groups ('siidas') in explaining the social relationships revealed through gift-giving. Belonging to the same siida was the stronger predictor of gift-giving; relatedness had a positive but weaker effect. This result is likely to reflect the importance of herding groups in daily subsistence for Saami pastoralists. There is increasing quantitative evidence for the pivotal role played by reciprocal exchange in human cooperation, especially as regards the sharing of food, even when food is shared with kin (Allen-Arave et al. 2008; Jaeggi & Gurven 2013; Kasper & Borgerhoff Mulder 2015). My work reflects and extends these findings by marshalling evidence from new field experiments to show the importance of this interplay in other forms of cooperative network.

Participants gave nearly one third of gifts to non-kin who were members of other siidas. Most of these gifts were for people who were considered good herders, suggesting reputational factors were also at play. In addition, participants gave gifts to newly established herders. It is possible that some of these patterns can be explained through affinal ties (which I did not measure). Speculatively, participants may also have wanted to forge future reciprocal relationships or be giving gifts due to normative obligations towards younger, inexperienced herders. Future investigations into the cooperative dynamics within and between herding groups should therefore try to tease apart the roles of reputation, fictive kinship and social duties, alongside the reciprocity and kin selection explanations studied in this thesis.

In Chapter 5, I showed how cooperativeness towards siidas was contingent on group size, which may affect the perceived marginal returns of donating to a public goods game (PGG). Smaller groups were more cooperative in that they contributed more to the public good. This result is consistent with theoretical expectations, since people in smaller groups could expect a higher return rate for every unit (in this case, every litre of petrol) they contributed to the PGG (Ledyard 1995). I described this as 'perceived' returns because although information about contributions and group composition was private (i.e. the PGGs were anonymous), participants knew they would be playing with fellow siida members and thus knew and had experience of working with

the pool of potential players. It is possible that herders were not thinking about marginal returns and instead contributed because of other factors related to their previous experiences with fellow siida members. Since I was interested in meaningful social groups, it would have been difficult to experimentally control expected returns. Future work could, however, attempt to quantify cooperative behaviour through observing contributions to a real public good such as time and effort spent on fence repairs or winter herding activities.

Relatedness to the siida was not associated with PGG contributions, contrary to predictions that higher relatedness would favour cooperation. The sample size for these analyses was small ($n = 30$) and so may not have had the statistical power to detect an effect of relatedness. Unfortunately, the bulk of field experiments using PGGs either do not measure relatedness or simply control for it. However, I conducted a reanalysis of Waring & Bell's (2013) study of public goods provisioning within and across castes in India, and found that people who were more related to others in their group also contributed more to the PGG (Figure 2.1). The role of relatedness in social dilemmas remains a topic for further exploration.

The second part of this thesis looked at the cooperative networks of Mosuo farmers in southwest China. In Chapter 7, I investigated the factors predicting a real-world measure of cooperation: helping on another household's farm during planting or harvesting seasons. A household was more likely to receive help on its farm from people living in the homes of residents' reproductive partners. This result provides quantitative evidence backing up previous ethnographic observations that affinal networks are important for cooperation between households in Mosuo villages (Shih 2009). Households were also more likely to help on farms associated with households that contained children belonging to any residents of the former household. However, help became less likely if the children lived with other people who were related to the helping household. (Children, in this case, referred to offspring of any age, not just people who were under a certain age.) These patterns suggest that labour investment on farms might double as parental investment in children who live with fewer relatives.

Households were more likely to help nearby neighbours as well as households containing closer relatives. Neighbours also tend to be kin, especially in small-scale societies, which may underestimate the effect of relatedness when looking at the effect of distance on cooperation (Ziker & Schnegg 2005). I accounted for this by including an interaction term between relatedness and distance; the estimate suggested that people were willing to travel further to help relatives. Overall, there was moderate reciprocity in observed farm help. Reciprocity varied considerably between villages, which may have been due to the random sampling of a subset of households. Anthropological studies conducted elsewhere have similarly highlighted the importance of spatial proximity, relatedness and affinal ties for cooperation in the form of sharing food (Koster & Leckie 2014; Koster et al. 2015; Ziker & Schnegg 2005).

Analyses of a gift game played with Mosuo participants showed that gifts were reciprocated more often than farm labour. This suggests that the games picked up on social relationships based around reciprocity, whereas helping on farms—especially farms associated with partners and children—was a form of cooperation not contingent on reciprocal exchange. The presence of children in another household was more strongly correlated with gift-giving compared to the presence of reproductive partners. Gifts given between households were not associated with observations of farm labour, suggesting that the two measured different kinds of cooperation (see section 9.2.1 for further discussion of this issue).

Chapter 8 investigated how withholding labour from other households' farms might function as a form of indirect, costless punishment, a key assumption of indirect reciprocity models of cooperation (Balafoutas et al. 2014; Ohtsuki et al. 2009). I used a measure of poor standing in the community—for Mosuo people, being thought of as somebody who poisons food—to show weak detrimental effects on fertility for female heads of households, but not for males. These people with bad reputations, known locally as *zhubo*, were more likely to intermarry and have children together, as well as work on each other's farms and give gifts to one another, suggesting a certain resilience to potential ostracism. Their households were not spatially clustered within vil-

lages, nor were they banished to the margins.

Zhubo households received less help on their farms and fewer gifts, although these effects were statistically weak and uncertain. Non-*zhubo* households did not completely withhold help, however. Overall, *zhubo* households tended to be wealthier – a pattern with striking similarities to societies where accusations of witchcraft act as a response to wealth inequalities and target the relatively well-off (Geschiere 1997; Smith 2001). The relative wealth of households was not associated with observations of farm help, suggesting that in this case wealth was not confounding the effect of poor reputation.

9.2 Furthering the study of cooperation in the real world

In this section, I consider issues arising from the work presented in this thesis and suggest future avenues for studying cooperation in the field.

9.2.1 Are economic games fit for purpose in the field?

Chapter 5 found no associations between contributions to a public goods game and the outcomes of real-world collective actions (measures of herd productivity), while Chapter 7 found weak links between gift-giving and costly cooperative behaviour (labour investment on other households' farms). Similarly, evidence is mounting that lab-in-the-field experiments may not correspond to real-world cooperative behaviours (Bouma et al. 2014; Gurven & Winking 2008; Hill & Gurven 2004; Voors et al. 2012a).

Despite the poor predictive power of gift-giving on cooperation, gift game behaviour was selected as a predictor in the best-fitting models (Chapter 7). Thus, field-based games may have explanatory power, even if they do not directly map onto the cooperative behaviours or outcomes of interest. While the games presented in Part I used a relatively meagre stake in terms of purchasing power in Norway, the Mosuo participants in Part II were able to win a substantial portion of their daily wages. This suggests that endowment size or potential winnings are not necessarily driving the lack of relationship to real-world cooperative behaviours observed here, although the effect of endowment size

might differ from population to population (Raihani et al. 2013).

It is perhaps an inalienable fact of economic games that behaviour will be guided by existing preferences and beliefs (Cárdenas & Ostrom 2004; Henrich et al. 2005). Even when researchers employ devices such as anonymity to control for factors such as reputations, they still interpret the variance in their results in terms of these cultural systems (Smith 2005).

Levitt and List (2007) identified five factors that influence decision-making (other than calculations about payoffs), the first three of which are socio-cultural: (i) moral and ethical systems; (ii) the ability to observe and appraise a player's actions; (iii) the context of a decision; (iv) the subject pool; and (v) the stakes of a decision. Self-interested decisions can be shaped and constrained by culturally influenced factors such as reputations and expectations (Chibnik 2005; Gilmore 1978). In the real world, it is not only the outcomes of decisions that matter but the process by which decisions are made (Levitt & List 2007). As we are inherently and inextricably social, cultured creatures, I argue that experimenters should place less weight on factors such as anonymity when analysing decision-making. In the words of Cronk and Leech (2013: 43), "Humans did not evolve in a world of one-shot anonymous interactions and laboratory experiments."

Researchers should not assume that all cooperation is equal. Not all community or communal activities have the same purpose and may not elicit the same behaviours. In some situations, people might experience motivations or incentives to collaborate, while in other contexts people might prefer to invest more selfishly (Bouma et al. 2014). Different social institutions have different purposes: some might be dedicated to managing, sharing or pooling risk (Aktipis et al. 2011); some will focus on monitoring and governance (Rustagi et al. 2010); and others will tackle neighbourhood security, social services, or developing or maintaining infrastructure (Muller & Vothknecht 2012). Thus, we must also bear in mind the purpose of cooperative behaviours in terms of the social institutions—formal or informal—in which cooperation takes place.

One pattern commonly observed in laboratory-based public goods games (PGGs) played over repeated rounds is that contributions decline over time

in the absence of reinforcement mechanisms such as punishment or sanctioning (Chaudhuri 2010). Researchers have explained this pattern as evidence of pro-sociality (Camerer 2013) or mistakes (Burton-Chellew & West 2013; Burton-Chellew et al. 2015). Another alternative hypothesis—one that to the best of my knowledge is yet to be explored—is that games involving a single public good miss the delayed and diversified nature of human cooperation. That is, real-world cooperative groups may not 'play' repeatedly for the same public good but rather work together to provision many kinds of public good. To take a feasible example from Saami pastoralism, some siida members might spend a few days making bales of dried hay to feed their herds but sit out when it comes to repairing fences around their pastures, although everybody will band together when shepherding reindeer to the corral for earmarking.

Role diversification might mean that individuals play many overlapping games simultaneously, dealing with delayed reciprocity across many domains and with many currencies. Thus, researchers could try to design an iterated PGG in which participants assort into or are assigned into groups with public or private information (these could form part of the experimental treatment or be held constant, depending on the research question) whose composition remains stable over repeated rounds but where the common project changes over time. While the logistics of such an experiment would no doubt be difficult, an ethnographer combining quantitative and qualitative methods might be uniquely placed to attempt this, given enough time and experience to map out the games people play in their everyday lives.

To properly test evolutionary hypotheses regarding cooperation, we must seek disconfirming evidence rather than just analyse correlations. I argue that this should entail randomised controlled experiments tailored more precisely to particular contexts in which participants play for meaningful stakes beyond money. For example, a study in Liberia conducted a randomised public goods experiment—in collaboration with a non-governmental organisation—in which participants in the treatment condition directly contributed to a community-driven reconstruction programme (Fearon et al. 2009). We might expect more meaningful insights into social behaviour where experiments have

meaningful outcomes. Anthropologists might not want to run 'true' randomised controlled trials (RCTs) in the field if we are interested in non-random groups; we might therefore look into the possibility of randomly assigning groups (that are themselves not randomly formed) into treatment or control conditions.

This style of experimentation—not quite a 'true' experiment but more rigorous than a quasi-experiment (Bernard 2006)—might sacrifice ease of cross-cultural comparability for a more localised game structure. However, an ethnographically informed, RCT-esque approach would not only introduce quantifiable measures of risk and cost (and thus provide a more refined measure of cooperation) and strongly link individual decision-making to social institutions, but might also have applied value in terms of informing future policy and developmental interventions.

On the surface, the idea of toying with a community's future welfare might seem fraught with ethical quandaries; however, in a world where evidence-based policy—in essence, applying randomised controlled trials to the domain of social science—is gaining traction and might become the norm, evolutionary anthropologists are in a prime position to provide a more nuanced and theory-driven understanding of human decision-making.

9.2.2 The role of relatedness in kin selection

As I discussed in section 1.4.1.1, the concept of relatedness in Hamilton's rule (which states that a social behaviour evolves when the coefficient of relatedness $\times$ indirect fitness benefit $>$ direct fitness cost; Hamilton 1964) has been generalised beyond shared ancestry (pedigree or genealogical relatedness) to include all forms of assortment on genotype (Fletcher & Zwick 2006). This theoretical advance has redefined relatedness as a statistical concept capturing the idea that two individuals might be less or more related to one another than either is to its local group (Krupp & Taylor 2015) and is not contingent on shared ancestry. However, there appears to be something 'special' about relatedness through shared ancestry compared to sharing alleles at particular loci for other reasons because genealogical relatives are equally related across

the whole genome (more or less), allowing adaptations fuelled by multiple interacting genes to evolve (West & Gardner 2013). In addition, humans recognise extensive networks of non-relatives who are considered family, including affinal ties (see section 1.4.1.2), as well as people who become 'cultural kin' through social learning mechanisms (Allison 1992), which might also change the calculus of cooperative decisions.

Given the increasing availability and affordability of sequencing equipment, coupled with the relative ease of collecting DNA samples—not to mention the profusion of free online bioinformatics courses—evolutionary anthropologists are in a good position (bar ethical clearance and participants' informed consent) to empirically test for differences in the explanatory power of genealogical relatives, genetic relatives without shared ancestry, and cultural relatives including fictive kin in predicting cooperative behaviour and reproductive success.

9.2.3 Other routes to cooperation

Evolutionary approaches to understanding how natural selection can influence cooperative behaviours are not limited to kin selection, reciprocal altruism and indirect reciprocity – the theoretical cornerstones of this thesis. In this section I will briefly discuss how coordination, partner choice, signalling and biological markets can also lead to cooperation and how these ideas might inform future research.

Cronk and Leech (2013) argue that studies of cooperation should investigate coordination problems alongside the traditional fare of social evolution research: dilemmas of conflicting interests. One method of achieving coordination is through sharing knowledge and meta-knowledge (but see Binmore 2008), and researchers are beginning to explore how traditional knowledge about resources and norms interact with observed behaviours (Ziker et al. 2015). In the Saami case, herders share knowledge about herd movements, husbandry decisions, weather patterns, earmarks etc. and it would be enlightening to understand the ways in which such knowledge is shared or withheld from others, and how this cultural transmission affects cooperative behaviour

and outcomes. Similarly, as discussed in section 8.4, future work investigating reputation systems should take a longitudinal and ethnographic approach to understand how gossipy accusations might be weaponised as a form of punishment, potentially leading to detrimental effects on reproductive success for the victims of accusations.

The freedom and ability to choose partners has been posited as a major component of cooperation (Barclay 2013). Partner choice is sometimes contrasted with partner control, the latter referring to the management of existing partners to prevent cheating (Baumard et al. 2013). Both choice and control are associated with reciprocal cooperation; partners must be chosen in order for reciprocity to get underway, while control can occur in the sense that individuals might sanction uncooperative partners by withholding future investments or punish defectors at a cost to themselves (Raihani et al. 2012).

Individuals may be chosen based on more than their capacity or willingness to reciprocate cooperative behaviours. Individuals can promote themselves as desirable partners (in all senses of the word) by signalling intent to cooperate (Barclay & Willer 2007). Signals, here, mean behaviours or physiological traits that alter the behaviour of others who respond to the signal (Davies et al. 2012). Honest and/or costly signals allow discrimination between individuals' qualities, and a cooperative temperament might signal facts about status, skill, prestige, resource-holding potential, or reproductive value. These characteristics can be thought of as giving individuals some value as potential partners, where value can vary over the lifetime as well as over ecological and evolutionary time (Barclay 2013), not to mention from culture to culture. Potential cooperative partners can also distinguish themselves by building good reputations through high contributions or sacrificing potential earnings in order to increase their probability of being chosen (Barclay & Willer 2007; Stiff & Van Vugt 2008).

One such form of signalling would be public, prodigal and prodigious generosity, perhaps in the form of hosting feasts or donating to charity. In such cases, people might be seen as competing for enhanced social status or reproductive partners (Bliege Bird & Smith 2005; Raihani & Smith 2015). This form of

competition could potentially lead to coordinated cultural standards by which to judge signalled quality in order to compare and contrast competitors (Bliege Bird & Smith 2005). When it comes to choosing partners, an individual's cooperativeness relative to others can lead to a form of 'price war' in cooperation (Schino & Aureli 2010).

Signals need not just be a strategy of individuals. According to Bliege Bird and Smith (2005), signals such as funerary feasts might present a social dilemma in that the feast's scale and extravagance (the 'intensity' of the signal) will be maximised if all group members provision this common or club good, although individuals may face temptations to defect if the feast will be provided regardless of their contributions. Theoretical work has shown that costly signalling through provisioning a public good can be evolutionarily stable even in the absence of assortment (Gintis et al. 2001). It would be interesting for future evolutionary studies of cooperation to investigate the interplay between individualistic and group-focussed signals, especially for scenarios in which coordinated signalling might create social dilemmas. One potential method would be through designing a field-based public goods game where the common project takes the form of a ritual rather than a pot of money.

Partner choice and signalling can lead to social behaviour being understood as taking place within a biological market (Noë & Hammerstein 1994). Markets arise when individuals voluntarily exchange goods yet differ in their preferences and in their state (factors that vary between individuals, such as wealth, genetic quality, or resource-holding potential). Goods may be exchanged in kind (e.g. reciprocal grooming in primates) or not (e.g. aphids exchanging honeydew with ants in return for protection) (Werner et al. 2014).

More than being just a metaphor, the paradigm of biological markets centres on trade-like behaviours in which partner choice plays a central role. This is a burgeoning area of research which is gaining support from animals, plants and microbes engaging in all manner of inter- and intra-specific market interactions (Barclay 2013; Noë & Hammerstein 1994; Werner et al. 2014)[1]. To date,

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[1]Ronald Noë, one of the architects of biological market theory, maintains a collection of papers related to the topic: http://www.scoop.it/t/biological-markets

empirical research using a biological market perspective to investigate human behaviour has mostly focussed on mating (e.g. Schacht & Borgerhoff Mulder 2015), although there is experimental evidence that partner choice and the availability of better options elsewhere ('outside options') play a role in establishing fairness norms (Debove et al. 2015).

To the best of my knowledge there is currently no evolutionary anthropology research quantifying the role of partner choice and market forces in real-world cooperative systems. Future studies adopting biological market theory might investigate cooperation from this angle, looking into the extent partner choice is adaptive and/or constrained in different societies. For example, partner choice may be more limited for sedentary populations such as farmers compared to hunter-gatherer societies in which mobility might spur cooperation (Aktipis 2011; Lewis et al. 2014). One approach would be to employ biological market theory in interpreting systems of marital transfers (bridewealth, dowry and *mahr*, or indirect dowry; Goody & Tambiah 1973) in terms of families choosing partners for younger generations, perhaps partly as a kind of 'lineage partner choice' that forges affinal bonds with desirable families.

9.3 Concluding remarks

Studying cooperation in the field is fraught with challenges. Abstracted field experiments have proven useful but researchers must move beyond simply transplanting experimental economic games into the field. Our cooperative tendencies and behaviours are flexible, responding to social, historical and ecological factors. Evolutionary anthropologists should consider a more holistic approach to studying real-world cooperation. Humans are cultured and agentive. We make decisions based on our motivations, beliefs, preferences, emotional states, cultural and familial upbringing, received and adapted norms, morals, etc., all of which have been shaped by evolutionary forces. Understanding the interacting (and perhaps conflicting) nature of these factors requires an explicitly multilevel and flexible approach. Being methodologically promiscuous and mindful of local ethnographic contexts could prove the most effective way for anthropologists to gain insights into the collective action prob-

lems humanity may have to solve now and in the future.

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Appendix A

A dynamic framework for the study of optimal birth intervals reveals the importance of sibling competition and mortality risks

Appendix B

Survey and game scripts

This appendix contains the English-language originals of the information sheet, survey and game scripts used to collect the data in Part I.

Information Sheet for License Owners

Title of Project: The Dynamics of Cooperation among Saami Reindeer Herders in Finnmark, Norway

This study has been approved by the UCL Research Ethics Committee (Project ID Number): 4536/001

Names of Researchers: Matthew Thomas, Marius Warg Næss, Bård-Jørgen Bårdsen, Ruth Mace

Contact details:

Details of Study:

We are studying how reindeer herders in your siida work together and work with herders in other siidas. We want to look at how people herding together in summer and winter pastures cooperate and find out under what circumstances herders might leave or join siidas.

We have selected the license owners in your district, including you. If you agree to take part, we would like to ask a few questions about your summer and winter siidas, your family and you. To thank you for taking part, we would like to offer you money for 10 litres of gasoline.

After the questions, we will play a game where you can potentially win a further 15 litres of gasoline. The amount you win will depend on how others play the game, but you will not lose any money by taking part in this study.

It will only take about 45 minutes of your time to play the game and answer our questions.

Everything you tell us is private and we will not share any personal data except with the named researchers from London. When the project is finished and results are reported, no individual will be identified in any way. You may not get any direct personal gain from this research and you will not suffer any cost if you do not take part.

We are doing this research to understand how you live and work with other people at different times of the year. We are interested in why you work with the people you do, and what reasons people might have for joining or leaving siidas.

Please discuss the information above with others if you wish or ask us if there is anything that is not clear or if you would like more information.

It is up to you to decide whether to take part or not; choosing not to take part will not disadvantage you in any way. If you do decide to take part you are still free to withdraw at any time and without giving a reason.

All data will be collected and stored in accordance with the UK Data Protection Act 1998.

My name is Matthew Thomas and I'm a researcher at University College London in the UK. Because I don't speak Norwegian so well, I've asked *[name]* to be my translator. Jeg vil gjerne snakke med deg om [reindeer husbandry and the siida system].

Introduction

We would like to talk about how and why Saami herders work in siidas, how they help each other out and why people leave or join siidas. We will play three games and do a quick questionnaire. The games and the questions will take about 45 minutes of your time.

We will give you money for 10 litres of gasoline just for taking part in the study. We will also play three games where you can win some more money for gasoline. You will not lose any money by taking part in this study.

We know that Saami herders have experienced trouble in the past from people abusing their written statements. Everything you tell us today will be confidential and we will not write down your name or anything else that can identify you.

[ACTION: Hand over information sheet]

This sheet explains what the study is about and tells you how to contact us if you have any questions or want to talk about anything we discuss today.

You are free to stop us at any time and clarify questions. You don't have to answer a question if you don't want to – we can just move on to the next one.

Before we start, we need you to sign the front of the questionnaire…

If you don't have any questions, we will start.

Games 1 & 2

To begin with, we would like to play two of the three games. By playing you can win some money for gasoline.

We will give you some vouchers for gasoline. In the first game, you will decide how much gasoline to share with your district. In the second game, you will decide show much gasoline to share with your summer siida.

Today, you will decide how much gasoline to share with these two groups. Once we have played the game with other people in your siida and your district -- and they have made their decisions -- Matthew will calculate how much each person gets and give them the money they won.

The total amount you win will depend on the amount of gasoline you give to your district and to your siida, as well as how much other people give. Matthew will add up all the contributions, increase them by 50% and split the increased amount equally among all the herders who play these games.

In total, you could earn money for up to 15 more litres of gasoline on top of the 10 litres we're giving you for participating. We will pay you in cash in one month's time – after everybody has made their decisions. I will deliver the cash to your postal address.

No one in either of the groups will know exactly who they are playing with. All you know is that the first group is made of six people – including you – randomly chosen from your district and the

second group is made of up to six people – including you – randomly chosen from your summer siida.

[ACTION: Show vouchers]

I will give you vouchers for five litres of gasoline, in one litre units, before each of these two games. You will decide how much of the five litres to share – first with your district and second with your summer siida. Everyone will receive the same amount of gasoline money and will have to make the same decision.

[ACTION: Show diagram of game to participant]

You can choose to give nothing to the group, or you can give 1, 2, 3, 4 or all 5 litres. The amount that you do not share with the group will be yours to keep, once everyone in the group has made their decisions.

The money for the gasoline that you will receive does not belong to me. It has been given to me by my university to conduct this research project. It does not matter to the university whether this money is spent or not.

You will make your decision independently from everyone else and no one else will know how much you gave to the group. No-one will know how much of the total anybody contributed. Only the researchers from London will know how much you shared with your district and with your siida.

Now I will ask you some questions to check whether you have understood the rules of the game.

1. How much gasoline does each player have to play with at the beginning of each game?
2. What decision must each player make about these 5 litres?
3. What are the two groups you can share gasoline with?
4. On top of the money for 10 litres of gasoline we will give you for participating, what will your total earnings consist of?

[ACTION: If participant answers all questions correctly, continue.
Otherwise, move on to questionnaire]

[ACTION: Give participant first set of vouchers and envelopes]

Here are vouchers for 5 litres of gasoline. You now have to decide how much of these 5 litres of gasoline you want to give to your district and how much you want to keep for yourself. Please put the amount you want to share with your district into <u>this</u> envelope and put the amount you want to keep in <u>this</u> envelope.

[ACTION: Player makes decision]

Thank you. Why did you choose to donate that amount of gasoline to your district?

[ACTION: Write down reason]

[ACTION: Give participant second set of vouchers and envelopes]

Here are vouchers for five more litres of gasoline. In this second part of the game, you now have to decide how much of these 5 litres of gasoline you want to give to your summer siida and how much you want to keep for yourself. Please put the amount you want to share with your summer siida into <u>this</u> envelope and put the amount you want to keep in <u>this</u> envelope.

[ACTION: Player makes decision]

Thank you. Why did you choose to donate that amount of gasoline to your summer siida?

[ACTION: Write down reason)

Game 3

Now for the final game.

[ACTION: give participant three 5-litre vouchers]

Here are 3 vouchers, each for 5 litres of gasoline. I would like you to choose one, two or three people from this list of other license owners in your district *[ACTION: show list]* to give these to, as gifts. You may not keep any of this gasoline for yourself.

The person or people you choose will not know that the gift came from you. You may choose to give all 3 tokens to just one person, give 2 to one person and 1 to another, or 1 token to three different people.

Please read out the ID numbers for 1, 2 or 3 people from this list who you would like to give a gift to and how much you would like to give them. Only the researchers from London will know who you give gifts to.

[ACTION: Write down herder ID numbers and amounts given to each]

Thank you. Why did you make that decision?

[ACTION: Write down reason]

That's the end of the game. Please do not discuss the game with other people who haven't yet played. We would now like to ask a few simple questions about working in siidas.

[ACTION: Go to questionnaire]

Living and Working in Siidas ⛫ UCL

Official Title of Project:

The Dynamics of Cooperation among Saami Reindeer Herders in Finnmark, Norway

This study has been approved by the UCL Research Ethics Committee (Project ID Number): 4536/001

We would like to ask about how and why Saami herders work in siidas, how they help each other out and why people leave or join siidas. The answers you give will form part of Matthew Thomas's PhD project and may be used in future scientific publications.

It is up to you to decide whether to take part or not; choosing not to take part will not disadvantage you in any way. If you do decide to take part, you are still free to withdraw at any time and without giving a reason.

By continuing, you are giving us your consent that the information you provide will only be used for the purposes of this project and not transferred to an organisation outside of UCL. The information will be treated as strictly confidential and handled in accordance with the provisions of the UK Data Protection Act 1998.

Signature: _____

Interviewer's signature: _____

Date: _____

Interview Coding

Location of interview (person's home etc.): _____

Town: _____

Game 1

Reason for size of donation:

Game 2

Reason for size of donation:

Game 3

Recipient 1 *(enter ID number)*: _____ Amount given: _____

Recipient 2 *(enter ID number)*: _____ Amount given: _____

Recipient 3 *(enter ID number)*: _____ Amount given: _____

Reason for decisions:

About you

We'd like to begin with a couple of simple questions about you.

1. What town were you born in? _____

2. What year were you born? _____

Working in a siida

We would now like to ask about how you schedule and share work in your siida.

3. Over the last year, how often did you take part in _____ in your own siida? Please choose one option from this card **[Show card 1]**

	Activity	Never						Every day	DK	NA
		1	2	3	4	5	6	7		
A	Herding activities									
B	Finding lost/wandering reindeer									
C	Taking animals to slaughterhouse									
D	Repairing vehicles									
E	Repairing fences/corrals/cabins									
F	Other (specify)									

4. Over the last year, how often did you do _____ for a siida you don't belong to? Please choose one option from this card **[Show card 1]**

	Activity	Never						Every day	DK	NA
		1	2	3	4	5	6	7		
A	Herding activities									
B	Finding lost/wandering reindeer									
C	Taking animals to slaughterhouse									
D	Repairing vehicles									
E	Repairing fences/corrals/cabins									
F	Other (specify)									

Siida history

This next set of questions is about the summer and winter siidas you have belonged to over the last eight years. We want to understand how often herders change siida and their reasons for leaving one and joining another.

5.   Are you part of your summer siida's leadership board?

☐ Yes   ☐ No   ☐ Don't know   ☐ No answer

6.   In 2005, our records say you were a member of **_____** summer siida. Please can you tell us which summer siidas you have been a part of from 2005 until now?

INTERVIEWER: *If interviewee has moved between summer siidas, ask **Q7**, otherwise skip to **Q8**.*

7.   Could you please tell us why you left each siida when you moved, and why you moved to the siida you joined?

Year	Reason for joining new siida	Summer siida	Reason for leaving siida
2005			
2006			
2007			
2008			
2009			
2010			
2011			
2012			
2013			

8.   Now I'd like to ask the same question but about your winter siida. In 2005, our records say you were a member of **_____** winter siida. Please can you tell us which winter siidas you have been a part of from 2005 until now?

INTERVIEWER: *If interviewee has moved between winter siidas, ask **Q9**, otherwise skip to **Q10**.*

9.   Could you please tell us why you left each siida when you moved, and why you moved to the siida you joined?

Year	Reason for joining new siida	Winter siida	Reason for leaving siida
2005			
2006			
2007			
2008			
2009			
2010			
2011			
2012			
2013			

About your household

We would now like to ask about your household's sources of income as well as what tools and technologies you use.

10. **[Show card 2]** Please look at this list of items. Which of these were sources of income for your household in the last year?
    (Tick all relevant)

11. Which one brought in the most money to your household in the last year? *(Tick one)*

	10	11
Reindeer sold alive		
Reindeer meat		
Other bits of deer (milk, hide, antlers, bone)		
Fishing		
Tourism (selling handicrafts etc.)		
Labouring, construction		
Transport		
Working in shops, petrol stations, …		
Welfare		
Government subsidies (compensation for losses, pasture loss)		
Other (specify)		

12. **[Show card 3]** Roughly how many reindeer does your household own?
    (Circle one)

0-100	101-200	201-300	301-400	401-500	501-600	601-700	700+	DK	NA

13. **[Show card 4]** Which of these items did you own, rent or borrow in the last year? *(Write O, R or B)*		14. In the last year, did you share the item with other members of your _____ siida? *(Tick all applicable)*	
		Summer	Winter
Snowmobile			
All-Terrain Vehicle (ATV)			
Helicopter			
Other vehicle (specify)			
Smartphone (iPhone, Android etc.)			
Satellite Phone			
GPS			
Walkie talkie			
Computer			
Internet			

About you: family

We would now like to ask a couple of questions about whether you are married and if you have any children.

15. **[Show card 5]** What is your marital status?
    a. Never married
    b. Married
    c. Cohabiting but unmarried
    d. Widowed
    e. Separated/divorced
    f. Other (specify)

INTERVIEWER: *If respondent answered 'Married', continue, otherwise* ***skip to Q17.***

16. After you got married, where did you live?
    a. Your parents' household
    b. Spouse's parents' household
    c. With both sets of parents
    d. Moved into own household
    e. Other (specify)

17. **[Ask for each parent]** Is your father/mother still alive?
    a. Do they live in your household/summer siida/winter siida?

18. **[Ask for each sibling/child]** How many brothers/sisters/sons/daughters do you have?
    a. Do they live in your household/summer siida/winter siida?

	Living? (enter number)	Same household? (tick)	Same summer siida? (tick)	Same winter siida? (tick)
Father				
Mother				
Brother (full)				
Sister (full)				
Son				
Daughter				

About you: education

Finally, we would like to finish with a couple of questions about your education.

19. **[Show card 6]** What is your highest level of education?
    a. Primary school / secondary school (*norsk: Grunnskole*)
    b. Upper secondary school (*norsk: VG skole*)
    c. University or similar (*norsk: Høyskole/Universitet*)

20. What age were you when you left school/university? _____

Thank you for taking the time to speak with us and answer our questions. Is there anything you would like to add to what you have already told us?

[Additional comments:]

You will be paid in cash within a month from now. We first need everybody to play the game you played earlier so we can work out how much money you won from the game. This will be added to the money you receive for taking part in our study, as well as the amount that you chose to keep instead of donating. I will deliver the cash to your postal address.

That's the end of the interview. Thank you again for taking part in my study.

END OF INTERVIEW

Appendix C

Colophon

This thesis was typeset with LaTeX and BibTeX, using Ian Kirker's UCL Thesis LaTeX Template and Hermann Zapf's *Palatino* typeface.