Cooperative Dynamics among Hunter-Gatherers: An Experimental Investigation of Adaptive Hypotheses

By

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

Abstract

From small-scale food-sharing among hunter-gatherers to large-scale institutions in modern industrial societies, cooperation is central to human success. This thesis focuses on the former, exploring cooperative dynamics among the Agta, a Filipino hunter-gatherer population. I develop a novel experimental approach to exploring hunter-gatherer cooperative behaviour which simultaneously assesses the amount individuals cooperate and who they cooperate with. In contrast to much previous experimental literature, this non-anonymous design permits tests of specific theories for the evolution of cooperation, including: kin selection (cooperating with related individuals); reciprocity (cooperating with others who cooperate in return); and tolerated theft/demand sharing (taking from those with more resources), among other adaptive hypotheses. Using two experimental games – one exploring giving behaviour (donating resources *to* others) and another exploring demand sharing behaviour (taking resources *from* others) – I find that individuals from camps with a greater probability of repeated interactions give more to and take less from others. When individuals give to others it is directed towards kin and reciprocating partners, while when individuals take they do so from those with more resources, regardless of kinship or reciprocity. As predicted by theoretical models, this suggests that reciprocal transfers occur when interactions are repeated, while demand sharing occurs when repeated interactions are less likely. Differences in the frequency of repeated interactions may therefore explain some cross-cultural variation in forager food-sharing practices. This thesis also explores the effects of reputation on cooperative and interaction networks, finding that many aspects of forager social networks may reflect the trade of commodities in biological markets. Additionally, assessment of the ontogenetic roots of Agta cooperative behaviour suggests that who children cooperate with, but not overall levels of cooperation, change over childhood in ways which are consistent with adaptive evolutionary hypotheses. These findings provide an insight into the evolutionary and ecological roots of hunter-gatherer cooperation.

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In a roundabout way this all happened because of Richard Dawkins. As a rather aimless Psychology undergraduate I happened upon 'The Selfish Gene' which sparked my interest in evolutionary approaches to understanding human behaviour. From there I pursued a Master's in Human Evolution and Behaviour at UCL, to which I owe a debt of gratitude to many wonderful lecturers for helping to develop my knowledge in several aspects of human evolution. I especially would like to thank Volker Sommer (course coordinator) and James Steele (my dissertation supervisor) for their enthusiasm and support. Highlighting the viscosity of social networks (that is, 'it's not what you know, it's who you know'), after completing the Master's course Andrea Migliano (who taught 'Human Behavioural Ecology' on the MSc) received funding for the 'Hunter-Gatherer Resilience Project' and I was fortunate enough to apply for and be offered the opportunity to undertake this PhD. As this whole cavalcade of events was triggered by 'The Selfish Gene', I heartily thank Richard Dawkins for inspiring myself (and innumerable others) into the field of Evolutionary Biology and setting the wheels of this journey in motion.

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Chapter 1 Introduction

This chapter introduces two approaches to the study of cooperation, one theoretical and the other methodological. Theoretical approaches to the evolution of cooperation are discussed first, which include why cooperation is a central problem in biology and ways in which cooperation has been theorised to evolve in spite of individual self-interest. Using this theoretical background, the literature on hunter-gatherer cooperation, particularly regarding food-sharing, will also be introduced. Methodological approaches to investigate cooperation, predominantly in small-scale societies, are then detailed, focusing on the role of experimental games in understanding and explaining patterns of human cooperation. Despite their potential limitations, in recent years experimental games have been used extensively to explore cooperation in small-scale societies as they offer a quick, simple and standardised assessment of cooperative behaviour which can be compared between multiple study sites. In this brief review particular focus will be given to the interpretation of these games and whether they are valid measures of cooperation. I conclude that interpretation of these games is currently somewhat ambiguous and lacking clear theoretical cohesion, especially when applied in small-scale societies. It will then be argued that, despite the similarity in subject matter between the two approaches, experimental indices of cooperation have often been underused in broadly testing theories of cooperative evolution, particularly in small-scale societies. I end this chapter by introducing the aims of my research, which are to devise valid experimental measures of cooperation which can be used to explore and test theories of cooperation among hunter-gatherers to further our understanding of human cooperative evolution.

Evolutionary Theories of Cooperation

Cooperation is widespread in biology, from aphids (Abbot *et al.* 2001) to bacteria (Kümmerli *et al.* 2009), and from yeast (Smukalla *et al.* 2008) to zebra finches (St-Pierre *et al.* 2009). Humans are no different, and it could plausibly be argued that cooperation is even more important among humans than in many other animals. This is true for all humans, and especially so for hunter-gatherers (the terms 'foragers' and 'hunter-gatherers' are used interchangeably throughout this thesis). Cooperation among foragers is ubiquitous, including behaviours such as food-sharing (Gurven 2004d; Hill & Hurtado 2009), allocare (individuals other than the mother looking after children; Hrdy 2009; Meehan *et al.* 2013), cooperative hunting (Alvard 2002), coalition formation (Patton 2005), and many other aspects of daily social life.

Cooperation can be defined as the result of an interaction between two or more organisms where both parties receive inclusive fitness gains (Bshary & Bergmüller 2008; Connor 2010). This is an inclusive definition of 'cooperation', encompassing interactions which are both costly to the actor (altruism) as well as those which also benefit the actor (mutual benefit). It is important here to distinguish between 'cooperation' and 'cooperative behaviour' (Bshary & Bergmüller 2008). Cooperative behaviour (an individual's actions) may not necessarily result in cooperation, in terms of the outcome of an interaction. For instance, in the 'prisoner's dilemma' scenario (discussed below; Box 1.1) one individual may display cooperative behaviour (i.e., they cooperate), but if the other individual defects then cooperation does not occur (although depending on the circumstances this may be a form of altruism). In other situations, such as deciding whether or not to share resource with others, cooperation is independent of the actions of others (at least in the short-term) as the recipient will receive resources regardless of their behaviour towards the donor. In these situations cooperativeness (an individual's behaviour) is equivalent to cooperation (the outcome of an interaction).

A further important caveat to be made here regarding definitions of cooperation is that cooperative behaviour must be an action which *evolved* to benefit others (West *et al.* 2007b). A behaviour which benefits others but did not evolve to do so is not therefore cooperative under this definition as the help derived by others is incidental. The benefit to others in this instance should be regarded as a 'by-product' for selection on otherwise self-interested behaviours (Clutton-Brock 2009). For instance, imagine a scenario where a group of four organisms are being attacked; if none of the group retaliate, then the whole group perishes, while each individual who does retaliate increases their own probability of dying by 10%, while increasing the probability of group survival by 25% (Clutton-Brock 2009). In this scenario the best strategy is for individuals to retaliate, regardless of the actions of others, as the costs to retaliation (a 10% increase in mortality risk) are outweighed by the benefits (a 25% decrease in mortality risk). Thus, even though this retaliatory behaviour may seem cooperative as it increases the survival of other group members, the benefits derived by others are incidental, so this should not be categorised as 'cooperation'.

Despite the seeming ubiquity of cooperation in the biological world, the evolution of cooperation is perceived as a problem in biology (Hamilton 1964; Nowak 2006; West *et al.* 2007a). This is because of the free-rider problem; within a group, individuals have higher fitness if they receive the benefits of cooperation from others without paying the costs. All else being equal, this then causes the selfish phenotype to have higher fitness and replicate faster, outcompeting cooperative phenotypes until only defectors remain. A famous instance of this is the 'tragedy of the commons' (Hardin 1968), in which various actors take resources from a common pool. To use a hypothetical agricultural example, if farmers have cattle which graze on a plot of land, it would be optimal in the long-run for individuals to only allow the cattle to graze as much as can be grown back. This would mean that resources remain stable over time, sustaining the long-term future of the population. However, if one farmer purchases more cattle and allows them to graze on the land, their short-term material pay-off will be higher than the other farmers. Therefore, other farmers must also obtain extra cattle in order to compete, causing the resources of the pasture to deplete past sustainable levels. Thus, cooperation should not evolve as defectors will have higher fitness, even if in the long-term it is detrimental to both themselves and the population (Nowak 2006). Similar reasoning applies to cooperative behaviour among hunter-gatherers, such that individuals which do not hunt or share food, yet reap the spoils of other's foraging efforts, would have higher fitness (all else being equal). Obviously, however, given the ubiquitous nature of cooperation in biology, this tragedy can be resolved, meaning that there are resolutions to this apparent pessimistic inevitability. Many theories have now been proposed which explain how cooperation can emerge, despite the free-rider problem. It appears that there are myriad ways in which this problem can be overcome, some of which will be detailed now, with a specific focus on how they apply to hunter-gatherer cooperation and food-sharing. It should also be noted that the pay-off structure utilised when modelling cooperative evolution can greatly alter the subsequent evolutionary dynamics, as demonstrated in Box 1.1.

Box 1.1: Altering the Pay-Off Structure to Cooperation

The majority of models regarding the evolution of cooperation apply a similar framework to that of the 'tragedy of the commons' above (Hardin 1968). For simplicity, if we assume that this process only involves two players, this can then be modelled as a 'prisoner's dilemma' scenario. In this situation two suspected criminals are brought in for questioning regarding a serious crime and taken to separate rooms. The police have enough evidence to convict them of a minor crime, but not enough for conviction of a serious crime. Each prisoner is then offered a bargain and can either cooperate with the other prisoner (keep quiet) or defect (testify that the other prisoner committed the serious crime). The outcomes of these actions depend on the behaviour of the other player. If both cooperate, then each get charged with the minor offence and serve one year in jail. If one cooperates and the other defects, then the defector walks away free while the cooperator spends five years in jail for the serious crime. While if they both defect then they both get two years in prison. The pay-off ranking, with prisoner 1's actions first and prisoner 2's actions second (where 'D'=defect and 'C'=cooperate), reads DC>CC>DD>CD. Even though mutual cooperation results in the best average pay-off for both individuals, an individual would do better if they defect while their partner cooperates. Thus, as defection results in higher pay-offs, regardless of their partner's behaviour, defection is the only stable (or rational) strategy (Doebeli & Hauert 2005). Similar reasoning applies in multi-player settings, such as with public goods or common-pool resources, such that defection is the optimal strategy in one-shot interactions.

While the majority of research regarding the evolution of cooperation has utilised this pay-off structure, others are also possible. For instance, imagine a 'snowdrift' situation where two drivers are stuck behind a snowdrift. As with the prisoner's dilemma, individuals can either cooperate (dig through the snowdrift) or defect (not dig). While joint cooperation would mean clearing the snow faster, defecting and letting the other dig would be a superior strategy as no energy would be expended. However, in this case being the 'sucker' (the individual who cooperates while the other defects) is superior to mutual defection, as they still benefit by clearing the snow and getting home. The pay-off structure for this scenario is therefore DC>CC>CD>DD. In the snowdrift game defection is not the optimal strategy in one-shot interactions, resulting in a mixed population of cooperators and defectors (Doebeli & Hauert 2005). When 'cooperating' in this situation the benefit to the partner is incidental, meaning that these situations may not be strictly cooperative as behaviour is purely self-interested (West *et al.* 2007b). Although cooperation in this scenario benefits others, it did not evolve to do so as the effect on the other player is a by-product. These alternative pay-off structures have been under-researched compared to prisoner's dilemma scenarios, despite their seeming applicability to several kinds of social interactions among a number of taxa (Doebeli & Hauert 2005; Clutton-Brock 2009; McNamara & Doodson 2015).

There are two routes by which cooperation can evolve: by increasing an organism's direct fitness, or increasing their indirect fitness. Both of these impact *inclusive fitness*, which is an individual's lifetime reproductive success via both direct and indirect fitness effects (Hamilton 1964; West *et al.* 2007a). Direct fitness benefits to cooperation occur when the cooperative act benefits the actor by increasing *their* reproductive success; in this instance cooperation is mutually beneficial, as it increases the fitness of both the actor and the recipient (to be discussed below). One of the most common mechanisms proposed to explain cooperation in humans and other organisms, however, is kin selection, which enhances indirect fitness (Hamilton 1964). This is an indirect fitness benefit because the cooperative act does not increase the actor's reproductive success, but rather increases the reproductive success of *others*. As suggested by the name, kin selection is where individuals preferentially assist close kin over more distant kin or unrelated individuals to help pass on shared genes, thus increasing the actor's *inclusive* fitness, even though their individual fitness may be reduced. Helping another is therefore expected if the benefits to the recipient of a cooperative act, as a function of relatedness (0.5 for parents/full siblings/offspring, 0.125 for cousins, etc.), outweigh the costs of the action, neatly summarised as $b*r>c$. To take an abstract example, if the cost of a cooperative act is a one unit reduction in reproductive success for the actor, but a three unit increase for the recipient, the actor is likely to cooperate if the recipient is a sibling, but not a niece or nephew. This is because, for a sibling, 3 (the benefit to the recipient) times 0.5 (relatedness between siblings) is 1.5, which is larger than 1 (the cost to the actor), so the benefits outweigh the costs. For a niece or nephew, however, the benefit is 3 times 0.25 (0.75), which is lower than the cost to the actor, so cooperation would not be expected in this instance.

Three further caveats can be added to this formulation. Firstly, the *reproductive value* of an individual is likely to influence cooperation between kin, even if genetic relatedness is identical (Rogers 1993). That is, even though a child and a parent share the same amount of genetic material, it may be better to invest in the child as they are younger and therefore have more chance of reproducing and passing on shared genes. Secondly, shared reproductive interests, and not merely shared genealogical descent, are likely to influence cooperation for indirect fitness benefits (Chapais 2010). Although an individual may share food with affinal kin (e.g., a brother-in-law) who is not genetically related, the actual target of the provisioning may be the brother-in-law's offspring, the individual's niece or nephew, meaning that cooperation among affines may still be construed as a form of indirect fitness benefit. Lastly, relatedness is not always conducive to cooperation, as limited kin dispersal can result in an increased competition for resources between relatives, negating the usual positive effect of increased relatedness promoting cooperation (Queller 1994; West *et al.* 2002). Analysis of reproductive success among the Mosuo, Chinese agriculturalists with a duolocal residence pattern where kin do not disperse from their natal household, suggests that increased competition among female kin does occur and can reduce fitness (Ji *et al.* 2013; Mace 2013). Kin presence does not therefore necessarily increase cooperation under *all* conditions, especially when dispersal is limited.

Despite the ubiquity of kin selection for explaining cooperative behaviour across biological kingdoms (Nowak 2006; West *et al.* 2007a), the role of kin selection in predicting patterns of food-sharing in hunter-gatherers has produced mixed results. Some studies report that kin selection does not explain the flow of resource transfers between households (Kaplan & Hill 1985; Bliege Bird & Bird 1997; Allen-Arave *et al.*

2008; Koster *et al.* 2015), while others find an effect of preferential sharing among kin but attribute this to proximity or other effects, rather than a kin bias (Gurven *et al.* 2000b). Despite this negative evidence, several other reports of kin-mediated transfers have been found (Wiessner 2002; Patton 2005; Nolin 2010; Wood & Marlowe 2013; Hooper *et al.* 2015). Reviews and meta-analyses comparing across several forager populations have found relatedness to be a significant predictor of between-household food-sharing (Gurven 2004d; Jaeggi & Gurven 2013), although there is great variation across societies in the strength of this kin-bias. It is important to note that these results pertain to food-sharing *between* households. The majority of food-sharing occurs *within* households (between parents and offspring) meaning that kin selection does play a fundamental role in resource distributions (Gurven *et al.* 2000b; Wood & Marlowe 2013; Dyble *et al.* 2016).

We now turn to direct fitness benefits, in which the cooperative act increases the *actor's* reproductive success, as well as that of the recipient. One of the most well-known theories for the evolution of cooperation among unrelated individuals is direct reciprocity (or simply 'reciprocity'), in which individuals cooperate with others who have previously cooperated with them (Trivers 1971; Axelrod & Hamilton 1981). Reciprocity is most likely to occur when individuals have repeated interactions which foster trust and a reputation for cooperating, as well as when the cost to the giver of cooperating is lower than the benefits to the recipient (Trivers 1971; Doebeli & Knowlton 1998). Reciprocity therefore solves the free-rider problem as the long-term gains from exchanges outweigh the short-term benefits to defection. While indirect fitness benefits are ubiquitous in nature (West *et al.* 2007a), despite the intuitive appeal of reciprocity as a broad explanation for cooperation, it is considered predominantly applicable only to humans as a result of the complex cognitive architecture and psychological mechanisms required, such as language, theory-of-mind, temporal discounting, memory and co-ordination (Stevens & Hauser 2004; Clutton-Brock 2009). Although more recent evidence suggests that non-human animals such as non-human primates (Schino & Aureli 2010; Jaeggi & Gurven 2013), bats (Carter & Wilkinson 2013, 2015) and birds (St-Pierre *et al.* 2009) display reciprocity, the mechanisms underlying reciprocity may be best understood by focusing on humans.

Direct reciprocity has particular resonance in hunter-gatherer societies. As a consequence of high levels of resource variability in big-game hunting, reciprocal sharing has been thought to be essential for ensuring that individuals still receive resources from others, even when they return with no food themselves (Winterhalder 1986; Smith 1988; Hill & Hurtado 2009). Although intuitive, observations of food-sharing tend to find that some individuals provision others significantly more than they receive in return (Kaplan & Hill 1985; Bliege Bird & Bird 1997; Hawkes *et al.* 2001). However, even though there may be asymmetries in the *amount* of resources given and received, reciprocal sharing relationships can still be adaptive if the relative *value* of resources traded are approximately equivalent (Gurven 2006). For those with a surplus of resources, sharing one kilogram of food is less costly than the equivalent benefit for receiving one kilogram of food for someone in dire need of resources. This resource value asymmetry means that the amount of food transferred between individuals does not need to be equal for reciprocity to evolve. Consequently, reciprocal sharing relationships are found among several foraging societies (Wiessner 2002; Gurven 2004c, d; Patton 2005; Allen-Arave *et al.* 2008; Nolin 2010; Jaeggi & Gurven 2013), even if the amounts shared are unequal.

Recently there has been a shift towards explaining patterns of cooperation, especially in small-scale societies, as instances of needs-based sharing. This occurs when those with a greater supply of, or less need for, resources provision those in greater need of additional resources (Hao *et al.* 2015; Aktipis *et al.* 2016). This can take the form of food-sharing, such that differences in productivity and need over the life-course influence resource transfers. For instance, individuals less energetically-burdened with children, and therefore at a net-calorific surplus, provision those with many dependent children who otherwise would not have enough food to support themselves (Hill & Hurtado 2009; Hooper *et al.* 2015). Larger families or households also receive a greater proportion of resources than small families or households, again reflecting differences in need (Aspelin 1979; Kaplan & Hill 1985). Needs-based cooperation has also been modelled as a risk-reduction mechanism among Maasai pastoralists to aid herd survival in times of stress (Aktipis *et al.* 2011; Hao *et al.* 2015). However, needs-based sharing is a description of cooperation, not an evolutionary explanation for why it is adaptive. A strategy in which individuals give altruistically to those in need, without any subsequent future fitness gain, would possess lower fitness than an alternative strategy which did not give to those in need. The adaptive mechanism underlying this needs-based sharing could be: kin selection, if those helped in need are predominantly kin (Hamilton 1964); direct reciprocity, as due to resource value asymmetry the costs of sharing for those with many resources are low relative to the benefits gained by those in need, who may reciprocate in the future (Trivers 1971); tolerated theft (discussed below); or possibly other explanations discussed later such as sharers gaining reputation, status or mating opportunities (Allen-Arave *et al.* 2008).

In addition to direct reciprocity, other kinds of reciprocity may also promote the evolution of cooperation among non-relatives (although they are only reciprocal in name as there is nothing strictly reciprocal about them; Cronk & Leech 2013; 75-77). One theory is indirect reciprocity, in which individuals cooperate with those who have a reputation for cooperation (Nowak & Sigmund 1998; Nowak 2006; Milinski 2016). This goes beyond direct reciprocity by modelling the conditions which permit cooperation between unrelated individuals who have not met before and will not interact again in the future. If individuals acquire a reputation for cooperation by being cooperative, and this reputation is known by others, those with a reputation for cooperation are more likely to be cooperated with, irrespective of a lack of previous encounters. Theoretical models have indicated that cooperation can evolve via this process (Nowak & Sigmund 1998; Panchanathan & Boyd 2003; Roberts 2015), and results from several empirical studies (reviewed in Nowak & Sigmund 2005 and Milinski 2016) have found results consistent with indirect reciprocity. For example, non-cooperative individuals are less likely to be cooperated with in the future (Wedekind & Milinski 2000), while individuals also appear to engage in 'reputation management': if their behaviour will be made public to others they are more likely to cooperate (Seinen & Schram 2006).

Due to the cognitive constraints required for transmitting and keeping track of reputations, indirect reciprocity may be most developed in humans (Nowak & Sigmund 2005), although its influence may be pervasive among human societies (Cronk & Leech 2013). There has been little research explicitly testing theories of indirect reciprocity in hunter-gatherers, although in those that have the evidence is mixed. For instance, among the Ache, good hunters received more food when they were ill or injured compared to poor hunters, suggesting that a reputation for acquiring and sharing resources results in receiving greater cooperation in times of need (Gurven *et al.* 2000a). However, among the Hadza, after playing a Public Goods Game, those who were cooperative in the game were not more likely to be chosen in a subsequent gift or camp-mate network, indicating that cooperative individuals were not actively sought out as social partners (Apicella *et al.* 2012). Similarly, free-riding Meriam foragers, who received food from others but gave little in return, were equally as likely to receive food as industrious and generous individuals, suggesting little preferential cooperation towards known cooperators (Bliege Bird *et al.* 2002).

A further theory which takes social structure into consideration is network or spatial reciprocity (Nowak 2006), in which clusters of cooperative individuals assort together to the exclusion of defectors. The ability to migrate between groups or shift partners can promote cooperation, as models indicate that variants of a ‘win stay, lose shift’ strategy can produce positive assortment with cooperators associating preferentially with other cooperators (Pepper & Smuts 2002; Hamilton & Taborsky 2005; Ohtsuki *et al.* 2006; Pepper 2007; Aktipis 2011; Lewis *et al.* 2014). Empirical evidence from student populations (Sylwester & Roberts 2010; Fehl *et al.* 2011; Efferson *et al.* 2015) suggests that assortativity by cooperativeness does occur, with cooperators assorting with other cooperators, while in the Hadza individuals of a similar cooperative level clustered together (Apicella *et al.* 2012). Each of the above mechanisms is dependent upon assortativity or partner choice: the preferential selection of certain individuals as recipients of cooperation over others. This may be via relatedness (kin selection), previous sharing partnerships (direct reciprocity), cooperative reputation (indirect reciprocity) or the exclusion of defectors (network/spatial reciprocity).

Demand sharing and tolerated theft are further mechanisms which have been proposed to explain food-sharing in hunter-gatherers. Although often discussed separately, with ‘demand sharing’ more frequently used by social anthropologists and ‘tolerated theft’ employed by behavioural ecologists, there is an obvious correspondence between the two and both theories predict similar patterns of behaviour. Tolerated theft – more commonly known as ‘scrounging’ in the biological literature (Caraco & Giraldea 1991; Vickery *et al.* 1991) – posits that individuals take resources from others and are not reprimanded for doing so because the costs of defending the resource are higher than the marginal gains from successfully defending it. As marginal returns diminish with consumption (figure 1 in Blurton Jones 1987), a hungry scrounger will be more willing to contest a resource than a more satiated producer will wish to defend (Winterhalder 1996). This particularly applies to larger game as small resources can be consumed prior to scroungers knowing about them, while it is much more difficult to hide larger packets which cannot be consumed in one sitting (Blurton Jones 1984, 1987). While returns may even out over time given variation in foraging return rates, making tolerated theft appear similar to reciprocity (Blurton Jones 1987), this is not necessarily so as some individuals may forage more or be more efficient foragers (Winterhalder 1997). Group size also has an important effect on the proportion of producers to scroungers. Smaller groups (with around five or less foragers) are likely to have a larger proportion of producers, making these groups possess a higher average per-capita calorific consumption than larger groups (Blurton Jones 1987).

Compared to tolerated theft, which is also referred to as ‘passive sharing’ (Blurton Jones 1984), demand sharing is a more active process, whereby individuals with resources are forced – or demanded – by others to share for fear of ridicule, ostracism or other social sanctions (Peterson 1993; Hawkes 2000). However, other than a more explicit discussion of the proximate mechanisms involved, tolerated theft and demand sharing are fundamentally alike and make similar predictions regarding patterns of food-sharing (and thus will be used interchangeably through the course of this thesis). Note, also, that demand sharing or tolerated theft do not necessitate confrontation; they merely require an expectation that food will be shared among camp-mates, meaning that distribution is demanded, regardless of reciprocity and the wishes of the producer. This may include the pre-emptive giving of resources (Bird & Bliege Bird 2010). Although unlikely to be the sole mechanism explaining food transfers in hunter-gatherers, due to the roles of kin selection and reciprocity discussed above, and others discussed below (Gurven 2004d), tolerated theft/demand sharing has been used to explain food-sharing in several foraging societies (Bliege Bird & Bird 1997; Hawkes 2000; Bird & Bliege Bird 2010; Jaeggi & Gurven 2013). This is especially likely to occur when producer control over distribution is low, meaning that the procurer of the resource cannot control over who it is distributed to (Gurven 2004d). As with other mechanisms, assortativity may also play a role in tolerated theft/demand sharing. A recent model testing the conditions under which this can evolve found that high levels of mobility were essential for demand sharing to be viable as mobility was required to avoid non-hunting free-riders (Lewis *et al.* 2014; see also Efferson *et al.* (2015) for an experimental test of this ‘walk away’ mechanism). Demand sharing may also explain several apparent instances of needs-based sharing, as those in greater need are more likely to demand share relative to those less in need of resources (Hao *et al.* 2015).

Compared to other mechanisms for cooperation, which tend to be modelled on prisoner’s dilemma-style scenarios, tolerated theft/demand sharing appear to better approximate the snowdrift model pay-off structure (Doebeli & Hauert 2005: Box 1.1). This is because foraging (cooperating) and having some of the resources taken by scroungers (defectors), is superior than mutual defection where no-one forages (Blurton Jones 1987). The food-sharing resulting from tolerated theft may therefore be better characterised as a ‘by-product’ (Clutton-Brock 2009), rather than strictly cooperative, as being a producer would not evolve to benefit others, but would rather be an incidental consequence (West *et al.* 2007b). While neither party may wish to forage and have food taken by others, the costs to not foraging are greater for some individuals, meaning that these individuals would ‘blink’ first in this proverbial game of chicken. An example would be foraging by an individual with multiple dependent offspring against another individual with no dependants. In this scenario the second individual has less need to forage compared to the first as the costs to not foraging for the first individual are larger as their household would be in greater need of resources. Consistent with this perspective, men from Ifaluk atoll with more dependent offspring were more likely to fish compared to those with few dependants, as the costs to not foraging were greater for these men (Sosis *et al.* 1998).

An alternative explanation perceives tolerated theft as a description of resource transfers, rather than an evolutionary mechanism. By sharing food widely, or allowing food to be taken freely, proficient hunters make their efforts a public good of which non-hunters can free-ride, theoretically increasing the free-riders’ fitness relative to the hunters (Hawkes 1992). Ethnographic data suggest that individuals in forager bands both spend considerable time hunting and share their spoils widely, with some individuals hunting and sharing more than others (Kaplan & Hill 1985; Gurven *et al.* 2000a; Bird & Bliege Bird 2010; Bliege Bird & Power 2015). Why would individuals hunt in the knowledge that much of the resource would be taken from them and with little control over subsequent distribution? Given the importance of assortativity discussed above it would appear beneficial to only give to those who would also cooperate or for good hunters to lower their hunting rates (Hawkes 1991, 1992), yet this does not appear to be the case among many societies (Kaplan & Hill 1985; Bird & Power 2015; although see Wiessner 2002). A potential answer may be that cooperative ventures, such as hunting and food-sharing, are forms of 'costly signalling', or showing off, in order to attract mates or other social benefits via reputation or prestige which subsequently increase reproductive success.

Data from the Hadza indicate that males preferentially hunt large game, to the detriment of small game and other foraged resources, even though the return rates of large game are lower (Hawkes *et al.* 1991). This suggests that provisioning may not be the sole aim of male's hunting effort. Big-game hunting, and other costly activities, may act as an 'honest signal' displaying a male's phenotypic quality, and thus a social or mating strategy as opposed to a provisioning one (Hawkes 1991; Smith & Bliege Bird 2000; Bliege Bird *et al.* 2001; Hawkes & Bliege Bird 2002; Nolin 2012). Indeed, better hunters often possess increased reproductive success, although the exact mechanism underlying this finding is unclear (Smith 2004). However, other studies, including a more recent investigation of Hadza food-sharing (Wood & Marlowe 2013), suggest that hunters keep a larger proportion of game for their household, indicating a role for family provisioning (Hill & Kaplan 1993). Thus, costly signalling as a form of mating strategy, although prevalent in some societies, is unlikely to have universal application as an explanation for forager food-sharing patterns (Gurven 2004d).

Costly signalling theory can also be applied, not just as a mating strategy, but as a cooperative strategy, whereby high-producing or generous individuals are preferred cooperative partners, via a process of ‘reputation-based partner choice’ (also known as ‘competitive altruism’: Roberts 1998; Sylwester & Roberts 2013). When applied in this cooperative context reputation-based partner choice and indirect reciprocity make similar predictions, such that seemingly costly displays of cooperation will be rewarded by cooperation in future encounters, yet the mechanisms of indirect reciprocity and reputation-based partner choice are markedly different. In reputation-based partner choice, individuals preferentially interact with cooperative individuals for future mutually-beneficial cooperative interactions with said cooperator. In contrast, indirect reciprocity assumes that individuals help cooperative others solely to enhance their own cooperative reputation so that others will cooperate with them, irrespective of future interactions with the individual they originally cooperated with (Nowak & Sigmund 1998, 2005). It should also be noted that indirect reciprocity applies only to receiving cooperative acts in the future, while costly signalling is more general; the returns may not be in terms of cooperation, but rather conferring status or prestige upon the actor (see below for further discussion regarding this ‘not-in-kind’ cooperation).

Other theories have been put forward to explain patterns of cooperation and food-transfers in hunter-gatherers. A form of ‘generalised reciprocity’, in which cooperation is extended to all without concern for reciprocation from specific partners, has been proposed as characterising hunter-gatherer cooperation (Sahlins 1972). It has been suggested that, as a result of a history of cooperative breeding producing prosocial tendencies in humans, cooperation may extend to all group members (Burkart *et al.* 2014). Modelling has indicated that generalised reciprocity can evolve, although it requires the rather limiting constraints of both: i) small groups, and; ii) stable group composition (Pfeiffer *et al.* 2005). This mechanism has been touted as a possible explanation for cooperation between non-kin in non-human animals as the complex cognitive machinery associated with direct or indirect reciprocity (score-keeping, etc.; Trivers 1971; Stevens & Hauser 2004; Nowak & Sigmund 2005) is not required (Pfeiffer *et al.* 2005; van Doorn & Taborsky 2012). Indeed, generalised reciprocity, based on the simple rule of ‘help anyone, if helped by someone’ (or ‘paying it forward’), has been observed in both rats (Rutte & Taborsky 2007) and humans (Gray *et al.* 2014), although not in macaques (Majolo *et al.* 2012). However, despite claims that generalised reciprocity explains hunter-gatherer cooperation (Sahlins 1972), no quantitative research has confirmed this, and the evidence presented above suggests that cooperation is not generalised to all, but rather is targeted to specific individuals (kin, reciprocating partners, etc.).

Thus far, the majority of these theories have focused on ‘in-kind’ cooperation, such that individuals base their decisions on whether to cooperate on the cooperation of others. However, there are several other factors beyond this which may explain cooperation that is not returned ‘in-kind’. This can take several forms, which can be grouped under one of two categories: mating effort or cooperative market value. Cooperation as a form of mating effort has already been discussed above, under the section on costly signalling (Bliege Bird *et al.* 2001; Hawkes & Bliege Bird 2002), where individuals display their phenotypic prowess by ‘showing-off’ in order to attract mates. A second aspect of ‘not-in-kind’ cooperation concerns one’s ‘market value’ as a recipient of cooperation. This is based on the logic of ‘biological market theory’ (Noë & Hammerstein 1994; Barclay 2013, 2016), in which individuals with a greater ability or willingness to assist others (a greater ‘market value’) are preferred cooperative partners. This can include factors discussed above, such as reciprocity or possessing a cooperative reputation (e.g., via indirect reciprocity or reputation-based partner choice).

Biological market theory can also encompass ‘not-in-kind’ commodities, such that an individual with great hunting knowledge may be a preferred recipient of cooperation as an individual can learn from them, irrespective of whether share food or not (Barclay 2013; see also Henrich & Gil-White 2001). These ‘not-in-kind’ transfers have been studied extensively in non-human primates. For instance, chimpanzees exchange meat for coalitional support (Gomes & Boesch 2011), while female macaques exchange grooming by males for sex (Gumert 2007). However, they have not been explored in great detail among humans, despite their potential relevance for explaining patterns of resource transfers in foraging populations (Kaplan & Hill 1985). One exception are the forager-horticulturalists from Conambo, Ecuador, in which resources were preferentially given to political allies in return for coalitional support (Patton 2005). Similarly, Bird and Bliege Bird (2010) hypothesise that sharing magnanimity among the Martu is associated with increasing one’s political reputation (although see Bird and Power (2015) for a re-interpretation suggesting that magnanimity instead enhances one's position in cooperative networks). Recent work among the Tsimane, forager-horticulturalists from Bolivia, has found that reciprocal sharing among different cooperative domains occurs, such as exchanging meat for agricultural produce, or labour for childcare (Jaeggi *et al.* 2016). In contrast to indirect reciprocity, where individuals with a cooperative reputation are sought as prospective partners, market models predict that other forms of reputation are also important, such as competency or knowledge (see also Sugiyama & Chacon 2000). Although little work has been conducted on this topic with foragers, research from Dominican bay-oil producers and Peruvian agro-pastoralists suggests that individuals with a reputation for competency are preferred social partner over those with a reputation for cooperativeness (Macfarlan & Lyle 2015). The influence of ‘market value’, especially regarding ‘not-in-kind’ commodities, in explaining patterns of cooperation and forager food-sharing is an area in great need of further empirical research.

A final theory to be discussed regarding the evolution of cooperation is group selection. Group selection is a complex topic with several different interpretations which can easily become conflated and confused, so a brief historical sketch is required to separate and understand these differences (for additional discussion on this topic see: West *et al.* 2007b, 2008, 2011; Leigh Jr 2010). ‘Old’ group selection, prevalent until the 1960’s, contested that traits evolved for the ‘good of the species’ (or group: Wynne-Edwards 1962). Thus, ‘group adapted’ behaviour would flourish as cooperative groups would outcompete groups filled with selfish individuals. However, due to the free-rider problem selfish individuals within these groups would have a selective advantage as defectors would out-compete altruists (Hamilton 1964). This form of group selection and group-level adaptation has been shown to be possible, but only under very restrictive constraints, such that within-group competition must be non-existent or the population consist entirely of clones (Gardner & Grafen 2009). Thus, on theoretical and empirical grounds, organisms appear adapted to maximise inclusive fitness, not group fitness (West *et al.* 2007b, 2011). ‘Old’ group selection is therefore a highly improbably candidate to explain the evolution of cooperation.

Rather than focus solely at the group level, a ‘new’ group selection originating in the 1970’s and 1980’s – known as multi-level selection – attempted to explain adaptation, particularly of cooperation, as emerging from the interaction of several different levels of selection, most pertinently individual and group-level selection (Wilson 1975; Wilson & Dugatkin 1997; Traulsen & Nowak 2006). According to this theory, if the strength of between-group selection outweighs within-group selection, then traits which benefit the group can evolve. However, this 'new' group selection has been shown to be mathematically identical to an inclusive fitness approach (Hamilton 1975; Lehmann *et al.* 2007a; West *et al.* 2008; Gardner & Grafen 2009), such that strong between-group selection is equivalent to maximising indirect fitness, while strong within-group selection favours maximising direct fitness. This does not mean that the 'new' group selection approach is incorrect, only that it is formally equivalent to existing approaches based on inclusive fitness (West *et al.* 2008; Frank 2012). As the approaches are equivalent, and the models much more tractable and widely applicable using an inclusive fitness approach, it is this approach which has been utilised much more widely in evolutionary biology; the difference is in perspective, not process (West *et al.* 2007b, 2011). It should be noted that the conditions in which between-group selection outweigh individual-level selection may be quite limited in nature. For instance, it requires low migration between groups and suppression of within-group competition (Gardner & Grafen 2009), and within the animal kingdom may apply primarily to eusocial insects (Leigh Jr 2010). Given that these conditions are not met in humans – there is within-group competition, high migration rates and groups are relatively fluid – multilevel selection may be an unlikely explanation for the evolution of cooperation among humans.

A 'newer' theory of group selection is allied to theories of 'gene-culture co-evolution' and group selection at the cultural, rather than the genetic, level (Boyd & Richerson 1985, 2009; Henrich 2004a; Richerson *et al.* 2010, 2016). This approach again stresses the importance of competition between groups in explaining group-level cooperative behaviour, but these can be cultural traits, so is predominantly applied to humans (although for sperm whales see Cantor, Maurício, Shoemaker *et al.* 2015). While genetic selection is generally relatively slow, cultural group selection can be much faster. This is because between-group differences can be amplified, and within-group differences minimised, by social learning processes such as conformism and imitating successful individuals (Boyd & Richerson 1985; Henrich & Boyd 1998, 2001) and other proximate mechanisms which promote cooperation such as policing (Kümmerli 2011) and punishment (Gintis 2000; Boyd *et al.* 2003; Lehmann *et al.* 2007b). These between-group differences in cultural behaviour mean that traits which appear costly for the individual but beneficial to the group can then spread as cooperative groups out-compete uncooperative groups. Various models have demonstrated that this process is possible, such that apparently costly behaviours can spread at the group level, despite being selected against at the individual level, via the process of within-group phenotypic homogenisation by cultural transmission and subsequent selection between groups (Boyd *et al.* 2003, 2011; Henrich 2004a). However, just because transmission is cultural rather than genetic, it does not necessarily follow that cultural transmission results in cooperation (Lehmann *et al.* 2007b, 2008). Indeed, cultural transmission mechanisms may even be *detrimental* to cooperation if cultural success is independent of genetic success by increasing an agent's local level of competition (Lehmann *et al.* 2008). Furthermore, the importance of inclusive fitness should not be disregarded when assessing the effect of cultural transmission on cooperation; even when explicitly modelling cooperative evolution via cultural mechanisms, inclusive fitness benefits are still required for cooperation to evolve (Lehmann *et al.* 2007b). Thus, while cultural group selection (and group selection more generally) may be possible in theory, it is currently unclear whether group-level processes played a role in the evolution of human cooperation, especially given the restrictive constraints required for it to operate (low within-group and high between-group competition). Nevertheless, there is currently considerable debate as to whether human cooperative capabilities are consistent with adaptation at the group or individual level (Krasnow *et al.* 2012, 2015; Richerson *et al.* 2016).

Five main conclusions can be drawn from this brief literature review: i) the evolution of cooperation and overcoming the free-rider problem is possible by several routes, utilising either direct or indirect fitness benefits (while by-product mutualisms may explain other instances of seemingly cooperative behaviour); ii) no single perspective can explain the totality of food-sharing in hunter-gatherers; iii) the relative importance of each approach appears to vary by society (for a more in-depth discussion, see Gurven (2004d)); iv) greater attention should be given to the exchange of other commodities, not merely 'in-kind' cooperation, to explain the evolution and maintenance of cooperative partnerships; and v) the contribution of group selection to the evolution of human cooperation is currently intensely-debated.

Cooperation among hunter-gatherers, especially in terms of food-sharing, is usually collected by observation or interviews. Little empirical research has been conducted using experimental methods as a tool for understanding resource transfers and other forms of forager cooperation. Experimental economic games have been employed to explore cooperation more generally in these societies, yet these results can be difficult to interpret and are often inadequate to explore many of the theories discussed above. It is to this topic, the application of experimental games in hunter-gatherer and other small-scale societies, to which I turn next.

Experimental Games in Small-Scale Societies

Experimental economic games to explore and quantify cooperation in small-scale societies (broadly defined here to include all non-industrial societies) have been widely adopted across the behavioural sciences in an attempt to both discover and explain cross-cultural variation in cooperative behaviour (Henrich *et al.* 2001, 2004b, 2005, 2010a; Ensminger & Henrich 2014). These games predominantly consist of one-shot, anonymous, scenarios in which participants are asked to make a choice between dividing resources (usually money) between themselves and another (or others: Camerer & Fehr 2004). The resulting situation is a ‘social dilemma’ (Kollock 1998) as there is a conflict between individual and group interests: helping others involves incurring a cost to self. The methods most often employed, the Dictator Game (DG), Ultimatum Game (UG), Third-Party Punishment Game (TPG) and the Public Goods Game (PGG), are described in table 1.1, along with the rationale of what each game intends to measure. Despite their superficial differences, all of these protocols are intended to quantify levels of cooperation, with the assumption that game behaviour reflects real-life social dilemmas and is therefore applicable to behaviour outside the experimental context. However, there is a lack of underlying consensus as to what these games actually signify. The intention of this review is an attempt to explore some of these issues and hopefully point the way towards more productive research in the future.

Table 1.1: A summary of common experimental games used to assess cooperation (adapted from Camerer & Fehr 2004, table 3.1; Levitt & List 2007, table 1).

Game	Protocol	Interpretation	Typical Findings[a]
Dictator Game (DG)	Proposer divides a resource between self and responder (e.g., £10 in £1 increments). Responder cannot reject offer.	'Pure' altruism/fairness (without threat of punishment), inequality aversion	Proposers often offer ~20% of the stake
Ultimatum Game (UG)	Same as DG, but responder can reject offer if they wish, in which case both players receive nothing.	*Proposer*: Fairness, offer amount to maximise own pay-offs yet avoid punishment. *Responder*: Punish offers deemed unfair (inequality aversion)	*Proposers*: Offer 30-50% of stake. *Responders*: Reject low offers
Third-Party Punishment Game (TPG)	Identical to DG, but a third player receives half the stake. Player 3 can then use 20% of their earnings to reduce the amount the proposer keeps by 30%	*Proposer*: Fairness, offer amount to maximise own pay-offs yet avoid punishment by third-party. *Player 3*: Punish unfair offers to others at cost to self, norm enforcement, inequality aversion	*Proposers*: Offer ~25% *Player 3*: Punishment of unfair (i.e., non-50/50) splits[b]
Public Goods Game (PGG)	All players in a group receive an initial endowment, then decide how much to keep for self and how much to invest in a group pot. Earnings in the group pot are increased and divided equally between all players, adding to the amount they individually kept.[c]	Fairness, trust, risk aversion	First round offers usually ~50% of endowment, but often drops to 0% when iterated without punishment.[d]

[a] Typical responses from university students in western industrialised societies, that is.
[b] Results from Fehr & Fischbacher (2004a).
[c] Thus, defecting (not investing) is the safer option, as if an individual invests and no-one else does, then pay-offs are lower than defection, although the pay-offs would be higher than mutual defection if everyone invested, hence the dilemma.
[d] See Fehr & Gächter (2002).

This section aims to critically examine the assumptions of these experimental games by assessing: 1) whether different games measure similar underlying constructs (convergent validity); 2) whether game behaviour correlates with real-life behaviour (external validity), and under what conditions an association should even be expected; 3) explanations for cross-cultural variation in game behaviour; and 4) how these games can inform us about the evolution of cooperation, utilising the theories outlined above. Prior to exploring these issues, a short history on the use of experimental games in small-scale societies is provided. However, before beginning it is important to note that this review is primarily intended to elucidate the issues surrounding the adoption of these experimental methodologies in small-scale societies, and not larger industrial state societies (see Levitt & List (2007) for a general critique of laboratory experiments using experimental games).

Background to Experimental Games in Small-Scale Societies

The use of such games to investigate cooperation has increased dramatically since their inception in the 1960's. However, most studies, even cross-cultural ones (Roth *et al.* 1991; Brandts *et al.* 2004), have focused primarily on Western societies. In all populations tested, levels of cooperation were both quite high and reasonably stable. In the UG, for example, most participants offer 40-50% of the stake, with a mode of 50% (Camerer 2003). The Machiguenga, Peruvian forager-horticulturalists, were the first small-scale society tested using these methods, and were found to deviate significantly from previous societies, with an average UG offer of only 26% (with a mode of 15%: Henrich 2000). Consequently, further research in additional small-scale societies from various subsistence and ecological backgrounds, primarily employing the UG (but also the DG, TPG and PGG), reported a great deal of previously unidentified cross-cultural variation in cooperative behaviour (Henrich *et al.* 2001, 2004b, 2005, 2010a; Ensminger & Henrich 2014). This research was conducted by the *Roots of Human Sociality* team (Henrich *et al.* 2004b; Ensminger & Henrich 2014), from which the majority of studies presented here are taken.

In Phase I of the project, which focused on UG behaviour over 15 small-scale societies, significant between-society variation was reported (Henrich *et al.* 2004b, 2005). This variation was associated with market integration (a combination of frequency of market exchange, settlement size and socio-political complexity) and pay-offs to cooperation (a subjectively ranked measure assessing, based on the local ecology, “what is the potential benefit to cooperative as opposed to solitary or family-based productive activities?” (Henrich *et al.* 2004a: 29)). Both of these society-level measures were positively associated with increased UG offers, while individual-level traits, such as age, sex, wealth and education, explained little of the variance. In Phase II of the project (Henrich *et al.* 2010a; Ensminger & Henrich 2014), the DG, UG and TPG were conducted over 14 small-scale societies (some different from Phase I; note that games were played in 15 societies, but the rural US population is excluded here as this is an industrial society). Both increased market integration (now operationalised as percentage of food purchased from a market) and adherence to a world religion were associated with increased offers (the variable ‘payoffs to cooperation’ was dropped from Phase II). Again, individual-level variables appeared to explain little of the variation in results. The authors interpret these patterns as evidence for cultural group selection acting on cooperative norms and perceptions of fairness (the topic of interpretation of these games will be returned to in a later section). Several of the assumptions underlying these experimental economic games will now be explored.

Convergent Validity

Although individual games may measure specific aspects of social interactions, for example, the UG measures cooperation given the threat of punishment while the DG removes this threat (table 1.1), each of the games intends to elicit general levels of cooperation both within- and between-groups (Henrich *et al.* 2005). Thus, if these games measure similar cooperative tendencies, then results from two games ought to be correlated and similar explanatory variables should be predictive of behaviour in both games (Peysakhovich *et al.* 2014); that is, they should display convergent validity. Although the mean offer for a society is the most commonly interpreted statistic in these experiments, several researchers (Marlowe 2009; Gurven 2014) have proposed that, as these studies aim to investigate social norms, the modal value is also of great interest and may be a better measure of social preferences (although see Lamba & Mace 2013; Lamba 2014). Therefore, between-population comparisons discussed below will be explored using both mean and modal offers.

Firstly, to assess how two seemingly different methods compare, PGG and UG values for each society were correlated using data from Henrich *et al.* (2005). Despite a small sample size (*n*=5), mean values displayed a significant positive correlation (*r*=0.956, *p*=0.011), although modal values no longer reached significance (*r*=0.429, *p*=0.47). When a similar within-society analysis using these two games was conducted on five different Tsimane camps (Gurven 2004b), neither the means (*r*=-0.065, *p*=0.92) or modes (*r*=-0.49, *p*=0.4) were significantly correlated, suggesting little relationship between PGG and UG behaviour in this society.

Furthermore, when the significant predictors of PGG and UG behaviour in societies which played both games are contrasted, as evinced by multivariate regressions, there is little overlap in results (table 1.2). This suggests that although there may possibly be a society-wide correlation between mean PGG and UG offers, within each society individuals behaved differently in each game. If these games were tapping in to shared constructs, the predictor variables of the regressions should be analogous. Supporting this, when individual UG offers were plotted against private PGG offers in the Ache, no correlation was reported (however, it should be noted that a weak positive correlation was found between UG offers and public PGG offers; Hill & Gurven 2004). Similarly, among the Tsimane there was no correlation between individual PGG and UG behaviour when all offers were pooled together, although when divided by sex males displayed a non-significant positive trend between offers, while for females there was no relationship (Gurven 2004a, b).

Table 1.2: Comparison of predictor variables for the Public Goods Game (PGG) and Ultimatum Game (UG) over five small-scale societies. 'Pos' or 'Neg' indicate whether a predictor variable was positively or negatively associated with donations.

Society	PGG Predictors[a]	UG Predictors
Ache (Hill & Gurven 2004)	Male (pos), Public (pos), Times played (neg)[b]	None
Machiguenga (Henrich & Smith 2004)	Not reported	None
Mapuche (Henrich & Smith 2004)	Belief that others would also contribute (pos)	None
Orma (Ensminger 2004)	Household wealth (pos)	Involved in wage labour (pos), Education (neg)[c]
Tsimane (Gurven 2004a)	Village residence	Village residence, Male (pos), Spanish fluency (pos), Education (neg)

[a] For the Machiguenga a Common-Pool Resource game was employed, which is identical to the PGG, other than individuals extract, rather than deposit, resources.
[b] For the Ache, a private round of the games were first played, followed by a public version.
[c] Education for the Orma has a *p*-value of 0.058, so was approaching significance.

Adopting a different pair of methods with the Pahari Kowra forager-horticulturalists of India, Lamba and Mace (2011) performed a PGG and a naturalistic common-pool resource game. In the latter, each camp was allocated 1kg of salt per person. Each individual could then extract as much as they wished, which would leave less than 1kg per person for subsequent participants if they took more than 1kg for themselves. Each of the 16 communities were ranked from 1-16 (from most to least cooperative) for both games based on the ordering of mean PGG contributions and mean salt deviations (see figures 1 and 2 in Lamba & Mace 2011). Due to the ranked nature of this data, the correlation was performed using spearman's *rho*. No significant relationship between PGG offers and amount of salt taken was reported (r_s=0.162, p=0.55). Correspondingly, in a multilevel model the predictors for each game were different; age and a measure of network size were positively associated with increased PGG contributions, while increasing village size and number of sisters living in the village increased the amount of salt taken. Thus, although games are often intended to assess cooperation levels in general, it appears that different games may evoke different cooperative constructs, making comparisons between games difficult to interpret.

Next, the convergent validity of the UG, DG and TPG was examined across 13 societies from Phase II (Henrich *et al.* 2010a). Results suggest that they are all significantly positively correlated with one another at both the mean and modal values (table 1.3; see also Marlowe *et al.* 2011). Additionally, individual-level data from the Tsimane (Gurven 2014), Sanquianga (Cardenas 2014), Hadza (Marlowe 2009) and Yasawa (Henrich & Henrich 2014) each reported a significant positive correlation between DG and UG offers. Individual-level data were not available for comparisons with the TPG as the DG and UG were played sequentially (with DG prior to UG), while the TPG was conducted later, often with different individuals.

Table 1.3: Correlations between Dictator Game (DG), Ultimatum Game (UG) and Third-party Punishment Game (TPG) offers over 13 small-scale societies (Henrich *et al.* 2010a). Mean offers are displayed above the diagonal, with modal offers below. Correlation coefficients are presented first, with *p*-values in brackets.

	DG (*n*=13) [a]	**UG (*n*=13)**	**TPG (*n*=12)** [b]
DG (*n*=13)	-	0.79 (0.001)	0.68 (0.015)
UG (*n*=13)	0.84 (<0.001)	-	0.58 (0.049)
TPG (*n*=12)	0.81 (0.001)	0.79 (0.002)	-

[a] In Phase II of the *Roots of Human Sociality* project, the Orma only played the DG, and not the UG or TPG, hence why sample size is 13.

[b] Sample size is 12 for the TPG as the Dolgan/Nganasan only played the DG and UG.

Investigation of predictor variables from multivariate regressions across all societies combined (table 1.4; adapted from Henrich *et al.* 2014) indicate a broadly similar pattern for DG and UG offers, with market integration and world religion associated with an increase in DG and UG offers (although for the DG world religion only approaches significance). The only substantial difference is that age was positively associated with increased UG, but not DG offers. When compared to the

TPG, however, although market integration remains significant, increased income and household size were associated with decreased TPG offers, while higher household wealth increased TPG offers. Comparing within-societies indicates a similar profile. With the Sanquianga of Columbia, increased DG offers were predicted by increased education, larger household size and lower wealth, while for the UG these same variables were again reported, but additionally finding that older individuals gave more while income decreased offers. In contrast, for the TPG both increased education and income were associated with reduced offers, while wealth increased donations. Thus, education and wealth have opposite effects for the TPG compared to the UG and DG for the Sanquianga (Cardenas 2014). Among the Tsimane, UG offers were associated quadratically with income (such that high and low earners gave less) and positively with household size, while DG donations were also related with income quadratically and also negatively with wealth. The TPG presents a different profile, with increased Spanish language competency associated with decreased offers, as well as attending church, which had a positive impact on offers, although both were only approaching statistical significance (Gurven 2014).

Table 1.4: Results of regressions for predicting Dictator Game (DG), Ultimatum Game (UG) and Third-party Punishment Game (TPG) offers across multiple small-scale societies. Adapted from tables 4.3 (DG), 4.4 (UG) and 4.5 (TPG) in Henrich *et al.* (2014). *P*-value codes: $^{\cdot}$ $p<0.1$ * $p<0.05$ ** $p<0.01$

Variables	**DG**	**UG**	**TPG**
Market Integration	0.17 (0.04)**	0.14 (0.07)*	0.1 (0.05)*
World Religion (Adherence=1)	6.43 (3.64)$^{\cdot}$	9.96 (2.72)**	0.84 (3.03)
Sex (Female=1)	-2.58 (2.2)	-1.36 (1.96)	-1.04 (2.62)
Household Size	-0.11 (0.31)	-0.25 (0.27)	-1.1 (0.44)*
Education	1.15 (1.16)	0.96 (0.88)	-0.5 (1.45)
Individual Income	-0.003 (0.15)	0.14 (0.11)	-2.2 (0.97)*
Age	-0.02 (0.08)	0.14 (0.07)*	0.05 (0.09)
Community Size	-0.06 (0.09)	-0.26 (0.22)	0.13 (0.1)
Household Wealth	0.001 (0.01)	-0.007 (0.01)	1.28 (0.26)**
R^2	0.102	0.148	0.102

It therefore appears that although there is quite a strong correspondence between UG and DG behaviour, the association of both to the TPG is substantially weaker. This result, however, may in part be due to methodological differences. As noted above, the DG and UG were always played together, with the DG first, while the TPG was conducted at a later time with different individuals. Thus, it is possible that DG and UG scores and predictor variables were similar as a result of ‘order effects’. Individuals may have used their previous DG offer as a guide for their subsequent UG offer, similar to the ‘anchoring and adjustment’ bias reported in the human reasoning literature when making decisions under uncertainty (Tversky & Kahneman 1974). As supporting evidence of this effect, in Phase I of the project when the UG was not preceded directly by the DG, mean UG offers across the 3 societies who played both games were higher than DG offers by 37% (average mean UG offer=38%; average mean DG offer=27.7%), while modal offers in the UG were 47% higher (average modal UG offer=36.7%; average modal DG offer=25%: Hadza (Marlowe 2004a); Orma (Ensminger 2004); Tsimane (Gurven 2004b)). Conversely, across 13 societies in Phase II, mean UG offers were only 5% larger than DG offers (average mean UG offer=39%; average mean DG offer=37.2%), while modal UG offers were 6% larger (average modal UG offer=39.3%; average modal DG offer=37%: Henrich *et al.* (2010a)).

This pattern of results also questions the validity of these games as the threat of punishment is believed to increase cooperation (Fehr & Gächter 2002), yet in Phase II the threat of punishment did not significantly increase UG offers compared to the DG, while TPG offers were significantly lower than both (average mean TPG offer=32.1%; average modal TPG offer=31.7%: Henrich *et al.* 2010a). Indeed, the authors state that “offers in the UG and TPG measure some combination of internalized motivations (regarding fairness, equality, relative payoffs, etc.) and beliefs about the likelihood of punishment or rejection. In the DG there is no punishment … so we assume the DG measures intrinsic motivation" (Henrich *et al.* 2014: 115). Yet this is not what the observed pattern of offers indicates. Furthermore, when a 'threat of punishment' variable (using the mean 'minimum acceptable offer' for each population) was added to the regression for UG and TPG offers, the effect was not significant (see table S17 in Henrich *et al.* (2010a)). This indicates that threat of punishment had little impact on both UG and TPG offers, arguing that, in small-scale societies at least, these games may not be measuring what they intend to measure (Delton *et al.* 2010).

Thus, the conclusion previously drawn that "these [cooperative] values are widely internalized and expressed is exemplified by the fact that group-level average UG offers and PGG contributions are highly correlated across the societies in which both games were played" (Henrich *et al.* 2005: 813), may not be warranted, and cannot extend to all games used to investigate cooperative behaviour. Although some games appear to possess convergent validity – namely the DG and UG, and, perhaps more distantly, the TPG – this may be a result of methodological biases which need to be explored further. In sum, researchers wishing to compare levels of cooperation using different experimental games must do so with caution as the comparisons may not be valid; different games may not necessarily measure the same cooperative constructs. This may apply particularly to small-scale societies, as in large Western industrial societies convergent validity between different cooperative games appears relatively high (Peysakhovich *et al.* 2014). Furthermore, many of these games do not appear to measure the constructs they intend to measure, specifically regarding the threat of punishment in the UG and TPG.

External Validity

There is currently debate regarding to what extent game behaviour reflects real-life behaviour, and under what circumstances the two should in fact be expected to correlate. Beginning with the first topic, several studies have reported that these games possess little external validity. In the Ache, for example, no association was found between PGG or UG behaviour and real-world measures of food-production or food-sharing (Hill & Gurven 2004). Similarly, Wiessner (2009) reported that the Ju/'hoansi gave low offers and rarely punished in the UG and DG, yet when the earnings were subsequently divided between individuals and followed in real-life, high levels of both generosity and punishment were observed. In the most thorough study investigating the external validity of these games in small-scale societies, with the Tsimane, there was little correspondence between UG, DG or TPG behaviours when compared against several real-life measures of cooperation, including: participation in a communal project (well-digging); food-sharing; beer provisioning; consumption of other's beer; and provisioning for a village feast (Gurven & Winking 2008). The only significant results were that UG offers predicted the amount of food given to non-family members and that lower DG offers predicted an increased in beer consumption, although the latter was only approaching significance. However, both were non-significant once Bonferroni adjustments were made to account for multiple comparisons, indicating that these trends may have been statistical anomalies. This lack of association suggests that that factors which predict real-world cooperation may not be the same that predict cooperation in these games.

In spite of these seemingly negative results, an UG comparing two Tanzanian populations, the Pimbwe and the Sukuma, found evidence for external validity (Paciotti & Hadley 2003). Ethnographically, the Sukuma have been described as very generous relative to the Pimbwe, and this was reflected in mean UG offers, with Pimbwe offering 43% and Sukuma offering 61%. Similarly, offers in the DG and UG from New Guinea populations, such as the Sursurunga and the Au, are generally high, where norms of generosity are particularly pronounced (Tracer 2004; Bolyanatz 2014; Tracer *et al.* 2014). The evidence is thus equivocal, suggesting that these games may or may not reflect patterns of real-world interactions, potentially varying depending on the population or the measure of real-world cooperation used.

This then leads to the latter question; *should* everyday cooperative behaviour and game behaviour correlate? Despite previously claiming that "in many cases experimental play appears to reflect the common interactional patterns of everyday life" (Henrich *et al.* 2005; 795), and thus intimating that external validity should be relatively high, in more recent publications the *Roots of Human Sociality* team have stated that the experiments "may only apply to contexts involving monetary transactions and lacking long-term relationship-specific demands (for example, status, kinship) or reciprocity motivations. Our experiments probably do not, for example, generally cue and measure the social norms associated with complex kinship relationships, food sharing, or cooperative fishing" (Henrich *et al.* 2014; 90). They also add that these games reflect "contexts involving ephemeral interactions and money" (*ibid*; 91). According to this interpretation it is no surprise if game behaviour is uncorrelated with certain everyday cooperative interactions. It is therefore unclear what precisely these games are expected to measure, be it norms pertaining to market interactions specifically, or more generally to the wider social milieu. This ambiguity is, however, to be somewhat expected, given the variable nature of the results; in some societies real-world social dynamics appear to be reflected in these games, while in other societies they seemingly do not.

On this note it is worthwhile to add that one experiment which compared game behaviour using both money and a medium used in local exchange (betel nut) found no difference in either DG or UG behaviour between the two resources (Bolyanatz 2010). This suggests that the behaviour in these games is not just applicable to transactions involving money, but potentially to other goods as well. However, in other societies, such as among Samburu pastoralists, the medium of exchange can influence patterns of cooperation, as when the DG was framed in terms of meat-sharing (a local and widely-exchanged medium), offers were lower relative to an uncontextualised version using money (Lesorogol 2007). How different currencies influence cooperation in these games therefore remains relatively underexplored and in need of further empirical research to understand whether these games reflect everyday social dynamics or market interactions more specifically.

Although there has been a shift away from explaining behaviour in these games in terms of everyday dynamics by some (Henrich *et al.* 2014), most authors still interpret game behaviour in terms of everyday interactions. In the Hadza, for instance, low offers and high UG rejection rates were interpreted in terms of everyday interactions surrounding demand sharing of food (Marlowe 2004c, 2009). Similarly, the high levels of cooperation found within the Sanquianga were discussed in terms of long-term reciprocation and fairness with close others (Cardenas 2014). In fact, other than this change of emphasis by Henrich *et al.* (2014), the majority of researchers from Phase I (Henrich *et al.* 2004b) and Phase II (Ensminger & Henrich 2014) attempt to explain game behaviour in terms of everyday interactions (see also Gerkey 2013). This approach has intuitive appeal, yet the results pertaining to consistent a lack of external validity make these explanations tentative at best.

This shift in focus away from everyday dynamics may also explain why the 'pay-offs to cooperation' variable was dropped from Phase II of the project. However, given that everyday social dynamics appear to explain some of the variation in game behaviour, this choice is somewhat puzzling. Indeed, if both market integration and pay-offs to cooperation variables from Phase I are taken separately and regressed against UG offers (using data from Henrich *et al.* (2005)), the latter appears to explain more of the group-level variation in cooperative behaviour than market integration (table 1.5). In univariate models the adjusted R^2 value for pay-offs to cooperation is over twice that of market integration, suggesting that this variable is a better predictor of UG offers. Thus, despite playing down the potential role of everyday cooperative dynamics in explaining game behaviour in recent publications (Henrich *et al.* 2014), their own previous data suggest that general cooperative levels may be even more influential in predicting game behaviour than norms pertaining to markets. Thus, it is currently unclear to what extent everyday cooperative dynamics (i.e., those not specific to market interactions) explain behaviour in these games.

Table 1.5: Regression models predicting Ultimatum Game offers in three models containing combinations of market integration and pay-offs to cooperation variables (n=15). Data obtained from Henrich *et al.* (2005). *P*-value codes: ˙ $p<0.1$, * $p<0.05$, ** $p<0.01$, *** $p<0.001$

Variable	Market Int. Model	Pay-offs to Coop. Model	Combined Model[a]
Market Integration	0.013 (0.007) ˙	-	0.012 (0.005)*
Pay-offs to Coop.	-	0.027 (0.009)**	0.026 (0.008)**
Constant	0.312 (0.046)***	0.315 (0.3)***	0.246 (0.04)***
Adjusted R^2	0.147	0.367	0.522

[a] The coefficients for the equivalent model in Henrich *et al.* (2005) differ slightly, but are qualitatively similar. This is because the authors do not specify which populations or sub-groups they use in their analysis. Here I take the values from tables 1 and 2 from their publication, subsuming all sub-groups into the same population (e.g., grouping Sangu farmers and Sangu herders together).

Additional Influences on Game Behaviour

The above section suggests that everyday cooperative dynamics may only be partial explanations for game behaviour in small-scale societies. Additionally, although the *Roots of Human Sociality* team found that market integration and world religion (in Phase II) predicted variation in cooperation between societies (Henrich *et al.* 2005, 2010a), the data concerning differences at the individual-level within societies regarding market integration do not necessarily conform to theoretical predictions from this perspective (Smith, 2005). For instance, the Au and Gnau from Papua New Guinea are socioecologically similar, except that the Au possess higher levels of market integration (Tracer 2004). Contrary to expectations, however, differences in game behaviour were not particularly prevalent. Although the Au gave slightly more than the Gnau on average (Au=43%; Gnau=38%), the Gnau had a larger modal value (Au=30%; Gnau=40%), suggesting that differences in market integration had little effect on cooperation between these societies. Conversely, the Quichua and the Achuar live in the same village and have identical levels of market integration (Patton 2004), yet the Achuar gave significantly more than the Quichua (Achuar, mean=43%, mode=50%; Quichua, mean=25%, mode=25%).

Furthermore, focusing on within-society analyses, of the populations in which market integration data was obtained, only the Orma and the Shuar reported any individual-level association between market integration, indexed by participation in wage labour, and increased UG and DG offers (Ensminger 2004; Barrett & Haley 2014). In the Ache (Hill & Gurven 2004), Yasawa (Henrich & Henrich 2014), the Au and Gnau (Tracer 2004), and the Machiguenga and Mapuche (Henrich & Smith 2004) no effects of market integration (including participation in wage labour, cash-crops and proximity to markets) were reported to be significant at the individual level. A further exception is the Tsimane, and the results are somewhat counter-theoretical. Regarding distance to market, a crude proxy for market integration, Gurven (2004a, b) reported that individuals *farther* from a market town had higher median (by 10%) and modal (by 20%) offers than those closer to the market, although this only approached significance (*p*=0.06). Similarly, among the Pahari Kowra distance from main town had no effect on cooperation (Lamba & Mace 2011).

These results raise an apparent difficulty for market integration theory as to how exposure to markets can have little effect at the individual level, yet simultaneously explain a significant proportion of group-level behaviour (Smith 2005; Yamagishi 2005). For instance, R^2 values indicate that market integration explains 51% of the group-level variance in mean DG offers from Phase II (Henrich *et al.* 2010), yet the R^2 values across the games using individual offers are much lower and only explain between 10-15% of the variation when all variables are included, such as market integration, adherence to a world religion, age, sex, etc. (table 1.4). Furthermore, this strong group-level association between game offers and market integration in Phase II only holds for the DG, as simple Pearson correlations between market integration and mean and modal values of the other games (UG and TPG), although in the predicted direction, are non-significant (table 1.6). Thus, the proposed group-level association between market integration and game behaviour in Phase II only holds for the DG, while in Phase I the association between market integration and UG behaviour only approaches significance in a univariate analysis, although increases in significance when combined in a model with the 'pay-offs to cooperation' variable (table 1.5).

Table 1.6: Correlations between mean and modal Dictator Game (DG), Ultimatum Game (UG) and Third-party Punishment Game (TPG) offers and market integration. For consistency with Henrich *et al.* (2010a) the rural US population is included here. *P*-values are displayed in brackets.

	UG Mean (*n*=14)	**UG Mode (*n*=14)**	**DG Mean (*n*=15)**	**DG Mode (*n*=14)[a]**	**TPG Mean (*n*=12)**	**TPG Mode (*n*=12)**
Market Integration	0.43 (0.122)	0.34 (0.238)	0.71 (0.003)	0.48 (0.086)	0.31 (0.326)	0.3 (0.347)

[a] The Orma only played the DG and only mean offers were presented, meaning that modal DG offers for the Orma could not be obtaining and entered in to this analysis.

Related to the topic of within- and between-society inconsistency, a further variable reported to significantly predict an increase in DG and UG offers in Phase II, adherence to a world religion (Henrich *et al.* 2010, 2014), will be discussed. There is some inconsistency between how market integration and world religion variables were defined. Market integration was entered as a society-level variable, which the authors state is "to remain consistent with our definition of norms (as local equilibria)" (Henrich *et al.* 2010; 1482). Despite this claim, world religion was used as an individual-level variable in their analyses, seemingly for no theoretically justifiable reason; religion is also a norm, so for consistency ought to be analysed at the society level. When non-parametric Spearman's *rho* correlations are conducted between society-level world religion and DG, UG and TPG offers – due to world religion violating the assumption of normality (Shapiro-Wilk test; $p<0.001$), as for 10 of the societies levels of adherence to a world religion were >95%) – world religion is no longer significantly associated with increased offers in any game (table 1.7; data obtained from tables 3 & S3 of Henrich *et al.* (2010a)). Here we appear to run in to the opposite problem of that found with market integration: significance at the individual level yet a lack of significance at the between-society level. Furthermore, in the DG and UG, world religion loses significance when continent is entered as a control variable, which may partially control for shared history or similar environment. In the TPG the reverse occurs; a lack of association when not controlling for continent but statistical significance when continent is controlled for (tables 4.3, 4.4, & 4.5 in Henrich *et al.* (2014); see also SOM of Henrich *et al.* (2010a)). This suggests that adherence to a world religion may be confounded with continental differences, meaning that it is difficult to assess whether this effect is associated with religion specifically or is a consequence of similar environments or shared history.

Table 1.7: Correlations between mean and modal Dictator Game (DG), Ultimatum Game (UG) and Third-party Punishment Game (TPG) offers and society-level adherence to a world religion. Spearman's *rho* correlations were conducted due to the non-normal distribution of world religion. For consistency with Henrich *et al.* (2010a) the rural US population is included here. *P*-values are displayed in brackets.

	UG Mean (*n*=14)	**UG Mode (*n*=14)**	**DG Mean (*n*=15)**	**DG Mode (*n*=14)[a]**	**TPG Mean (*n*=12)**	**TPG Mode (*n*=12)**
Adherence to World Religion	0.23 (0.44)	0.08 (0.79)	0.08 (0.79)	0.2 (0.5)	0.03 (0.92)	0.08 (0.8)

[a] The Orma only played the DG, and only mean offers were presented, meaning that modal DG offers for the Orma could not be obtained and entered in to this analysis.

Although market integration, religious adherence and everyday cooperative dynamics may explain some of the variation in game behaviour, much is left to be understood. Other effects which may influence game behaviour will now be discussed, including context/framing effects and reputational influences (a specific form of everyday cooperative dynamics). Although discussed sequentially, these factors share a common theme: cross-cultural variation reflecting differences in how the game is perceived, as opposed to differences in cooperativeness if interpretation was constant across societies. In essence, without an understanding of how each society comprehends each game, cross-cultural comparisons are difficult to interpret as they may be measuring different constructs (Hagen & Hammerstein 2006; Baumard & Sperber 2010; Rai & Fiske 2010; Shweder 2010). The discussed effects by no means exhaust the range of possibilities of how societies may interpret the games differently, but are intended to elucidate this general principle.

Regarding contextual (or framing) effects, whether individuals or societies drew parallels between the games and real-world situations appears to greatly influence sharing behaviour. In the Orma, for example, the PGG was perceived as analogous to their *Harambee*, in which individuals donate money in aid of a public good. As such, Orma PGG behaviour strongly corresponded to real-life behaviour as wealthier individuals gave more than poorer individuals in the PGG, just as they would in an ordinary *Harambee* situation (Ensminger 2004). Similarly, in Kamchatka, Russia, individuals contributed highly to a PGG as they interpreted the game as analogous to everyday common-pool resource extraction (Gerkey 2013). Among the Sursurunga many players perceived the games (UG and DG) as analogous to everyday life, and consequently these individuals gave more than those who reported no connection (Bolyanatz 2014). Conversely, interviews revealed little association between the UG or DG and real-life interactions among Tsimane individuals (Gurven 2014), suggesting that they had no 'anchor' on which to base their behaviour in these games. Amongst the Ache, informants were explicitly informed, in an effort to ensure comprehension, that the UG was similar to food-sharing regarding the division of resources (Hill & Gurven 2004). As all other societies were devoid of this contextualisation, Ache results may not be directly comparable to other societies, although this is difficult to assess without a no-prime control condition. Although methods across field sites in Phase II were standardised in an attempt to prevent these contextualisation effects from occurring (Ensminger *et al.* 2014), it is impossible to control which societies perceive a resemblance between games and real-life, which appears to greatly influence levels of cooperation.

In terms of more formal manipulations of context within small-scale societies, Cronk (2007) conducted a trust game with the Maasai. In this game, one player can give a proportion of their stock to an 'investor', who subsequently multiplies this amount, and then decides whether to give player one back some money or not. By trusting the investor, the first player can gain more money by investing as opposed to merely keeping the stock, but only if they believe that the investor is trustworthy. The context was altered by either the inclusion or exclusion of the Maasai concept of *osotua*, which is a norm pertaining to sharing goods with others based on "obligation, need, respect, and restraint" (Cronk 2007: 352). It was found that when the *osotua* concept was made explicit, both transfers and expected investment returns declined, reflecting the norm that *osotua* sharing is based on need rather than equality. Similarly, Lesorogol (2007) performed contextualised and uncontextualised DGs on the Samburu pastoralists from Kenya, using sharing of a goat as the contextual cue. In everyday life a 'fair' share of a goat when asked by extra-familial members is usually the hind-leg, or about 20%. Correspondingly, in the contextualised DG the mean offer was 19.3%, while in the uncontextualised version the mean was 41.3%, with an increase in offer variance. It is also interesting to note that contextualising these games may actually *decrease* offers. As suggested by Cronk (2007) and Lesorogol (2007), the concept of 'fairness' as reflecting an equal split of the resources in these games may also be culturally and contextually dependent.

The role of reputation-management is a factor which Henrich *et al.* (2005) claim is not confounding their results because the games are both one-shot and anonymous. Yet stating that real-world dynamics can influence game behaviour, but that because of anonymity these games do not reflect reputational effects, is somewhat inconsistent (Smith 2005). Indeed, one of the authors from the *Roots of Human Sociality* team states that "it may be difficult to control for reputation effects and expectations about future interactions" (Lesorogol 2014: 357). Although later appearing to recant their view that games reflect everyday interactions (Henrich *et al.* 2014), the evidence amassed above suggests at least some role for everyday interactions influencing behaviour. Therefore the role of reputational differences between societies explaining the inter-cultural variability must be considered (Heintz 2005; Smith 2005).

Consistent with the hypothesis that reputational influences affect game behaviour, the Quichua and the Achuar are similar in terms of ecology and market integration, yet the Achuar gave significantly more than the Quichua (Patton 2004). Despite their surface-level similarities, among the Achuar there is a strong association between status and food-sharing, as well as a stronger focus on coalition formation, while these are less obvious among the Quichua (Patton 2004). It is therefore possible that differences in the importance of reputation drove the disparity in UG offers between these groups. To take the reverse situation, both the Au and Gnau gave similar offers regardless of differences in market integration (Tracer 2004), potentially because the effects of reputation are equally salient in both societies. As noted above when discussing theories for the evolution of cooperation, reputation and trust are particularly important components of both direct (Trivers 1971) and indirect (Nowak & Sigmund 1998, 2005) reciprocity. It is therefore interesting to note that among foraging populations where food-sharing data has been collected, both the Ache (Gurven *et al.* 2001; Allen-Arave *et al.* 2008) and the Lamalera (Nolin 2010) display significant levels of reciprocity, and both of these societies were particularly cooperative in the UG (Ache=48%; Lamalera=57%; Henrich *et al.* 2005). In contrast, food-sharing among the Hadza is less reciprocal (Hawkes *et al.* 2001), which may reflect a demand sharing/tolerated theft system (Hawkes 2000). Correspondingly, the Hadza were much less cooperative in these games, giving an average of only 33% in the UG in Phase I (Marlowe 2004a, c) and 26% in each of the three games played in Phase II (Henrich *et al.* 2014). As demand sharing is not contingent upon reputation and trust, signalling cooperativeness may be less important under this system, especially as individuals *take* from others, rather than give to them, so the benefit to displaying generosity is lower. Despite the claim of Henrich *et al.* (2014), these games may indeed reflect food-sharing dynamics to some extent, although this evidence is currently only suggestive at present.

This discussion also brings up the question of whether players believed that they were in a one-shot environment. If reputational influences impact cooperation in these games, as appears possible, then individuals do not act as if they are in an anonymous one-shot encounter. The potential role that reputation plays suggests that they may in fact act as if the game(s) may be repeated. An agent-based model exploring cooperative decision-making under uncertainty found that a cognitive bias towards cooperation in one-shot encounters can evolve when the cost of mistaking a one-shot interaction for a repeated interaction is higher than the potential benefit of repeated interactions (Delton *et al.* 2011). When potential gains from repeated cooperative interactions are high, a tendency towards ‘irrational’ cooperation in one-shot encounters can evolve.

Thus, it appears that societies may play the games differently from one another, depending on factors such as context/framing and reputational effects. Multiple other factors not considered here are also likely to influence game behaviour, including: group size (Boyd & Richerson 1988; Kollock 1998); socio-economic status (Nettle *et al.* 2011; Holland *et al.* 2012; Silva & Mace 2014); competition for resources (West *et al.* 2006); recent cooperative interactions (Fowler & Christakis 2010); and so on, potentially *ad infinitum.* If different societies are using different frames of reference when playing these experimental games, then cross-cultural results are not directly comparable as they reflect differences in interpretation of the game, as opposed to actual behavioural differences if the interpretation was held constant across societies (Baumard & Sperber 2010; Rai & Fiske 2010; Shweder 2010). Each population brings its own norms, expectations and interpretations to the experimental game, and the correspondence of these between each society has thus far been assumed based on maintaining a static protocol across all field-sites (Henrich *et al.* 2010a; Ensminger *et al.* 2014). However, this assumption may not be warranted, as not all societies appear to play the games identically. Indeed, Henrich *et al.* (2010b) note that “it seems likely that in New Guinea, behavioral games map onto prosocial norms that have little or nothing to do with markets or complex societies” (pp. 116). If, as would appear probable, this line of reasoning can be extended beyond merely Papua New Guinea, then this is a major problem for the *Roots of Human Sociality* team as it questions both their methodological assumptions and their subsequent conclusions. Without more thorough and systematic research investigating these influences within each society in which the games are employed, it is impossible to guarantee that what is being measured is identical across all sites.

Theoretical Interpretation of Results

We now turn to how these games have been interpreted and assimilated with the theories of cooperation outlined in the first section of this chapter. The *Roots of Human Sociality* team interpret the positive association between market integration and game offers as a result of a set of ‘market norms’ which co-evolved with increasing societal complexity to facilitate exchange between unrelated and unknown others (Henrich *et al.* 2005, 2014). According to this interpretation, these cooperative sentiments extend to strangers, permitting large-scale cooperative projects to occur, which are essential for the existence of modern complex societies. Meanwhile, adherence to a world religion is believed to be associated with cooperativeness due to a co-evolutionary process whereby cooperation in large-scale societies is driven by norms of fairness towards unrelated individuals propounded by world religions (Atran & Henrich 2010; Henrich *et al.* 2010a). These results have been interpreted as evidence for cultural group selection (CGS) as individuals are believed to acquire these norms by social learning, and then that "competition among social groups, religions, and institutions has sculpted these group-beneficial social norms over the course of cultural evolution" (Henrich *et al.* 2014: 134). However, there are several potential problems associated with this interpretation which will be discussed in greater detail below. These include: i) the interpretation of game behaviour; ii) that cooperative behaviour is acquired via cultural transmission; iii) an assumption that group differences are a result of between-group competition; iv) ignoring within-group differences in cooperative behaviour; v) the assumption that cooperation is only beneficial to the group, not the individual; and vi) a lack of testing alternative theories.

i) *Interpretation of game behaviour.* Interpretation of these games as evidence for CGS in response to market norms rests upon these games reflecting "ephemeral interactions and money" (Henrich *et al.* 2014: 91). If they reflect everyday social dynamics then this 'market norm' interpretation may not be warranted. However, the evidence discussed above suggests that individuals may act as if the games will be repeated (Delton *et al.* 2011), particularly regarding the role of reputation (meaning that they are not ephemeral interactions). Additionally, participants may play similarly with money relative to everyday trade items, such as betel nut, meaning these results may not be specific to monetary transactions (Bolyanatz 2010). This suggests that game behaviour may represent more general norms of distribution and cooperation, not just ephemeral ones involving money. These games, therefore, may not tap specifically into 'market norms', meaning that the interpretation of them as such may be erroneous. If true, these games cannot be used as evidence for evolved market norms promoting cooperation in association with increased social complexity.

Additionally, everyday social dynamics may explain *more* of the variation in group-level game behaviour than market integration (table 1.5), while the explanatory power of market integration, although somewhat consistent, appears quite low (tables 1.4 & 1.6). The evidence for adherence to a world religion in explaining game behaviour is even less compelling, as individual-level religious adherence appears confounded with geography, while group-level religious adherence is uncorrelated with offers in the DG, UG and TPG (table 1.7). Thus, in addition to potential misinterpretations over how individuals play these games, the evidence also suggests that the association between cooperation and market integration is weaker than often presented, while religion may play even less of a role in promoting cooperative behaviour in these games.

ii) *Individuals learn cooperative behaviour via social learning*. This is central to CGS hypotheses, as biased social transmission is essential for minimising within-group differences, making selection between groups stronger than selection within groups. This is generally theorised to be a result of either conformism (copying the most common behaviour: Henrich & Boyd 1998) or pay-off based transmission (e.g., copying prestigious or successful individuals: Henrich & Gil-White 2001), both of which can homogenise behaviour in groups (Boyd & Richerson 1985; Richerson *et al.* 2016), although other transmission mechanisms are possible. Although Western populations display some evidence for these social learning strategies (Efferson *et al.* 2008; Molleman *et al.* 2014), when similar protocols were conducted among Bolivian pastoralists the effects of conformism and pay-off based transmission were minimal (Efferson *et al.* 2007). In the one study which explored whether small-scale societies specifically learn cooperative behaviour socially, using a repeated PGG, little evidence of conformism or pay-off based transmission was found (Lamba 2014). This indicates that cooperative behaviour, especially in small-scale societies, may not be learned to a great extent via biased transmission, questioning the validity of this assumption (although further tests are required). Without this mechanism to homogenise behaviour within groups, individual-level selection is stronger and the potential for cultural group selection is significantly weakened.

iii) G*roup differences are a result of between-group competition.* The CGS approach seemingly equates group differences with group selection. For example, in a recent review Richerson *et al.* (2016) cite large differences in UG behaviour between the Pimbwe and Sukuma (Paciotti & Hadley 2003) as resulting from stronger institutional norms which promote cooperation and the sharing of public goods in the Sukuma. While this may be true, contrary to their interpretation it is not necessarily evidence for CGS. Differences between groups stem from various factors, which could be either genetic, socioecological or cultural (Whiten *et al.* 1999). Without controlling for genetic and socioecological differences it is impossible to determine whether a behaviour is a result of cultural transmission or not (and even then, behaviours which are the result of cultural transmission need not be a result of CGS). For example, among the Sukuma cooperation may be more prevalent in everyday life, while Pimbwe households may be more economically independent and self-reliant (note that this is just hypothetical). As a more concrete example, rice farming requires more cooperation than wheat farming, which can be done relatively independently. Over hundreds or thousands of years these differences in subsistence have resulted in descendants of rice farmers seemingly possessing a more ‘collectivistic’ mentality, while descendants of wheat farmers are much more ‘individualistic’ (Talhelm *et al.* 2014). These differences are based on subsistence and ecology, not necessarily CGS. Thus, group differences are not evidence for group selection. One must be wary about confusing group-level differences for group selection; a ‘herd of fleet deer’ will also appear as a ‘fleet herd’. However, as individual-level selection is usually a stronger force (Gardner & Grafen 2009) it is the fleetness of individuals (an individual-level explanation) which is being selected for, rather than the fleetness of the herd (a group-level explanation: Williams 1966), although this needs to be assessed on a case-by-case basis.

iv) *Within-group differences are often ignored.* Further arguing against this CGS interpretation is evidence amassed from looking at variation *within* groups. Although the ‘group’ in group selection can refer to several different levels (e.g., band nested within region nested within state; hence the theory of ‘multi-level’ selection), within CGS ‘group’ generally refers to the larger ethnolinguistic unit under which individuals define their identity (Richerson & Boyd 2005; Richerson *et al.* 2016). Examples include the Nuer, Hadza, Maasai, etc. Thus, for CGS to operate at this level, within-society variation needs to be low across multiple camps and localities. However, when multiple camps are sampled from within a single small-scale society, large amounts of variation in cooperativeness are often reported (Marlowe 2004a; Gurven *et al.* 2008; Lamba & Mace 2011, 2013). In the most comprehensive within-society study to date among the Pahari Kowra, ~4% of the variation in PGG donations, ~18% of variation in salt distributions and ~14% of variation in UG offers occurred at the village level (Lamba & Mace 2011, 2013). In comparison, the amount of between-society variance in UG behaviour from Phase I over 15 societies was ~12% (Henrich *et al.* 2005). This suggests that within-group variation in cooperative behaviour can equal, or even exceed, between-group variation. CGS may therefore not be required to explain variation in cooperative behaviour between different populations.

v) *Cooperation is only beneficial to the group, not the individual.* It is a common claim in the CGS literature that human cooperative capabilities do not increase an individual's inclusive fitness, so must have evolved by CGS and are therefore 'group adaptations' (Boyd *et al.* 2003; Boyd & Richerson 2009; Henrich *et al.* 2014; Richerson *et al.* 2016). This is most clearly seen in the literature regarding 'strong reciprocity', meaning a tendency to punish non-cooperators at a personal cost, which is claimed to require group selection (cultural or genetic) to evolve (Gintis 2000; Fehr *et al.* 2002; Boyd *et al.* 2003; Fehr & Henrich 2003; Bowles & Gintis 2004; Fehr & Fischbacher 2004b). However, when these models are reformulated they can be shown to rely upon inclusive fitness benefits, so do not necessarily require group selection (Lehmann *et al.* 2007b; West *et al.* 2007b, 2011; Powers & Lehmann 2013). Similarly, experimental studies (e.g., Fehr *et al.* 2002; Fehr & Fischbacher 2004b; Henrich *et al.* 2005, 2010a) often claim that cooperation or punishment is 'altruistic' (i.e., against individual self-interest) from one-shot encounters. Yet in repeated situations these seemingly 'altruistic' individuals increase levels of cooperation, resulting in greater pay-offs for themselves (Gürerk *et al.* 2006; Krasnow *et al.* 2012), meaning that the behaviour is consistent with self-interest and mutual benefit, rather than group-interest and altruism (Trivers 2004; Hagen & Hammerstein 2006; Delton *et al.* 2011). Furthermore, recent experiments have explicitly pitted predictions of a CGS-evolved 'norm psychology' (in which punitive behaviours benefit the group) against predictions from a self-interested model (in which punishment brings greater future cooperation (a direct fitness benefit) to the punisher). These studies found that behaviour conformed to the latter, suggesting that cooperative behaviour is not for the good of the group, but a way to maximise individual fitness (Krasnow *et al.* 2012; see also Burton-Chellew *et al.* 2015). Proponents of CGS often seem to conflate the occurrence of group-level traits, such as institutions or food-sharing norms, with group-level adaptations (West *et al.* 2011), yet just because there are group-level traits it does not mean that they are group adaptations. Many such phenomena can be explained via inclusive fitness benefits. For instance, Powers & Lehmann (2013) devised a model to demonstrate how institutions and punishment can evolve via individual-level selection, without the need for group selection.

vi) *A lack of testing alternative theories.* While these economic games are useful for assessing levels of cooperation and punishment, the results are often difficult to fit into the wider literature on the evolution of cooperation. This is because many of these theories require assortativity of cooperative partners: that is, preferentially interacting with certain individuals over others. This could be kin (kin selection: Hamilton 1964), previous sharing partners (reciprocity: Trivers 1971), those with a reputation for cooperativeness (indirect reciprocity: Nowak & Sigmund 2005), etc. Given the anonymous nature of these games, such that individuals do not know who they are cooperating with, it is difficult to test these theories to assess whether they fit the data better than a CGS approach (although the importance of reputation discussed above suggests that reciprocity (direct or indirect) may in fact play a significant role (see also Delton *et al.* (2011)).

When comparing theories of cooperation many researchers who espouse a CGS approach to cooperative evolution often contrast CGS with a ‘mismatch’ hypothesis (Chudek *et al.* 2013; Henrich *et al.* 2014; Zefferman 2014; Richerson *et al.* 2016). They state this ‘mismatch’ hypothesis posits that “prosocial preferences evolved genetically in our hunter-gatherer past where one-shot anonymous interactions were rare and these preferences are misapplied in modern laboratory settings" (Zefferman 2014: 358). This is misleading for two reasons. Firstly, the 'mismatch' interpretation is fundamentally a debate not over evolutionary rationale, but over human cognitive capabilities (Hagen & Hammerstein 2006). The debate concerns whether the cooperative behaviours observed in these anonymous one-shot experiments are the behaviours of 'rational' actors who understand the experimental context and display group-beneficial behaviours (the CGS interpretation: e.g., Chudek *et al.* 2013; Henrich *et al.* 2014; Zefferman 2014), or whether game behaviour reflects 'misfiring' behaviours adapted for other contexts, such as those involving reputation or reciprocity in repeated interactions, which may otherwise be adaptive (the 'mismatch' interpretation; e.g., Hagen & Hammerstein 2006; Delton *et al.* 2011; West *et al.* 2011). If game behaviour is not a consequence of altruistic prosocial preferences towards the wider group, but rather a misfiring of otherwise individually-adaptive strategies, then these cooperative behaviours towards the wider group are not altruistic and no longer require group selection to be explained (Krasnow *et al.* 2012; Burton-Chellew *et al.* 2015).

A second reason this CGS-mismatch dichotomy is misleading is because it only compares a cultural evolution approach (CGS) to an 'evolutionary psychology' approach (that human behaviour evolved in small-scale hunter-gatherer societies, so may now misfire in modern environments to which we are not adapted). There are three main disciplines by which to study human behaviour from an evolutionary perspective: cultural evolution, evolutionary psychology and human behavioural ecology (Sear *et al.* 2007; Brown *et al.* 2011). By only contrasting two of these approaches, this debate ignores the role that behavioural ecology can play in predicting cooperative behaviour. Human behavioural ecology simply assumes that humans adapt their behaviour to their current environment in order to maximise reproductive success (Winterhalder & Smith 2000; Borgerhoff Mulder & Schacht 2012; Nettle *et al.* 2013a). This approach is 'mechanism neutral', such that the proximate mechanisms resulting in this adaptation are often unspecified, meaning they could be genetic, culturally learned, individually learned, resulting from phenotypic plasticity, or otherwise (Brown *et al.* 2011; Mace 2014). By merely contrasting CGS and mismatch hypotheses, one is given the misleading impression that cross-cultural variation in cooperative behaviour must be a result of social learning, and, by extension, CGS (e.g., Zefferman 2014). However, human behavioural ecology makes similar predictions regarding differences between groups, such that they will exist when faced with a different socioecology. As evidenced from the food-sharing data above, even among hunter-gatherers cooperative behaviour can be incredibly variable, with some societies sharing food according to reciprocity (Allen-Arave *et al.* 2008; Nolin 2010), while in others tolerated theft/demand sharing appear to explain patterns of resource distribution (Peterson 1993; Bliege Bird & Bird 1997; Hawkes *et al.* 2001). Furthermore, differences in socioecology can also explain patterns of cooperation *within* societies – such as variation between camps in experimental games with the Pahari Kowra (Lamba & Mace 2011) or socio-economic status being associated with differential levels of cooperation within UK cities (Nettle *et al.* 2011; Holland *et al.* 2012; Silva & Mace 2014) – where cultural norms at the ethnolinguistic level ought to be held relatively constant. Thus, a human behavioural ecology approach predicts that different cooperative mechanisms (kin selection, reciprocity, demand sharing, reputation, etc.) may be at work in different environments, meaning that these theories need to be considered when contrasted with CGS, not just potential ‘mismatch’ hypotheses rooted in evolutionary psychology.

In sum, the interpretation that economic game behaviour among small-scale societies is evidence for cultural group selection can be questioned on several fronts. Together, these criticisms weaken the case that human cooperative tendencies evolved via CGS. Cooperative behaviour does not appear beneficial solely to the group, meaning that group-level selection is not required to explain how individually-costly behaviours evolved, because these behaviours only appear costly in the short-term: in the long-term these behaviours may increase an individual’s inclusive fitness. This is not to say that CGS played no role in the evolution of human cooperation, only that the current evidence does not provide conclusive proof to exclude individual-level selection as a plausible alternative explanation. Additionally, one of the most important problems highlighted here is that, given that the majority of economic games are anonymous (i.e., individuals do not know who they are giving to), the current stock of these games may be insufficient to test many of the other theories for the evolution of cooperation against one another.

Conclusions

The results of this review can be summarised as follows:

1) *Convergent validity*. Simply because two games appear, or are designed, to measure cooperation, it is no guarantee that they assess the same underlying cooperative constructs. Some methodologies show little association between one another, making comparisons using different experimental games problematic. The DG and UG appear similar, although this is possibly a methodological artefact of order effects. The TPG also appears related to the UG and DG, although not as strongly. Thus, different games seemingly do not tap into a single unitary construct

of ‘cooperation’, meaning that different games may be measuring different forms of cooperative behaviour.

2) *Game results can be contrary to theoretical expectations*. The finding that UG offers were identical to DG offers in Phase II, as well as TPG offers also being lower than the DG, is worrisome as both the UG and TPG contain a threat of punishment which should increase offers. As the threat of punishment had little effect on both TPG and UG offers, this highlights that these games may not be measuring what researchers intend them to measure, at least when applied in small-scale societies.

3) *External validity*. Game behaviour may be unrelated to real-life cooperative dynamics in some societies, although in others an association may exist. The extent to which games are conceptualised is currently unclear, with some authors stating that games reflect short-term monetary interactions and not everyday life, while others interpret behaviour using the latter. This review finds that although both market integration and everyday social dynamics may have an effect on game behaviour, the effects appear inconsistent across societies and vary in magnitude.

4) *Other sources of cross-cultural variation*. Effects unrelated to market integration, and which vary considerably across societies, are likely to influence behaviour in these games. This includes the extent to which individuals or societies draw parallels between the game and real-life (framing effects) and the impact of reputational influences on cooperative behaviour. These effects are likely to vary between populations, meaning that different societies may not be playing the same game. Behaviour from different societies may not therefore be directly comparable, making cross-cultural variation difficult to interpret.

5) *Theoretical interpretation of results.* Despite generally being interpreted as support for cultural group selection, the evidence presented here suggests that many

of the foundations upon which these claims are made can be questioned. These include: i) misinterpreting game behaviour as solely reflecting ‘market norms’, and not everyday social interactions; ii) a lack of evidence that cooperative norms are learned by cultural transmission; iii) mistakenly equating group differences with group selection; iv) ignoring differences in cooperation within-groups, which cannot be explained by CGS; and v) Interpreting behaviours as group-beneficial when they can be explained by inclusive fitness benefits; and vi) not testing other theories for the evolution of cooperation.

Future Directions for Experimental Games and Aims of PhD

For potential future experiments utilising games in small-scale societies, recommendations largely depend on what one wishes to extract from these games. To investigate market-based norms specifically, these anonymous, one-shot, methodologies may be somewhat adequate. However, it does appear that everyday social dynamics do influence behaviour in these games to some extent, meaning that they do not solely measure ‘market norms’. Alternatively, if one wishes to explore cooperative behaviour more generally, although there does appear to be some correspondence between games and everyday social life, this association is quite variable across different populations. Thus, alternative methods may be required. One such method is to employ a semi-anonymous approach, in which players know with whom they are cooperating. This approach has been applied with the Tsimane to investigate conflict and cooperation among women, using a game where individuals took beads off one another (Rucas *et al.* 2010). This non-anonymity allows an exploration of how the relationship between two individuals affects cooperation, such as the role of kinship, reciprocity and reputation. Non-anonymity also increases the ecological validity of the measure, as individuals in small-scale societies rarely interact anonymously. Combining this with making the games simpler and more intuitive to comprehend would also not only lower the possibility of misunderstandings, but also reduces the risk of different societies interpreting the game in different ways. An example of this increased simplicity is the 'gift game', in which individuals are given a number of resources and asked who they would like to share them with. This has been conducted with the Hadza (Apicella *et al.* 2012), Saami reindeer herders (Thomas *et al.* 2015), Mosuo agriculturalists from China (He *et al.* 2016) and the BaYaka hunter-gatherers in Congo (Chaudhary *et al.* 2015, 2016) in order to investigate social dynamics and social networks. It should be noted, however, that the gift game is not a social dilemma (Kollock 1998) as individuals cannot keep any resources for themselves, so it is not a measure of how cooperative an individual is (although it may be informative regarding cooperative social networks).

To date, experimental games have largely been used to explore general levels of cooperation in small-scale societies, rather than test specific theories regarding the evolution of cooperation (other than CGS). One exception is Marlowe (2004b), who analysed patterns of Hadza economic game behaviour against several hypotheses of food-sharing. He concluded that their low offers in the game reflected a system of demand sharing, where resources were demanded by others, even if they did not want to share. A further notable example of testing explicit evolutionary theories with these games occurred with agro-pastoralists in China (Wu *et al.* 2015). This study investigated the role of kin dispersal on cooperation (using a DG, PGG and a resource dilemma game with tea, similar to the salt distribution protocol described above from Lamba & Mace (2011)) using different populations living in the same area but with different levels of female dispersal. They found that villages with low female dispersal rates were less cooperative, suggesting that limited kin dispersal has the potential to increase competition for resources, not merely promote cooperation. Additionally, UG's conducted in Dominica with a horticultural population explored how kinship influenced cooperation (Macfarlan & Quinlan 2008). Men with more brothers in the community were found to donate more, while women with more brothers donated less, suggesting that kinship bonds can influence patterns of cooperation, albeit in different directions depending on sex.

With these more specific tests of evolutionary hypotheses in mind, it has been argued that "future experimental methods should be tailored to specific research questions [and] show reduced anonymity … to inform and redirect ethnographic study and build scientific theory" (Gurven & Winking 2008: 179). Building upon this, the aim of this PhD is to devise an ecologically valid experimental method for exploring cooperative dynamics, with specific application regarding food-sharing among hunter-gatherers. Here, I develop two games which explicitly test theories of cooperation among foragers using a semi-anonymous methodology. I devised these games to allow both an exploration of how cooperative individuals are (i.e., how many resources they share with others), as well as who they cooperate with (e.g., kin, reciprocating partners, etc.). This combination allows one to bridge the gap between traditional experimental economic games on one side (Henrich *et al.* 2004b, 2005; Ensminger & Henrich 2014), and research regarding the evolution of cooperation and food-sharing patterns among hunter-gatherers on the other (Kaplan & Hill 1985; Bliege Bird & Bird 1997; Hawkes *et al.* 2001; Gurven 2004d). Despite some notable exceptions (Marlowe 2004c; Macfarlan & Quinlan 2008; Wu *et al.* 2015), in small-scale societies these have tended to remain somewhat distinct enterprises; the present work aims to build upon this previous work and further connect these academic traditions. It is hoped that this thesis will introduce a novel and externally valid experimental measure of cooperation which can be used to inform and further scientific theory regarding the evolution of cooperation, particularly food-sharing, among hunter-gatherers specifically, and humans more broadly.

Structure of Thesis

This thesis aims to explore the role of experimental games in understanding the evolution of human cooperation, with particular application to food-sharing in hunter-gatherer societies. The next chapter (Chapter 2) focuses on the study population, the Agta, giving an ethnographic background and a brief introduction to hunter-gatherer research more generally. Chapter 3 details the field site and research methods used during fieldwork. Subsequent chapters detail the substantive results of this study and test hypotheses derived from the theories for the evolution of cooperation detailed above to explain patterns of cooperation among the Agta. A brief synopsis of the aims for each of these chapters will be given now, with more detailed theoretical background and hypotheses discussed in the specific chapters.

In Chapter 4 I explore variation in levels of cooperation (the amount individuals cooperate) among individuals and camps. This chapter aims to explicitly test predictions made by cultural group selection, specifically that between-camp variation ought to be low as social learning mechanisms homogenise cooperative behaviour among ethnolinguistic groups. Alternative hypotheses derived from human behavioural ecology are also assessed to explore whether variation in cooperative behaviour is consistent with individuals attempting to maximise their inclusive fitness in a given socioecology.

In the next chapter (Chapter 5) I present an analysis of the factors which predict who individuals cooperate with, exploring the respective roles of kin selection, direct reciprocity, indirect reciprocity and cooperative homophily in explaining hunter-gatherer food-sharing. In this chapter, levels of producer control – whether resources are *given to* others (high producer control) or *taken by* others (low producer control) – are also contrasted to explore how patterns of resource transfers differ under these two systems, with implications for understanding cross-cultural variation in food-sharing practices among hunter-gatherers.

Chapter 6 takes a biological market approach to understanding social dynamics and aims to moves beyond ‘in-kind’ cooperative exchanges to explore how differences in an individual’s ‘market value’ influences decisions with whom to cooperate and interact. This includes an investigation of how reputational factors, such as foraging skill, storytelling ability, medicinal knowledge and camp influence, affect who individuals choose to cooperate and interact with.

In the final results chapter (Chapter 7) I adopt an ontogenetic perspective to examine the development of both levels of cooperation and who individuals cooperate with, a perspective often absent from studies investigating cooperative behaviour. As such, this chapter provides a novel insight into how cooperative behaviour is acquired and alters over the life-course among a foraging population.

A final chapter summarises the main findings of this research project, integrates the findings into the wider literature regarding the evolution of cooperation and provides suggestions for future research employing similar experimental methods.

Chapter 2 Agta Ethnography

This chapter presents an ethnographic description of the Agta from north-east Luzon, the Philippines, and is intended to provide a general and broad background to the study population covering several aspects of Agta life. Topics discussed include: location, history, demography, life history, social organisation, subsistence, marriage, religious and ritual life, and external influences affecting the Agta. Prior to this, a brief introduction to the topic of hunter-gatherer research will be provided to place this study within a wider conceptual, historic and evolutionary context.

Why Study Hunter-Gatherers?

Hunter-gatherers (or foragers) are particularly important targets of study as they best approximate the subsistence and social organisation lived by humans for ~95% of our species' existence (Lee & Daly 1999) before the development of agriculture ~12,000 years ago. Hunter-gatherer populations are therefore our best extant models for understanding the context in which many of our species' derived traits evolved (although these comparisons are by no means straightforward, as discussed below). Compared to our closest living common ancestors, the African apes, these derived phenotypes include: life-history traits, such as extended lifespan, female reproductive senescence (menopause), increased infant dependency and shorter inter-birth intervals (Gurven *et al.* 2000b; Kaplan *et al.* 2009; Kramer 2010); socio-cognitive capabilities, such as extensive cooperation, especially among non-kin, reliance on tools and cumulative culture, and enhanced other-regarding preferences (Burkart *et al.* 2009; Tennie *et al.* 2009; Tomasello *et al.* 2012); and differences in social organisation, including pair-bonding, multi-level societies and increased group sizes (Chapais 2010; Hill *et al.* 2011; Dyble *et al.* 2015).

Despite their theoretical importance, modern hunter-gatherers are notoriously difficult to characterise across one dimension (although each likely contains a kernel of truth). Foraging societies appear simple to define according to subsistence, in that they procure all of their calories from wild food without recourse to agriculture. However, this simple definition belies much variability in behaviour and social organisation (Bettinger 2001; Ames 2004; Kelly 2013), questioning how useful a conceptual tool this definition is for explaining hunter-gatherer behaviour. Additionally, it is difficult to strike a definitive line between foragers and food-producers as many foraging populations derive some resources from agriculture, either grown by foragers or traded with neighbouring farmers (Spielmann 1986; Headland 1987b). Many small-scale societies also practice a mixed-economy of foraging and small-scale horticulture (so called 'forager-horticulturalists'), making definitions based solely on subsistence problematic, especially in the present day.

The most prominent depiction of forager societies stems from the 1968 *Man the Hunter* conference in which it was proposed that "(1) they live in small groups and (2) they move around a lot" (Lee & DeVore 1968: 18). However, this definition does not typify all hunter-gatherers, such as those from the northwest coast of North America who lived in large groups and were largely sedentary (Ames 1994, 2003). Others define hunter-gatherers more psychologically, stating that there is a forager 'mode of thought', which prioritises autonomy, sharing and other traits common to many forager societies, even when these populations have recently given up a foraging mode of subsistence (Barnard 2004). The extent to which this characterises hunter-gatherers from larger and more settled populations (e.g., the northwest coast) is unclear, however. As an aside, given this lack of a universal consensus, perhaps the most useful definition of hunter-gatherers was given by Nurit Bird-David during the 10th Conference on Hunting and Gathering Societies in 2013, who suggested, somewhat tongue-in-cheek, that "hunter-gatherer societies are what hunter-gatherer researchers study". Nonetheless, it does appear that, despite many attempts, it is difficult to define all hunter-gatherers according to one universal criterion.

One approach to simplify this variability is to subdivide hunter-gather populations into either 'simple' or 'complex' societies (Keeley 1988), although note that 'simple' merely refers to social structure and does not mean that it was necessarily the basal human state, such that 'complex' hunter-gatherers evolved from 'simple' ones (Rowley-Conwy 2001). This dichotomy also corresponds well with other forager categorisations, such as between immediate- and delayed-return societies (Woodburn 1982), or foragers which either store or do not store resources (Testart 1982). 'Simple', or immediate-return, hunter-gatherers are those most-closely allied with traditional definitions of hunter-gatherers, such as from the *Man the Hunter* conference, as they live in small highly-mobile bands, are egalitarian and do not store food. In contrast, 'complex', or delayed-return, hunter-gatherers live in larger societies with increased sedentarisation, food storage, and often a stratified social structure with increased territoriality. While the majority of extant forager societies conform to the 'simple' hunter-gatherer category, ethnographically known 'complex' hunter-gatherers existed predominantly in the northwest coast of North America (Ames 2003), but also include the Ainu from northern Japan (Sakaguchi 2009).

One must also be cautious regarding generalisations when using modern hunter-gatherers to infer our evolutionary past. Although it is often assumed that 'simple' hunter-gatherers most closely represent our species-typical ancestors (Rowley-Conwy 2001), the form hunter-gatherer societies take is highly variable and greatly dependent on social and ecological circumstances (Kelly 2013). Furthermore, modern hunter-gatherers are not pristine primitives unaffected by external social factors, but are embedded within wider societies with whom they have contact, trade and cultural exchanges (Spielmann 1986; Headland 1987b; Headland & Reid 1989; Kent 1992; Solway & Lee 1992; Stiles 1992; Spielmann & Eder 1994; Guenther 2007). One should therefore be cautious about extrapolating the patterns found today among 'simple' hunter-gatherers into the past, especially before the advent of farming and interaction with agricultural populations.

Further muddying these waters, the Pleistocene (prior to 11,500 year ago) climate was colder, less productive and more variable compared to the present day (Bettinger 2001). The environmental conditions faced by Pleistocene foragers would therefore have been dramatically different to those faced today, potentially necessitating differences in behaviour, such as an increased reliance on storage, especially in higher latitudes. Food storage among hunter-gatherers appears particularly widespread in colder and more seasonal habitats, such as in Palaeolithic Europe (~30,000 to 10,000 years ago; Soffer 1989) and ethnographically-known hunter-gatherers from North America (Morgan 2012). As described above, this is associated with a social structure considerably different from that of many present-day hunter-gatherers, such as decreased mobility and food storage. This may have resulted in patterns of social and economic stratification not observed in many 'simple' egalitarian hunter-gatherers today. Indeed, archaeological studies have found evidence for wealth inequality (and, by inference, social stratification) in forager groups (e.g., Mesolithic Siberia 6,000-7,000 BC; O'Shea & Zvelebil 1984: late Palaeolithic Europe ~15,500 BC; Vanhaeren & d'Errico 2005), indicating that some Eurasian societies may have been 'complex' hunter-gatherers. Similarly, Ames (2010) discusses the archaeological bias that the occurrence of 'simple' hunter-gatherers is often assumed in archaeological assemblages, while for 'complex' societies the evidence has to be actively sought. This may potentially give the misleading impression that all hunter-gatherers in the archaeological record are of the 'simple' variety, at least until proven otherwise. Rowley-Conwy (2001) presents a similar discussion, arguing that the progressivist notion of a transition from 'simple' to 'complex' hunter-gatherers in the archaeological record should not be assumed, but rather propounds a behavioural ecological interpretation in which different types of society can exist under different socioecological conditions. Indeed, recent archaeological evidence has demonstrated that large sedentarised hunter-gatherer settlements in the Levant occurred ~20,000 years ago, long before the advent of agriculture (Maher *et al.* 2012a, b). Despite this, it is still often assumed that prior to the Holocene era (~11,500 years ago) the majority of forager bands were of the 'simple' kind (Shultziner *et al.* 2010).

Extinct hunter-gatherers may therefore have been very different and more variable than the predominantly 'simple' hunter-gatherers observed today, although this requires further empirical work by archaeologists and paleoanthropologists. The take-home message from this brief discussion is that forager societies can be incredibly variable in response to socioecological differences. It is this plasticity, rather than over-simplified extrapolation of current states to human evolutionary history, which should be the focus of scientific study in hunter-gatherer research (Kelly 2013). The hunter-gatherers of today are probably vastly different to hunter-gatherers 20,000 years ago, yet they likely respond to socioecological challenges in similar ways. Despite the arguments against using modern forager populations to infer our evolutionary history, they still remain our best analogue for modelling the selective pressures humans faced prior to agriculture. However, given the diversity of forager societies such inferences should not be naively accepted at face-value. This thesis therefore adopts a ‘behavioural ecology’ approach and predominantly focuses on whether Agta cooperative behaviour is adaptive in their present environment, rather than using the Agta as a direct ‘window into our evolutionary past’ to infer past forager behavioural adaptations (Caro & Borgerhoff Mulder 1987; Foley 1995), although the latter can be made with caution and may be valid if the social and ecological contexts are comparable. With this background in mind, we now turn to an ethnography of the Agta, an extant hunter-gatherer population and the focus of the current research project.

Agta Ethnography

Location

Several Agta – also known as ‘dumagat’ (meaning ‘people of the sea’) – populations exist on Luzon island, the Philippines (figure 2.1), such as in Casiguran (Headland 1989; Early & Headland 1998) and Cagayan (Estioko-Griffin 1985). However, the Agta population which are the focus of this study are from Isabela Province north-east Luzon, situated in the Northern Sierra Madre Natural Park (NSMNP: figure 2.2). Specifically, the current research focuses on the Agta from the municipalities (local government areas) of Palanan and Maconacon (as well as one camp from south Divilican, near the northern border of Palanan). These populations, especially in Palanan, have been the subject of research by several anthropologists over the past 40 years (Peterson 1978, 1981; Griffin 1996; Minter 2010).

The NSMNP is one of the few remaining rainforest areas in the Philippines and received national park status in 1997 due to its biological importance (DENR 1997). The park extends across four coastal municipalities, which, starting from the south-most, are Dinapigue (only the northern-most parts of which are in the NSMNP), Palanan, Divilican and Maconacon (a small part of the inland municipality of San Mariano also extends to the coast between Dinapigue and Palanan). Palanan, Divilican and Maconacon are located entirely within the park's boundaries (figure 2.2). Other municipalities which overlap with the park's borders on the mainland side are San Mariano, Ilagan, Tumauini, San Pablo and Cabagan, although the majority of these municipalities lie outside the park boundary and were not visited during the present study. The Sierra Madre mountain chain extends from north to south across this area, meaning that the coastal side is to a large extent independent from the mainland. Currently, the only ways to reach these coastal areas from the mainland are by: i) a 6-10 hour boat trip either north from Dilasag to Palanan, or south from Santa Ana to Maconacon; ii) a small plane from either Cauayan or Tuguegarao in the mainland to Palanan or Maconacon; or iii) a 3-5 day hike across the mountain range from San Mariano to Palanan (although plans for a road linking Ilagan to Divilican and Maconacon are currently underway, as is a larger airport in Divilican). Thus, inhabitants of these coastal communities are currently relatively isolated from the wider Filipino population in the mainland. This is especially true in the rainy season when boats and flights are less frequent and trekking more hazardous.

The NSMNP itself is covered in forests of several types, including lowland dipterocarp rainforest, mangrove forest, limestone forest, beach forest and montane forest, as well as other ecosystems such as coral reefs (DENR 1997). The park is home to several medium-sized animals, such as wild pig, deer and monkey, which are hunted by the Agta, as well as other endemic and endangered species. The park was created because it is one of the few remaining forested areas left in Luzon, especially as a result of extensive logging, particularly in the western side from ~1950's until the 1990's (at which time a moratorium on logging was announced, although some illegal logging still continues). When crossing the Sierra Madre mountain range, the drop-off to the coast is quite sudden, often leaving little viable non-mountainous land between the mountain and the coast suitable for agriculture. The majority of farmland in the coastal municipalities is contained within Palanan, hence why population and population densities are higher there compared to the other coastal municipalities within the NSMNP (table 2.1).

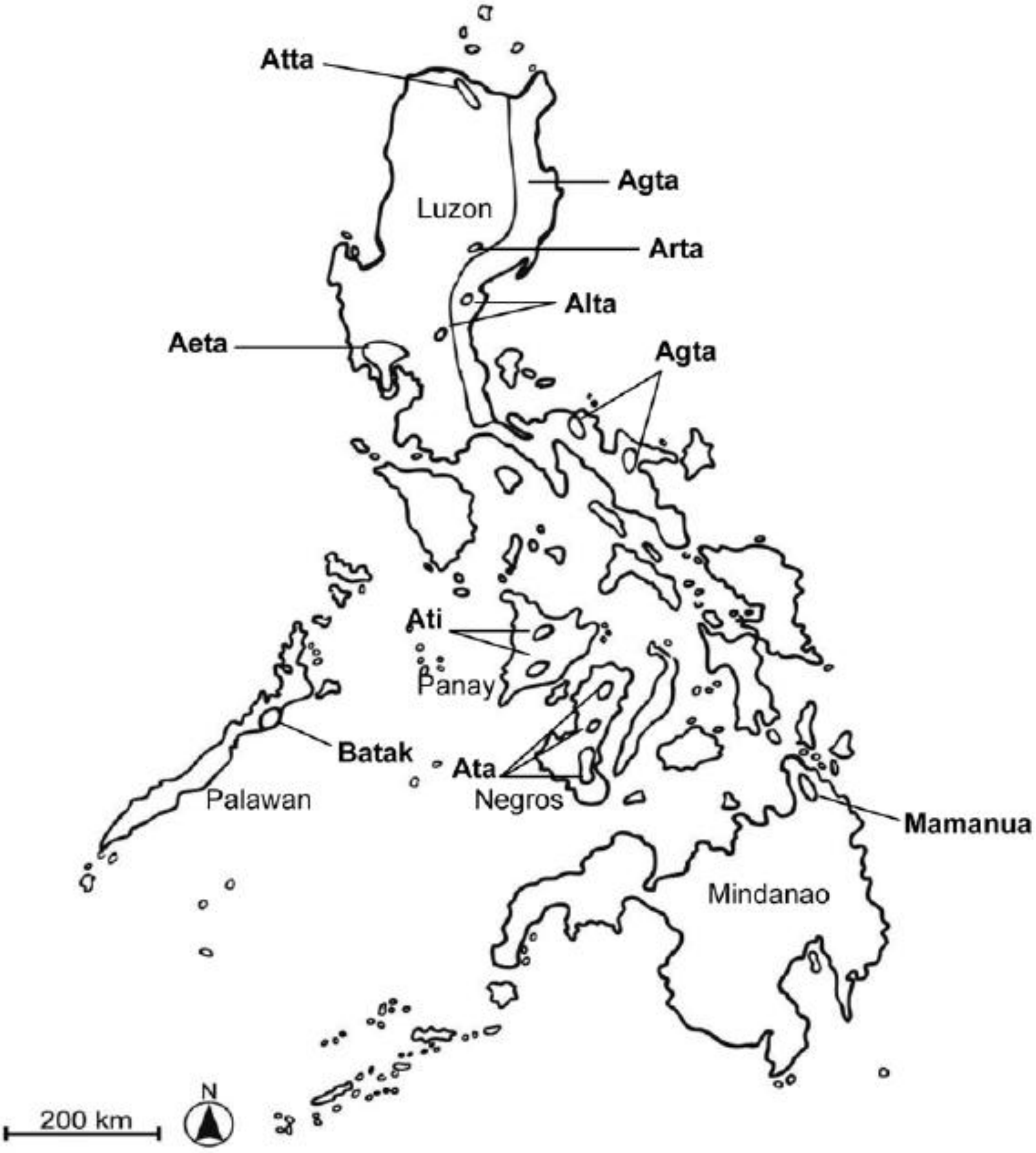

Figure 2.1: Current distribution of Negrito groups in the Philippines (taken from Minter (2010), page 44, map 2.1)

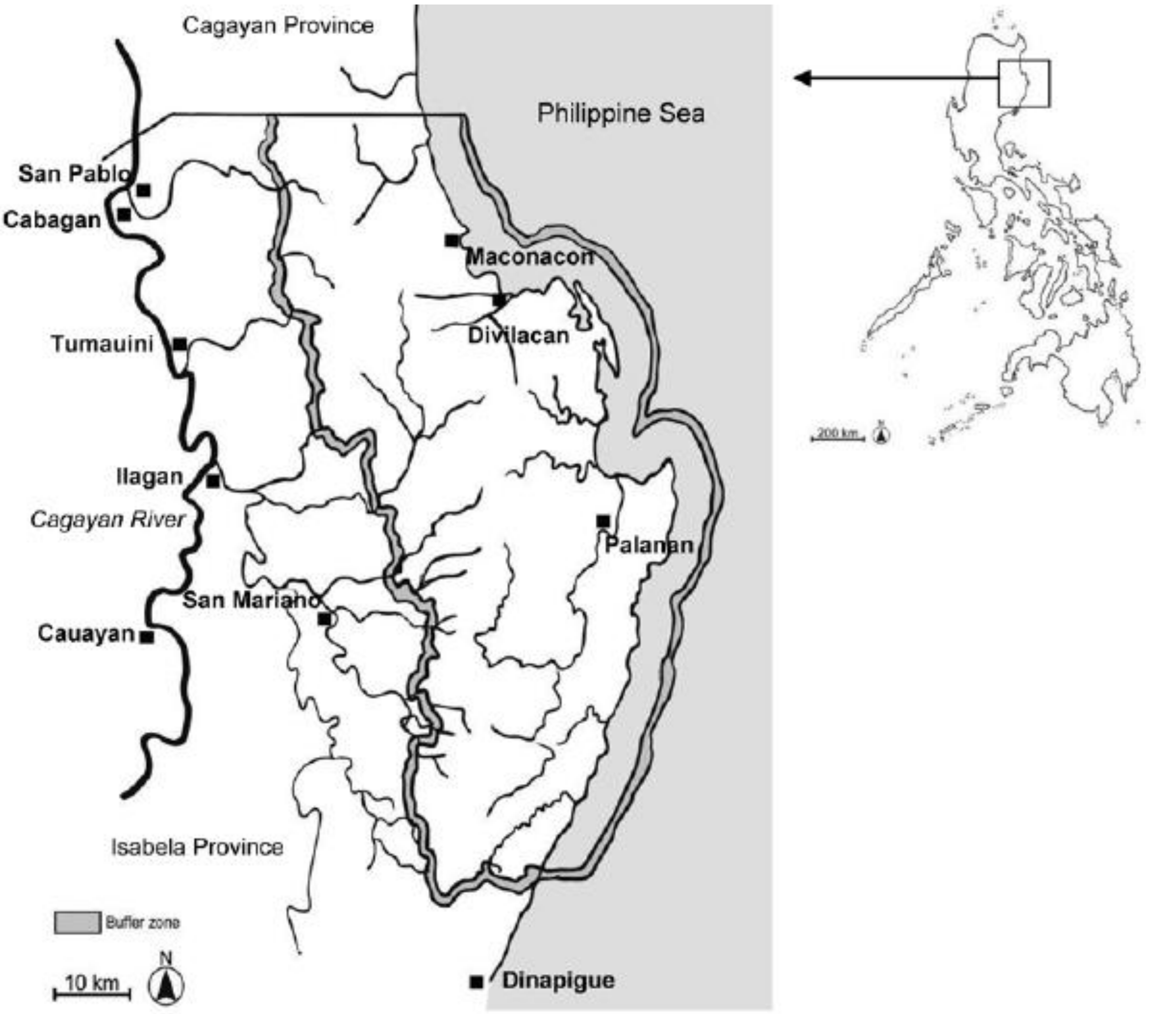

Figure 2.2: Location of study area within the Philippines (right) and close-up of study area (left). The thick grey line denotes the boundary of the Northern Sierra Madre Natural Park (NSMNP). Each of the labelled squares (other than Cauayan) indicates the capital of a municipality within the NSMNP boundary. The current research took place in the municipalities of Palanan, Divilican and Maconacon, all of which are found completely within NSMNP boundaries. The Sierra Madre mountain range runs north to south approximately down the centre of the NSMNP (taken from Minter (2010), page 2, map 1.1).

Climatically, there are two distinct seasons: dry and rainy. The rainy season lasts from approximately September/October to February/March, in which large amounts of rain occur on the majority of days. These downpours can cause rivers to swell up to over a metre above their level in the dry season, making navigation more difficult and treacherous during these months. Due to its coastal location facing the Pacific, these areas also face tropical storms (typhoons), which usually occur between

October and December. As reported in the news on a near-yearly basis, these storms which hit the Philippines can be extremely powerful, as seen by the devastation caused by Typhoon Haiyan in Leyte in 2013. In the NSMNP the last serious typhoon (Typhoon Juan) made land-fall in 2010, destroying many of the houses in the municipalities of Divilican and Maconacon. The dry season lasts from approximately March to September, in which temperatures often exceed 35^{0}C. During this season rain is less frequent, but still occurs.

Table 2.1: Population size, area and population density for the Philippines, Isabela province and municipalities in the Northern Sierra Madre Natural Park.

Area	Population (2010)[a]	Area (km^2)[b]	Population Density (Population per km^2)	± Isabela Average Population Density (%)
Philippines	92,337,852	300,000	307.79	+135.51%
Isabela	1,622,449	12,414.93	130.69	NA
Palanan	16,094	880.24	18.28	-86.01%
Divilican	5,034	889.49	5.66	-95.67%
Maconacon	3,615	538.66	6.71	-94.87%
San Mariano	51,438	1,469.5	35	-73.22%
Dinapigue	5,484	574.4	9.55	-92.69%
Ilagan	135,174	1,166.26	115.9	-11.32%
Tumauini	58,463	467.3	125.11	-4.27%
Cabagan	45,732	430.4	106.25	-18.7%
San Pablo	22,040	637.9	34.55	-73.56%
Coastal Municipalities[c]	30,227	2,882.79	10.49	-91.97%
Inland Municipalities[d]	312,847	4,171.36	75	-42.61%

[a] Population sizes obtained from the Philippine Statistics Authority (2010).
[b] Area sizes obtained from the Philippine National Statistical Coordination Board (2016).
[c] Coastal municipalities within the NSMNP are Palanan, Divilican, Maconacon and Dinapigue.
[d] Inland municipalities within the NSMNP are San Mariano, Ilagan, Tumauini, Cabagan and San Pablo. Although a small section of San Mariano extends to the coast, the majority of this municipality is located inland, so is included here as an inland municipality.

History

Descendents of the Agta, grouped together under the term ‘Negrito’ (meaning ‘little black’ in Spanish), are believed to have reached the Philippines ~35,000 years ago (Bellwood 1999). These ‘Negrito’ groups are thus called because of their distinctive phenotype: short ‘pygmy’ stature, dark skin and tightly-coiled frizzy hair (in contrast to the more common Asian phenotype of lighter skin, straight black hair and taller stature). In addition to the Philippines (figure 2.1), many other Negrito populations are found in South-East Asia, such as Semang and Batek from Peninsular Malaysia, Maniq from Thailand, and the Andamanese (Higham 2013; Reid 2013). The term ‘Negrito’ is frequently used by both social and biological anthropologists to refer to South-East Asian populations possessing this phenotype (Endicott 2013). Although the pejorative and colonial connotations of this term make its continued adoption somewhat unfortunate, it has remained in use given a lack of alternatives to adequately demarcate these populations from neighbouring non-Negrito groups. As there are no well-known or agreed-upon alternatives, I therefore follow convention and use the term ‘Negrito’ to refer to these populations, while noting that this term carries less-than-ideal social and political connotations.

The first known non-Negrito populations to reach the Philippines most likely originated from Taiwan during the Austronesian expansion ~5,000 years ago, bringing agriculture with them (Diamond & Bellwood 2003). As will be detailed in greater depth below, interactions between these colonising agricultural populations and Negritos were likely extensive and relatively rapid, as evidenced by modern day Negrito populations having adopted Austronesian languages soon after colonisation (Headland & Reid 1989; Reid 2013). Over time, from this contact and increasing population pressure from expanding agricultural populations it is likely that many Negrito populations either went extinct or became increasingly dependent on agriculture rather than foraging, such as the Ayta from Zambales (Brosius 1983). One example of this transition occurred recently with the Casiguran Agta (in Aurora

Province, south of Isabela). In the 1960's they were foragers who, like the NSMNP Agta, traded some of their foraged goods for carbohydrates from neighbouring non-Agta. However, over the ensuing decades new roads to Casiguran paved the way for loggers and agricultural migrants to occupy land which was previously only utilised by the Agta, resulting in the abandonment of foraging and increasingly becoming a peasant population in an agricultural economy (Early & Headland 1998). As a result of this Austronesian expansion, Negrito groups currently occupy few areas in the Philippines (figure 2.1), and even 100 years ago Negrito groups in Luzon appeared more widespread than their current distribution (Worcester 1906).

In coastal areas of the NSMNP, however, this tide has washed over much more slowly. Although it is likely that the Agta in these areas have interacted with agricultural neighbours for thousands of years (Peterson 1974; Headland & Reid 1989; Reid 2013), the pressure on them is likely to have been reduced compared to other foragers on the mainland. The Agta in these coastal areas appear to have maintained their cultural identity and foraging livelihood for longer than other Agta or Negrito populations. For example, on the eastern coastal side of the Sierra Madre mountain range there is little flat land suitable for agriculture, meaning that farming population densities are lower. Figures from the most recent Philippine census (2010) indicate that population density is much lower in these coastal regions compared to in the mainland (table 2.1). Thus, as a result of geography the Agta from the NSMNP are one of the few hunter-gatherer populations in the Philippines, and also worldwide, to continue subsisting predominantly by foraging in the present day. This does not mean that the NSMNP Agta are 'pristine isolates'; exchange with agricultural populations and more recent interventions (such as Christianisation, education, non-governmental organisation initiatives, government interventions, logging, etc.) have occurred which affect the Agta and include them in the wider Philippine and global economy. These schemes have also influenced different groups to varying extents, meaning that there is also great variability among the NSMNP Agta (see Kent (1992) for a similar example of how history and ecological circumstance influenced Bushmen groups differently regarding their foraging subsistence and assimilation within the wider economy). These themes of within-society variability will be discussed in greater detail below.

Demography

The last census of the Agta in the NSMNP was conducted between the years of 2002-2005 (Minter 2010). Including just *barangays* (local governmental subdivisions within municipalities) in which Agta reside, Minter reported 1,777 Agta living in the NSMNP and statistics from the Philippine government census indicated a total of 21,409 residents (Minter 2010). However, given that census conductors frequently do not visit Agta camps as they can be difficult to reach (Minter 2010: 42), it is impossible to know precisely how many Agta were included in these census estimates. Within the NSMNP, Minter found that the Agta made up approximately 8% of the total population in *barangays* where Agta reside. As these figures do not include population centres where Agta do not live, such as the main towns of Palanan, Divilican and Maconacon, the total percentage of Agta living in the NSMNP is likely to be lower (e.g., in the whole of Palanan the Agta comprise ~5% of the total population: table 2.2). Given the influx of migrants and high population growth in non-Negrito farming populations over the past decades (tables 2.3 & 2.4), the relative population size of the Agta was probably much larger in earlier times. As an example of the magnitude of this change, the population of Palanan has increased by over 600% in the past century, from 2,410 in 1918 to 16,094 in 2010 (table 2.3).

Table 2.2: Population sizes of Agta and non-Agta for both Palanan and Maconacon municipalities and *barangays* from a 2000 Philippine census and Minter's 2002-2005 census (adapted from table 2.4 in Minter 2010). Only *barangays* in which Agta reside are included here. Total *barangays* is included here and comprises all *barangays* within the NSMNP as a whole in which Agta live (*barangays* in which Agta do not reside, such as population centres, are therefore not included here). Given that it is debatable whether census figures contain Agta, the proportion of Agta to non-Agta are calculated twice: the first assuming that Agta population numbers are included in census figures and the other assuming that they are not. The actual proportion probably lies somewhere between these two values.

Municipality (in bold) and *Barangays*	**Reported Population (2000 Census)**	**Agta Population 2002-2005 (Minter)**	**Proportion of Agta:Non-Agta (If census included Agta)**	**Proportion of Agta:Non-Agta (If census excluded Agta)**
Palanan	15,317	728	0.048 (4.8%)	0.045 (4.5%)
Bisag	643	31	0.048 (4.8%)	0.046 (4.6%)
Centro West	2,282	10	0.004 (0.4%)	0.004 (0.4%)
Culasi	962	27	0.028 (2.8%)	0.027 (2.7%)
Dialomanay	548	75	0.137 (13.7%)	0.12 (12%)
Diddadungan	724	154	0.213 (21.3%)	0.175 (17.5%)
Didian	1,112	141	0.127 (12.7%)	0.112 (11.2%)
Marikit	892	121	0.136 (13.6%)	0.119 (11.9%)
San Isidro	569	169	0.297 (29.7%)	0.229 (22.9%)
Maconacon	3,721	149	0.04 (4%)	0.039 (3.9%)
Flores/Canadam	206	37	0.18 (18%)	0.152 (15.2%)
Reina Mercedes	457	34	0.074 (7.4%)	0.069 (6.9%)
Santa Marina	264	78	0.295 (29.5%)	0.228 (22.8%)
Total *Barangays* in NSMNP	21,409	1,777	0.083 (8.3%)	0.077 (7.7%)

Table 2.3: Changes in the population size of municipalities within the Northern Sierra Madre Natural Park over the past century (from Minter (2010) table 2.5 and Philippine Statistics Authority (2010)).

Municipality	**1918**	**1960**	**1975**	**1990**	**1995**	**2000**	**2007**	**2010**
Palanan	2,410	5,599	8,930	11,431	13,220	15,317	16,254	16,094
Maconacon	-	-	-	7,259	5,895	3,721	3,991	3,615
Divilican	-	-	1,207	2,479	2,593	3,413	4,602	5,034
Dinapigue	-	-	932	-	-	3,171	4,807	5,484
San Pablo	4,994	8,349	12,402	16,680	17,122	19,090	20,561	22,040
Cabagan	13,112	17,924	24,987	34,983	35,054	41,536	43,562	47,732
Tumauini	7,147	16,606	27,669	40,664	45,551	50,256	55,041	58,463
Ilagan	23,447	35,384	-	-	-	119,990	131,243	135,174
San Mariano	1,486	15,064	25,157	36,295	37,861	41,309	44,718	51,438

Table 2.4: Net change in population size and percentage change per annum (in brackets) of municipalities within the Northern Sierra Madre Natural Park over time.

Municipality	1918 - 1960	1960 – 1975	1975 - 1990	1990 - 1995	1995 - 2000	2000 - 2007	2007 - 2010
Palanan	+3,189 (+3.15%)	+3,331 (+3.97%)	+1,601 (+1.2%)	+1,789 (+3.13%)	+2,097 (+3.15%)	+937 (+0.87%)	-150 (-0.31%)
Maconacon	NA	NA	NA	-1,364 (-3.76%)	-2,174 (-7.38%)	+270 (+1.04%)	-376 (-3.14%)
Divilican	NA	NA	+1,272 (+7.03%)	+114 (+0.92%)	+820 (+6.32%)	+1,189 (+4.98%)	+432 (+3.13%)
Dinapigue	NA	NA	NA	NA	+2,239 (+9.61%)[a]	+1,636 (+7.37%)	+677 (+4.69%)
San Pablo	+3,355 (+1.6%)	+4,053 (+3.24%)	+4,278 (+2.3%)	+442 (+0.53%)	+1,968 (+2.3%)	+1,471 (+1.1%)	+1,479 (+2.4%)
Cabagan	+4,812 (+0.87%)	+7,063 (+2.63%)	+9,996 (+2.67%)	+71 (+0.04%)	+6,482 (+3.7%)	+2,026 (+0.7%)	+4,170 (+3.19%)
Tumauini	+9,459 (+3.15%)	+11,063 (+4.44%)	+12,995 (+3.13%)	+4,887 (+2.4%)	+4,705 (+2.07%)	+4,785 (+1.36%)	+3422 (+2.07%)
Ilagan	+11,937 (+1.21%)	NA	NA	NA	+84,606 (+5.98%)[b]	+11,253 (+1.34%)	+3,931 (+1%)
San Mariano	+13,578 (+21.76%)	+10,093 (+4.47%)	+11,138 (+2.95%)	+1,566 (+0.86%)	+3,448 (+1.82%)	+3,409 (+1.18%)	+6,720 (+5.01%)

[a] Population change measured from 1975 to 2000 due to missing data.
[b] Population change measured from 1960 to 2000 due to missing data.

While the relative population size of the Agta may have decreased, the total population size of the Agta in the NSMNP appears to have increased from 1,644 during a census by Rai (1990) conducted in 1979/1980 to 1,777 during Minter's (2010) census conducted between 2002-2005: a 0.34% increase in population size per year (table 2.5). As this table separates the Agta populations by municipality, it can be seen that the Agta population appear to be shifting away from mainland municipalities, such as San Mariano and Ilagan, towards coastal municipalities, such as Palanan and Divilican. While the current research was not intended as a census of the NSMNP, Agta populations from 2013-2014 can be ascertained for the whole of Palanan and two *barangays* in Maconacon (only two known Agta camps were not visited in Palanan, and the population of these camps were estimated based on genealogical knowledge and Agta informants familiar with these camps: table 2.6). Focusing just on Palanan, it appears that the Agta population was increasing at a rate of 3.43% per year during this 10 year period between ~2004 and 2014. Although some authors speculate that Philippine Negrito populations, such as the Agta and the Batak, are bound for extinction, both culturally and as distinct populations (see Minter 2010: 6-15), the NSMNP Agta do not appear to conform to this dire prediction. While the Agta population may be decreasing relative to the non-Agta population, in absolute numbers the Agta population appears to be increasing. However, whether this is due to an increasing population size, in-migration or simply missing individuals from previous censuses is currently unknown.

Table 2.5: Absolute population increase, yet relative decline, of the Agta within the Northern Sierra Madre Natural Park (from table 2.7 in Minter 2010). The proportion of Agta assumes that Agta are included in census figures.

Municipality	**# Agta 1979-1980**	**# Agta 2002-2005**	**Agta Change (Net & % per year)**	**Total Census 1975**	**Total Census 2000**	**Proportion Agta in 1975-1980**	**Proportion Agta in 2000-2005**
Palanan	669	728	+59 (+0.37%)	8,930	15,317	0.075 (7.5%)	0.048 (4.8%)
Maconacon	259	149	-110 (-1.77%)	7,259[a]	3,721	0.036 (3.6%)	0.04 (4%)
Divilican	230	526	+296 (+5.36%)	1,207	3,413	0.191 (19.1%)	0.154 (15.4%)
Dinapigue	45	71	+26 (+2.41%)	932	3,171	0.048 (4.8%)	0.022 (2.2%)
San Pablo	NA	24	NA	12,402	19,090	NA	0.001 (0.01%)
Cabagan	NA	0	NA	24,987	41,536	NA	0 (0%)
Tumauini	11	19	+8 (+3.03%)	27,669	50,256	0.0004 (0.04%)	0.0004 (0.04%)
Ilagan	68	38	-30 (-1.84%)	35,384[b]	119,990	0.0019 (0.19%)	0.0003 (0.03%)
San Mariano	332	222	-110 (-1.38%)	25,157	41,309	0.013 (1.3%)	0.005 (0.05%)
Total	1,644	1,777	+133 (+0.34%)	143,927	297,803	0.011 (1.1%)	0.006 (0.6%)

[a] Population size are not available for Maconacon in 1975, so the nearest available year (1990) is used.
[b] Population sizes are not available for Ilagan in 1975, so the nearest available year (1960) is used.

Table 2.6: Comparison of Agta population sizes in Palanan and two *barangays* in Maconacon from Minter's 2002-2005 census and present census data from 2013-2014. Note that the aim of the current research was not a complete census of the population, so not all camps in the *barangays* below were visited. *Barangays* where a complete census was not conducted are noted by a 'NC' (meaning not complete), but are estimated based on knowledge of Agta informants familiar with those non-visited camps.

Municipality (in bold) and *Barangay*	**Minter Census (2002-2005)**	**Current Research (2013-2014)**	**Total Population Change (Percentage change)**	**Percentage Population Change Per Annum (Over 10 years)**
Palanan	728	978	+250 (+34.3%)	+3.43%
Bisag	31	67	+36 (+116.1%)	+11.61 %
Centro West	10	25	+15 (+150%)	+15%
Culasi	27	57	+30 (+111.1%)	+11.11%
Dialomanay	75	92	+17 (+22.7%)	+2.27%
Diddadungan	154	180 (NC)[b]	+26 (+16.9%)	+1.69%
Didian	141	155	+14 (+9.9%)	+0.99%
Marikit	121	154	+33 (+27.3%)	+2.73%
San Isidro	169	229	+60 (+35.5%)	+3.55%
Dibewan	NA [a]	19	+19 (NA)	NA
Maconacon	149	175 [c]	+26 (+1.7%)	+0.17%
Flores/Canadam	37	35	-2 (-5.4%)	-0.54%
Reina Mercedes	34	140	+106 (+311.8%)	+31.18%
Santa Marina	78	NA [d]	NA	NA

[a] According to Minter, no Agta were living in Dibewan during her census.
[b] 29 of these were not visited in the present study but are inferred from genealogical records and knowledge from Agta informants.
[c] 175 is a minimum estimate for the whole of Maconacon as it does not include *barangay* Santa Marina where many Agta are known to live. It is likely that at least 50 Agta or so live in Santa Marina, although this is a very crude estimate and should not be considered precise in any way.
[d] This *barangay* was not visited during the current research, so population size cannot be estimated.

Life History

We next turn to life history parameters of the NSMNP Agta. Life history is central to understanding several aspects of human behaviour and evolution, including cooperation. As mentioned above, human life history is highly-derived relative to other primates, including an extended life-span, increased childhood dependency, multiple co-resident dependent offspring, shorter inter-birth intervals and female reproductive senescence (menopause). These life history parameters necessitate extensive cooperation, particularly in terms of food-sharing and childcare. Without cooperation, extended childhood dependence, multiple dependent offspring and increased fertility rates would not be possible (Hawkes *et al.* 1998; Kaplan *et al.* 2000; Kramer 2005). Given the co-evolution of human cooperation and life history, several key life history parameters of the Agta will now be described and referred back to later when interpreting patterns of cooperation.

As many life history traits require accurate ages, the aging process will be introduced here briefly (and explained in greater detail in the methods chapter). Ages for the Agta met in Palanan (and the one camp visited in Divilican) were estimated using Bayesian methods based on relative age rankings and age estimates attributed to individuals. Ages for these individuals are therefore likely to be more accurate than aging based solely on visual examinations. Ages for Agta from Maconacon (and Dibungko camp in Palanan) were not estimated using this method (due to differences in data collection: see methods chapter for further details). Rather, ages for some of these Agta were based on known ages, as many Agta under the age of ~25 in these two areas knew their own and their children's ages with some degree of accuracy. Alternatively, for individuals without known precise ages, especially older individuals, visual estimates, life-stage details and other information (e.g., number of children/grandchildren, cessation of reproduction (menopause), known ages of siblings, etc.) were used to assign approximate ages. Ages from these camps should therefore be treated more cautiously as there is likely to be greater error. For life history events requiring accurate aging, only age estimates using the Bayesian method are used (therefore excluding aging based on visual estimation or other subjective methods). These include: age at first birth, age at last birth, inter-birth intervals, age difference to spouse and age at menarche. For other demographic and life history traits which do not rely upon precise age estimates, such as completed fertility and population pyramids, data from all individuals are used. Life history theory is a multifaceted topic, the analysis of which could easily be the sole focus of a PhD regarding the Agta. However, as this is not the main focus here, life history parameters will only be broadly introduced, with further in-depth analysis and cross-cultural comparison to occur in subsequent publications. Thus, the following is predominantly descriptive in nature and little integration is made with the wider life history literature, although comparisons to neighbouring Agta populations are noted where relevant.

As population pyramids describing the age-structure of the population by sex require individuals to be categorised into age groups of 5 year intervals (e.g., 0-5, 5-10, etc.), precise age estimation is less essential than for other demographic or life history traits. The resulting population pyramid (figure 2.3) is therefore based upon all 1,081 individuals met (exact frequencies are displayed in table 2.7). A large proportion of the population (over 50%) are children under the age of 15. The population pyramid also displays a tapering shape, as the amount of individuals in each age group decreases with age. Both of these patterns are common in natural fertility populations with high mortality rates, and have been reported in other hunter-gatherer populations (Hill & Hurtado 1996). Less expected was the greater number of males compared to females (586 vs. 495), meaning that the total sex ratio is 118 males for every 100 females. This trend is particularly pronounced in children, and especially under 5's where the sex ratio is 147:100. A similar trend was noticed by Headland (1989) with the Casiguran Agta, and comparable trends of male-biased sex ratios are common in many societies (Cronk 1991). The cause of this sex-skew is currently unclear. Female infanticide is an unlikely explanation, as no strong preference for either sex was noted during fieldwork. Instances of infanticide (or passive neglect) were also not observed during the project or reported in Headland's extensive fieldwork with the Casiguran Agta (Headland 1989). One potential explanation may be that child mortality (under 15) is higher among males than females, with a ratio of 132:100. Thus, more males may be born as they are more likely to die in childhood, potentially because males require greater investment relative to females (Clutton-Brock 1991). Male children may also be more likely to die an accidental death (Kruger & Nesse 2006). Regardless of the cause of this male-biased child sex ratio, as would be expected (Fisher 1930) the operational sex ratio in adults is much less skewed (adults (over 15)=111:100; children=126:100).

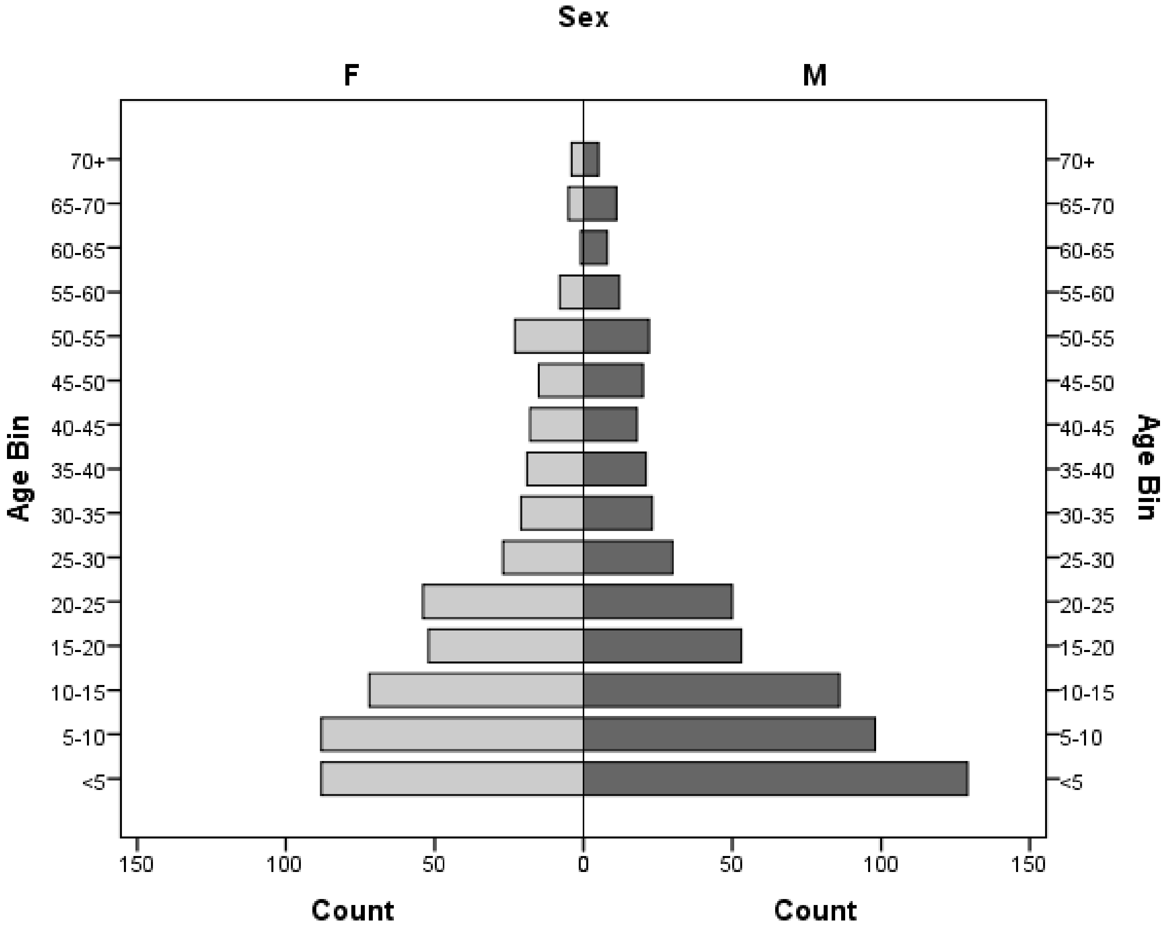

Figure 2.3: Population pyramid for the entire study population (*n*=1,081; males (dark grey)=586; females (light grey)=495). Note the higher proportion of males to females, especially in the <5 category.

Table 2.7: Age structure of the Agta population in 5-year-intervals for the total population, as well as male and female populations separately. Differences between male and female population sizes for each age category are also displayed.

Age Cat.	**Total**			**Male**			**Female**			**M to F Diff**	**Ratio M to F**
	Freq	**%**	**Cum %**	**Freq**	**%**	**Cum %**	**Freq**	**%**	**Cum %**		
<5	217	20.1	20.1	129	22	22	88	17.8	17.8	+51	1.47
5-10	186	17.2	37.3	98	16.7	38.7	88	17.8	35.6	+10	1.11
10-15	158	14.6	51.9	86	14.7	53.4	72	14.5	50.1	+14	1.19
15-20	105	9.7	61.6	53	9	62.4	52	10.5	60.6	+1	1.02
20-25	104	9.6	71.2	50	8.5	70.9	54	10.9	71.5	-4	0.93
25-30	57	5.3	76.5	30	5.1	76	27	5.5	77	+3	1.11
30-35	44	4.1	80.6	23	3.9	79.9	21	4.2	81.2	+2	1.1
35-40	40	3.7	84.3	21	3.6	83.5	19	3.8	85.1	+2	1.11
40-45	36	3.3	87.6	18	3.1	86.6	18	3.6	88.7	0	1
45-50	35	3.2	90.8	20	3.4	90	15	3	91.7	+5	1.33
50-55	45	4.2	95	22	3.8	93.8	23	4.6	96.4	-1	0.96
55-60	20	1.9	96.9	12	2	95.8	8	1.6	98	+4	1.5
60-65	9	0.8	97.7	8	1.4	97.2	1	0.2	98.2	+7	8
65-70	16	1.5	99.2	11	1.9	99.1	5	1	99.2	+6	2.2
>70	9	0.8	100	5	0.9	100	4	0.8	100	+1	1.25
<15	561	51.9	-	313	53.4	-	248	50.1	-	+65	1.26
>15	520	48.1	-	273	46.6	-	247	49.9	-	+26	1.11
Total	1081	100	100	586	100	100	495	100	100	+91	1.18

The average number of conceptions for 56 post-menopausal women whose reproductive histories were collected was 8.1 (SD=3.2, range=0-14, mode=9), of which 7.5 resulted in a live birth (not miscarriage or stillborn: SD=2.8, range=0-13, modes=7 & 8: figure 2.4). The average number of conceptions for 58 post-reproductive men was 7.3 (SD=3.6, range=0-14, mode=6), of which 6.7 resulted in a live birth (SD=3.2, range=0-13, mode=6: figure 2.5). Although biologically capable of reproduction, post-reproductive aged men were classified as those either divorced or widowed over the age of 45, or married to a post-reproductive aged wife and therefore unlikely to reproduce. It should be noted that this sample only includes post-reproductive aged individuals, so the average fertility rate is likely to be lower due to mortality of reproductive aged individuals. Two-sample Kolmogorov-Smirnov tests reported no significant difference between the distributions of post-reproductive men and women for both number of conceptions (Kolmogorov-Smirnov Z=0.683, p=0.738) or number of live births (Kolmogorov-Smirnov Z=0.169, p=0.595). Male and female reproductive skews are therefore approximately equivalent, as may be expected given the Agta's monogamous marriage system where few men are unable to monopolise reproduction. Interestingly, however, even in other hunter-gatherer societies which are serially monogamous, males do tend to have a wider variance in reproductive success than females (Betzig 2012), indicating that sex differences in reproductive skew among the Agta are especially minimal.

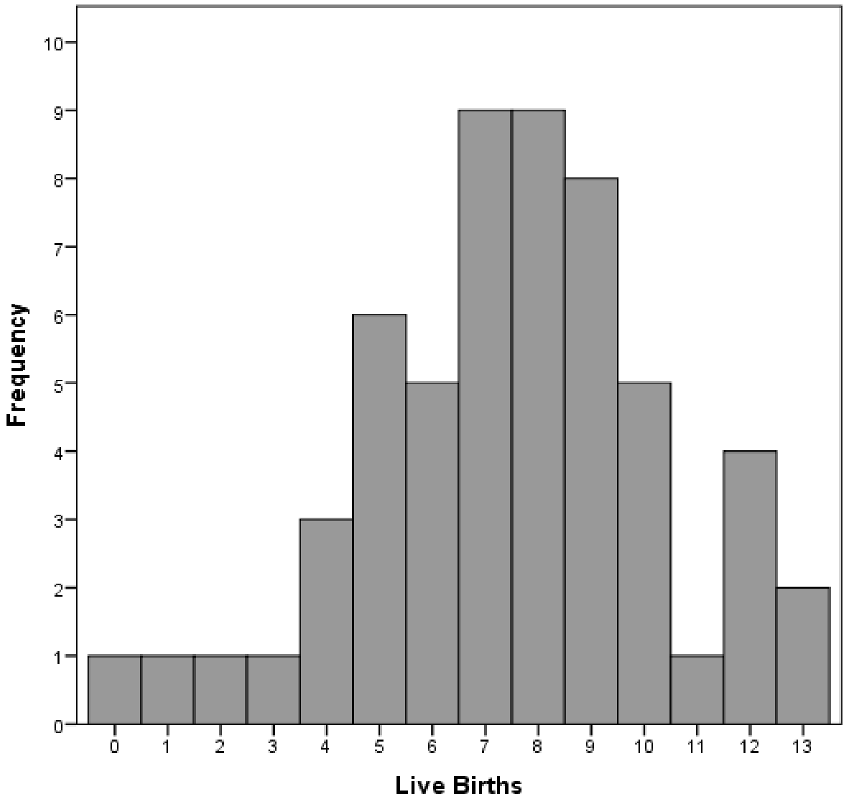

Figure 2.4: Histogram of number of live births for post-reproductive women (n=56).

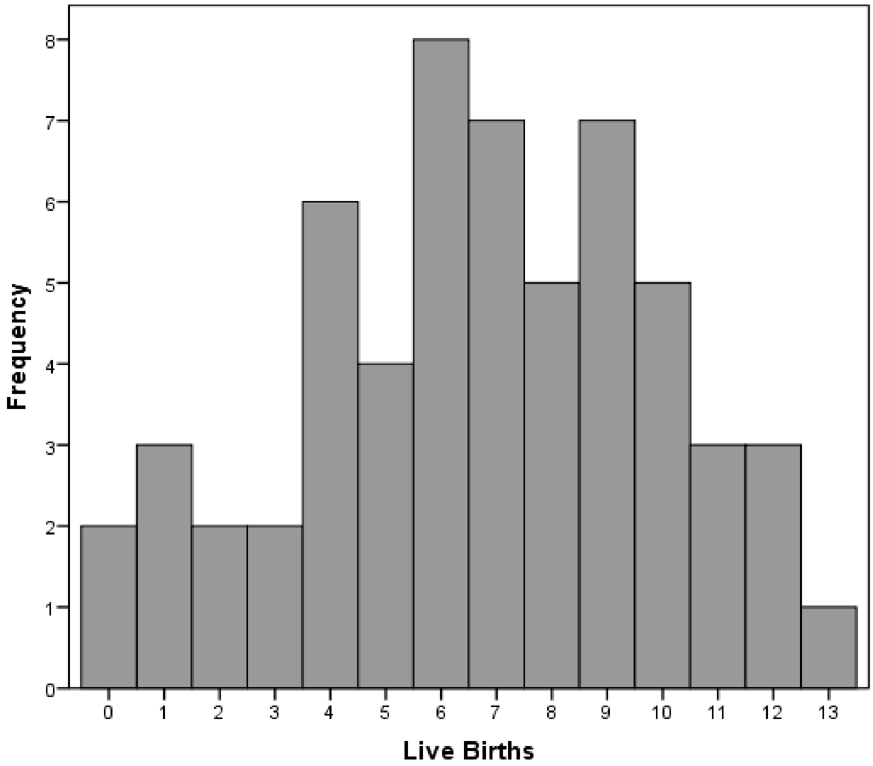

Figure 2.5: Histogram of number of live births for post-reproductive men (*n*=58).

I next explore mortality rates among the Agta. In an attempt to ensure accuracy, only deceased children of living parents are used to calculate the following figures. This is because individuals are likely to forget or not even know about other deaths, such as from siblings born before them or distant kin they were less familiar with. By focusing on this sub-set of living informants, it is possible to approximate child mortality, but not adult mortality. Although a sample of adult causes of mortality are presented below, from these it is only possible to infer causes of death, and not mortality rates for specific age groups. Devising life-tables for this population is currently a work-in-progress and will provide more accurate age-specific mortality rates for both children and adults. It should also be noted that ages of death are currently only approximations (methods for accurately aging deceased individuals are also currently under development). Ages of death are therefore based upon estimates given by parents or are based upon crude developmental stage (walking, weaned, teenager, married, etc.) and comparison to living siblings if age at death was not known.

Of all living women of reproductive or post-reproductive age in our sample (that is, aged over ~15 years; *n*=232), 1,002 live births were recorded (from a total of 1,088 conceptions). Of these 1,002 live births, 88 ended in death before reaching one year of age. As 66 children were currently less than one year old, once these were excluded this meant that 88 of 936 children died in their first year: an under one mortality rate of 9.4%. From conception – that is, including pregnancies that resulted in death, as well as either ending in miscarriage or a still-born foetus (i.e., non-live birth) – 174 foetuses did not survive beyond their first birthday, providing an under one mortality rate from conception of 17%. Applying the same criteria to mortality rates of children under the age of 15, 189 deaths were reported. As there were 513 living children aged under 15, these living children were removed, as were deceased children who would currently be aged under 15 had they survived. This resulted in 106 deaths from 488 live births; a 21.7% under 15 mortality rate. If similar criteria are applied from conception, then 138 pregnancies out of 574 did not survive beyond the age of 15, giving an under 15 mortality rate from conception of 24%.

Although these figures give an indication of Agta mortality rates, life-tables are required to accurately assess mortality rates in further detail, especially regarding adult mortality. Furthermore, as all of these births for calculating under 15 mortality occurred over 15 years prior to fieldwork (pre 1998), it is possible that young children may have been forgotten about due to the greater length of intervening time, so the actual mortality rate, especially among infants, miscarriages and stillborns, may be higher. Assuming that these figures are approximately correct, while undoubtedly high compared to Western standards, these mortality rates from birth of ~9% for under 1's and ~22% for under 15's are significantly lower than corresponding figures for the Casiguran Agta, where the under one mortality rate was 30% and 50% of children died before their tenth birthday (table 8.1 in Early and Headland 1998). These figures are also much lower than survivorship to age 15 in several other hunter-gatherers and other small-scale societies, in which under 15 mortality averages ~42% (Marlowe 2005; Migliano 2005; Walker *et al.* 2006; Migliano *et al.* 2007). Again, life-tables are required to definitively answer this question and assess whether these rates are representative of NSMNP Agta child mortality (although I suspect that infant and child mortality rates are significantly higher).

For a sub-set (*n*=230) of offspring deaths it was possible to attach a cause of mortality (table 2.8). However, these causes should be taken as crude approximations given that Agta often do not possess enough medical knowledge to diagnose illness correctly and some of our post-interview diagnoses based on associated symptoms may be incorrect. This is particularly true for infants and young children. For instance, many of the causes of death for children attributed to 'bad spirits/witchcraft' are likely disease-based. As can be seen from the table, the majority of mortality in childhood is caused by disease. If unknown causes and witchcraft are attributed to disease (as is highly likely), then 96% of all deaths under one year of age were a consequence of disease. Many of these diseases were infectious, but some were nutritional. In particular, a thiamine deficiency known as 'subi-subi' (or 'beri-beri') resulted in 17% of all infant deaths. While the majority of deaths were disease-based, a significant minority of them were a result of accidents, with over 10% of deaths between the ages of 1-15 attributed as accidental.

Causes of death for adults were obtained from primary kin and spouses, in addition to the adult offspring of living parents included in table 2.8. From this, causes of mortality for 221 adults (those aged over 15) were ascertained (table 2.9). Mirroring the offspring mortality data, infectious diseases were a significant cause of death, with approximately two-thirds of adults dying from this cause. Older Agta were more susceptible to infectious disease, with three-quarters of over 45 mortality attributed to disease, compared to half among younger adults. This table also highlights how dangerous child-birth can be among the Agta, resulting in ~22% of all deaths in reproductive-aged adults. Homicide, both by Agta and non-Agta was prevalent, although relatively rare, resulting in ~5% of all adult deaths. Approximately 6% of adult deaths were claimed to be a result of intoxication.

Table 2.8: Causes of mortality for offspring of living individuals. Absolute numbers are given first, with percentages presented in brackets (*n*=230).

Cause	<1	1-5	5-15	Adult	Total
Disease	70 (70.7%)	51 (70.8%)	26 (83.9%)	14 (53.85%)	161 (70.6%)
Respiratory	20 (20.2%)	7 (9.7%)	6 (19.4%)	6 (23.1%)	39 (17.1%)
Fever/Malaria	9 (9.1%)	10 (13.9%)	5 (16.1%)	3 (11.5%)	27 (11.8%)
Subi-Subi	17 (17.2%)	3 (4.2%)	0 (0%)	0 (0%)	20 (8.8%)
Measles	10 (10.1%)	15 (20.8%)	7 (22.6%)	1 (3.9%)	33 (14.5%)
Infection	6 (6.1%)	0 (0%)	0 (0%)	0 (0%)	6 (2.6%)
Gastro-Intestinal	8 (8.1%)	12 (16.7%)	4 (12.9%)	1 (3.9%)	25 (11%)
Hepatitis A	0 (0%)	2 (2.8%)	3 (9.7%)	0 (0%)	5 (2.2%)
Other	0 (0%)	2 (2.8%)	1 (3.2%)	3 (11.5%)	6 (2.6%)
Child Birth	NA	NA	NA	6 (23.1%)	6 (2.6%)
Drink-Related	0 (0%)	0 (0%)	0 (0%)	2 (7.7%)	2 (0.9%)
Accident	4 (4%)	11 (15.3%)	4 (12.9%)	4 (15.4%)	23 (10.1%)
Bad Spirit/ Witchcraft	2 (2%)	4 (5.6%)	0 (0%)	0 (0%)	6 (2.6%)
Homicide	0 (0%)	0 (0%)	0 (0%)	1 (3.9%)	1 (0.4%)
Unknown	23 (23.2%)	6 (8.3%)	1 (3.2%)	1 (3.9%)	31 (13.6%)
Total	99 (100%)	72 (100%)	31 (100%)	28 (100%)	230 (100%)

Table 2.9: Causes of mortality for adults, as evinced from primary kin and spouses (adults from the above table are also included here). Absolute numbers are given first, with percentages presented in brackets (*n*=221).

Cause	Young Adults (15-45)	Old Adults (45+)	All Adults
Disease	54 (50%)	88 (77.9%)	142 (64.3%)
Respiratory	23 (21.3%)	48 (42.5%)	71 (32.1%)
Fever/Malaria	7 (6.5%)	8 (7.1%)	15 (6.8%)
Subi-Subi	1 (0.9%)	0 (0%)	1 (0.5%)
Measles	2 (1.9%)	0 (0%)	2 (0.9%)
Infection	1 (0.9%)	1 (0.9%)	2 (0.9%)
Gastro-Intestinal	7 (6.5%)	8 (7.1%)	15 (6.8%)
Hepatitis A	0 (0%)	0 (0%)	0 (0%)
Other	13 (12%)	23 (20.35%)	36 (16.3%)
Child Birth	24 (22.2%)	NA	24 (10.9%)
Drink-Related	6 (5.6%)	8 (7.1%)	14 (6.3%)
Accident	10 (9.3%)	5 (4.4%)	15 (6.8%)
Bad Spirit/ Witchcraft	2 (1.9%)	0 (0%)	2 (0.9%)
Homicide	8 (7.4%)	2 (1.8%)	10 (4.5%)
Unknown	4 (3.7%)	10 (8.8%)	14 (6.3%)
Total	108 (100%)	113 (100%)	221 (100%)

I next explore life history traits for which accurate ages are required. Thus, for this section only individuals with known or estimated ages using the Bayesian method introduced above are included. Regarding the onset of reproduction, of 130 women who had given birth the mean age at first birth was 20.2 (SD=4.3), while for 129 men the age was 23.9 (SD=5.1). Mirroring this difference in ages, men were on average 4.3 years older than their wives (SD=5.3, *n*=133). Regarding age at last birth, the average age for 37 post-reproductive women was 40.7 (SD=5.9), while for 41 post-reproductive men the corresponding average was 42 (SD=8.8). Using data from post-reproductive individuals, the average fertile period (between first and last birth) was 17.9 years (SD=6.1) for women (*n*=37), and 17.5 years (SD=8) for men (*n*=41). Other than a slight delay in age of first birth for men, these figures, along with fertility measures above, suggest that male and female reproductive timings are relatively synchronous (although the standard deviations suggest that the variation in these indices is slightly higher among males). These ages at last birth and average fertile period only include living individuals who reached post-reproductive age; if individuals who died during reproductive age were included, both of these values would likely be reduced.

Using these more accurate age estimates it is also possible to assess age at onset of reproductive potential in women: i.e., menarche. Previous methods with the Cagayan Agta population to the north of Isabela reported that mean menarche age was ~17 (Goodman *et al.* 1985a). However, this was assessed indirectly, by asking if ego was the age of another individual when they began menstruating. This method can result in two sources of error, as i) the target's age was not known with precision, and ii) ego may misremember their age when they began menstruating. To overcome these methodological short-comings, we asked individuals with known or precisely-estimated ages between the ages of 10 and 20 whether or not they had begun menstruating. This sample includes 57 individuals and is displayed in figure 2.6. As can be seen, all individuals were found to have begun menstruating by the age of 16, while the youngest was menstruating at age 12.5. Thus, menarche appears to occur between the ages of 13-15. Supporting this, a probit analysis on this data found that 50% of females began menarche by the age of 13.78 (95% CI: [13.18; 14.64]).

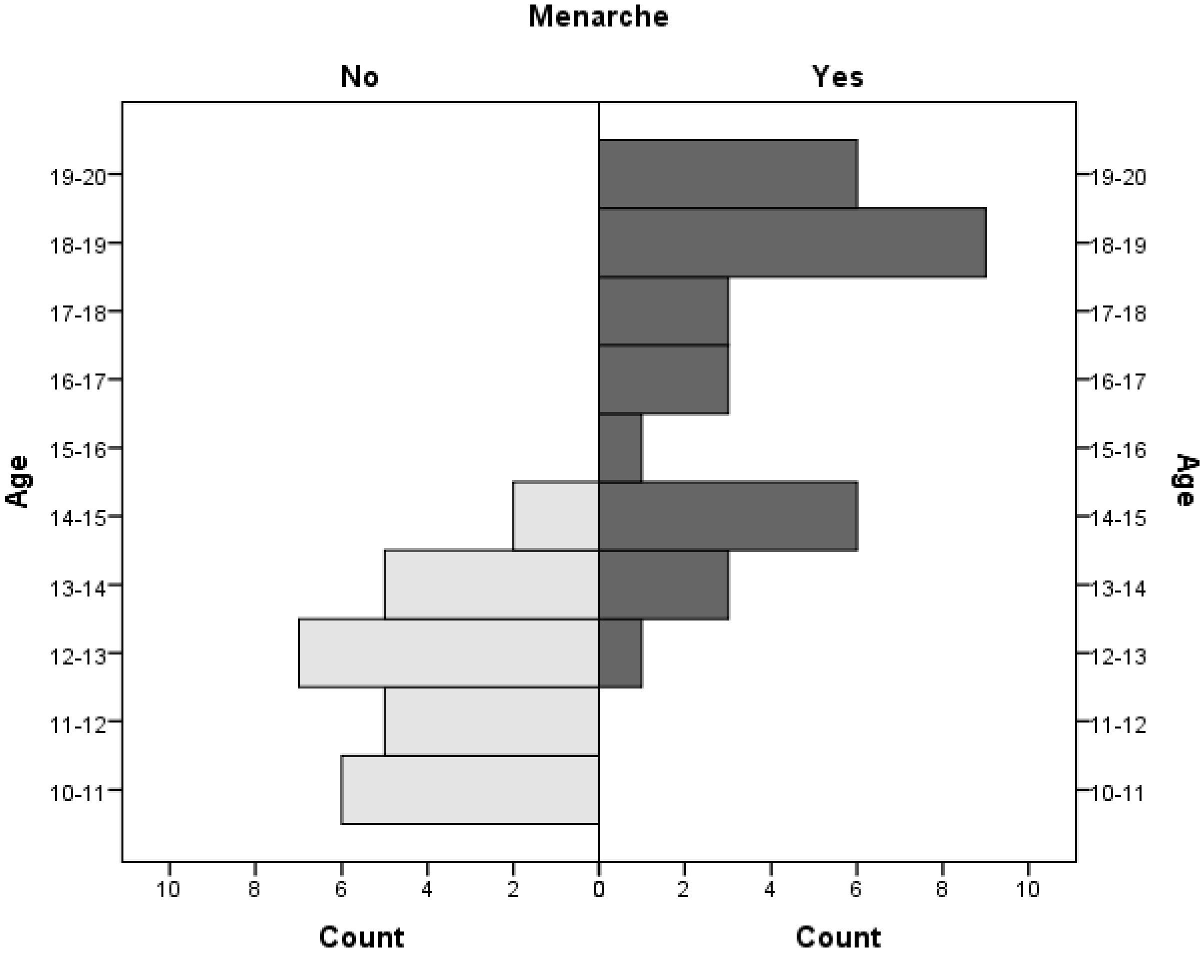

Figure 2.6: Plot displaying the frequency of females between the ages of 10 and 20 and menarche status (reached menarche (dark grey) or not reached menarche (light grey): *n*=57).

Only using individuals for which ages where either known or assigned using the aging method (meaning that ages are likely to be more accurate) and for which genealogies were given by parents (as children are likely to forget or not know siblings who died young), the average inter-birth interval (IBI) was 2.7 years (SD=1.4, *n*=258). The average IBI for when there was a miscarriage, stillborn or death under 1 year of age between siblings was 3.7 years (SD=1.7, *n*=23). On average, this suggests that miscarriages or infant deaths add ~1 year to IBI's between living siblings. Interestingly, IBI's between children (average age of two subsequent siblings below 16 years) and adults (average age of two subsequent siblings over 16 years) found that IBI's were significantly shorter for children than for adults, using an independent samples *t*-test (child; mean IBI=2.5, SD=1.1, *n*=215: adult; mean IBI=3.5, SD=2.2, *n*=43: *t*=4.369, *df*=256, *p*<0.001). As genealogies were conducted with parents, this makes forgetting children a less likely reason for this trend (although still a possibility, especially for miscarriages and infant deaths). This suggests that IBI's may have decreased over the past generation, supporting a recent study among the Palanan Agta which found that increasing sedentarisation was associated with increased fertility among this population (Page *et al.* 2016).

A final life history trait which can be explored with the current data is growth rates. This includes both height and weight, which can be combined to form a composite measure of body-mass index (BMI: weight (in kilograms) divided by height (in meters) squared). As can be seen in figure 2.7 for height, growth rates are broadly similar for both males and females under the age of 15, but while females appear to stop growing at this point, males continue into their early 20's. A similar pattern emerges regarding weight (figure 2.8). Weights are comparable during early to mid-childhood (ages 0-10), but then females put on weight faster than males during early adolescence (10-14), after which female weight gain decelerates while for males it surpasses females and continues through later adolescence and into early adulthood. These growth trends can also be seen in adult stature (between the ages of 20 and 60), as males are both taller and heavier than females (table 2.10), and are comparable to those of the San Ildefonso Agta from Casiguran (Early & Headland 1998). The weight figure also indicates growth spurt in adolescence, as around the age of 10 both sexes begin putting more weight on per year (a trend which continues for longer in males). BMI appears slightly larger in males in early childhood, similar between the sexes in mid-childhood, and larger in females in later childhood and adolescence (figure 2.9), although in adulthood males again have a larger BMI (table 2.10). As can be seen from these graphs, when the height, weight and BMI are compared against median values from UK children (Royal College of Pediatrics and Child Health 2015a, b), the Agta have lower values in all cases, although the growth curves appear broadly similar. Again, however, this requires additional in-depth analysis to explore further.

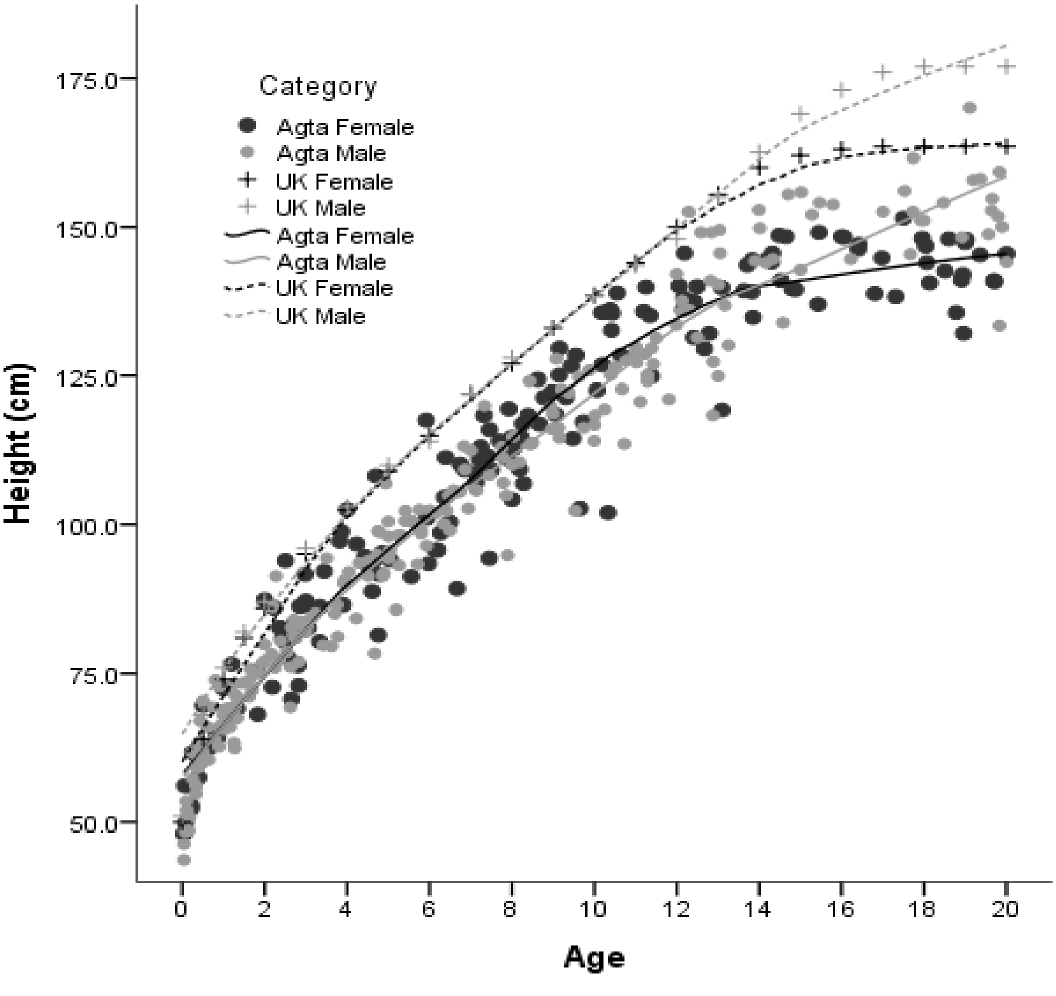

Figure 2.7: Growth curves for height for individuals aged under 20. Agta males are grey circles (*n*=219) and females are black circles (*n*=169). Median height values for UK children are also displayed (males=grey crosses; females=black crosses).

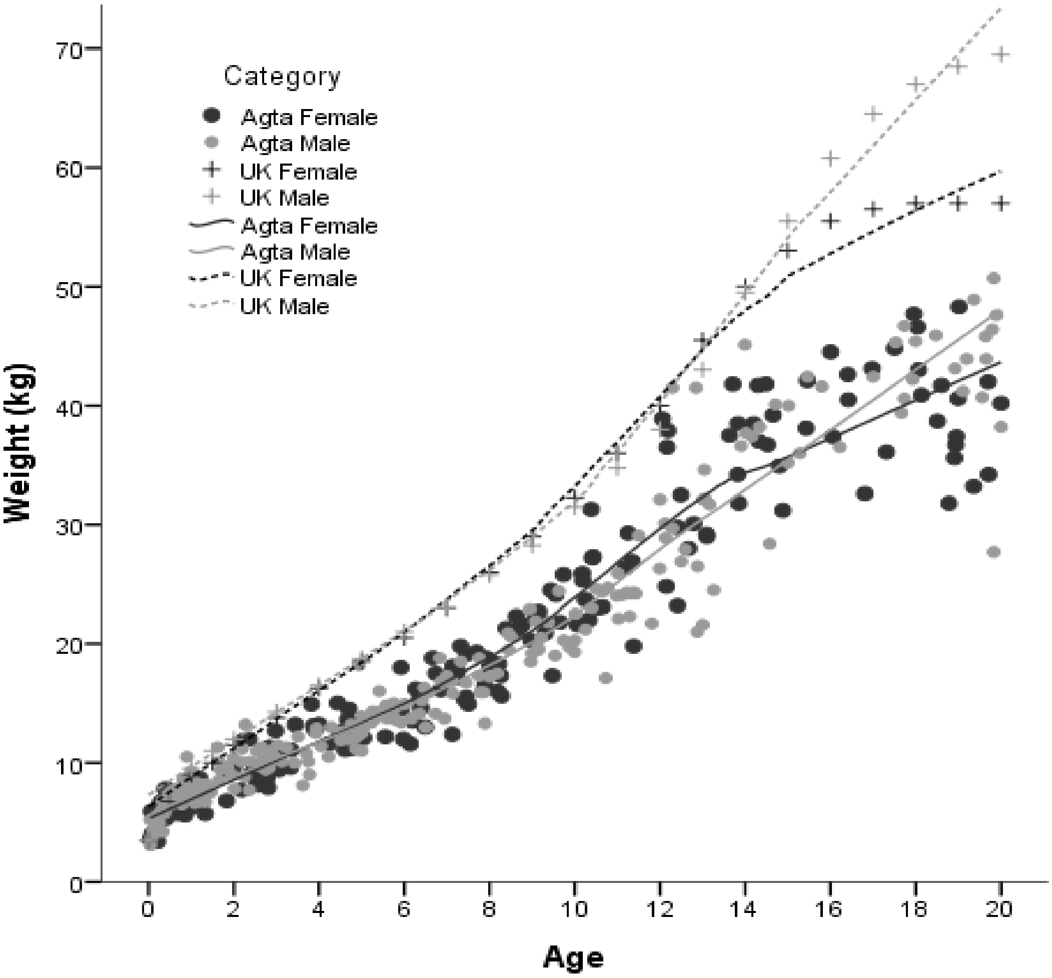

Figure 2.8: Growth curves for weight for individuals aged under 20. Agta males are grey circles (*n*=219) and females are black circles (*n*=169). Median weight values for UK children are also displayed (males=grey crosses; females=black crosses).

Table 2.10: Average height, weight and body mass index (BMI) for Agta adults (aged 20-60) divided by sex from both the Northern Sierra Madre Natural Park (NSMNP) Agta population (males=104; females=104) and the San Ildefonso Agta population from Casiguran (Early & Headland 1998).

Population	Sex	Height (cm)	Weight (kg)	BMI
NSMNP Agta	Male	154.2	46.4	19.5
	Female	143.7	38.7	18.7
San Ildefonso Agta (Casiguran)	Male	154.4	46.2	19.5
	Female	143.8	39.3	19

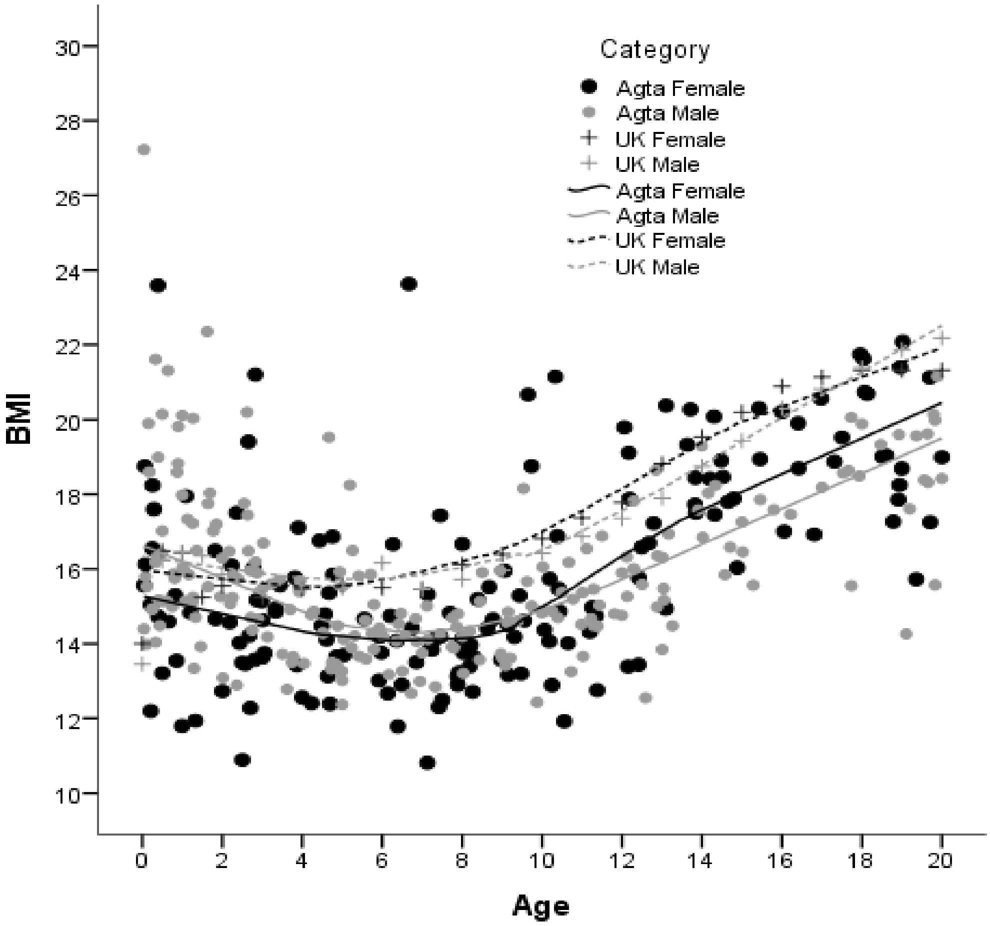

Figure 2.9: Growth curves for body mass index (BMI) for individuals aged under 20. Agta males are grey circles (*n*=219) and females are black circles (*n*=169). Median BMI values for UK children are also displayed (males=grey crosses; females=black crosses).

Social Organisation

As can be seen from a map detailing the locations of Agta camps within Palanan, they are widely dispersed over a large area of the NSMNP (figure 2.10; the camps visited in Maconacon are displayed in figure 2.11). While the Agta tend to avoid living in close proximity to large commercial centres, such as the main town (*bayan*) of the municipality, they often live next to or within short walking distance of smaller agricultural villages (*sitios*) where they can trade their foraged resources for rice and other bartered goods. In addition to trading partnerships, living near non-Agta farmers also allows them to work as farm labourers when crops need to be harvested, where they receive cash payment or, as is more frequent, a share of the harvest. As has been documented previously for the Palanan Agta, these forager-farmer relations appear somewhat beneficial for both the Agta, as they obtain carbohydrates, and for the farmers, as they acquire protein (Peterson 1978). The Agta tend to reside in either coastal or riverine locales: coastal-dwelling Agta live either directly on the beach or behind a line of vegetation, while riverine-dwelling Agta live inland, usually adjacent to rivers on cleared plots of land.

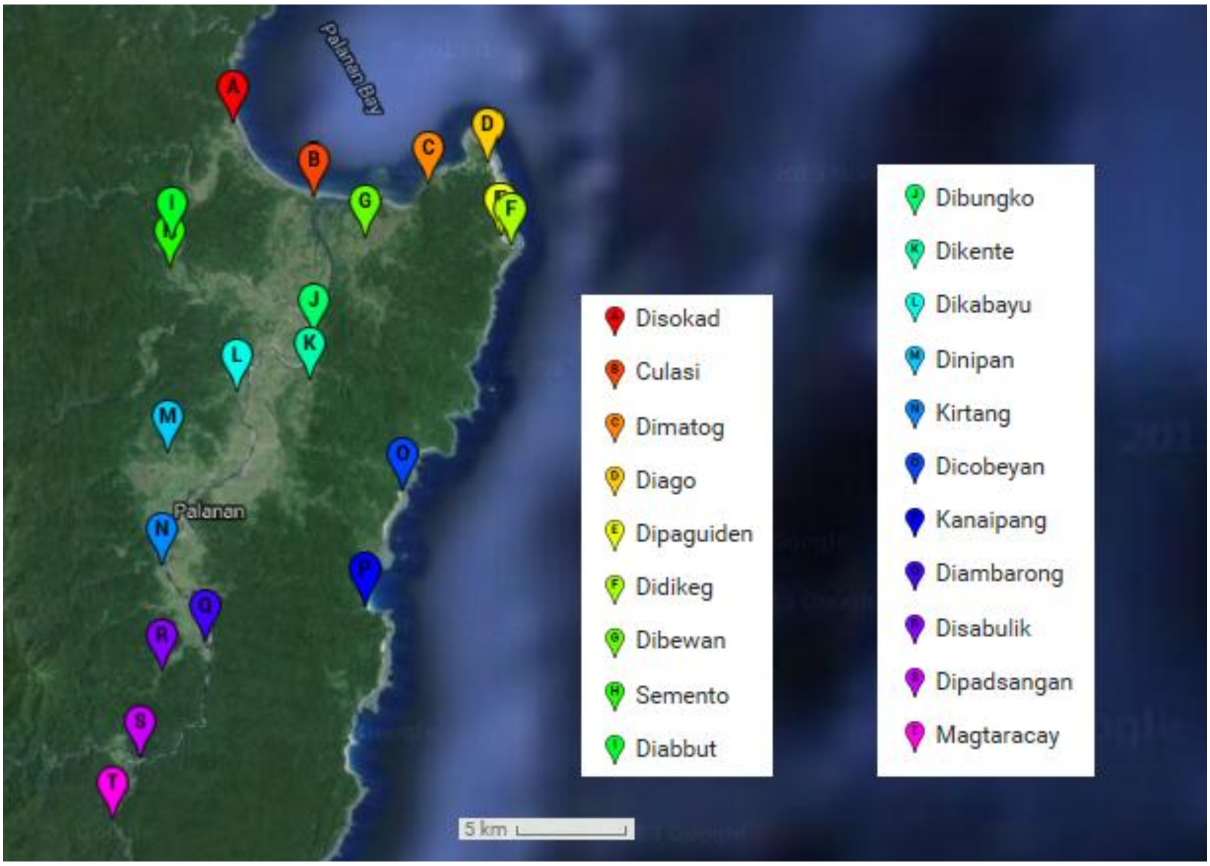

Figure 2.10: Distribution of Agta camps visited in the municipality of Palanan (although camp A (Disokad) lies just in the municipality of Divilican). Note that not all camps visited or known about are displayed here. For instance, many solitary dwellings are not displayed, such as Lucban and a further camp with an unknown name in Didian (near Dipadsangan (S)), two camps in *barangay* Centro West (in the vicinity of Dikabayu (L)), and Dimelmel (slightly south of Didikeg (F)). The marker for Dibewan (G) includes two separate camps in close proximity. To the best of our knowledge, only two camps were not visited, Cacawayanan and Disumangit, both of which lie on the coast between Didikeg (F) and Dicobeyan (O). The main town of Palanan lies approximately equidistant between Dibungko (J) and Dikabayu (L).

Figure 2.11: Distribution of Agta camps visited in the municipality of Maconacon, specifically focusing on *barangays* Reina Mercedes (north of the river) and Flores (south of the river). Other Agta camps exist north of this map in *barangay* Santa Marina, but were not visited during the present study. Note from the scale that these camps are located in relatively close proximity to one another. The main town of Maconacon is approximately 15kms south.

As is common in many other present-day hunter-gatherer societies, Agta social organisation can be characterised by high mobility, relatively small camp size and egalitarian social relations (Lee & DeVore 1968; Testart 1982; Woodburn 1982; Kaplan *et al.* 2009). Although all Agta are mobile to some extent, the level of mobility varies greatly between camps. Individuals in some camps appear relatively sedentary, living in large wooden houses similar to non-Agta farmers (figure 2.12). At the opposite extreme, other individuals move very frequently, sometimes only staying in a camp for one night before moving on. These individuals, if not staying in another's house, tend to build simple lean-to shelters, made simply of a stick in the ground holding up a cover made of dried leaves to keep out wind and rain (figure 2.13). In between these two extremes, many Agta live in semi-permanent dwellings, consisting of a small 'hut' with a raised floor and a palm-leaf roof (walls are optional; figure 2.14). These dwellings are associated with intermediate levels of mobility. Rather than whole camps being mobile and moving as a single unit, resulting in ephemeral camp locations, Agta mobility is generally based on movement between recognised and stable camps, such that a family (or group of families) will move from one camp to another. This means that, while camp locations rarely change, the composition of these camps can vary greatly. Differences in mobility between individuals and camps are largely a function of involvement in the wider Philippine economy and the impact of outside institutions, such as schooling, church, healthcare, involvement in agriculture (usually on behalf of non-Agta farmers) and wage labour opportunities. Camps which are more involved in these enterprises are generally less mobile. Reasons for moving tend to be either economic, such as extended hunting expeditions, fishing in different areas or the potential for agricultural work (e.g., harvesting rice or rattan), or social, such as visiting family in other localities or moving away from unseemly neighbours. Mobility tends to be greater in the dry season, while it is reduced in the rainy season, resulting in larger and more stable camps with more permanent-style housing (Minter 2010).

Figure 2.12: Example of a large Agta house, indicating more permanent residence and lower rates of mobility.

Figure 2.13: Example of a lean-to dwelling, which are quick to construct and are associated with higher rates of mobility.

Figure 2.14: Example of a 'hut' style dwelling, associated with intermediate levels of mobility.

Of 31 camps visited, the average number of individuals in a camp was 36.5 (SD=34, median=25.5), with 6.7 families (SD=6.1, median=5) and 5.7 houses (SD=5.5, median=4: table 2.11). These local group size figures are remarkably similar to averages produced over 130 warm-climate non-equestrian foraging groups, with a mean of 37.5 and median of 25.6 (Marlowe 2005). Similar to mobility levels, camp size is also highly variable among the Agta. The smallest camps consisted of solitary houses, while the largest camp numbered 156 individuals in 24 households. Small camps consisting of just one or two houses are often either elderly individuals who invest more in gardening and small-scale horticulture and less in foraging, or are individuals more involved in wage labour and often live closer to population centres (for instance, two individuals from *barangay* Centro West, the closest *barangay* to the main town in which Agta live, work in town as house-keepers and domestic staff). Thus, camps consisting of solitary dwellings tend to rely on agriculture or wage labour for subsistence, rather than foraging. Conversely, many of the larger camps, such as Dibungko, Culasi, Diago and Kanaipang, are associated with evangelical church groups, which appear to attract Agta from neighbouring camps. If these large camps and solitary dwellings are excluded, of the remaining 20 camps the average group size is 29.5 (SD=15, median=28), with 6.3 families (SD=2.9, median=6) and 5.2 houses (SD=2.5, median=4).

From a total of 1,039 individuals censured, we found 208 families (defined as individuals currently or previously married; unmarried adult offspring are not included as a separate family unless living separately from parents) in 178 houses, giving an average family size of 5 individuals and an average household size of 5.8. Of these 178 households, over three-quarters (137; 77%) are composed solely of nuclear family units (NFU's), meaning spouses and offspring (figure 2.15). Of the 15 households composed of two NFU's (8.4%), the majority were parents and married offspring. Divorced or widowed parents either lived alone (12 households; 6.7%) or with married offspring (11 households; 6.2%). The remaining three households (1.7%) did not fit any of these categories, and consisted of one household with four NFU's, one household with an NFU living with their widowed daughter and a final household of an NFU plus a young unrelated adult male living with them. As is common in many extant hunter-gatherer societies (Hill *et al.* 2011), the Agta display a flexible multilocal residence pattern, where NFU's can live with either husband's or wife's kin (Dyble *et al.* 2015), and high mobility means they often move between the two.

Table 2.11: Number of individuals, families and houses in each of the camps visited. Number of families is calculated as number of nuclear families (either husband and wife or widowed/divorced spouses), while unmarried adult offspring living with parents were not counted separately. As some camps in Palanan were visited multiple times, camp size figures are calculated from the first time they were visited in 2014 (other than for Dimatog, Dicobeyan and Disokad, which were only visited in 2013).

Camp	*Barangay*	Municipality	Number of Individuals	Number of Families	Number of Houses
Diabbut	Alomanay	Palanan	33	7	5
Semento	Alomanay	Palanan	25	6	3
Dikabayu	Centro West	Palanan	12	2	2
Dikangrayan	Centro West	Palanan	4	1	1
Centro 1	Centro West	Palanan	7	1	1
Dibungko	Marikit	Palanan	156	26	24
Dinipan	Bisag	Palanan	38	5	4
Kirtang	Bisag	Palanan	7	1	1
Culasi	Culasi	Palanan	66	12	10
Dimatog	San Isidro	Palanan	38	9	6
Diago	San Isidro	Palanan	69	13	13
Dipaguiden	San Isidro	Palanan	26	6	5
Didikeg	San Isidro	Palanan	61	10	9
Dicobeyan	Diddadungan	Palanan	17	5	4
Kanaipang	Diddadungan	Palanan	119	24	20
Diambarong	Didian	Palanan	30	6	3
Magtaracay	Didian	Palanan	41	8	8
Dipadsangan	Didian	Palanan	63	13	9
Lucban	Didian	Palanan	2	1	1
Didian 1	Didian	Palanan	2	1	1
Disibulik	Didian	Palanan	8	2	2
Dibewan 1	Dibewan	Palanan	7	1	1
Dibewan 2	Dibewan	Palanan	10	2	1
Palanan Average (SD)			36.6 (38.8)	7 (7)	5.8 (6.2)
Palanan Median			26	6	4
Mundora	Reina Mercedes	Maconacon	42	10	10
Putar	Reina Mercedes	Maconacon	33	7	6
Karayan	Reina Mercedes	Maconacon	19	4	3
Kamanggaan 1	Reina Mercedes	Maconacon	11	3	3
Kamanggaan 2	Reina Mercedes	Maconacon	28	5	5
Canadam	Flores	Maconacon	18	4	4
Kapanikian	Flores	Maconacon	16	4	4
Maconacon Average (SD)			23.9 (10.9)	5.3 (2.4)	5 (2.4)
Maconacon Median			19	4	4
Disokad	Dimapnat	Divilican	31	9	9
Total Average (SD)			33.5 (34)	6.7 (6.1)	5.7 (5.5)
Total Median			25.5	5	4

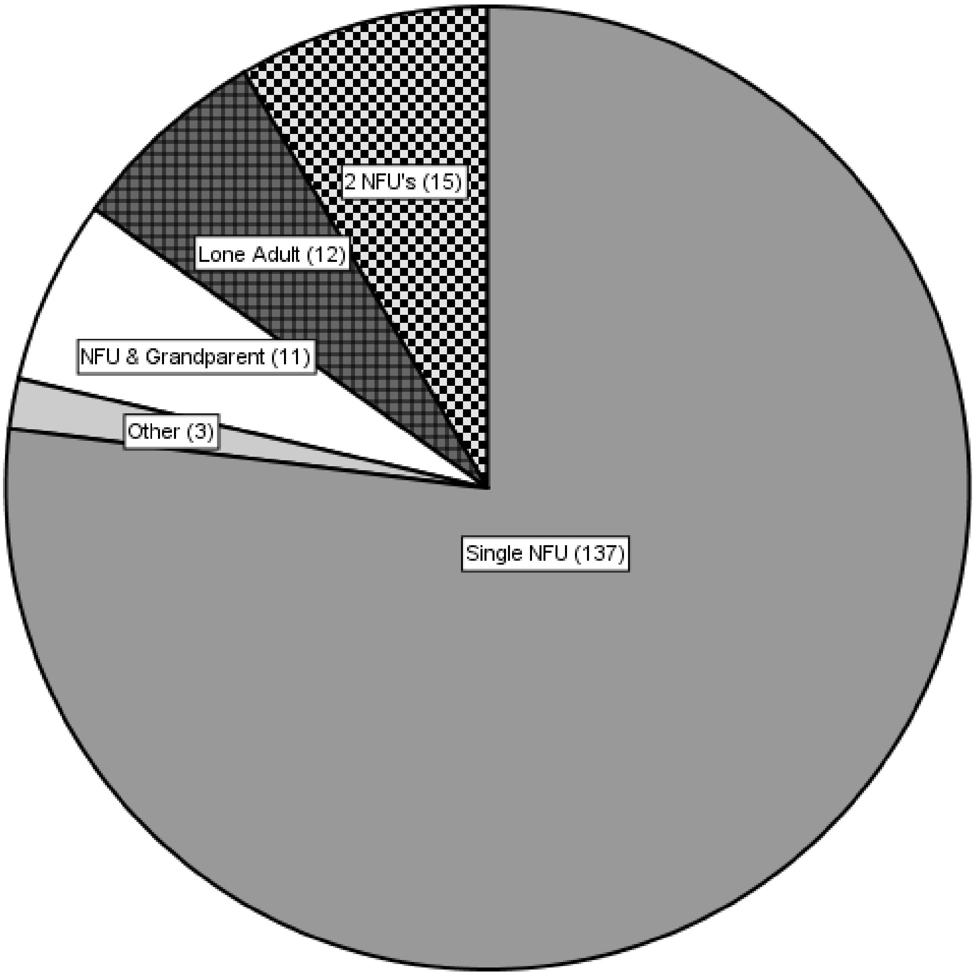

Figure 2.15: Breakdown of household composition (*n*=178). NFU refers to nuclear family unit (i.e., spouses residing together). Numbers in brackets denote the number of households in each category.

A final aspect of Agta social organisation to be discussed is egalitarianism. Again, as is common with many other 'simple' hunter-gatherer populations, social relations among the Agta are egalitarian, in that all adults in the population are afforded roughly equal standing and there is no social stratification or hereditary positions (Woodburn 1982; Boehm 1993, 1999). A central concept here is 'autonomy', such that other individuals cannot coerce others in to doing something that is against their wishes (Gardner 1991). One of the main reasons for this egalitarian social system is that, given high forager mobility, if an individual begins to act despotically camp-mates can simply ‘vote with their feet’ and move away from the problem individual, thus preventing the accumulation of power (Woodburn 1982). This is not to say that all Agta are equally knowledgeable, adept at foraging or prestigious. There certainly are individual differences in these qualities which the Agta are cognizant of, but these differences do not permit any individual to dictate the actions of others. At first glance this may appear counter to the fact that many Agta camps possess chiefs, but these chiefs are often appointed by government agencies or church groups and have little control over the behaviour of others. These chiefs are generally spokesmen (they are all male) for the camp who attend meetings on behalf of their camp and represent the Agta, as well as talk to camp visitors. Within camp they may act as arbitrators if disagreements or arguments occur, or their opinions may be given greater weight than others in discussions, but their influence rarely stretches beyond this. This role of chief as primarily mediator rather than leader was exemplified by the chief of Dibungko who, when asked about the decision-making process in camp, replied that “everyone has a voice, and whoever is the best, they [will] follow, because even though I am the chief, it’s not good if my decision is the only one to be followed as I may not be right”.

Subsistence

The Agta engage predominantly in hunting and gathering for subsistence, although some engage in wage labour, commercial gathering and small-scale agriculture. Traditionally the Agta were known for their skill in hunting using the bow-and-arrow (Worcester 1912; Vanoverbergh 1933), particularly of wild pig, deer and monkey. While hunting is still practiced widely in Maconacon, many informants from Palanan told us that hunting is becoming less common due to over-hunting and declining game populations. Indeed, many men from Palanan do not hunt whatsoever, while those that do often use traps or guns, with bows-and-arrows largely the preserve of the older generation (although in Maconacon the majority of men still engage in bow-and-arrow hunting; table 2.12). Our fieldwork occurred during the dry season, where hunting is less successful as pigs are leaner and less likely to be caught, as in the wet season the rain prevents them from being aware of the hunter for longer (the rain masks sounds and smells, meaning that animals can be tracked easier). It is therefore probable that more hunting occurs in the rainy season, as was confirmed by Agta informants. Even in the rainy season many men, particularly younger ones, do not hunt, but focus on fishing for subsistence. Despite this reduction in hunting, the Agta still attach great importance to it, as will be described in the 'Ritual Life' section below.

Table 2.12: Percentage of males who hunt, and of those that hunt, the method used (note that for 'method used' percentages add up to over 100% as often individuals utilise two or more hunting techniques).

		Palanan (*n*=109)	**Maconacon (*n*=30)**	**Total (*n*=139)**
Engages in hunting	Yes	75 (68.8%)	28 (93.3%)	103 (74.1%)
	No	34 (31.2%)	2 (6.67%)	36 (25.9%)
Method (of those that hunt)	Bow-and-arrow	36 (48%)	23 (82.1%)	59 (57.3%)
	Traps	56 (75.7%)	23 (82.1%)	79 (76.7%)
	Gun	45 (60%)	3 (10.7%)	48 (46.6%)

The Agta have been famed in the anthropological world because they combine female hunting with no apparent decline in female fertility (Estioko-Griffin 1985; Goodman *et al.* 1985b), seemingly disproving the assumption that childcare is largely incompatible with hunting (although in many other foraging societies women do engage in hunting, such as the Mbuti (Noss & Hewlett 2001) and the Australian Martu (Bliege Bird & Bird 2008)). While Agta women did hunt, they did so half as often as, and differently to, males. Males tended to hunt alone with a bow-and-arrow while women hunted in groups with dogs (Goodman *et al.* 1985b), a potentially less risky strategy. This Agta population was studied in Cagayan province, north of Isabela, and this region has strong ties with the Agta from Maconacon. Despite this apparent history of female hunting, very few cases of female Agta engaging in hunting were either observed or elicited during the present fieldwork. In Palanan, few women ever claimed to have hunted in their life, and active hunting by females was only observed on one occasion. In Maconacon there appears to be a longer history of women hunting, as some of the older women claimed to have hunted when they were younger, although this was usually with their husband and was often in a supporting role with a machete and dogs, rather than a bow-and-arrow. Still, many women claimed never to have hunted. Only one female informant from Maconacon (aged ~40) claimed to still actively hunt with a bow-and-arrow. None of the younger females reported to have ever engaged in hunting.

Spear-fishing is also predominantly a male arena. Although teenage girls are quite proficient at spear-fishing, once they begin to reproduce the amount of time spent spear-fishing decreases as a result of childcare commitments, as was noted by several Agta during interviews (although they still spend considerable time foraging for other aquatic resources, such as shrimps, octopus and shellfish, which are less intensive than spear-fishing and can thus be coupled with childcare duties more easily). This suggests that childcare responsibilities do somewhat limit participation in both hunting and fishing for Agta women, *contra* previous research (Estioko-Griffin 1985; Goodman *et al.* 1985b), and that hunting is rarely practised by Agta women nowadays. Gathering is predominantly practiced by women and juveniles, and will be discussed in more detail below. These trends can be seen from activity budgets using data collected from camp-scans, in which little time is spent hunting and much is devoted to fishing (figure 2.16). A division of labour also occurs; men hunt and fish more than women, while women participate more frequently in gathering (figure 2.17).

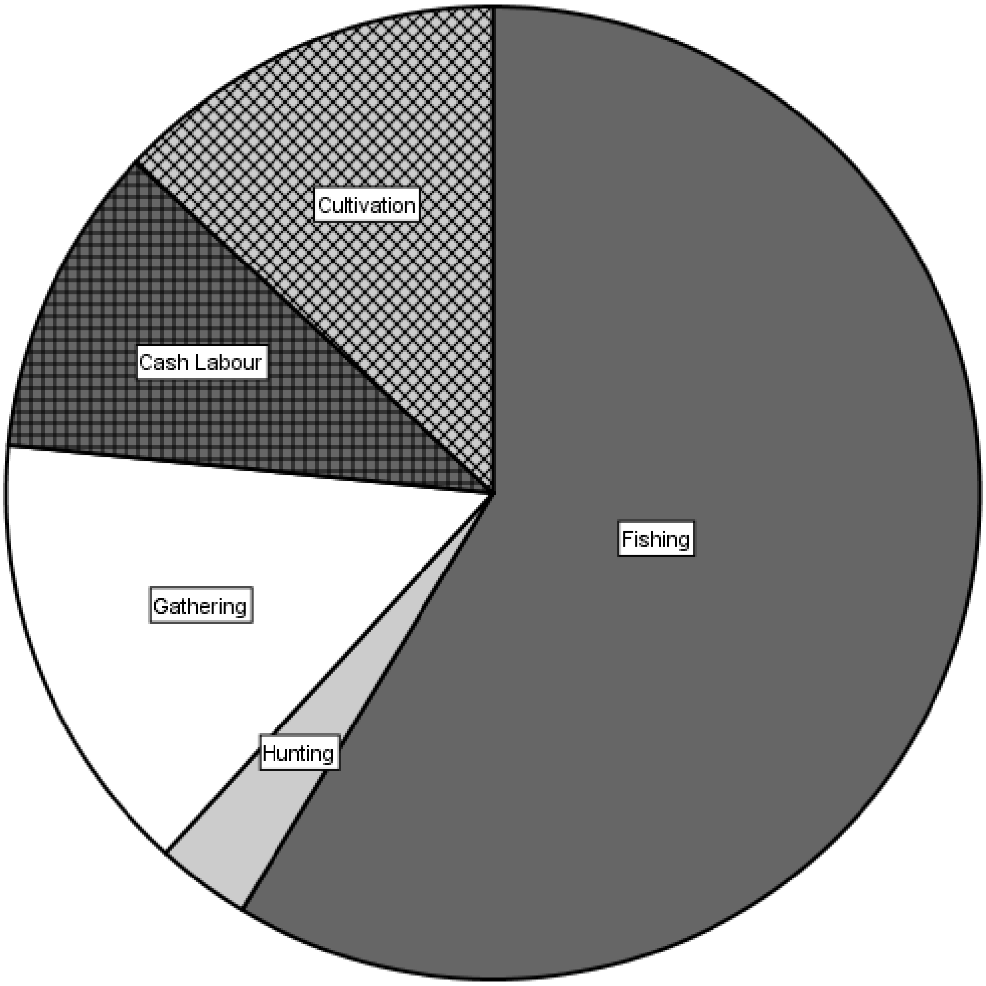

Figure 2.16: Activity budget of time spent in subsistence activities for all Agta (including children) out of 1.984 events. The exact percentages for each activity are: hunting=3.1%, fishing=58.6%, gathering, 14.8%, cash labour=10.3%, and cultivation=13.1%. Note that cultivation may either be of gardens owned by Agta, or cultivating land for non-Agta.

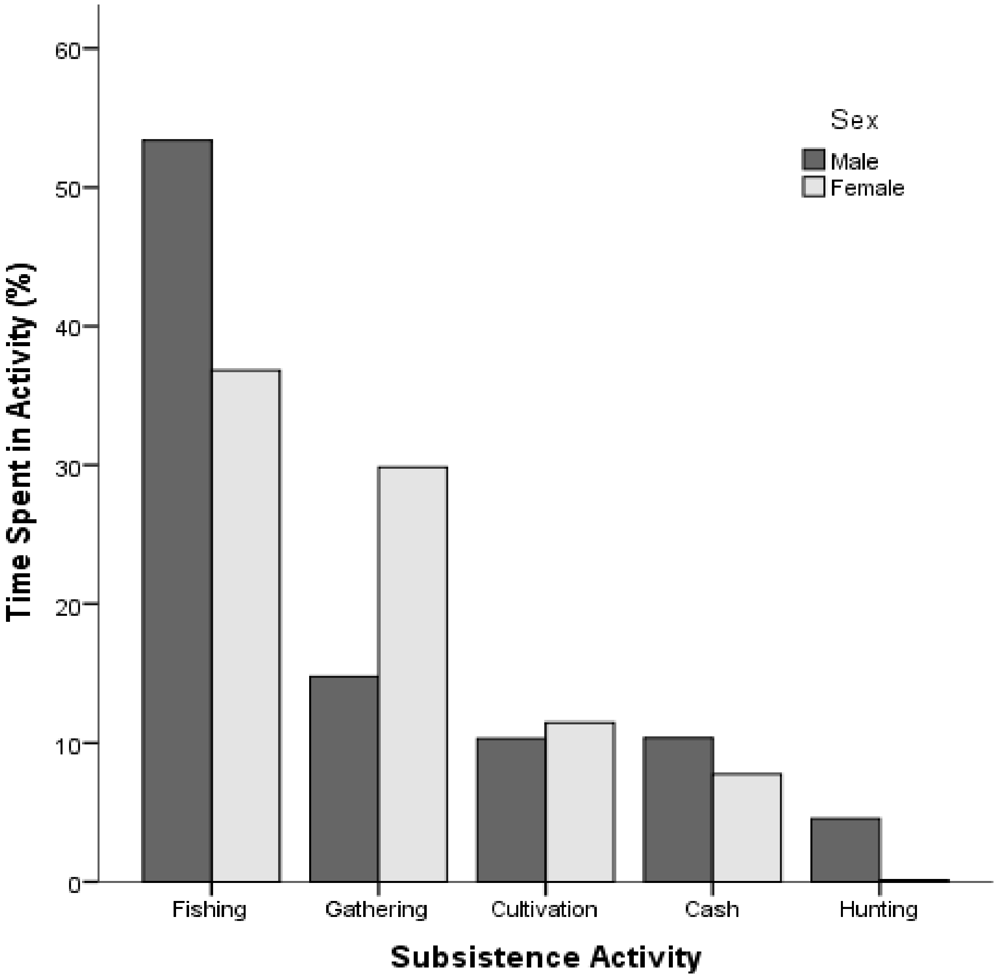

Figure 2.17: The percent of time adults were engaged in subsistence activities while out of camp, split by sex, using camp-scan data. Note the division of labour between fishing, gathering, and hunting. Cultivation may either be of gardens owned by Agta, or cultivating land for non-Agta.

As more time is spent fishing, as opposed to gathering, foraged resources obtained by the Agta predominantly contain protein rather than carbohydrates. To obtain carbohydrates the Agta have three options, each of which is practised to a varying extent depending on season and location: i) trade meat/fish with non-Agta agricultural neighbours for carbohydrates; ii) forage for wild plants and tubers; or iii) grow their own carbohydrate source. Regarding option one, as noted above, Agta subsistence cannot be understood without recourse to interaction and trade between their non-Agta agricultural neighbours. The Agta have been in contact with farming populations for thousands of years (Peterson 1974; Headland & Reid 1989; Griffin 1996), trading foraged meat and fish for carbohydrates and other household and luxury goods. Thus, while the majority of their food-acquisition activity budget is spent foraging, many calories come from agricultural products, especially rice, as is common for other Agta populations (Early & Headland 1998).

This discussion is associated with the ‘wild yam’ hypothesis, proposed by Thomas Headland, and states that hunter-gatherers would not be able to survive in rainforest environments due to a lack of naturally-occurring carbohydrates. This argument suggests that it is only with the advent of agriculture and trade between foragers and farmers that hunter-gatherers could have survived in rainforests (Headland 1987b; Bailey *et al.* 1989). This may mean that option two stated above (gathering) is less viable for the Agta. Although exceptions have been observed, such as the Penan from Borneo who subsist by foraging in rainforests without domesticated plants (Brosius 1991), it is very difficult to know whether the observed inter-dependence between Agta and non-Agta is a result of preference or necessity. It may be that the Agta can survive solely on foraged forest products but choose not to because rice has higher calorific-returns (and they prefer the taste). One Agta informant said that there were many gathered forest products which they could eat, such as tubers, wild bananas and pith to make flour, and that if they had no rice they would eat these and have enough to survive (although of course this should not be taken as a statement of fact). Although gathered goods are foraged, less time is spent gathering than fishing, suggesting that gathered foods are less important to Agta diet (figure 2.16). Overall, gathered produce appears subsidiary to traded rice as a source of carbohydrates, and many gathered products such as honey or forest fruits are consumed as luxuries or snacks (or sold, in the case of honey) rather than as staple foods. Whether this reliance on traded carbohydrates, rather than gathered resources, is a result of choice or necessity on behalf of the Agta is currently an open question.

A final option available to the Agta to secure carbohydrates is to grow them. Many Agta have small-scale swidden patches, but these are often neglected or only used in times of emergency as fall-back food. Mobility also mitigates against intensive agriculture; few Agta remain in one place for long enough to successfully cultivate crops such as rice, which require a significant time investment. Many of the products grown by Agta are relatively unintensive labour-wise (such as sweet potato, *taro*, coconut and banana), require little attention and can be returned to after lengthy trips away. In addition to their mobility, outside forces may also act to stop the Agta investing more heavily in agriculture. Headland (1986) posits that non-Agta agriculturalists would not like Agta to become farmers as this would increase competition for suitable arable land, lower the amount of protein obtained via trade with the Agta and reduce the number of Agta available as seasonal land workers. Non-Agta may prefer the Agta to remain as foragers, in a process known as the ‘competitive exclusion principle’ (Headland & Headland 1997). Thus, as a result of the Agta’s social organisation and resistance from non-Agta populations, direct horticulture is only a small source of calories for the Agta.

Indirectly, however, Agta may obtain carbohydrates by harvesting the fields of non-Agta and receiving some of the crop as payment. Sometimes Agta are highly mobile at this time and harvest multiple fields in a season, while others tend the land over longer periods of time and effectively manage the land on behalf of the non-Agta. As an example of this latter system, two camps in *barangay* Alomanay live on non-Agta-owned land, but work the field and are permitted to keep half of all harvests. They also look after some *carabao* (water buffalo), also owned by non-Agta, which they can use to help plough fields, as well as keeping one-quarter of the profits if a *carabao* is sold (~5,000 pesos, or ~£70) and are allowed to own all first-born females. These relationships – known as *ibay* (translated as 'special friend' and based upon mutually-beneficial exchange) – appear relatively symbiotic for both the Agta and non-Agta (Peterson 1978, 1981). This possibility is more available to inland populations, given the greater amount of land suitable for farming near riverine systems rather than by the coast (figure 2.18).

In addition to these modes of subsistence, some Agta are also involved in the market economy and have jobs, such helping government projects or as domestic help, although these are relatively few in number and are often only temporary. Other Agta also engage in commercial gathering, such as of rattan, swift nests or honey, which they can then sell. Although currently not prevalent in Palanan, many Agta in the NSMNP, especially in San Mariano, assist with illegal logging operations. As exemplified by Minter (2010), Agta subsistence is highly varied and flexible depending upon the prevailing local conditions. For instance, inland Agta engage more in hunting and cultivation (either for self or on behalf of non-Agta) as there are more opportunities for these activities inland, while coastal Agta spend more time fishing (figure 2.18). It is important to note that both individuals and camps which are more involved in agriculture or wage labour do not partake in these roles exclusively, but rather combine them with foraging. Thus, an individual who harvests rice one day may spend all of the next day fishing, then the next day in wage labour, and so on. This displays a great degree of adaptability and resilience on behalf of the Agta in a changeable socioecological climate.

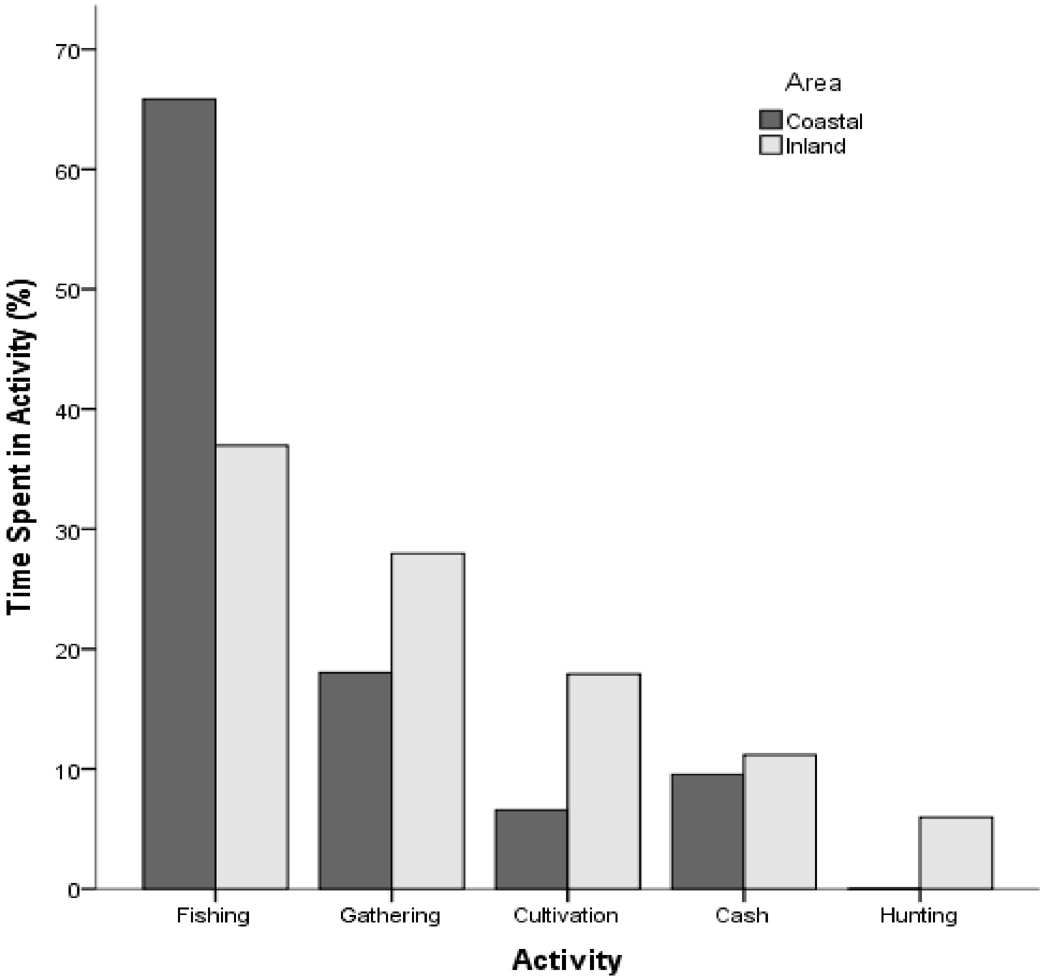

Figure 2.18: The percent of time adults were engaged in subsistence activities while out of camp, split by camp location (coastal or inland), combining male and female data. Note that coastal camps engage much more in fishing than inland camps, while inland camps gather, cultivate and hunt more than coastal camps. The proportion of time spent in cash labour is approximately the same between the two areas. Again, cultivation may either be of gardens owned by Agta or cultivating land for non-Agta.

Marriage

In common with other hunter-gatherer groups (Chapais 2010; Wiessner 2014) Agta marriage is generally exogamous, in that individuals tend to marry outside their local group, increasing the number of kin ties individuals have to call upon in times of need (Headland 1987a; Early & Headland 1998). This is manifest among the Agta in proscriptions against marrying anyone named by a kin term, either consanguineal or affinal (Headland 1987a) This greatly reduces the number of available marriage partners, although in many instances these social rules are flouted. In small groups this effectively means that all camp-mates are off limits as potential partners, necessitating marriage between distant camps, although in larger camps exogamy is not always practised as enough suitable marriage partners may be available within camp. As mentioned above, post-marital residence among the Agta is multilocal, in that married couples either live with husband's kin, wife's kin or both of their kin (or neither's kin: Dyble *et al.* 2015), as is present in many other forager populations (Marlowe 2004b; Hill *et al.* 2011).

For prospective first-time marriage partners there are two paths to spousal choice: arranged by parents or their own decision. Rather than dichotomous, these should be thought of as two extremes on a spectrum, from purely parental choice to purely offspring's choice. At the one extreme there are marriages which are arranged by the parents of the potential spouses, regardless of the wishes of their offspring. Many wives in this situation claimed to be unhappy with their parents' choice at the time, but were happier once they had children. Other 'arranged' marriages were predominantly chosen by parents, but in which the potential spouses could choose not to marry if they wished. When offspring had greater control over mate choice they could choose their own partner, but parents could say whether they were happy with the choice or not. In each of these situations, once a potential spouse was agreed upon the parents of both parties would meet to discuss the prospective marriage in a process known as *nanacad* (in Palanan) or *umil-uli* (in Maconacon).

One of the items to be discussed would be the length and type of bride service (*magservi*) provided by the future husband for the wife-to-be's family. This would generally be a period of a few days to a few years, depending on the quality of the husband and how much the prospective wife's parents approve of him. The prospective husband would live with and provide for the wife's family by completing domestic tasks, such as fetching water, cleaning and cooking, as well as economic tasks, such as providing meat/fish/coffee, engaging in wage labour to earn money or assisting in crop harvests and giving the proceeds to the wife's family. This is to show the wife-to-be's parents that the husband is hard-working (*masipag*) and can take care of their daughter and provide for a family. Although less common in the present-day, many older Agta informants said that some arranged marriages occurred prior to the wife's menstruation, and the male would do bride service for her family until menarche occurred.

In one situation neither *nanacad* nor *magservi* would be performed, and that is when a couple would run away together, often because the parents did not like their prospective mate. In this situation the couple would 'elope' to a different camp for a period of one night to a couple of weeks, after which they would return and apologise to her parents and sometimes bring a small gift of coffee or rice. They would then co-habit as husband and wife, with no need for *nanacad* or bride service. Splitting marriages into those decided by parents or chosen by the couple, there is an approximately equal split, although more marriages in Maconacon are decided by parents compared to in Palanan (table 2.13). In the same table we also see that there are many instances where bride service does not occur, although this is largely confined to Palanan, and that the length of bride service averages 5.6 months, but is greater in Maconacon. Traditionally there was little ceremony upon marriage other than a feast, but recently marriages have become increasingly formalised. Many are now either conducted in the Mayor's office or in a church (figure 2.19), especially in camps closer to town or with a greater Christian influence.

Table 2.13: Data on marriage decisions (own or parents), whether bride service (*magservi*) occurred and approximate length of bride service (if occurred: *n*=177).

		Palanan	**Maconacon**	**Total**
Marriage Decision	Parents	61 (42.4%)	23 (69.7%)	84 (47.5%)
	Own	83 (57.6%)	10 (30.3%)	93 (52.5%)
Bride Service	Yes	101 (70.1%)	31 (93.9%)	132 (74.6%)
	No	43 (29.9%)	2 (6.1%)	45 (25.4%)
Bride Service Length (if occurred)	-	4.6 months (SD=7.2)	8.8 months (SD=11.2)	5.6 months (SD=8.5)

Magas - Infiel Nuptials

Mr. & Mrs. Joning & Melda Magas
and
Mrs. Uklis Infiel

request the honor of your presence
at the ceremony uniting their children

Ariel & Mariel

on Wednesday, April 30, 2014 @8:00pm
at Kag. Steve Manuel's Residence
Del Pilar, San Mariano, Isabela.

Reception to follow
at the same place.

To stand as Principal Witnesses
to our Exchange of Marriage Vows

PB Jesell Wanol
Kag. Lary Padre
Mr. Noli Enipto
Mr. Joel Gallo
Mr. Basangyo Allaga
Mr. Eleng Etchore
Mr. Jhony Yadao
Mr. Lito Izon
Mr. Eduardo Paguirigan
Ms. Perling Cabalteja
Ms. Lilia Gallo
Ms. Sonya Garcia

Mr. Erning Ayson
Mr. Jose Wanol
Mrs. Gina Wanol
Mr. Jessie Gallo
Mr. Faustino Nebrida
Mr. Sammy Gonzales
Mrs. Leni Garcia
Mr. Inggo Etchore
Ms. Melinda Marron
Ms. Ludy Gammad

Figure 2.19: Example of a wedding invitation for a couple in San Mariano, indicating changing Agta marriage practices. This was shown to us by a family from Dipadsangan, Didian, who have kinship ties with the to-be newly-wed couple.

Divorce is relatively rare among the Agta. Out of all marriages, few are known to have ended once one child had been born, and even fewer divorces occurred when there was more than one child. Thus, pair-bonds are relatively stable once one, and definitely two, children have been born. Although precise numbers are not available, many young individuals go through a number of ‘trial marriages’ which are often quite transient and appear to function as a test of the couple’s compatibility. These ‘trial marriages’ often end because of conflict between the couple, intervention by parents or one of them finds a more suitable partner. Mobility between camps is particularly high in teenage years as Agta seek out prospective partners.

Once a couple have children the main reason a marriage will end is because of death. Due to high levels of Agta mortality this is a relatively common occurrence, even among reproductively-aged individuals. Among the San Ildefonso Agta one-third of individuals who reached the age of 20 died before they were 40 (Early & Headland 1998). If the wife dies, then widowers will often have to go through the process of *nanacad* and bride service again if they wish to marry a young female (likely due to their high reproductive value). On the other hand, unless they are still very young, marriage to widows does not entail bride service (again, likely reflecting differences in reproductive value). It is also not uncommon for post-menopausal widows and older widowers to live together in seeming ‘marriages of convenience’. These unions are even sometimes instigated by children (or other kin), and as with widow re-marriages no bride service or formal ceremony is required.

Religious and Ritual Life

To a casual observer the Agta seem quite devoid of ritual life. There are no obvious rituals, cosmology, spiritual beliefs or even apparent attachment to current beliefs or practices. In some places where Evangelical church groups have greater influence there appears little resistance to dropping old customs in favour of newer Christianised ones. One of the few exceptions was an older man from Dibungko, who, when asked why many others in the camp no longer gave offerings while hunting, replied that it is because they are religious, but he didn’t believe their religion (Born Again Christianity), because religion changes his culture and he doesn't like it (however, when asked if he was a Born Again, he replied that no, he is Catholic!). Thus, as noted by other researchers, "the Agta are not highly defensive of their cultural ways" (Early & Headland 1998; 163). While the Agta appear willing to embrace these new customs, they will seemingly be equally as willing to drop them again if the circumstances change. For instance, in Maconacon there was an evangelical church group which gained quite an Agta following, but after leaving the area in the 1990's the Agta there appeared to have lost interest and reverted back to their old ways (or to a different church group active in the area), as no-one there in the present-day continues to follow this denomination (Minter 2010: 249). Regarding religious and ritual life the Agta appear to take the 'path of least resistance', at least when it comes to dealing with non-Agta, by going along with what appears easiest and most beneficial at the time.

Other than Dibungko and a few other camps where the Born Again presence is greatest, one aspect of ritual life appears relatively resilient among the Agta: their hunting practices. This predominantly relates to offerings and good luck rituals. Even in the Born Again camps many individuals still practice these, despite suggestions not to from religious leaders. If an individual successfully catches game then part of the animal and/or a small portion of rice is offered to the *anito* (spirit) accompanied by reciting words to the effect of 'you come and eat. You will give me luck again'. This is generally reserved for larger game, such as wild pig or deer, while it is not performed for fishing or other game (such as monkey or birds). Of 111 adult men that hunt, 81 claim to still leave an offering (73%), although the proportion is higher in Maconacon (25 of 28; 89.3%) compared to Palanan (56 of 83; 67.5%). In addition to these offerings, many Agta perform good luck rituals prior to hunting.

The form of these rituals can vary: some Agta burn items in a fire then either inhale the smoke or wave their bow and/or feet over the flames; others make a paste from water and various plants which they wash themselves with; some Agta leave small offerings such as liquor or betel nut alongside traps for good luck; while many of the Christianised Agta simply pray. Of those that hunt, 65% perform good luck rituals (67 of 103), with equal proportions in both Maconacon (18 of 28; 64.3%) and Palanan (49 of 75; 65.3%).

A further aspect of Agta ritual life concerns medicines and 'bad spirits' (or *anito* – *anito* is a general term for 'spirits'). There are broadly two types of traditional medicines: *magbuga/magtapal* and *magduprak.* *Magbuga* and *magtapal* are basic healing practices used when someone is sick. *Magbuga* consists of combining several plants (which vary depending on individual and camp), chewing or pounding them together, then rubbing the mixture on the sick individual. This is mainly used to try and treat intestinal afflictions, such as diarrhoea. *Magtapal* is similar to *magbuga* in that it aims to treat sickness (generally fever), but is performed by rubbing oils and placing a big leaf on an individual's chest or back. *Magduprak*, meanwhile, aims to treat sickness that is believed to be caused bad spirits. *Magduprak* can only be performed by certain individuals with special 'gifts' (often given in a dream) who perform similar acts to *magbuga* (rubbing plants on an individual) but combine it with dancing and chanting to compel the 'good spirits' to defeat the 'bad spirits'. This can be dangerous for the healer, as upon leaving the sick individual the bad spirit may enter their body. As with many practices in Agta ritual life, *magduprak* is rarely practiced anymore, especially in the Born Again camps. This was highlighted by an old woman from Dibungko who used to perform *magduprak* but informed us that she no longer practices it as missionaries told her to pray to God instead.

Despite seemingly lacking a strong shared belief system, Agta ritual life is peppered with several small practices aimed to improve health and social well-being, although knowledge of and adherence to these practices is highly variable within and between camps. Many of these relate to avoidance of misfortune, such as believing that it is bad luck to leave camp if someone sneezes as accidents will occur. As noted in Casiguran, some Agta possess taboos about mentioning in-laws by name (Headland 1987a), although this norm is not strictly adhered to by many of the NSMNP population. Widows usually wear bracelets and/or necklaces made of black cloth, and sometimes wear black clothes, for approximately one year as a sign of mourning and to show that they have recently become a widow. Family members also wear black thread, although to a lesser extent than widows, as a sign of mourning and recent loss in their family (a practice borrowed from non-Agta populations). Many Agta also wear *manik* (beaded necklaces or bracelets), which some older women use as an additional source for curing illness, although many wear it simply for decoration in order to look *maganda* (beautiful). Teenagers of both sexes in particular wear a lot of jewellery, potentially to attract mates. This may act as a costly signal because *manik* require money to acquire, so displays an individual's resources (or lack thereof). Other body modification practices used to be performed by the Agta, although younger Agta do not partake in them anymore. One example is *gap-gap,* in which the upper incisors and canines are filed away and stained black (Headland 1977), ostensibly for beauty. A further example is scarification, often consisting of simple geometric shapes on a woman's arms or chest, which is claimed to be a signal of strength, particularly in child-birth, which may also act as a costly signal (see also Ludvico & Kurland 1995).

Other practices revolve around childhood and ensuring strong and healthy offspring. One such practice is *upig*, which consists of placing various objects, often animals, against a young child in order for them to acquire some of those traits. For instance: a monkey will make the child good at climbing; a specific tree will make them grow strong; while a deer will make them walk well. A similar practice is known as *dumanay*, in which a string of bark is tied around a child's waist in order to promote growth and health. Surprisingly, many Agta are circumcised (Vanoverbergh 1937), a practice which continues in the present-day. This appears to occur in mid-childhood around 8-10 years of age (according to our field assistants circumcision is common in the Philippines, and males are not seen as 'real men' unless they are circumcised). Thus, Agta ritual life is certainly not non-existent, despite a lack of obvious cosmology or elaborate ceremonies. However, many, if not all, of the foregoing are not specific to the Agta, as according to our informants they are (or were formerly) practiced by non-Agta, suggesting that few of these customs are indigenous to the Agta (see also Vanoverbergh 1933).

External Influences to Agta Livelihood

Looking at the history of hunter-gatherer groups worldwide, and Negrito groups in the Philippines in particular, one may reasonably become pessimistic. These groups are often marginalised and coerced (whether intentionally or not) into giving up a hunting and gathering way of life. Focusing on Filipino Negrito groups, the Batak from Palawan (Eder 1987) and Casiguran Agta (Headland 1989; Early & Headland 1998) cases are instructive. In both instances these formerly foraging groups, although varying in their dependency on traded agricultural products, have faced increased pressure from in-migrating non-Negrito populations, resulting in both the threat of cultural extinction and the loss of the Batak and Casiguran Agta as distinct populations. Taking cultural extinction first, although cultural change is an ordinary and inevitable process, the increased population pressure prevented both populations from continuing to live a foraging subsistence. For the Batak this resulted in an increased reliance on swiddening and trade with lowland farmers (Eder 1987), while for the Casiguran Agta it meant that they could only subsist as labourers for non-Agta (Early & Headland 1998). Regarding the loss of the Batak and Casiguran Agta as distinct populations, the biggest threat to both is out-marriage to non-Negrito's, as the proportion of these inter-group marriages increased in both populations. For the Casiguran Agta this mainly concerned non-Agta men marrying Agta women who subsequently assimilated within the agricultural population, meaning that the pool of potential mates for Agta males decreased (Headland 1989; Early & Headland 1998). In both cases the remaining populations of Batak and Agta not lost to out-marriage declined (Eder 1987; Headland 1989), although for one specific sub-group of the Casiguran Agta, from San Ildefonso, the population rose slightly despite these out-marriages (Early & Headland 1998: it should be noted, however, that since this research the Casiguran Agta population has since collapsed as a result of land-grabbing (Andrea Migliano, Personal Communication)).

However, not all Negrito populations appear fated to extinction. Despite having largely given up a foraging subsistence, the Ayta from Zambales in eastern Luzon are still a successful and self-sufficient independent group of swidden agriculturalists (Brosius 1983). As described above, the NSMNP Agta population appears to be increasing, suggesting that – for now – they may remain a viable and distinct population. Furthermore, the problem of out-marriage appears less of an issue for the NSMNP Agta. Of 212 marriages recorded, nearly 90% were between 'full' Agta (table 2.14), while only ~6% of marriages were to non-Agta. Additionally, while in

Casiguran out-marriages were usually one-way (Agta women marrying non-Agta men and moving away from Agta camps), among the NSMNP Agta this pattern is not observed. Of the 13 marriages to non-Agta, seven were to male non-Agta and six were to female non-Agta, suggesting little sex bias in inter-group marriage. Many non-Agta also live in Agta camps, therefore not removing their offspring from the pool of potential future Agta marriage partners. Thus, the problems of out-marriage faced by the Casiguran Agta are seemingly not present for the NSMNP Agta. Indeed, one of the non-Agta men married to an Agta woman from Kanaipang claimed that it was easier for a non-Agta to live with Agta than for the reverse.

Table 2.14: Frequency and percent of marriages between Agta and non-Agta in the Northern Sierra Madre Natural Park (*n*=212).

Marriage Type	Count	Percent
Both Agta	190	89.6%
Agta to Non-Agta	11	5.2%
Agta to Half-Agta	8	3.8%
Half-Agta to Non-Agta	2	0.9%
Half-Agta to Half-Agta	1	0.5%
Total	212	100%

Even though the NSMNP Agta do not appear to be in as immediate danger of extinction compared to the Batak or the Casiguran Agta, there are reasons to be cautious. Firstly, although they are in no imminent danger of extinction as a distinct ethnic group, as detailed above many of their practices and customs are no longer being practiced by younger Agta or those more associated with Evangelical Born Again church groups. These customs include (but are not limited to): a reduction in hunting, especially with bow-and-arrows, and associated rituals such as offerings; changes in marriage practices; changes in attire away from traditional g-strings to shorts and t-shirt (figure 2.20); and a loss of *magduprak* healing rituals. Many older Agta ascribe these differences to changes in the younger Agta’s mentality, saying that ‘they want to live and act like non-Agta’.

Figure 2.20: Photograph showing changing patterns of Agta clothing. Traditional Agta clothing and decoration (g-string, *biskal* (upper-arm bands), *manik* (beaded necklace) and *pinanes* (cloth bracelets)) as worn by the older gentleman (right) and clothing worn by many younger Agta who are claimed to want to act like non-Agta (t-shirt, shorts and baseball cap) as worn by the younger man (left). This photo is of a grandfather and grandson.

Exogenous changes are also occurring in the Agta's environment which may affect their culture and social dynamics. One factor already alluded to is Evangelical missionaries, which are influencing Agta customs and settlement patterns. Other factors include development projects such as education and 4P's (*Pantawid Pamilyang Pilipino Program*; English: Bridging Program for the Filipino Family), which encourage sedentism and punish mobility. The latter is a 'conditional cash transfer' scheme in which poor families receive cash incentives in return for enrolling their children in school and partaking in health initiatives. While schemes such as 4P's aim to assist impoverished and marginalised groups such as the Agta, they do so by forcing the Agta to adapt, rather than by adapting to the specific needs and circumstances of the Agta (Minter 2010: 249-253).

Population increases over the past few decades have likely put pressure on the Agta (tables 2.3 & 2.4), but one of the reasons they have remained predominantly hunter-gatherers for so long is because of their relative isolation from the Filipino 'mainland'. However, plans to build a new road through the Sierra Madre mountains from Ilagan to Divilican have recently been passed, suggesting that in a few years migration may increase even more, putting further pressure on the Agta. In both the Batak from Palawan (Eder 1987) and the Casiguran Agta (Early & Headland 1998) one of the causes of their transition was roads opening up through their land for economic development. In theory the designation of the NSMNP as a protected area, with specific rights for the Agta to hunt and utilise areas off-limits to agricultural populations, ought to prevent, or at least slow, this transitioning process. However, a lack of enforcement by officials or knowledge by the local population means that the NSMNP is essentially a 'paper park' (Minter 2010; 270) which does very little to actually help the Agta or the protected area. Although the Agta are adaptable and resilient to changing ecological conditions (Minter 2010), no society is infinitely resilient. The impact that these external initiatives will have on the Agta remains to be played out.

Summary and Next Chapter

This chapter has provided a brief ethnographic description of the NSMNP Agta. Each of the topics has been covered in a relatively superficial manner in order to provide a very general background to Agta livelihood, life history, subsistence and interactions with external non-Agta agencies and populations. It is within this ethnographic context that the hypotheses regarding the evolution of cooperation introduced in the preceding chapter will be explored. One important and recurring theme, which will have major prominence throughout this thesis, is the great amount of variability displayed among different Agta camps in terms of mobility, subsistence and social organisation. In addition to displaying resilience and adaptability on behalf of the NSMNP Agta in the face of different environmental circumstances, this variability also offers a ‘natural experiment’ investigating how socioecological differences influence hunter-gatherer behaviour within a single ethnolinguistic group. In contrast to cross-cultural studies between different populations, within-society designs do not confound cultural and ecological differences, as all participants are from the same ethnolinguistic group (Lamba & Mace 2011). This is important as populations such as the Agta can be used to explore and test between different hypotheses regarding the evolution of cooperation, such as the influence of group selection in explaining human cooperation (that is, whether ethnolinguistic group membership or local socioecological conditions better predict cooperative behaviour: Chapter 4). The large amount of variability can also be used to test other adaptive hypotheses regarding the evolution of cooperation. For instance, differences in mobility and camp stability mean that the frequency of repeated interactions between individuals varies between camps, which may have significant implications for understanding cooperation requiring repeated encounters, such as reciprocal cooperation (Chapter 5). Despite the egalitarian nature of Agta social organisation, differences in skill and reputation in domains such as hunting, fishing, medicinal knowledge and decision-making influence are present. These individual differences can be measured and explored to determine if these traits influence an individual's 'market value' as a cooperative or social partner (Chapter 6). The unique life history of humans is also inextricably linked to cooperation. These associations between life history and cooperation, specifically regarding the evolution of extended childhood dependency, will be considered in further detail in the chapter examining the ontogeny of cooperative behaviour among the Agta (Chapter 7). These (and additional) hypotheses will be discussed in greater depth in future chapters. Furthermore, as the Agta are a hunter-gatherer population, understanding their cooperative dynamics may also shed light on the evolutionary and ecological roots of human cooperation prior to the advent of agriculture and large-scale societies (although these inferences are not without difficulty, as discussed above). In the next chapter I introduce the research design and data collection methods used to measure and explore the factors underlying cooperative behaviour among the Agta.

Chapter 3 Field Methods and Data Collection

This chapter contains a description of the methods employed to collect the data used in subsequent chapters (in addition to some of the data in the previous ethnographic chapter). Several types of data were collected, including: genealogies, census information, aging, anthropometrics, camp scans, household questionnaires, experimental cooperative games (on both adults and children), measures of skill and data on social norms. Much of this data, especially regarding demography, was gathered collectively and shared between other members of the Hunter-Gatherer Resilience Project working with the Agta (Mark Dyble and Abigail Page), while other data specific to the current research were collected independently.

Fieldwork Timeline and Translation

A total of approximately 10 months was spent in the field, split between two seasons. The first occurred from April to June 2013, and the second longer stint occurred between February and October 2014 (with two short breaks on the Philippine mainland as respite). During the first phase, data collection focused on obtaining collective data for the project, such as demographic information, which would then act as a foundation for further analysis. During the second phase more specific data relating to cooperation and the specific aims of this thesis were collected, as well as demographic information when engaging with individuals or camps not met during the first period.

Collection of this data would not have been possible without the assistance of our translator field assistants. These were primarily non-Agta (although one Agta field assistant joined us during the second season of fieldwork) recruited from the main town in Palanan, and in most cases were students or graduates of the local Isabela

State University. Translators were proficient in English, as well as Tagalog, the *lingua franca* of the Philippines, and Paranan, the local language. In Palanan all Agta are fluent in Paranan, while the majority are also conversant in Tagalog. In Maconacon many Agta speak some Tagalog, although the main languages spoken there are Ilocano (introduced from mainland northern Luzon by Ilocano migrants over the past century) and Dupininan, the native dialect. Therefore, before departing for Maconacon it was ensured that at least one of our field assistants was fluent in Ilocano for conducting interviews with Agta that could not speak Tagalog. Prior to leaving the main municipal town, all field assistants were briefed over the data collection protocols to ensure that they understood the aims of the project and the data to be collected. As the majority of our interviews and data collection methods were structured, rather than unstructured, and repeated many times, they were learned very quickly by our field assistants.

Group Data Collection

Demographic information, such as age, sex, group composition and relatedness between individuals, are central to many evolutionary and ecological analyses. These data are a platform from which further research can be conducted; without this baseline data, testing these evolutionary hypotheses would be unfeasible. For instance, without knowledge of camp or kinship structure it would be impossible to assess the role of relatedness or proximity in explaining patterns of food-sharing (Allen-Arave *et al.* 2008; Nolin 2010). Thus, these data were obtained collectively by members of the Hunter-Gatherer Resilience Project working with the Agta as they would form the basis of all of our research projects.

Informed Consent and Ethical Approval

Upon entering a new camp, and prior to collecting data, we first sought out the chief of the camp (if there was one) or other highly-respected individuals to explain our research project and ask for permission to work in that camp. Once given approval, all available Agta from the camp were asked to attend a group meeting where members of the project introduced the research, explained the methods we planned to use and why we were collecting that data. Any questions or concerns raised at this time were answered. Only individuals that wished to participate were included in the research project, although the majority of individuals were happy and willing to take part (of over 1,000 Agta met, only ~15 declined to participate). Informed consent was given by each adult, and consent for children was given by their parent or guardian. Ethical clearance was granted by the University College London ethics review board (UCL Ethics Code 3086/003). Fieldwork permission was granted by local government units, including the Mayors of the municipalities visited and from the Department of Environment and Natural Resources (DENR) as the research took place in a protected area.

Genealogies

As detailed previously, knowledge of consanguineal and affinal kinship relations are core components required to explain and predict human cooperative behaviour. To this end, genealogical interviews were conducted with all adult individuals. This consisted of asking adults first whether their current spouse (if married) was their first partner, and if not to name any previous spouses. Beginning with the first spouse, individuals were then asked to list each of their pregnancies sequentially, including miscarriages and offspring deaths. The outcome of each pregnancy was noted (miscarriage, stillborn, deceased or living). For deceased offspring the approximate age at death was asked, and if unknown they were asked to name to another individual around camp who was around the same age when they died. Similarly, causes of death were also elicited, although in many cases these were unknown or simply said to be ‘illness/sickness’. Symptoms for these individuals (e.g., feverish, trouble breathing, diarrhoea, etc.) were ascertained where possible to attribute an approximate cause of death. We also asked whether the age of living offspring was known. After all offspring were recorded, these were repeated back to make sure that the order was correct and that no pregnancies had been missed out or forgotten. This was predominantly conducted with the wife, although often husbands or other family members were also present to aid recall. Husbands were explicitly consulted to ensure that they had no previous wives, and if so, reproductive histories were conducted for these marriages. Men were also the primary source of genealogical information if their wives were absent or the man was a widower. Thus, reproductive histories for all living adults met were obtained.

In addition to reproductive histories, genealogical interviews also enquired about the names and locations of other kin and their spouses. This was to link genealogies and infer relatedness coefficients (e.g., 0.5 for offspring, siblings, parents; 0.25 for aunts, uncles, etc.). Older individuals were especially useful for this as their knowledge possessed a longer temporal depth, so kinship links which would otherwise have been overlooked were obtained. This is especially important with the Agta, who have very limited genealogical knowledge (Headland 1987a) and often cannot name all four grandparents. Although this procedure was quite laborious at first, over time it was relatively uncommon to meet someone that we could not place as someone’s sibling or cousin. Note also that this procedure for constructing relatedness coefficients based on genealogies ignores the potential for extra-pair paternity, although recent genetic analyses suggest that its prevalence in humans may be as low as 1-2% (Larmuseau *et al.* 2016). For ego's parents, siblings, grandparents and aunts/uncles, causes of death and approximate age at death were also noted. However, for more distant kin, and even for grandparents, aunts and uncles, this information was often unknown, particularly if they died long ago. Where possible, cause and age of death for individuals other than offspring were taken from their closest living relative (e.g., sibling or child) in an attempt to ensure accuracy.

During these interviews we also asked females about menarche and menopause. For menarche, individuals between the ages of approximately 10 and 20 were asked whether they had begun menstruating (i.e., whether their periods had began). Menopause, in terms of whether women were still menstruating or not, was asked in older women between the ages of ~40-55. However, rather than a conspicuous cessation of menstruation many women could not answer when (or even if) they had become menopausal, as this is a gradual process, the experience and interpretation of which is also cross-culturally variable (Lock 1994). Given this imprecision, questions about menopause were dropped in later interviews.

Census

Upon entering each camp the names of all individuals living there, the number of houses and who lived in each house were ascertained. These data were used to calculate camp and household size, as presented in the ethnographic chapter. Although camp size and composition data were collected, as noted previously our research was not aimed to be a complete census of the NSMNP Agta population. There are camps, although relatively few in number in Palanan, which were not visited. Eleven Agta camps from Palanan were visited on multiple occasions, and on each visit the names of all individuals living in camp were noted. From this data it was possible to assess the level of in- and out-of-camp mobility for each camp, giving a measure of camp stability. As discussed in the ethnographic chapter, mobility and camp stability appear to vary considerably among the Agta (figures 2.12 to 2.14). Here, this variation in camp stability is quantified, providing a precise estimate of the level of turnover in camp composition. This index offers a measure of the frequency of repeated interactions within a camp, central to many theories regarding the evolution of cooperation, such as direct reciprocity (Trivers 1971).

To calculate this stability variable, during each visit to a camp individuals were coded as ‘1’ if they were present or as ‘0’ if absent (individuals first present at later visits were retrospectively assigned a ‘0’ for the preceding visits). Individuals who had moved either in or out of camp between visits were given a mobility value of ‘0’ for that period, while those who remained in the same camp received a value of ‘1’. For camps where only two visits were made, the camp stability metric was simply the average of those who had moved either in or out of camp (‘0’) and those who had not moved (‘1’). For example, in a camp originally consisting of ten individuals at time 1, if five had moved before our second visit, five individuals would have scored a ‘1’ (no change in camp) and five would have scored a ‘0’ (moved camp). This makes for a summed score of 5 ((5*1)+(5*0)), which, when divided by the number of camp-mates (10), gives an average of 0.5. Thus, the stability score for this camp would be 0.5. As another example, given a camp again consisting of ten individuals on the first visit, if five more individuals were to join the camp and none of the original members left, ten people would be given a score of ‘1’, and five would be given a ‘0’. The summed score is therefore 10 ((10*1)+(5*0)), and the average is 0.667 (the summed score (10), divided by the total number of camp-mates (15)). As a final example of a two-visit camp stability score, consider both in- and out-of-camp mobility simultaneously. Again, start with a camp of ten individuals at first visit, have five people leave and five new individuals join. The five people remaining across both visits would be given a '1', while both the five who left and the five who joined would be given a '0', so the summed score would be 5 ((5*1)+(10*0)), which, when divided by the total number of camp-mates (15), would give a stability score of 0.333.

This system becomes slightly more elaborate when considering three (or more) visits to a specific camp, although the principle remains the same. We can derive an estimate of individual mobility if we use the formula: 1-(ratio of 0's to 1's). For example, say an individual had the pattern 'present-absent-present' ('1-0-1'), the ratio of 0's to 1's is therefore 1:2, or 0.5, and 1-0.5=0.5, so they would receive an individual mobility score of '0.5'. 'Present-present-absent' ('1-1-0') or 'absent-present-present' ('0-1-1') would also receive a score of '0.5' via the same method. Given four visits, a string of 'absent-present-present-present' ('0-1-1-1') would produce a ratio of 1:3, or 0.333, which, when subtracted from 1, gives a score of 0.667. Meanwhile, a string of 'present-absent-present-absent' ('0-1-0-1') gives a ratio of 2:2, or 1, giving a score of '0' when subtracted from 1. However, when the number of 0's is larger than the amount of 1's, the formula does not work, but as these individuals are more often away from camp than present, their mobility is therefore high, so can be assigned a value of '0'. Thus, an individual who was 'absent-present-absent' ('0-1-0') would receive a score of '0'. As with the two-visit example in the previous paragraph, to calculate camp stability, simply sum up the individual mobility scores of each individual who lived in that camp at one time, and average this by the total number of individuals who had lived there.

Five of the camps were visited three times (once in 2013 and twice in 2014), two camps were visited twice in different years (once in 2013 and once in 2014), three of the camps were visited twice in the same year (2014) and one camp was visited four times (once in 2013 and three times in 2014). The minimum length of time between two visits was ~2 months. There was great variation in stability between camps, with a minimum stability of 0.12, meaning that nearly the whole camp had changed over visits, and a maximum stability of 0.79, meaning that the majority of individuals in that camp continually resided there over time. The average camp stability was 0.51 (SD=0.22). Although the number of visits and length between visits varied across camps, this is unlikely to bias the results. It may be expected that changes from one year to the next would be greater than changes over only a couple of months, yet this is not the pattern observed. The three camps visited in the same year showed greater instability than camps visited from one year to the next (same year average=0.28, *n*=3; different year average=0.59, *n*=8), a pattern likely found because the camps only visited in the same year were farther from the main town (as discussed in the preceding ethnographic chapter, camps more distant from town tended to possess greater mobility). Although seasonality can influence hunter-gatherer mobility patterns (Marlowe 2005), and the Agta are generally less mobile during the rainy season from October to February (Minter 2010), the present research was conducted during the dry season and there were no systematic biases between the months in which stable or unstable camps were visited (table 3.1). Differential mobility between camps cannot therefore be attributed to seasonality effects, such as climate or variation in wage labour opportunities (e.g., rice harvests).

To further verify this measure, each dwelling was ranked on a set of criteria (discussed below), with a low score meaning a simple and temporary residence and a high score indicating a larger and more stable dwelling. As would be expected, results from a linear regression between house type and camp stability indicated that individuals living in more basic and temporary dwellings were significantly more likely to reside in camps with increased instability, while individuals living in larger permanent houses were more likely to live in stable camps (b=4.04, SE=0.57, p<0.001, n=183). Thus, individuals living in temporary houses resided in less stable camps, as would be predicted if individual mobility was higher in these camps, providing further evidence that this index is a valid measure of camp stability.

Table 3.1: Dates of camp censuses and length of time between visits when constructing the 'camp stability' metric. Stability scores can vary between '0' (complete change in camp composition between visits) and '1' (no change in camp composition between visits). Note that there are no systematic biases in either the census dates or the length of time between visits for stable and unstable camps. Also note that all visits to camps were made in the dry season (from February to September). Seasonality or sampling biases are therefore unlikely to influence variation in camp stability.

Camp	Stability Score	Dates of Census	Length of Time Between Visits
Semento	0.6	05/2013, 03/2014, & 09/2014	10 months & 6 months
Dinipan	0.525	06/2013, 04/2014, & 09/2014	10 months & 5 months
Culasi	0.774	05/2013, 04/2014, & 09/2014	11 months & 5 months
Diago	0.732	04/2013, 04/2014, 06/2014, & 09/2014	12 months, 2 months, & 3 months
Dipaguiden	0.21	04/2013 & 07/2014	15 months
Didikeg	0.509	04/2013 & 07/2014	15 months
Kanaipang	0.612	05/2013, 05/2014, & 08/2014	12 months & 3 months
Diambarong	0.327	06/2014 & 08/2014	2 months
Magtaracay	0.122	06/2014 & 08/2014	2 months
Dipadsangan	0.384	06/2014 & 08/2014	2 months
Diabbut	0.789	06/2013, 03/2014, & 08/2014	9 months & 5 months

Aging Process

Accurate aging of a population is essential for several reasons, including inferring life-history events (menarche, marriage, first and last child, death, etc.), infant growth and development, as well as calculating the population structure of a society (e.g., population growth/decline, previous epidemics, etc.). Thus, in populations where individuals are largely unaware of their own ages – as is the case for the majority of hunter-gatherers– estimating individual ages poses a substantial problem. This is especially true when life history variables are of particular interest, regarding the evolution of human's derived life history (Kaplan *et al.* 2000). Even outside of life history studies, knowledge of age is essential as an independent or control variable in many analyses where age is likely to be associated with the dependent variable.

Several methods have been adopted in an attempt to estimate ages in small-scale populations (reviewed in Hill & Hurtado 1996). One such method is simple visual age estimates, while another is approximate groupings into age cohorts (e.g., infant, child, teen, adult and old age). However, these methods are likely to misattribute ages due to a lack of familiarity with differences in aging in these forager populations (e.g., children may appear younger than western age-mates or middle/old aged individuals may appear older). Additionally, these methods possess a lack of fine-grained resolution making comparisons of theoretically-relevant life history variables, such as age at menarche, first birth or death, problematic.

A method which aims to overcome these difficulties is a 'steady-state model', as applied by Howell (1979) with the Dobe !Kung. In this approach a static population structure is assumed, a relative age list of all individuals ascertained, and both the death and fertility rates of the population estimated. From the mortality and fertility rates it is possible to approximate the age structure of the population by mapping these factors on to several life-tables (in which 80% live to age 1, 75% live to age 2, etc.) and selecting the one with the best correspondence. However, there are several problems with this approach: the population structure may not be stable or none of the existing life tables may match the population structure. Additionally, the reasoning is somewhat circular, especially when exploring adaptive variation in life history parameters across human populations. For instance, the short stature of various pygmy populations may be a result of high mortality rates, which result in less investment in growth and a faster life history (Migliano *et al.* 2007). By assuming a static population model in which the proportion of individuals living to a certain age is pre-determined (e.g., 0.5% of the population live to age 85), these potentially significant differences in life history variation may be overlooked.

As a result of these problems, when determining ages for the Ache, Hill & Hurtado (1996; see also Blurton Jones *et al.* (1992) with the Hadza) employed a method which did not assume a static population. To achieve this, they first split the population into multiple age cohorts containing individuals of approximately the same age. Individuals then ranked others in their cohort (as well as the cohorts immediately above and below their own) as either older or younger than themselves. Within each cohort a relative age list was subsequently produced by minimising the number of contradictions in rank, followed by a master relative age list of all cohorts combined. To obtain absolute ages, estimates were made either by known events, birth certificates (for a few of the younger individuals) or by an age-difference chain (used for the majority of individuals with unknown ages, especially those born before ~1960 for which other age-relevant data was missing). For the latter method, the age of an individual was estimated by ego pointing to someone of a known age (person *A*) who was of a similar age to ego when another individual (also of a known age; person *B*) was born. The age of ego would then be the age of person *A* plus the age of person *B*. For example, if an individual said they were age of person *A* (who was, say, 12 years old) when somebody aged 18 (the age of person *B*) was born, their age would then be assigned as 30. Finally, the ages of ranked individuals without a previous age estimate were estimated by mapping them on a polynomial regression, using relative rank as the independent variable and age of known individuals as the dependent variable.

Similar methods were employed to estimate the ages of Agta individuals, although they differ in that the resulting age given by the analysis was not a single age, but a distribution of possible ages for the focal individual. Point estimates can then be derived from these, but it is also possible to utilise the age distribution and take this error into consideration (although point estimates, rather than age distributions, were used for all analyses in this thesis). For this aging process two pieces of information were required: i) a relative age list (or multiple lists) of individuals, ranked from youngest to oldest; and ii) age estimates associated with each individual in the relative age list.

In order to construct relative age rankings, photographs of all individuals in each camp were taken and printed. Individuals were then assigned to approximate age cohorts (0-4, 4-8, 8-12, 13-19, 20-45 and 45+). Those not easily assigned to one cohort were included in the two nearest cohorts (e.g., an individual aged ~45 would be included in both the 20-45 and 45+ cohorts). Either individually or in small groups, Agta were presented with photographs of individuals from a target cohort one at a time. The target cohort was the cohort ego was included in, as well as all cohorts younger than ego (so that individuals also ranked the ages of others younger than them). Sequential cohorts, especially for children, were often presented together (such that some rankings included, for instance, all individuals aged 0 to 12). Individuals from a specific camp were shown photos of others from their camp and neighbouring camps. More distant camps were not included due to a lack of familiarity, unless ego knew individuals from these camps particularly well (e.g., they grew up in said distant camp). For cohorts including ego, ego’s photo was displayed first. Participants were first asked if they knew the target individual. If so, they were then asked if they were familiar enough with the target to know their approximate age relative to other individuals. Each photograph was put into one of three categories: ‘don’t know’, ‘know but not the age’ and ‘know with age’. If ego knew both the target and their age, they were asked to rank the age of the target individual relative to others (with left meaning younger and right meaning older: figures 3.1 & 3.2). Although similar to Hill and Hurtado’s (1996) method, rather than having two categories of simply older and younger (with ego as reference), our method produced a continuous relative age list from youngest to oldest. This process was repeated multiple times, producing a total of 266 partial ranks which encompassed 587 Agta.

Figure 3.1: An example of the aging process being performed.

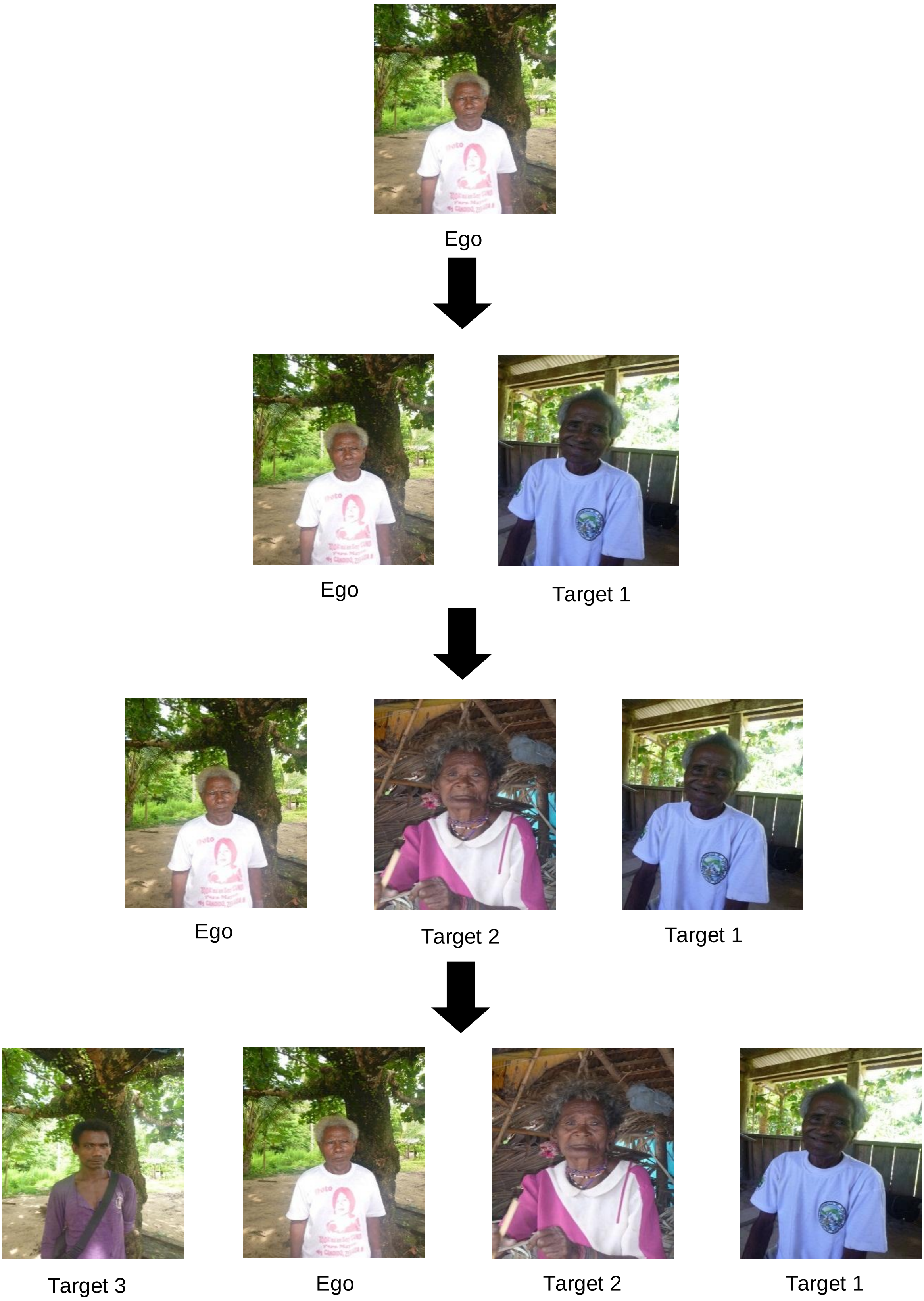

Figure 3.2: Example of the method used to construct a relative age list. Sequentially, ego placed individuals in order relative to others, from youngest (left) to oldest (right). In cohorts where ego's photo did not appear, their picture was omitted.

The second stage of the aging process involved deriving age estimates for these 587 individuals. One invaluable source of information, especially for older individuals, was Thomas Headland's database of Casiguran Agta (Headland *et al.* 2011). Some individuals from the NSMNP population were included in this database with relatively accurate dates of birth assigned. Absolute ages of individuals were ascertained via various other methods, including: asking individuals if they knew their own or their children's age (which could be from various sources, such as birth certificates, other documentation, school grade, own estimates, etc.); births near dated events (such as martial law in 1970, various known typhoons, etc.); and age-mates of individuals with known birthdays. For children up to the age of 12, it was also possible to estimate ages by dental development (see chart in Appendix 1).

However, there are many problems with trusting the answers of individuals via many of the above methods used to estimate absolute ages, especially for estimates given by individual Agta, dental development and school grades. For example, many individuals gave various conflicting dates or ages, including: stating a child was 4 years old, yet born in 2004 (meaning they were ~9 years old); giving a birth date for one child as 2004 (~9 years old) yet saying a younger sibling was 10 years old; or simple age conflicts between individuals (e.g., one child was given an age of 7 months by one parent and 2 years by another). For both teeth ages and school grades, the margins of error were often quite large (± 1/2 years). This was especially problematic regarding school ages, as the grade reached was often variable for individuals of a similar age. Therefore, strict criteria were used to select accurate ages and birth dates. Firstly, if an individual was given two markedly different birth dates, that person was excluded from the absolute age list. Secondly, if ages for an entire sib-set were provided, if even one age was illogical (e.g., did not correspond to teeth ages or did not allow 9 months pre- or post-birth of nearest sibling), then ages for the whole sib-set were excluded. Furthermore, given ages of children had to fall within the range of dental development ages to be accepted. Individuals with estimated ages from comparisons to those with a known birthday were given an age with a ± 1 year margin to account for error.

Using these methods, 98 individuals were given an exact birthday, while 93 others were given age estimates within ± 1 year (table 3.2). For individuals which a secure date or estimate could not be attached (*n*=396), three of the field researchers (myself, Abigail Page and Mark Dyble) and the principle investigator (Andrea Migliano) estimated the ages based on cues such as dental development, school grade, birth order (if older or younger siblings had a known age), age of ego's children (if known), number of children and visual inspection. Independently, each of the four assessors estimated an upper and lower bound based on the age range expected for the individual to fall between. In collating these estimates, the youngest lower bound and oldest upper bound of the four estimates were used in order to include as much uncertainty as possible. Obviously, with greater age comes greater uncertainty, as the average difference between upper and lower estimates increases with age (table 3.2).

Table 3.2: Average difference between upper and lower age estimates, and number of accurately known ages based on different age cohorts for the Agta (*n*=587). For the purposes of this table, the average of the upper and lower bound was taken as an individual's expected age used for grouping cohorts. Number of exact birth dates and birth dates accurate within ± 1 year are also displayed.

Age Cohort	Sample Size	Average Difference in Age Estimates	Number of Exact Birthdates	Percentage of Exact Birthdates	Number of Birthdates ± 1 year	Percentage of Birthdates ± 1 year
<1	20	0.16	15	75%	20	100%
1-5	103	1.73	30	29.13%	67	65.05%
5-10	103	3	19	18.45%	33	32.04%
10-20	116	4.1	13	11.21%	33	28.45%
20-45	164	9.47	18	10.98%	26	15.85%
45+	81	18.56	3	3.7%	12	14.81%
Total	587	6.85	98	16.7%	191	32.54%

The next stage involved combining the relative age lists and age estimates to assign specific ages to individuals. This stage of analysis was conducted by other project members (Yoan Diekmann, Pascale Gerbault and Mark Thomas) employing a Gibbs sampler Markov Chain Monte Carlo (MCMC) algorithm. Additional details of this methodology can be found in a forthcoming publication (Diekmann *et al.,* submitted). In brief, prior to the MCMC procedure each relative age list was checked for consistency. Individuals were subsequently removed from the age rank if they were either: i) placed in an incorrect order according to their age (e.g., an individual assigned an age between 3-5 ranked as older than an individual assigned an age of 6-8); or ii) placed in an incorrect order given known birth orders (for siblings).

A second process prior to the MCMC analysis involved collating lists which contained no contradictory information. This merging process was essential because without it individuals at either end of the partial rank could theoretically take any value within their distribution, as long as it was higher than the preceding individual (if at the end of the rank) or younger than the subsequent individual (if at the beginning of the rank, other than for the youngest cohort). By merging partial ranks between different age cohorts, this constrains the oldest individual in the younger cohort, making age estimation more accurate. For example, say an individual in the teenage cohort was believed to be between 16 and 21. If they were ranked as the oldest in this cohort and the next youngest was known to be 17, all ages between 17 and 21 were therefore possible. However, if this teenage cohort could be merged with the older adult cohort, and the youngest adult from this cohort was known to be 19, this would constrains the age of the focal individual to between 17 and 19, meaning that age estimation would be more accurate (e.g., two lists of ABCD and DEFG become ABCDEFG).

While merging is necessary for this reason between cohorts of different ages, it may also result in a loss of information *within* similar-aged ranks. For instance, if there are nine ABC ranks and only one BAC rank, one would be fairly certain that A was younger than B, yet by merging this would reduce the ten ranks to just two: ABC and BAC. This would entail a loss of information and make it appear that A being younger than B and B being younger than A were equally likely. However, this is only a toy example and our real-world data contains many more than three individuals per rank and the ordering is much more heterogeneous across individuals. To explore this, we applied the merging process using a sample of five ranks (between 17 and 28 individuals in length) of individuals of similar ages from a single camp and found that none of the ranks merged. This suggests that the merging process does not result in a loss of information regarding certainty of ordering *within* age cohorts, while simultaneously bracketing individuals and constraining ages at the ends of ranks *between* cohorts.

After this data preparation the Gibbs sampler MCMC method was employed. To start, all individuals in a relative age list were assigned fixed values from their distribution such that the resulting ages respected the ranking. Then, a randomly-selected age value was sampled from its distribution for each individual in turn, keeping all other ages fixed and again ensuring that the resulting ages respected the ranking. After each individual in a relative age list was assigned an age value, the process was iterated again, with newly-assigned fixed values given to each individual. This process of iterating over the individuals was repeated numerous times (15,000 iterations, in this instance) on each relative age list. The final age distribution for each individual was calculated by combining all valid ages sampled for that individual across all relative age lists in which they were included. Although a final age distribution was produced for each individual, the full information contained in the distribution can be reduced to point estimates if required, although with a concomitant loss of information. In a sample of individuals with a known age using data from the Casiguran Agta database (Headland *et al.* 2011), for which specific dates of birth and photos were available to make age estimates, this MCMC Gibbs Sampler approach found that the mean value approximated the actual age more closely than median or modal values. Analyses in this thesis therefore utilise mean point estimates as age values. This method was also found to result in more accurate point estimates than the regression-based approaches used with the Ache (Hill & Hurtado 1996) or the Hadza (Blurton Jones *et al.* 1992). The median difference between known and estimated values using this MCMC Gibbs Sampler approach was 0.3 years (around four months; mean difference=0.91 years), while the median difference using a fifth-order polynomial regression was 1.16 years (around 14 months; mean difference=2.66 years: Diekmann *et al.,* submitted).

Although we were able to assign ages to 587 Agta using this method, Agta from Maconacon and Dibungko, as well as additional individuals met after conducting the aging process, were not assigned ages via this procedure. Fortunately, as a result of greater integration with the wider non-Agta population, many of the individuals from Maconacon and Dibungko under the age of ~25 were aware of both their own and their children's ages with a relative degree of accuracy (approximately ±1 year or so). For other Agta, especially older individuals, ages were assigned based on birth order information (e.g., the age of their older and/or younger sibling may be known), approximate age of oldest child (e.g., if oldest child is ~8, then they are unlikely to be younger than ~24) or simple visual estimation if none of the former could be ascertained. Naturally, these estimates are likely to contain a greater amount of error than those produced from the MCMC procedure described above. When accurate ages are necessary, such as for certain life history analyses (as presented in the ethnographic chapter), the subset of Agta with known or accurately estimated ages can be used. As highly accurate ages are less vital for hypotheses regarding the evolution of cooperation, analyses in the following chapters use all age estimates derived from both the MCMC procedure and the less rigorous methods used to ascertain ages in Maconacon and Dibungko.

Anthropometrics

Several anthropometric measures were collected, including height and weight for the majority of individuals met. In Palanan height was measured using a Harpenden Anthropometer (manufactured by Holtain Ltd.) and weight measured using digital bathroom scales, both of which were recorded on a solid flat surface. Height was measured in centimetres to the nearest millimetre (0.1 cm) and weight in kilograms to the nearest 100 grams (0.1 kg). Height and weight were also measured for the Maconacon population (as well as Dibungko from Palanan), but using less precise apparatus. Height was measured using a tape measure fastened against an upright surface (measured to the nearest half-centimetre; figure 3.3) and weight recorded using mechanical bathroom scales (measured to the nearest half-kilogram). Heights and weights therefore carry greater error in the Maconacon (and Dibungko) population compared to the majority of Palanan. While all other height and weight data were obtained collectively, I was the only member of the team to visit Maconacon and Dibungko, so these data were collected solely by myself. Other anthropometric data were also collected for many individuals, including: hip width, shoulder width, head circumference (for children under the age of ~18), 2D:4D digit ratio and grip strength. See Appendix 2 for further details and specific protocols regarding collection of anthropometric measurements.

Figure 3.3: Example of anthropometric data collection in Maconacon.

Camp Scans

In order to explore time-budget and group composition information, camp-scans were conducted collectively in 10 of the Palanan camps. For this, the activity of every individual from camp was recorded, as well as all individuals in the social group. Activity was defined according to four broad categories, each of which was sub-divided into further activities: domestic activities (e.g., cooking, fetching water, processing food); childcare (e.g., breast-feeding, holding children); out of camp (e.g., hunting, fishing, gathering, wage labour); and non-work (e.g., socialising, playing, sleeping: see Appendix 3 for the data collection sheet). For individuals engaged in more than one activity, such as processing food and holding children, both activities were noted. Social group was defined as any individuals either in close proximity to another (~2 metres) or engaged in a shared goal (e.g., cooking, playing, hunting, etc.). For individuals currently out of camp, other camp members were asked of their whereabouts, including what they were doing and who they were with. If unknown, data for these individuals were retrospectively filled in when said individual(s) returned to camp. These scans were repeated four times a day, three hours apart, for the length of time the researchers were present in camp, with a minimum of six days (minimum total 24 scans per camp). The time of the first scan was staggered each day by 30 minutes (6:30, 7:00, 7:30, 8:00, 8:30 or 9:00), to ensure that time of day did not co-vary with activity.

Household Questionnaires

Questionnaires were also asked to each family in order to build up a database of familial variables (see Appendix 4). These questionnaires covered several different topics. Some questions required only one family representative to answer. For consistency, females in the family were consulted first for these questions (unless there were no women present, in which case men were interviewed). For other questions, answers from both sexes were sought. Regarding family-wide variables, it was first asked whether the family had any land for planting crops, and if so, approximately how large the area was and what they planted. Next, questions regarding whether the family had any food stored, and if so, which items and in what quantities were asked. The amount of money currently held (if any), and what it was to be used for, was also ascertained. In order to assess whether each family perceived that they had enough resources, questions regarding food security were asked. For this, ten statements such as “I did not eat for one day” or “I was worried that our food would run out” were answered on a Likert scale as either ‘always’, ‘sometimes’ or ‘never’. The amount of perceived food insecurity was then calculated by scoring and summing the answers. Church attendance was also enquired about. A final family-level variable collected was household wealth. For this, each family was asked whether they owned a list of 16 household items (including cooking pot, machete, blankets, etc.; see Appendix 4 for a full list), and if so, how many of each item they owned and which items were the most important to them. From the original list of 16 items, the 10 most important items were carried forward and used to construct an index of material wealth. For these 10 items, means and standard deviations (SD) were calculated. From this, each item in a household was given a value of ‘1’ if it was lower than 1 SD below the mean, ‘2’ it if it was between ±1 SD of the mean, and ‘3’ if it was higher than 1 SD above the mean. This was then averaged across each of the 10 items. Thus, the score for each family reflects whether the amount of material possessions was below average (closer to 1), average (closer to 2) or above average (closer to 3: raw *z*-scores were not calculated as extreme values would greatly distort comparisons).

Turning now to individual-level variables, each adult was asked which school grade (if any) they had reached, as well as the vaccinations they had received (if any). Similarly, the vaccination and educational history for each dependent offspring was also noted (as well as whether school grade was the current grade or the grade at which they stopped attending school). In order to explore social networks and relationships between camp-mates, all adults in each household were asked to name the five individuals they would most like to live with (similar to the ‘camp-mate’ network employed with the Hadza: Apicella *et al.* 2012). Agta were free to name whoever they wished: Agta or non-Agta, camp-mates or non-camp-mates. Residential histories were assessed by initially asking each adult where they were born. From there, it was asked where they next moved to, their approximate age, why they moved and whether they were living with consanguineal kin or affines (or neither). Mobility in this sense was generally from one region to another, rather than small moves within a given area (for instance, a long-term residential shift from one *barangay* to another, rather than mobility within a *barangay* between nearby camps). Each individual was also asked questions about their subsistence activities in order to assess the relative importance of each. For this, six cards were displayed, each containing a representation of a different subsistence activity: hunting, fishing, gathering, cash labour, gardening/agriculture and making products to sell (e.g., baskets, mats, etc.). Individuals were first asked to name any activity they never engaged in. After these were removed, they were asked to order the cards from the activity they spent most of their time in to the activity they spent the least of their time in. Additional questions about each activity were also asked to garner ethnographic information about the form and frequency of these subsistence activities. One last piece of information gathered from these questionnaires concerned the type of dwelling the family resided in. Each house was rated along several dimensions, including house type, construction materials, size and ownership. This was coded on a scale from ‘0’ (meaning a simple lean-to shared by more than one family; similar to figure 2.13) to ‘8’ (meaning large house with metal roof and wooden floors and walls, occupied by a single family; similar to figure 2.12).

Individual Data Collection

The above section described the methods employed for the collection of shared data for all members of the project. Methods utilised for collection of data specific to my research will now be presented. First, experimental data on cooperation in both children and adults, which form the bulk of the analysis chapters, were collected.

Second, data on reputation in different domains, such as hunting, fishing, medicinal knowledge, storytelling and camp influence, were obtained. Additional data relating to social norms were also collected through semi-structured interviews and observations. Data regarding these social norms have been presented in the ethnographic chapter to give a general background to the Agta, but will not be analysed in more detail in the subsequent analysis chapters which focus predominantly on cooperative behaviour.

Experimental Games with Adults

In designing experimental cooperative games there are several questions which need to be addressed. A central question is: which aspect of cooperation is one attempting to measure? If one is interested in exploring market norms and anonymous interactions with others, then traditional economic games, such as Dictator Game, Ultimatum Game and Public Goods Game, may suffice (Henrich *et al.* 2014), although as discussed in the introductory chapter it appears difficult to dissociate these from everyday social dynamics and other confounding influences. However, for examining cooperation within small social groups, such as food-sharing in hunter-gatherer bands, a different approach may be necessary given the apparent lack of correspondence between traditional economic game and real-world cooperative behaviour (Gurven & Winking 2008; Wiessner 2009). Furthermore, these traditional experimental games only measure levels of cooperation, while not exploring *who* individuals cooperate with as part of a wider social network. To examine who individuals preferentially cooperate with requires a non-anonymous methodology. Although games have been devised to measure cooperative networks, such as the gift game (Apicella *et al.* 2012; Chaudhary *et al.* 2015; Thomas *et al.* 2015; He *et al.* 2016), they offer no measure of cooperativeness, as individuals have to share resources regardless of whether they wish to or not. Alternatives must therefore be sought if one wishes to explore both levels of cooperation and who individuals share with. This is important as these are the types of cooperative decisions individuals have to make repeatedly on a day-to-day basis (i.e., how much to cooperate and who with). Two such games were therefore developed to explore cooperative dynamics among the Agta (described below).

A further question is: what currency should the games be conducted in? While the most common medium of exchange for these games is money (Henrich *et al.* 2004b; Ensminger & Henrich 2014), other currencies have also been utilised, such as: honey sticks (Apicella *et al.* 2012); cigarettes (Alvard 2004); rice (Thomae *et al.* 2013); salt (Lamba & Mace 2011); tea (Wu *et al.* 2015); and betel nut (Bolyanatz 2010). Money is rarely held by the Agta for long periods of time, or widely shared between camp-mates when obtained. As the aim of this project was to explore sharing behaviour among the Agta, money was therefore not used. In the first season of fieldwork in 2013, several preliminary games were tested with different currencies, including honey sticks, coffee, sugar and rice. In these preliminary trials individuals were given three resources and asked for each whether they would like to keep it for themselves or give it to someone else, and if so, to whom. Honey sticks were perceived to have little value to adults, being described as ‘just candy’, and were freely distributed to children. Although a small sample size (*n*=3), only one of the nine bags of sugar was given to others, suggesting that sugar may also not be shared widely. Rice and coffee were distributed more widely, as with a sample of eight individuals and 24 resource packets, 12 shares of rice were given to others (50%), as were 11 coffee packets (45.8%). Additionally, after discussing with the Agta which resources were most valued, rice was the unanimous choice. This was therefore the resource used for the actual experimental games during the second season of fieldwork in 2014. As described in the ethnographic chapter, although the Agta do not grow their own rice (though they may harvest it for neighbouring agricultural populations), it is one of the Agta's primary sources of calories and is highly-valued. The vast majority of meals are consumed with rice, and in some cases consist solely of rice. It is an interesting question whether different resources would have been shared in another way, as is the case with different resources acquired by foragers (Kaplan & Hill 1985). As described in the introductory chapter, some studies comparing distributions of different resources in small-scale societies find no significant differences (Bolyanatz 2010), while In other populations large differences are reported (Lesorogol 2007). Whether the patterns of Agta cooperation with rice described in subsequent chapters are generalisable to other resources will be returned to later in this thesis.

As was briefly mentioned in the introduction, and will be expanded upon in forthcoming chapters, the role of 'producer control' is of central importance in many theories of food-sharing and cooperation. For instance, direct reciprocity requires that individuals give to those who will reciprocate (Trivers 1971), meaning that a high degree of producer control over resource distribution is essential. On the other hand, tolerated theft/demand sharing (Blurton Jones 1987; Peterson 1993) is characterised by a lack of producer control, as producers cannot decide who receives resources. In order to explore this dimension of food-sharing two experimental games were devised; one exploring resource distributions under high producer control conditions (giving *to* others) and another exploring resource distributions under low producer control conditions (taking *from* others). Both scenarios are required to demonstrate that food transfers occur. For instance, if only the game concerning giving to others is conducted and low levels of cooperation are found, one may erroneously conclude that food transfers do not occur. However, by including the game where individuals take from others, if it is found that individuals take substantial amounts from camp-mates, one can conclude that resources are still distributed but the mechanism is via taking from others, rather than giving to them.

Two non-anonymous games, the ‘Sharing Game’ (SG) and the ‘Taking Game’ (TG), were designed to explore resource transfers among camp-mates. Both games can be thought of as variants of the Dictator Game, in which individuals allocate resources between themselves and a recipient (or recipients, in this instance), with no opportunity for rejection or punishment. Both games were designed to be as simple and intuitive to grasp as possible, in order to minimise the need for complex explanations which may lead to frustration, boredom and an increased risk of misunderstandings. The experimental set-up for both games was identical; participants were shown their own photograph, along with a maximum of 10 other randomly-selected adult camp-mates (these were taken and printed beforehand). Individuals from camps with ≤10 other camp-mates were shown all other adults.

For the Sharing Game (simulating high producer control), participants were then given a number of small wooden tokens representing rice equal to the number of camp-mate’s photos. This was chosen so that not every picture, including ego, could end up with rice on it, therefore introducing a social dilemma regarding whether to share; it would be impossible for everyone (including ego) to receive rice. Each token represented one-eighth of a kilo of rice (125g), described to participants as equivalent to a small cup of rice to facilitate understanding of the quantities involved. This amount was approximately the size of a portion for one individual. Participants then decided, token by token, whether to keep the rice for themselves or to give to a camp-mate, and if so, to who, until there were no tokens remaining (figure 3.4 upper). The SG is structurally similar to the gift game (Apicella *et al.* 2012), but with the added rule that individuals could keep resources for themselves. After each token was given to a camp-mate, participants were also asked why they gave to that specific person.

In the Taking Game (simulating low producer control), half of camp-mate's pictures had one token placed on them, while the other half had two tokens (in camps with an odd number of recipients the remaining individual received one token half of the time and received two tokens the other half). This was to explore the impact of resource quantity on taking behaviour. Allocation of receiving one or two tokens was random. To acquire rice, ego had to take tokens from others and place them on their own picture (figure 3.4 lower). The TG is comparable to the social strategy game played with the Tsimane (Rucas *et al.* 2010), in which women had to take beads off other women in order to receive beads for self. The present design builds on this protocol but varies the level of resource quantity to explore its impact on resource transfers (and alters the medium of exchange from beads to rice).

Previous studies have compared cooperation in Dictator Games framed as either 'giving' or 'taking', although the results are somewhat inconsistent and different methodologies have been used which may confound interpretation. Some studies include both frames in one game, such that both the dictator and the recipient begin the game with resources and the dictator can either give resources to, or take resources from, the recipient (List 2007; Bardsley 2008). These studies tend to find that the possibility of taking resources reduces the amount given. Here, rather than combine both frames in a single game, I designed two different games to separate the giving and taking of resources. Previous Dictator Game studies using comparable methods (i.e., separate giving and taking frames) have indicated no difference in cooperativeness between frames (Dreber *et al.* 2013; Grossman & Eckel 2015). The extent to which giving and taking frames influence cooperation is therefore somewhat unclear, but is not central to the hypotheses explored in this thesis.

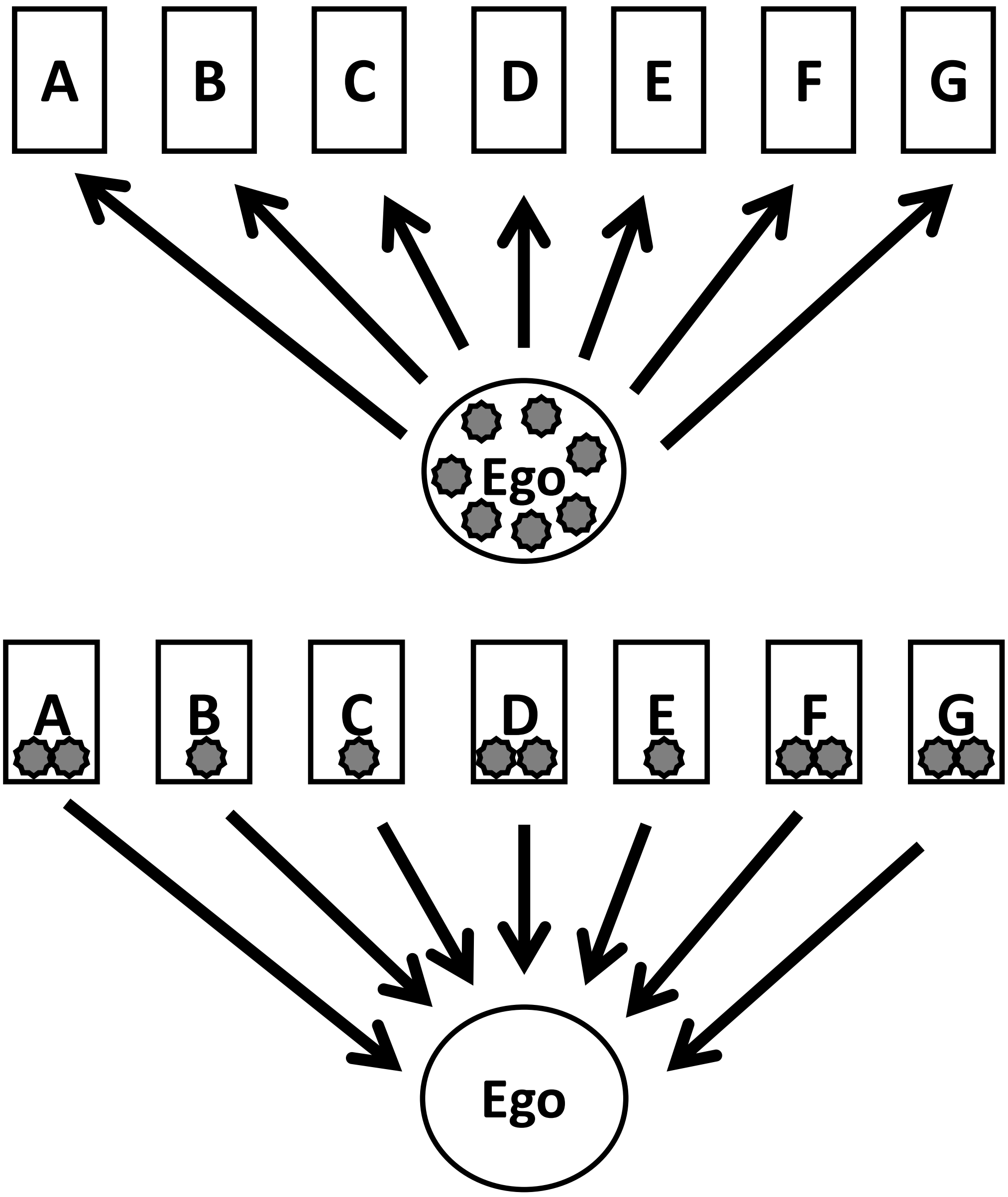

Figure 3.4: Schematic visualisation of the Sharing Game (upper) and Taking Game (lower) prior to play in a camp where *n*=8 (i.e., ego plus 7 camp-mates). Grey circles represent rice tokens and arrows denote direction in which the tokens are to be moved.

Only camps with eight or more adult members present were included in the games in order for statistical analyses comparing camps to possess sufficient sample sizes. As the majority of Agta do not know their exact ages, adults were defined as individuals who were married, divorced, or those believed to be over the age of ~16 (more precise ages were later assigned using the procedures described above). Games were played on the last few days in camp in order to maximise familiarity with the researchers and facilitate trust, as well as minimising the potential for collusion between camp-mates. This is unlikely to have occurred, as there were no sudden shifts in game behaviour towards uniformity in responses over time.

Although it may have been preferable to include all individuals from larger camps rather than a randomly-chosen sample of 10 individuals, this was chosen for practical and comparative reasons. Firstly, including all camp-mates from larger camps would have been logistically impossible as the quantities of rice needed would have increased exponentially with camp size. Secondly, although it would have been possible to limit the amount of rice by including all individuals in a large camp and only using 10 tokens, this would make comparisons between larger and smaller camps difficult as otherwise the rule of equal tokens to potential recipients would be violated. The TG would also not be possible if the amount of rice was limited in larger camps. Thus, in camp with 12 or more members, 10 randomly-selected camp-mates (in addition to ego) were chosen.

The games were conducted somewhere private, away from other camp-mates (figure 3.5). Only the participant, experimenter and translator were aware of an individual’s decisions. Participants were briefed on the games in a local language known to the individual. They were ensured that all decisions would remain secret from other camp-mates, told that there were no correct answers and that they, and whoever they gave rice to, would be given it before the researchers left camp (game scripts can be found in Appendix 5). If participants said they understood and had no further questions, the games were then played. Once both games were finished, participants were thanked and asked politely not to tell anyone else about how they played the games. In total, the procedure took approximately 10-15 minutes per participant. The order in which the games were played was alternated between participants. Prior to leaving camp, the quantities of rice earned by each participant were distributed, along with remuneration for their time and assistance in other aspects of the project conducted simultaneously.

Figure 3.5: Example of the adult cooperative games being conducted.

Studies of this kind also require ethical consideration, in terms of unanticipated consequences of playing such games and the impact on subsequent social dynamics. For instance, by asking participants to decide how much to cooperate and who with, afterwards camp-mates may want to know whether certain individuals shared with them, potentially causing friction and conflict. However, these are the cooperative decisions that individuals have to make everyday regarding who to share food with, who to help with childcare and who to cooperatively forage with, so these games are unlikely to introduce any additional conflict beyond that experienced in these everyday situations. As these games were private, if asked about how much they gave and who to individuals could simply lie. No obvious conflict as a result of these games was observed or reported either at the time or on revisits months later. A further potential ethical issue concerns differences in the amount of rice earned, which could cause conflict if high levels of inequality were present (e.g., an Agta who kept nothing for themselves, while everyone else kept everything, would receive little rice). However, as remuneration for participation in the wider study each family received two kilograms of rice, while rice earnings from the game were given out at a household level (i.e., pooling earnings between, say, husbands and wives). Inequalities would therefore be rather small and impossible to determine at an individual level, therefore mitigating the possibility of conflict or claims of unfairness. Measuring of the rice quantities was also carried out privately by the researchers, so that differences in earnings could not be known with any certainty. As such, we were not aware of any complaints of unfairness over the resources distributed. Furthermore, similar games have been played in dozens of small-scale societies and none have reported any unanticipated consequences of conflict as a result of these games (Paciotti & Hadley 2003; Henrich *et al.* 2004b;

Rucas *et al.* 2010; Apicella *et al.* 2012; Ensminger & Henrich 2014; Chaudhary *et al.* 2015; Thomas *et al.* 2015; Wu *et al.* 2015; He *et al.* 2016), suggesting that their impact on wider social dynamics is likely to be negligible.

While these games were designed to experimentally explore resource transfers, and may overcome some of the limitations of observational food-sharing methods, they do possess their own set of limitations. Foremost among these is that inferences about cooperative behaviour can be difficult to interpret from such games. As discussed in the introductory chapter, there is disagreement over whether participants fully understand the game structure and still behave altruistically, or whether they misapply otherwise adaptive strategies from the real-world, giving the illusion of group-beneficial altruistic prosocial preferences (Hagen & Hammerstein 2006). Based on the finding that individuals appear to use cooperative 'heuristics' taken from the real-world when first playing these games, hence why cooperation decreases with experience (Rand *et al.* 2014), the latter interpretation may be more parsimonious (although further empirical research is required, especially given the apparent lack of external validity regarding these games in small-scale societies). Therefore, although costly signalling was not possible as defined by the game structure (as decisions are private), high donations in the game may still be consistent with costly signalling or other reputational concerns if individuals behave like this in the real-world and (mis)apply these strategies in the games. Similarly, although taking behaviour is not strictly 'tolerated' in the TG, as camp-mates could not contest resources being taken from them, it is the act of *taking* (or demanding) resources from others which is the central prediction of tolerated theft/demand sharing. This is the only theory of resource transfers which predicts that individuals should take resources from camp-mates; that is, food-sharing is not necessarily cooperative. Thus, if everyday resource distributions are a result of demand sharing, participants may apply the same 'demand sharing heuristic' in the TG.

Additionally, even though the identity of the recipient was known to the participant, as these games were private this aspect of the experimental design may influence the strategies used. For instance, in real-life if a non-kin individual is standing next to ego then they are likely to receive resources, while in the game they may not be shared with. However, this real-world situation may reflect demand sharing; as the costs of competing for the resource (e.g., retribution from the by-stander) may be higher than the benefits to keeping it, this behaviour may not be strictly cooperative as they share not to help the by-stander but to avoid costs (what Connor (2010) refers to as 'extracted cooperative behaviour'). Here, in the SG specifically, I am interested in cooperation in the absence of these external costs in an attempt to separate cooperative behaviour (i.e., a behaviour which evolved to help another) from extracted or by-product benefits (i.e., a self-interested strategy where the benefit to the recipient is incidental). In contrast, in the TG I am specifically interested in seemingly cooperative behaviour which may be a result of extracted or by-product benefits (i.e., tolerated theft/demand sharing), rather than cooperative behaviour *sensu stricto*. Nonetheless, the private nature of these games may influence individual strategies, such as anonymity lowering levels of cooperation (Fehr & Gächter 2000). However, the few studies which have compared experimental game behaviour in small-scale societies under public and private conditions tend to find little difference in cooperative behaviour (Henrich & Smith 2004; Hill & Gurven 2004; Gurven *et al.* 2008; Lesorogol & Ensminger 2014), although public donations tend to be marginally greater. This suggests that cues of anonymity may not significantly alter the cooperative strategies used when conducting these games in small-scale societies.

Experimental Games with Children

To investigate the ontogeny of cooperation, a game analogous to the Sharing Game discussed above was conducted with children of different ages. For brevity and simplicity, this game was conducted without the use of photographs, and was played with small candies, rather than rice, to make it more straightforward for children. The number of resources was also reduced to five, as opposed to the 10 used with adults. Other than these differences, the protocol was largely the same. Children were told that there were five candies, and for each candy they had decide: i) if they wanted to keep it for themself or give to someone else; and ii) if they decided to give a candy to another, who this person was (see Appendix 6 for scripts). Games were conducted in private, out of sight and ear-shot of other children, with just the child, experimenter and translator (figure 3.6). Participants were told that their decisions were secret, so nobody else would know how much they kept or who they gave to, and that there were no right or wrong answers. The total number of candies earnt was given to each child after all games were played before we left camp. The game was played with as many children as possible in each camp visited, although some children did not take part because they were too shy, too young to fully understand or just did not want to.

Figure 3.6: Example of experimental protocol for cooperative games with children.

Reputational Measures

Although hunter-gatherers, especially of the ‘simple’ variety, are often portrayed as egalitarian (Woodburn 1982; Boehm 1993, 1999), differences in prestige, skill, knowledge and influence are still apparent (Sugiyama & Scalise Sugyiama 2003; Wiessner 2005; Smith *et al.* 2010, 2016b), and likely have fitness consequences (Smith 2004; Gurven & von Rueden 2006; von Rueden *et al.* 2011). Indices of reputation among the Agta were therefore obtained over several domains, including hunting, fishing, tuber-gathering, story-telling, medicinal knowledge and decision-making influence. For each of these domains, individuals were asked “who are the best hunters/fishers/tuber-gatherers/storytellers/at medicinal knowledge?”, after which all individuals believed to be the best at each skill were listed. Influence over camp decision-making was assessed slightly differently, by asking "if there is a discussion in camp whose opinions are listened to the most? Who is *malakas* (strong)?", again followed by listing individuals they thought were the most influential (see Macfarlan & Lyle (2015) for an analogous protocol with Peruvian agropastoralists and Marlowe (1999) for a similar study on assessing hunting skill among the Hadza). There were no limits on the number of nominations individuals could provide for each reputational domain. These interviews were conducted after the experimental games had been conducted. The proportion of nominations for each individual in camp can subsequently be calculated and skill/reputation levels inferred.

Social Norms

A final piece of independently-collected data concerned the nature of social norms possessed by the Agta. This was obtained via semi-structured interviews and observations regarding Agta beliefs, practices and traditions. These were aimed at exploring differences in social norms in a quantitative manner by asking all adults in camp (where possible) a series of questions relating to cultural norms and whether they engaged in said behaviour. Topics included a range of behaviours, including: childhood practices, marriage rites, hunting practices and rituals, taboo animals, division of labour, body adornment and hunting trophies (see table 3.3 for further details). Other aspects of these interviews were less quantitative, and aimed to obtain more qualitative data on topics such as: land rights/territories; *ngayaw* (indigenous warfare carried out between Agta from different areas, which ceased ~1950; Estioko & Griffin 1975); cultural change; *gaygay* (a length of string tied over a river to stop others entering that area, either because someone recently died there or to stop illegal activities, such as electric fishing); spirits; *ebuked* Agta (a group of

Agta recognised as distinct from other Agta as being more ‘wild’ (Estioko & Griffin 1975), although none remain today); other food taboos; medicinal knowledge; *gapgap* (dental modification; Headland 1977); burials; and any other interesting topics which arose during conversations. Some of the information gained from these interviews has been presented in the ethnographic chapter.

Table 3.3: A list of questions asked to the Agta during semi-structured interviews, aimed to elicit quantitative data regarding the prevalence and distribution of social norms among the Agta. Qualitative information, as discussed in text, covered many different areas and was elicited on a more ‘ad-hoc’ basis, so is not included here.

Topic	Target	Question(s)
Childhood (*upig* – practice to make child grow strong)	Women (or men if single/ divorced/ widowed)	Have you heard of *upig*? Have you ever used *upig* on your children? What did you use for *upig* (e.g., monkey, tree, etc.)? Who did you use this on? Did you ever use a monkey for *upig*? If not, why?
Marriage Rites	Women (or men if single/ divorced/ widowed)	Who decided that you and your spouse should marry, yourselves or your parents? Why did they/you choose them as a spouse? Did your husband do *nanacad* (bride service)? Did you husband do bride service? If so, what did they do and for how long?
Sneezing Superstition (*maggabben*)	All	Have you heard of *maggabben* (sneezing belief)? Do you believe that it brings good luck or bad luck?
Hunting Practices and Rituals	Men (or women who claimed to hunt)	Before going hunting, what rituals do you practice (if any)? Specifically, do you use *su-ub* (luck ritual) with a jaw bone? If you catch something while hunting, do you leave an offering? If yes, what do you leave? What do you hunt with (bow-and-arrow, gun or traps)?
Taboo Animals	All	Are there any animals which you do not eat? Prompt *musang* (civet cat), *ugsa* (deer), *biklat* (python), *adaw* (macaque), and *bannag* (water monitor)
Gender Roles	All	Asked to rate 12 activities according to whether they were performed: only by men, mostly by men, by either sex, mostly by women or only by women (small diagrams were displayed showing groups with different sex composition to aid understanding). Activities included: childcare, hunting, fishing, tuber gathering, honey collection, cooking, collecting firewood, building dwellings, deciding where to live, cash labour, housework and medicinal knowledge.
Bodily Adornment	All	If they wore *manik* (beaded necklace), they were asked why they wore it, or why not if they did not? Number of *manik* was also noted for each individual, from 0 (no *manik*), 1 (one *manik*), 2 (two/three *manik*), to 3 (multiple *manik*)
Hunting Trophies	Men	Asked to name the number of skulls (hunting trophies) in their house

A Brief Aside on Statistical Philosophy

In this section I briefly detail the ‘Information Theoretic’ (IT) approach used throughout the majority of this thesis. IT approaches are distinct from traditional ‘null hypothesis significance testing’ approaches (also known as ‘frequentist’ methods), in that multiple hypotheses (models) are simultaneously evaluated and model fit assessed (Burnham & Anderson 2002). Although several methods to assess model fit have been proposed (see Garamszegi 2011: 2), the most common method is based on the Akaike Information Criterion (AIC: Akaike 1998) and associated metrics such as the AICc (a derivation of AIC which corrects for small sample sizes: Grueber *et al.* 2011), the Bayesian Information Criterion (BIC: Burnham & Anderson 2004) and the Quasi-likelihood Information Criterion (QIC; for Generalised Estimation Equation (GEE) models which do not use maximum-likelihood estimation: Pan 2001). These methods estimate the amount of information contained in each model (i.e., how well the model predicts the dependent variable), with a lower value indicating increased model fit, with appropriate penalties for increased model complexity to prevent over-fitting (Burnham & Anderson 2002).

Use of these metrics permits comparison of multiple hypotheses in parallel, rather than stepwise selection of terms based on arbitrary *p*-value thresholds, as with frequentist approaches (Garamszegi 2011). A distinct advantage of this IT approach is that model uncertainty can be quantified and utilised in downstream analysis (Grueber *et al.* 2011). Based on the information criterion used, Akaike weights can then be quantified for each of the candidate models. This is a value between 0 and 1 which can be interpreted as the probability that a given model is the best fit to the data (Symonds & Moussalli 2011). Therefore, a model with an Akaike weight of 0.95 means that, of all models compared, there is a 95% chance that this is the best-fitting model. As this weight decreases there is less certainty that a given model is the best model, such that other models may be a better model fit (or that multiple models provide a similar fit).

If there is uncertainty over which is the ‘best’ model, model averaging over a set of these ‘top models’ can be used to obtain parameter estimates which takes this model uncertainty into consideration (Grueber *et al.* 2011). This procedure uses weighted parameter estimates, in that terms from weakly-predictive models (i.e., lower Akaike weights) are given lower weights than terms from models with greater predictive power (i.e., higher Akaike weights). I define the ‘top model set’ as any models within two information criterion values (e.g., 2 AICc or QIC values) of the best-fitting model (Grueber *et al.* 2011). I utilise a ‘zero method’ of model averaging, in which parameters absent in a subset of the top models are substituted with a value of ‘0’. This ‘zero method’ of model averaging is a more stringent method than the alternative ‘conditional method’ which only averages parameters over the models they appear in, while ignoring these parameters in top models in which they are absent. This ‘zero method’ therefore reduces the effect sizes of weakly predictive variables, meaning that the remaining predictive variables are those possessing the strongest association with the response variable, reducing the possibility of type I errors (Grueber *et al.* 2011; Barton 2015).

IT approaches are likely to be most useful in multivariate analyses where several variables may be associated with a specific response (Symonds & Moussalli 2011), as is the case here with multiple hypotheses derived from several different theories examined in tandem to explore the evolutionary and ecological roots of human cooperation. Therefore, other than a few supplementary analyses which utilise null hypothesis significance testing using *p*-values, the majority of analyses in this thesis employ an IT model selection approach, in conjunction with model averaging where appropriate.

Summary and Next Chapter

This chapter has presented a detailed description of how the data analysed in subsequent chapters (and to some extent in the preceding ethnographic chapter) were collected. Due to the nature of fieldwork, it was not possible to collect every kind of data described above in each of the camps visited. Therefore, a summary of the different types of data collected and from which camp is presented in table 3.4. The next chapter is the first substantive data chapter, which explores the factors underlying variation in cooperative game behaviour among adults. This chapter specifically tests between predictions made by cultural group selection and those based on adjusting cooperative behaviour in accordance with evolutionary expectations in response to socioecological variation (a human behavioural ecology approach).

Table 3.4: A summary of the different types of data collected in each of the camps visited. Note that some of the smaller camps consisting of solitary houses are not included here (although genealogical data were collected in these camps, where possible).

Camp	Geneal-ogies	Census Date(s)	Aging	Anthropometry	Camp Scans	Household Q'aires	Adult Games	Child Games	Skill Measures	Social Norms
50 (Disokad)	Y	05/2013	Y	All	N	N	N	N	N	N
54 (Semento)	Y	05/2013 03/2014 09/2014	Y	All	Y	Y	Y	Y	Y	Y
56 (Dikabayu)	Y	09/2014	N	None	N	Y	N	N	N	Y
59 (Dibungko)	Y	09/2014	N	Height & Weight	N	Y	Y	Y	Y	Y
62 (Dinipan)	Y	06/2013 04/2014 09/2014	Y	All	Y	Y	Y	Y	Y	Y
64 (Culasi)	Y	05/2013 04/2014 09/2014	Y	All	N	Y	Y	Y	Y	Y
65 (Dimatog)	Y	05/2013	Y	All	N	N	N	N	N	N
66 (Diago)	Y	04/2013 04/2014 06/2014 09/2014	Y	All	Y	Y	Y	Y	Y	Y
67 (Dipaguiden)	Y	04/2013 07/2014	Y	All	Y	Y	Y	N	Y	Y
67.2 (Didikeg)	Y	04/2013 07/2014	Y	All	Y	Y	Y	Y	Y	Y
73 (Dicobeyan)	Y	05/2013	Y	All	N	N	N	N	N	N
74 (Kanaipang)	Y	05/2013 05/2014 08/2014	Y	All	Y	Y	Y	Y	Y	Y
77 (Diambarong)	Y	06/2014 08/2014	Y	All	Y	Y	Y	Y	Y	Y
78 (Magtaracay)	Y	06/2014 08/2014	Y	All	Y	Y	Y	Y	Y	Y
79 (Dipadsangan)	Y	06/2014 08/2014	Y	All	Y	Y	Y	Y	Y	Y

84 (Diabbut)	Y	06/2013 03/2014 08/2014	Y	All	Y	Y	Y	Y	Y	Y
M1 (Mundora)	Y	08/2014	N	Height & Weight	N	Y	Y	Y	Y	Y
M2 (Putar)	Y	08/2014	N	Height & Weight	N	Y	Y	Y	Y	Y
M3.1 (Karayan)	Y	08/2014	N	Height & Weight	N	Y	Y	Y	Y	Y
M3.2 (Kamanggaan 1)	Y	08/2014	N	Height & Weight	N	Y	N	N	N	Y
M3.3 (Kamanggaan 2)	Y	08/2014	N	Height & Weight	N	Y	Y	N	Y	Y
M4 (Canadam)	Y	08/2014	N	Height & Weight	N	Y	Y	N	Y	Y
M5 (Kapanikian)	Y	08/2014	N	Height & Weight	N	Y	Y	N	Y	Y

Chapter 4 Exploring Variation in Agta Cooperative Behaviour [†]

This chapter explores cooperativeness among adult Agta across multiple camps, employing the two experimental games described in the previous methods chapter, to examine evolutionary hypotheses regarding hunter-gatherer cooperation. As a consequence of the substantial differences in socioecology between Agta camps described in the ethnographic chapter, particular focus will be given to exploring variation in cooperative behaviour between camps. This is of particular relevance when contrasting theories for the evolution of cooperation which focus on either population-wide social norms as the primary determinants of cooperative behaviour (the cultural group selection (CGS) approach), or behavioural ecology approaches which propose that cooperation is predominantly shaped by individuals adapting their behaviour to local demographic and ecological conditions in an attempt to maximise fitness. Societies such as the Agta, which form a single ethnolinguistic group, yet contain substantial internal socioecological variability, are ideal study sites to explore these competing approaches. I find substantial variation between camps, with camp stability a significant predictor of cooperation; camps with a greater probability of repeated interactions were more cooperative than camps with lower levels of stability. Levels of need (a proxy for increasing costs to cooperation) were also associated with cooperative behaviour, as individuals possessing fewer resources or more dependent offspring were less cooperative. These findings suggest that socioecological differences greatly influence Agta cooperative behaviour, arguing against CGS as an explanation for cooperative evolution in humans. Rather, individuals appear to adapt their cooperative behaviour to local

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[†] The research discussed in this and the following chapter has recently been published: see Smith, D., Dyble, M., Thompson, J., ... & Mace, R. (2016). Camp stability predicts patterns of hunter–gatherer cooperation. *Royal Society Open Science*, *3*(7), 160131.

socioecological conditions, even within a single ethnolinguistic population, consistent with a behavioural ecology approach.

Introduction

There are several theoretical approaches which have been developed to explain how cooperation can evolve in spite of the free-rider problem (discussed in the introductory chapter). As also noted in the introductory chapter when discussing previous experimental games, these methods have rarely been used to explore specific hypotheses relevant to resource transfers in hunter-gatherers, such as kin selection (Hamilton 1964), reciprocity (Trivers 1971; Axelrod & Hamilton 1981) or tolerated theft/demand sharing (Blurton Jones 1987; Peterson 1993; Lewis *et al.* 2014), among others (although see Marlowe 2004c). While it is not possible to explore who individuals share with (e.g., kin, reciprocating partners, cooperative individuals, etc.) from assessing overall levels of cooperation, analysing the amount individuals donate in these games can be used to explore the factors which influence cooperativeness and test whether they are consistent with these theories. It is variation in cooperativeness, or the *amount* individuals donate, which will be the focus of this chapter, while patterns of cooperation, or *who* individuals share with, will be explored in subsequent chapters.

Theories of Cooperative Evolution and Predictions for Game Behaviour

The majority of previous experimental studies exploring cooperative variation in small-scale societies have taken a CGS approach (eg., Henrich *et al.* 2004, 2005, 2010; Ensminger & Henrich 2014), so I will begin first by discussing predictions made by this theory. There is often ambiguity in group selection approaches regarding how to define a ‘group’ which is acted on by selection (Cronk & Leech

2013: 117); is it a cluster of houses, a village, a clan, a population, a nation state, those with a shared ideology? The most common usage concerns the ethnolinguistic group, such as the Hadza, Tsimane, Agta, Lamalera, etc., and CGS is usually said to occur at this level (see, for example, discussion of the Nuer expansion at the expense of the Dinka as a consequence of the Nuer's superior social system for co-ordinating warfare; Boyd & Richerson 2005; Richerson & Boyd 2005). In order for CGS to operate at this ethnolinguistic level, low within-group variation is essential (Henrich 2004a; Boyd & Richerson 2005; Richerson *et al.* 2016), meaning that cooperative behaviour ought to be relatively uniform within these groups. Thus, if CGS was responsible for the evolution of cooperative behaviour in humans, one would expect low levels of variation in cooperation within ethnolinguistic groups.

Although previous cross-cultural research has reported significant differences in cooperativeness between societies (Henrich *et al.* 2001, 2004b, 2005, 2010a; Ensminger & Henrich 2014), little attention has been given to variation *within* these societies. The lack of within-society comparisons may confound cultural and ecological differences, meaning that variation in cooperativeness may be a result of differences in local socioecology, rather than differences in population-wide norms of cooperation. Indeed, when multiple sites have been tested within societies, substantial between-camp variation is reported (Gurven *et al.* 2008; Lamba & Mace 2011, 2013). The amount of within-society variation in cooperative behaviour is comparable to that found between societies (Lamba & Mace 2011, 2013), suggesting that population-wide social norms acquired by CGS may not be necessary for explaining the observed distribution of cooperative behaviours. Rather, behaviour may be adapted to the prevailing socioecological conditions, regardless of ethnolinguistic affiliation, consistent with a human behavioural ecology perspective (Winterhalder & Smith 2000; Borgerhoff Mulder & Schacht 2012).

In order to test between these two hypotheses using a single ethnolinguistic population it is essential that there are differences in socioecology between camps or villages, otherwise cultural and ecological differences will be conflated once again. The present study with the Agta allows one to test between these competing theories as they form a single ethnolinguistic group (albeit with slight differences in language between the municipalities of Palanan and Maconacon), yet vary greatly in socioecology in terms of mobility, group size and subsistence. If CGS operates on society-wide cooperative norms then one would expect little variation in cooperative behaviour between camps, despite differences in socioecology. On the other hand, if local ecological conditions influence cooperativeness, then levels of cooperation ought to vary with socioecology, even though individuals are members of the same ethnolinguistic group who may live in close proximity to one another. Thus, the first aim of this chapter is to assess the relative merits of each of these approaches.

A second aim of this chapter is to explore within- and between-group differences in cooperation (should any variation arise) using the theories discussed in the introductory chapter. It is necessary to bear in mind throughout this chapter that inferences regarding certain theories may be indirect, at least before conducting the analyses in the following chapters which explore who individuals share with. For instance, from the amount given to others it cannot be ascertained whether individuals preferentially give to kin, but it can be shown whether the presence of kin impacts cooperation (see also MacFarlan & Quinlan 2008; Wu *et al.* 2015).

There are several factors which have been theorised to influence cooperation, of which kin selection is the most pervasive (Hamilton 1964; West *et al.* 2007a). The presence of kin is generally expected to increase cooperation, so it may be hypothesised that individuals with a greater relatedness to other camp-mates would be more cooperative. However, relatedness had no association with Dictator Game (DG), Ultimatum Game (UG) or Third-party Punishment Game (TPG) offers among the Yasawa from Fiji (Henrich & Henrich 2014). Similarly, among Dominican horticulturalists, increased relatedness to the group was associated with reduced UG offers for women and had no influence on male behaviour (although men with more brothers in the village were more cooperative; Macfarlan & Quinlan 2008). Furthermore, low levels of female dispersal among Chinese agro-pastoralists were associated with both decreased DG and Public Goods Game (PGG) offers, although individuals with more kin in the village were more cooperative in the DG (Wu *et al.* 2015). These findings suggest that increased kin presence may not necessarily promote cooperation, but can reduce cooperation in these experimental games, potentially as a result of increased competition between kin over resources (Queller 1994; West *et al.* 2002). Humans also have affinal kinship relations (Chapais 2010), which have been found to predict patterns of cooperation in some societies (Alvard 2009; Burton-Chellew & Dunbar 2011), so are also included here alongside genealogical relatedness.

While it is not possible to assess levels of reciprocity directly by analysing levels of cooperation, it can be inferred indirectly. Reciprocity requires repeated interactions which promote trust and a reputation for sharing (Trivers 1971). The concept of producer control (Gurven 2004d) is central here, as individuals must have control over distribution in order to allocate resources to reciprocating partners. Therefore, if reciprocity is present individuals should actively *give* resources to others (contrast with tolerated theft/demand sharing, below). In a reciprocal system one may therefore expect that participants would increasingly share resources with others. Reciprocity also requires repeated interactions, as when interactions are ephemeral there is no benefit to cooperating with others if there is little chance of future reciprocation. Despite the fundamental importance of repeated interactions for reciprocity – and cooperation more widely, as has been reported in experimental lab studies of cooperation (Dal Bo 2005; Kanagaretnam *et al.* 2010; Rand & Nowak 2013) – it is often overlooked in studies of forager food-sharing and cooperation. As data on camp composition for the Agta were collected over multiple visits, it is possible to assess whether individuals from camps with greater stability donate more than those from unstable camps, as would be expected should repeated interactions increase reciprocal cooperation. It should also be noted that a purported association between cooperation and repeated interactions is predicted by other theories, such as generalised reciprocity (Pfeiffer *et al.* 2005), although they predict different patterns of resource transfers, as will be explored in the following chapter.

Levels of cooperation in experimental games would be drastically different if they reflected a tolerated theft/demand sharing approach to resource transfers. Under this system there is low producer control, meaning that distributions are controlled by the recipient, rather than the producer, of the resource (Blurton Jones 1987; Peterson 1993). This suggests that even if the producer of a resource does not wish to share with others, they have little choice in the matter. Marlowe (2004c) interprets the low DG and UG donations by the Hadza as evidence for a tolerated theft system of food-sharing, whereby individuals do not wish to share food with others, but are coerced in to sharing (see also Hawkes 2000). The use of the two games described in the methods chapter is of particular relevance here, as one game, the Sharing Game (SG), simulates high producer control (unsolicited giving to others), while the other, the Taking Game (TG), simulates low producer control (taking from others, regardless of the wishes of the owner of the resource). Although low offers in a giving situation (the SG) are consistent with demand sharing, both scenarios are required to demonstrate that food transfers occur. For instance, if only the SG is conducted and low levels of cooperation are found, one may erroneously conclude that food transfers do not occur. However, by including the TG, if the reverse pattern is observed and individuals take lots from others, one can infer that resources are still distributed, even when individuals do not actively give to others. Tolerated theft/demand sharing therefore predict that the amount given to others in the SG will be low, while the amount taken from others in the TG will be high.

An alternative interpretation of widespread resource distributions without recourse to kinship, reciprocity or reputation is that it reflects showing off by individuals who acquire resources but then distribute them widely or let others take from them as a costly display of their phenotypic quality (Bliege Bird *et al.* 2001; Hawkes & Bliege Bird 2002). A simple prediction based on costly signalling theory is that overall levels of cooperation should be relatively high as individuals attempt to out-compete one another (Roberts 1998, 2015). From observational food-sharing data it is difficult to distinguish between demand sharing and costly signalling, as both predict that resources will be shared widely with little recourse to kinship or reciprocity. However, the motivations between the two are vastly different, and this is where an experimental approach pays dividends as it can be used to distinguish between these competing hypotheses. If food-sharing is a result of tolerated theft, then donations in these games should be low, while if widespread distributions are a result of costly signalling then donations in these games ought to be high.

In addition to these ‘traditional’ explanations for cooperation among foragers (kin selection, reciprocity, tolerated theft and costly signalling), there are several other factors believed to influence levels of cooperation which can be explored among the Agta. One such theory is ‘market integration’, which suggests that societies more heavily involved in market exchanges are more cooperative as a result of norms for trust and ‘prosociality’ co-evolving with markets and spreading via intergroup competition (where less cooperative groups are out-competed by more cooperative groups; Henrich *et al.* 2005, 2010). Although cross-cultural studies have found that market integration may explain some of the group-level variation in cooperative behaviour (Henrich *et al.* 2005, 2010), other within-society studies have found little evidence that it is associated with enhanced cooperation (Gurven 2004b; Lamba & Mace 2011; Henrich & Henrich 2014). Market integration is often operationalised as proportion of food obtained from markets (Henrich *et al.* 2010a), yet this is relatively constant among the Agta as all camps trade foraged food for rice and other agricultural products with their non-Agta farmer neighbours. Here, I therefore use involvement in the cash economy as a proxy for market integration.

Group size has also been theorised to mediate the evolution of cooperation, as strategies such as direct reciprocity and generalised reciprocity appear unsustainable in larger groups due to an increased risk of free-riders (Boyd & Richerson 1988; Pfeiffer *et al.* 2005), although assortativity and partner choice may overcome these group size limitations (Ohtsuki *et al.* 2006; Roberts 2015). Therefore, it may be expected that larger camps will be less cooperative than smaller camps (Thomas *et al.* 2016).

Two further concepts which can impact cooperation are resource competition and need. Research with student populations has found that local (within-group) competition for resources decreased cooperation in a Prisoner’s Dilemma game, while increased cooperation was reported when competition was global (between-groups; West *et al.* 2006). This is because cooperating under conditions of local resource competition decreases one's fitness relative to other group members, selecting against cooperation, while under global competition cooperation does not reduce one's fitness compared to local group members, promoting cooperation. Related to this concept is that of need, such that individuals who are less in need of additional resources may be more cooperative as the costs of cooperation are lower compared to those in greater need of resources (Aktipis *et al.* 2011; Hao *et al.* 2015). For instance, recent research on forager food-sharing suggests that individuals with fewer dependent offspring, who have less need for resources, provision individuals with more dependent offspring who possess a greater need of additional resources and who would otherwise not be able to sustain themselves (Hill & Hurtado 2009; Hooper *et al.* 2015). Similarly, research from experimental games suggests that, in some societies, such as the Dolgan/Nganasan (Ziker 2014), Maragoli (Gwako 2014) Samburu (Lesorogol 2014) and the Pahari Kowra (Lamba & Mace 2013), individuals with more children are less cooperative, although this trend does not hold across all societies examined (Henrich *et al.* 2010a; Ensminger & Henrich 2014). Analogously, deprived neighbourhoods in UK cities were less cooperative than more affluent neighbourhoods (Holland *et al.* 2012; Silva & Mace 2014), potentially because individuals in deprived neighbourhoods are in greater need of additional resources (or are in greater competition with one another for resources). Thus, when there is greater competition, or greater need, for resources, cooperation may decrease as the costs of cooperation increase under these circumstances. Among the Agta this can include factors such as number of dependent offspring, whether individuals possess any stored rice, or if the camp is currently engaged in harvesting rice (meaning that an existing stock of rice is secured, so need and resource competition will be lower).

Although exploring similar themes as other recent research, such as using within-society variation in cooperation to evaluate CGS as an explanation for the evolution of humans' derived cooperative capabilities (e.g., Lamba & Mace 2011, 2013), the current project builds upon this research in several ways. Firstly, it allows for a replication of previous studies which find substantial variation within ethnolinguistic groups (Gurven *et al.* 2008; Lamba & Mace 2011, 2013; Nettle *et al.* 2011; Holland *et al.* 2012; Silva & Mace 2014), while extending these findings by including novel factors believed to influence cooperation but which have not previously been explored among hunter-gatherers, such as the role of repeated interactions. Secondly, using two games to explore food-sharing – one where individuals give to others (the Sharing Game) and another where they take from them (the Taking Game) – means that the full spectrum of resource transfers can be observed, as theories such as tolerated theft/demand sharing posit that recipients take from producers, rather than simply rely on others giving to them. The games designed here explore both of these dimensions, making this a superior method for investigating resource transfers experimentally. A further novel aspect of this design is that it uses a semi-anonymous methodology where individuals know whom they are giving to or taking resources from. This is central for theories such as kin selection or reciprocity, where partner identity is likely to greatly influence cooperation. A summary of the hypotheses explored in this chapter is displayed in table 4.1.

Table 4.1: Summary of predictions made by each theory discussed above.

Theory	Prediction
Cultural Group Selection	As the Agta form a single ethnolinguistic group, between-camp variation ought to be low as population-wide social norms determine cooperative behaviour.
Kin Selection	Greater levels of cooperation when more kin are present (although kin can reduce cooperation by increasing competition for shared resources). Both genealogical and affinal kinship effects are explored here.
Reciprocity	Inferred indirectly by giving to others as a signal of trust and willingness to cooperate. Predict greater cooperation in camps with an increased probability of repeated interactions (generalised reciprocity also makes similar predictions).
Tolerated Theft/ Demand Sharing	Low levels of giving coupled with high levels of taking from others.
Costly Signalling	As individuals compete to 'out-cooperate' one another, cooperation will be high.
Market Integration	Greater market integration will be associated with increased cooperation.
Group Size	Reduced levels of cooperation in larger groups.
Resource Competition	More cooperation when local resource competition is reduced.
Needs-Based Cooperation	Individuals less in need of additional resources will be more cooperative (due to lower costs to cooperation).

To briefly summarise the results, I firstly find that levels of cooperation vary considerably between camps within a single ethnolinguistic population. This high level of within-society variation suggests that CGS may be an unlikely candidate for explaining cooperative behaviour among the Agta. Secondly, both individual- and camp-level variation can be explained by a small number of factors relating to differences in socioecology. Most notably, increased cooperation is associated with camp stability, suggesting that repeated interactions may foster trust and promote cooperation. Factors relating to need and resource competition may also influence cooperative behaviour, with those in greater need or increased competition displaying reduced cooperation. These findings shed light on the evolutionary and ecological factors which promote and inhibit cooperation in a foraging population. They also indicate that human behavioural ecology, rather than CGS, may be a superior framework with which to explore and understand variation in human cooperative behaviour.

Methods

Games were conducted with 324 Agta (mean age=37.1, range=16-70, males=160) over 18 separate camps (mean number of adults=18, range=8-46). All adult Agta were asked if they would like to participate. Individuals that did not wish to take part were excluded as potential recipients (although very few declined). However, due to high mobility some individuals who agreed to be included to begin with were not present when the games were conducted. Thus, even though 324 Agta were included as potential recipients, games were played with 290 Agta (mean age=37, males=140). All 290 Agta played both games. As the data collection methods have been described in the methods chapter, I refer the reader there for this information. The remainder of this section will describe the statistical methods used to analyse the data.

Statistical Analyses

For this analysis, response variables were percentage of rice kept for self in the Sharing Game and percentage of rice taken from others in the Taking Game, respectively. Thus, in both games a higher percentage is indicative of lower levels of cooperation. Although games were conducted in 18 camps, camp stability was only available for 11 of the camps in Palanan (*n*=183, male=90, average age=38). As camp stability is central to theories such as reciprocity, only analyses for this Palanan subset are presented here (other than when comparing null models exploring overall variation in cooperative behaviour between camps, which include all 18 camps). In addition to camp stability, other demographic, socioecological and behavioural variables associated with the theories discussed above were included in analyses to investigate how these impact levels of cooperation. These variables include: average consanguineal relatedness to sample, affinal closeness to sample, number of dependent offspring, two indices of resource availability (involvement in harvesting rice for agricultural neighbours and whether the house had any stored rice), camp size and observed involvement in cash labour (see table 4.2 for additional details and definitions of these variables).

Table 4.2: A list of independent variables included in analyses of how much individuals cooperated in these experimental games.

Variable	Level	Description
Camp Stability	Camp	Measure of how much camp composition varied over multiple visits to the same camp, from 0 to 1, with 1 meaning no change in membership and 0 meaning complete change.
# Dependent Offspring	Individual	Number of dependent offspring residing with parents (can also include grandchildren/adoptions) aged <15.
Harvesting Rice	Camp	Whether members of camp were engaged in harvesting rice.
Stored Rice	Individual	Whether the individual had any rice stored or not.
Camp Size	Camp	Number of families in camp.
Relatedness to Sample	Individual	Average relatedness to ego of individuals in the sample. A high value indicates increased average relatedness.
Affinal Closeness to Sample	Individual	Average affine depth to ego (player) of sample (excluding consanguineal kin). Spouse=1, Spouse's primary kin or primary kin's spouse=2, spouses distant kin or other affines (up to 5 degrees of separation)=3, not related=4. A higher average value indicates less affinal relatedness.
Cash Labour Involvement	Individual	During camp-scans, the proportion of time engaged in cash labour (of total time in subsistence).

Analyses were conducted using the statistical software *R* (R Development Core Team 2015). A multi-level approach using the package *lme4* (Bates *et al.* 2015) was utilised to explore behavioural variation at different hierarchical units (individuals nested within camps: Kreft & de Leeuw 1998). In order to assess whether there was camp-level variation in cooperativeness, null multi-level models were compared against null linear regression models without a multi-level component. Model averaging analyses were then conducted using the package *MuMIn* (Barton 2015).

Model averaging utilises an information-theoretic approach in which all potential models are weighted according to how well they fit the data. The best-fitting models (models within 2 AICc values of the top model) were then averaged, meaning that parameter estimates were obtained and weighted across different models. As described in the previous chapter, a ‘zero method’ of model averaging was used.

As a result of missing data, a multiple imputation procedure was employed to estimate missing values, creating five data sets. Although the amount of missing data was relatively small (17 cases out of 1,464, or 1.2% of all predictor variables), missing data renders comparisons between models impossible using the information theoretic approach employed here (Symonds & Moussalli 2011). A ‘multiple imputation’ procedure was therefore used in which missing data were imputed and *M* datasets created. Multiple imputation was carried out using the *R* package *Amelia* (Honaker *et al.* 2011), which uses an expectation maximisation algorithm to approximate maximum likelihood estimates for missing values. Using this method five datasets were created with no missing values, as it has been demonstrated that between 3-10 datasets is generally adequate to approximate variation in missing values (Rubin 2004). This multiple imputation method is less prone to error than other data imputation methods, such as removing all cases with missing values, using the mean for missing values or single imputation, and has been shown to recover accurate parameter estimates and information theoretic-related measures using a real biological dataset (Nakagawa & Freckleton 2011). Once analyses had been conducted on each of the imputed datasets, parameter estimates, standard errors and variable weights were then pooled across each of the five datasets.

Continuous input variables were standardised over two standard deviations (SD) while binary variables were mean-centred (Gelman 2008; Schielzeth 2010). This standardisation allows comparisons of effect sizes between both continuous and binary variables, as well as between continuous variables measured on different scales. However, it is important to remember that only unstandardised coefficients are biologically meaningful. Thus, unstandardised estimates are presented in the text to interpret the absolute effect sizes involved, while standardised estimates are also presented in tables to understand the relative effect sizes involved between different predictor variables.

Results

The mean amount of rice kept by individuals in the Sharing Game over all 18 camps was 62.6% (SD=30.5). This varied substantially between camps (figure 4.1 and table 4.3), from a minimum camp average of keeping just 26.8% (SD=20.8), to a maximum of 100% (SD=0), meaning that each individual in this camp kept all resources for themselves. A null multi-level formulation, with municipality as a control variable to account for differences between Palanan and Maconacon, possessed a lower AIC value (AIC=2714.6) than a non-multi-level null regression model (AIC=2738.1). Comparison of Akaike models weights indicated that the multi-level formulation was overwhelmingly a better fit to the data (w_i=1). Over these 18 camps, multi-level modelling found that 30% of the variance in cooperative behaviour in the null model occurred at the camp level. A Kruskal-Wallis test confirmed significant camp-level differences in donations (H=121.67, df=17, n=290, p<0.001).

Focussing on the 11 Palanan camps for which stability data were available, a null linear regression model without a multi-level structure possessed an AIC value of 1768.9, while a null multi-level model possessed an AIC value of 1725, suggesting a considerably better model fit for the multi-level formulation. Indeed, comparison of model weights again suggested that the multi-level model possessed significantly better model fit (w_i=1). Within this Palanan subset 40.2% of the variance in donations occurred between camps. Nearly half of the variation in cooperative behaviour among the Palanan Agta therefore occurred at the camp level. A Kruskal-Wallis test again confirmed significant differences in cooperative behaviour between camps (*H*=70.876, *df*=10, *n*=183, *p*<0.001).

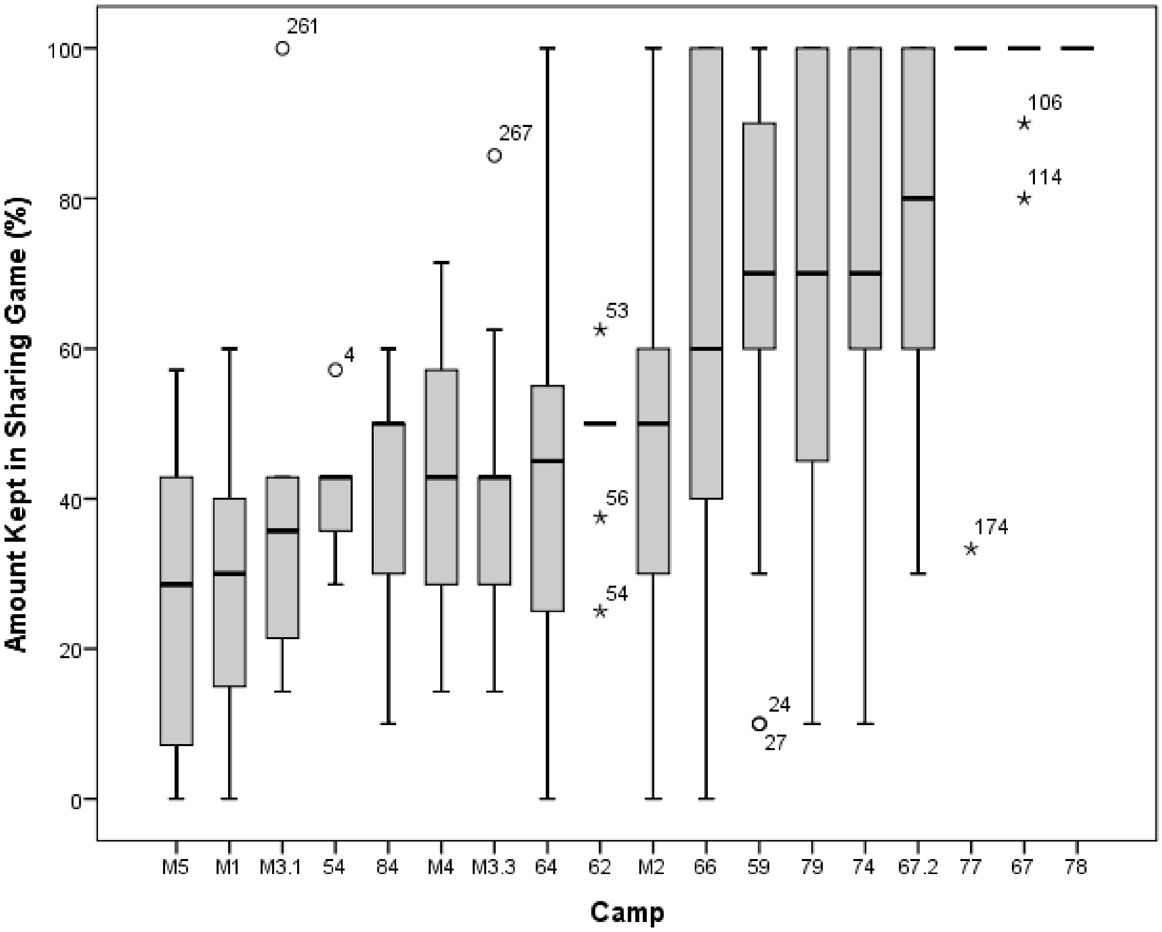

Figure 4.1: Box-plot displaying camp-level variation in the amount kept in the Sharing Game (camps=18, *n*=290). Sample size per camp varied between 7 and 44 (see table 4.3 for full list of sample sizes and summary statistics per camp). Boxes represent inter-quartile ranges with the horizontal black lines within bars indicating the median. Error bars extending above and below boxes display upper and lower quartile ranges, while numbered points represent outliers. Camps without boxes (62, 77, 67, and 78) had low variability in scores, so box-plots could not be produced. Camps are ordered from lowest mean amount kept (left) to highest mean amount kept (right).

Table 4.3: Sample sizes and summary statistics for each camp. An 'S' next to camp number indicates that stability data was available for this camp.

Camp	Sample size	Number of males	Mean % rice kept in Sharing Game (SD)	Mean % rice taken in Taking Game (SD)
54 (S)	7	3	40.8 (9.9)	40.8 (11.6)
62 (S)	9	5	47.2 (10.4)	61.1 (22.4)
64 (S)	16	8	43.1 (29.4)	44.6 (30.8)
66 (S)	26	14	61.5 (32.8)	67.2 (26.8)
67 (S)	12	6	97.5 (6.2)	94.4 (19.2)
67.2 (S)	18	8	78.3 (22)	76.7 (26.5)
74 (S)	38	19	71.8 (26.4)	61.6 (28.2)
77 (S)	10	4	93.3 (21.1)	94.6 (17)
78 (S)	14	7	100 (0)	96.7 (12.5)
79 (S)	23	11	69.6 (31.7)	73.9 (32.2)
84 (S)	10	5	41 (17.3)	42 (14.8)
59	44	20	68.6 (24)	67.9 (26.7)
M1	15	5	30.7 (17.5)	56.9 (34.4)
M2	14	8	50.7 (29.2)	47.6 (28.6)
M3.1	8	4	39.3 (27.3)	35.6 (15.1)
M3.3	10	5	43 (19.9)	75.4 (28.4)
M4	8	4	42.9 (20.2)	62.5 (31.2)
M5	8	4	26.8 (20.8)	44.5 (24.4)
Total (S)	183	90	69.1 (30.1)	68.7 (30)
Total (All)	290	140	62.6 (30.5)	65.4 (30)

Table 4.4 presents the results of the model averaging procedure, averaged across each of the five imputed datasets (see table A1 in Appendix 7 for AICc values and model weights for each of the top models over these imputed datasets). Results indicate that a combination of camp-level and individual-level variables were associated with cooperation in the SG. At the camp level, greater camp stability was strongly associated with increased cooperation. For instance, a camp with no changes in composition would be expected to give 63.7% points more rice than a camp which had changed composition completely (figure 4.2). A univariate linear regression between camp-average donations and camp stability corroborated this result (*b*=-87, SE=17.4, *n*=11, *p*=0.001), with this variable explaining a large proportion of camp-level variation in cooperative behaviour (adjusted R^2=0.71). A further camp-level variable found to predict cooperation was engagement in

harvesting rice, with camps participating in harvesting associated with an increase in donations to others by 19.9% points. At the individual level, each additional dependent offspring was associated with a reduction in cooperation, increasing the amount of rice kept by 1.8% points. Stored rice was also associated with sharing, as individuals without ancillary supplies kept on average 9.2% points more rice. Each one unit increase in affinal closeness was also associated with a 13.4% point decrease in amount given, meaning that individuals with closer affinal ties to potential recipients were less cooperative. Individuals who spent more time in cash labour were also observed to be more cooperative, with individuals who only participated in wage labour as their form of subsistence predicted to give 11.3% more rice than individuals who engaged in no wage labour. Neither camp size nor consanguineal relatedness to recipients were strong predictors of SG donations.

Table 4.4: Results of the model averaging procedure pooled across five imputed datasets for the Sharing Game, displaying both standardised and unstandardised coefficients (*n*=183, camps=11). Positive parameter estimates indicate an increase in rice kept for self (%) with an increase in the predictor variable. 95% confidence intervals are displayed in brackets. Relative importance denotes the summed Akaike weight (w_i) of each parameter in the top models used in model averaging, with a ‘1’ indicating that this term occurred in all of the top models. Note also that consanguineal relatedness to sample does not appear here as none of the top models contained this variable.

Variable	**Level**	**Std. Parameter Estimate (95% CI)**	**Unstd. Parameter Estimate (95% CI)**	**Relative Import. (w_i)**
Intercept	-	69.15 [65.81; 72.5]	120.11 [89.35; 150.86]	-
Camp Stability	Camp	-25.61 [-18.52; -32.71]	-63.66 [-46.03; -81.29]	1.00
Harvesting Rice (1=No)	Camp	19.91 [9.16; 30.67]	19.91 [9.16; 30.67]	1.00
Affinal Closeness	Individual	-10.77 [-3.88; -18.67]	-13.43 [-4.83; -22.02]	1.00
Stored Rice (1=No)	Individual	9.16 [2.21; 16.11]	9.16 [2.21; 16.11]	1.00
# Dependent Offspring	Individual	8.1 [1.05; 15.14]	1.76 [0.23; 3.29]	1.00
Cash Labour Involvement	Individual	-8.51 [-0.92; -16.11]	-11.31 [-1.19; -21.43]	0.94
Camp Size	Camp	0.11 [-4.52; 4.73]	0.008 [-0.36; 0.38]	0.04

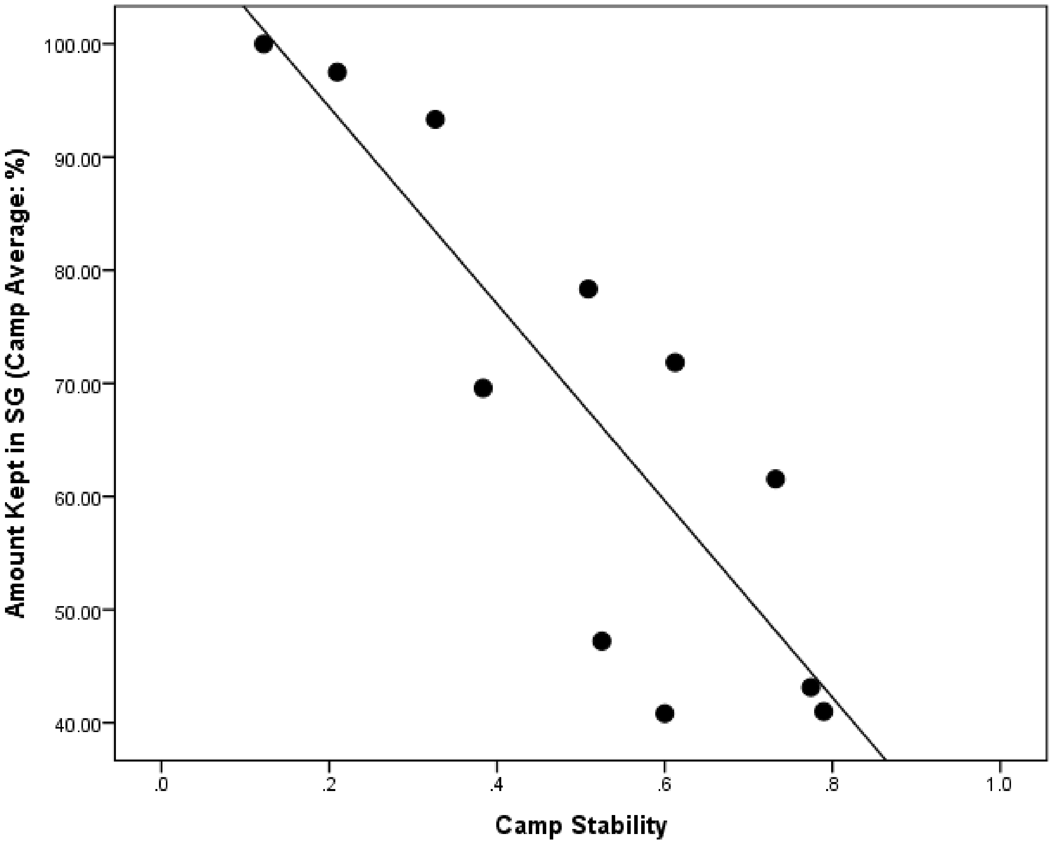

Figure 4.2: Association between camp average amount of rice kept in the Sharing Game (%) and camp stability (‘0’ indicates no individuals remained in that camp, while ‘1’ denotes camp membership was stable over multiple visits (minimum two month period); *n*=11). This plot demonstrates that an increase in camp stability was associated with an increase in donations to others (i.e., keeping less for self).

Similar trends emerged in the Taking Game. Over the 18 camps an average of 65.4% (SD=30) of rice was taken from others, with a minimum camp average of 35.6% (SD=15.1) and maximum of 96.7% (SD=12.5). AIC values for the null multi-level model (AIC=2761) were again lower than the equivalent non-multi-level model (AIC=2790), and models weights indicated that the multi-level model possessed superior model fit (w_i=1). 24.2% of the variance in TG behaviour over these 18 camps occurred at the camp level. Significant camp-level differences in taking behaviour were reported using a Kruskal-Wallis test (*H*=81.47, *df*=17, *n*=290, *p*<0.001).

The same patterns emerge when focusing on the 11 Palanan camps for which stability data were available. As with the SG, AIC values for the null regression model without a multi-level structure (AIC=1766.9) were higher than the AIC values for the null multi-level formulation (AIC=1734.5), with model weights again finding that the latter model was a better fit to the data (w_i=1). In the null multi-level model 28.1% of the variation in taking behaviour was accounted for by camp-level differences. A Kruskal-Wallis test again indicated significant between-camp differences in cooperative behaviour (*h*=60.674, *df*=10, *n*=183, *p*<0.001). Thus, similar to giving behaviour in the SG, a large proportion of the variation in taking behaviour in the TG was attributable to differences in cooperative behaviour between camps.

The model averaging results for the TG (table 4.5) mirrored those of the SG, with taking more rice significantly associated with reduced camp stability, no engagement in harvesting rice, more dependent offspring and no rice storage (see table A2 in Appendix 7 for AICc values and model weights for each of the top models over these imputed datasets). For example, a camp with a stability score of 1 would be predicted to take 62.6% points less rice than a camp with a stability score of 0, while engagement in harvesting rice decreased the amount of rice taken by 20.3% points. Similarly, individuals without stored rice were expected to take 11.9% points more rice in the TG, while each additional dependent offspring increased the amount taken by 3.1% points. Other variables entered in to the model averaging procedure were not strong predictors of cooperative behaviour in the TG (affinal closeness, cash labour involvement, camp size and consanguineal relatedness).

Table 4.5: Results of the model averaging procedure pooled across five imputed datasets for the Taking Game, displaying both standardised and unstandardised coefficients (*n*=183, camps=11). Positive parameter estimates indicate an increase in rice taken from others (%) with an increase in the predictor variable. 95% confidence intervals are displayed in brackets. Relative importance denotes the summed Akaike weight (w_i) of each parameter in the top models used in model averaging, with a '1' indicating that this term occurred in all of the top models.

Variable	Level	Std. Parameter Estimate (95% CI)	Unstd. Parameter Estimate (95% CI)	Relative Import. (w_i)
Intercept	-	68.79 [64.89; 72.68]	81.91 [47; 116.82]	-
Camp Stability	Camp	-25.2 [-16.16; -34.24]	-62.63 [-40.16; -85.1]	1.00
Harvesting Rice (1=No)	Camp	20.34 [6.71; 33.98]	20.34 [6.71; 33.98]	1.00
Stored Rice (1=No)	Individual	11.87 [4.5; 19.23]	11.87 [4.5; 19.23]	1.00
# Dependent Offspring	Individual	14.3 [6.94; 21.67]	3.11 [1.51; 4.71]	1.00
Consanguineal Relatedness	Individual	2.46 [-4.67; 9.59]	21.42 [-40.53; 83.37]	0.48
Affinal Closeness	Individual	-2.55 [-10.01; 4.91]	-3.18 [-12.48; 6.12]	0.46
Camp Size	Camp	-3.18 [-12.8; 6.44]	-0.25 [-1.02; 0.51]	0.44
Cash Labour Involvement	Individual	-0.06 [-3.19; 3.06]	-0.08 [-4.2; 4.03]	0.02

Thus, the only differences between the SG and TG, in terms of strongly predictive variables, was that affinal closeness and cash labour involvement were associated with SG, but not TG, offers. In neither game were camp size or consanguineal relatedness strongly predictive of cooperation. This correspondence in predictor variables indicates that both games are measuring similar aspects of cooperation, as also evidenced from the significant correlation between SG and TG scores (*r*=0.59, *n*=290, *p*<0.001). Thus, individuals who gave many resources to others in the SG took little from them in the TG. Additionally, although individuals were slightly more cooperative in the SG – with the average amount kept for self in the SG at 62.6% while the TG was 65.4% – a Wilcoxon signed-rank test found that the difference between games was not statistically significant, although a trend was apparent (*T*=10,440, *p*=0.087).

Mann-Whitney *U* tests reported that the order in which the games were conducted had no bearing on either SG (*U*=4430.5, *p*=0.47) or TG offers (*U*=3716, *p*=0.18), nor did familiarity with the researchers from fieldwork the previous year (SG; *U*=10,398.5, *p*=0.85: TG; *U*=9,303.5, *p*=0.16). Game order and familiarity are therefore unlikely to confound these results. None of the predictor variables in these analyses displayed heightened collinearity, suggesting that, for example, stored rice was not highly correlated with camp stability (table A3 in Appendix 7). Figures A1 and A2 in Appendix 7 display the residuals from both SG and TG null models using Q-Q plots. While both plots somewhat follow a normal distribution – especially compared against data from other economic games which often have bimodal distributions and a short tail (i.e., few offers above 50%; for example, see figure 2 in Henrich *et al.* 2005) – Shapiro-Wilk tests found that both SG and TG offers differed significantly from a normal distribution (SG; *p*<0.001: TG; *p*=0.003). Although regression-based methods are generally robust against violations of normality (Gelman & Hill 2007: 46), in tables A4 to A7 I nonetheless also show that results of model averaged ordinal logistic regression models – specifically, cumulative link models (Agresti 2002) – are qualitatively similar to those presented above. This suggests that these findings are statistically robust and unlikely to be a result of violating methodological assumptions.

Discussion

These results suggest that: i) there is significant variability in cooperative behaviour within a single ethnolinguistic group; and ii) this variation can be explained by socioecological factors, both at the camp and individual level. The amount of variability in cooperative behaviour displayed by the Agta is quite surprising, with some individuals in the SG giving all resources to camp-mates, while others kept all resources for themselves. This variability persists at the camp level, from a minimum average of 26.8% of gifts kept for self in one camp, to a maximum of 100% of gifts kept in another: a range of 73.2% points. Of the total variance in the null multi-level model for the SG over all 18 camps, 30% occurred at the camp level (rising to 40.2% if only including the 11 camps from Palanan). This range of scores and amount of group-level variance is larger than was found previously in Ultimatum Games conducted in small-scale societies, both between-societies, with a range of 31% points and group-level variance of 12% (Henrich *et al.* 2005), as well as within-societies, with a range of 21% points and group-level variance of 14.4% (Lamba & Mace 2013).

Given this great amount of variability, this study, in conjunction with previous research exploring within-society variation in cooperative behaviour (Gurven *et al.* 2008; Lamba & Mace 2011, 2013; Nettle *et al.* 2011; Holland *et al.* 2012; Silva & Mace 2014, 2015; Wu *et al.* 2015), suggests that group-selected population-wide social norms may not wholly explain cooperative behaviour displayed within ethnolinguistic groups. This argues against CGS as an explanation for cooperative behaviour among small-scale societies, at least in the populations observed. However, CGS requires groups to be in competition with one another, or to have been in the recent past, in order for between-group selection to outweigh within-group selection and altruistic social norms to spread (Henrich 2004a; Boyd & Richerson 2005; Richerson & Boyd 2005; Bowles 2006, 2009; Richerson *et al.* 2016). These conditions may not have been met in present small-scale populations tested, meaning that individual-level selection would carry greater importance in determining social behaviour. However, even in societies with a history of conflict – meaning that groups are in competition, increasing the strength of between-group selection – such as in Northern Ireland, great variation in cooperative behaviour is still observed (Silva & Mace 2014). Furthermore, this variation is not predicted by levels of conflict, but rather is associated with socioecological factors such as socioeconomic status (Silva & Mace 2014), while conflict *reduces* overall levels of cooperation (Silva & Mace 2015). Thus, even under the conditions expected to be most favourable to CGS, one finds little evidence for it having shaped human cooperative behaviour.

Most research exploring the potential influence of CGS has posited that it operates at the ethnolinguistic population level (Henrich *et al.* 2005; Richerson & Boyd 2005), hence why this is the level I focus on here. Nonetheless, group selection may operate at lower levels, such as between camps or between geographical groupings, such as clans (Mathew & Boyd 2011). However, CGS operating at either of these levels is unlikely to explain the pattern of results observed here for several reasons. Firstly, the high level of camp-level mobility makes group selection at the camp-level, in terms of one camp reproductively out-competing another camp, resulting in group extinction of the vanquished camp, highly unlikely. This high level of mobility also indicates a lack of competition between camps, meaning that between-group selection at the camp-level is unlikely to significantly outweigh within-group selection. Given that levels of cooperation are predicted by factors which likely fluctuate over time, such as resource availability and camp stability, these camp-level cooperative profiles are unlikely to be temporally stable, again mitigating against CGS. That is, camps may be cooperative when food is plentiful or repeated interactions likely, but less cooperative when food is scarce or interactions fleeting. This suggests that camp-level cooperation may not be determined by a fixed set of camp norms, but rather is flexible depending on the prevailing socioecological conditions, although this needs to be verified further using longitudinal research.

Secondly, although the Agta historically engaged in violent conflict (the practice ended over 50 years ago), in the forms of raids (*ngayaw*) between neighbouring Agta communities (Estioko & Griffin 1975), which may have increased the strength of between-group selection, this is also unlikely to explain these results. These raids occurred between different Agta 'clans' – congregations of camps from a widely-dispersed geographic area, such as Agta from San Mariano or Dinapigue raiding Palanan Agta – rather than between neighbouring camps within a given area. As the results of this chapter are drawn from camps within one localised area (Palanan), increased between-group selection resulting from these raids is an improbable explanation for the observed variation in cooperation displayed in these games as 'camp' was unlikely to be the potential unit of selection. Additionally, the extent to which these raids enhanced between-group selection at the clan-level – if at all – is unknown as *ngayaw* may have been largely symbolic and probably resulted in few casualties (Minter 2010: 85). For these reasons, CGS at levels other than the ethnolinguistic group is also an unlikely explanation for the observed variation in Agta cooperation.

If not CGS, what, then, explains this variation in cooperativeness? As discussed above, there are several potential mechanisms, some of which are consistent with the results found here (see table 4.6 for a summary). The variable associated most strongly with cooperation in both the SG and the TG was camp stability. Individuals from stable camps gave more in the SG and took less in the TG compared to individuals from unstable camps. This suggests that repeated interactions can facilitate cooperation, in line with theories such as direct reciprocity (Trivers 1971) and generalised reciprocity (Pfeiffer *et al.* 2005). Although these findings are consistent with direct reciprocity, a dyadic analysis of who individuals give to is required to conclusively test whether individuals give to others with the expectation that they will reciprocate (to be explored in the following chapter). Although some lab studies have reported that repeated interactions increase cooperation (Dal Bo 2005; Kanagaretnam *et al.* 2010; Rand & Nowak 2013), this is the first real-world study reporting an association between cooperation and camp stability in hunter-gatherers.

Table 4.6: Summary of results relative to predictions made by each theory regarding the evolution of cooperation.

Theory	Prediction	Findings
Cultural Group Selection	Low levels of between-camp variation in cooperative behaviour.	Not Supported
Kin Selection	Greater levels of cooperation when more kin are present.	Not Supported [a]
Reciprocity	Greater cooperation in camps with a higher probability of repeated interactions	Supported
Tolerated Theft/ Demand Sharing	Low levels of giving coupled with high levels of taking from others.	Supported (in unstable camps)
Costly Signalling	High levels of cooperation as a signal to 'out-compete' other camp-mates.	(Potentially) Not Supported
Market Integration	Greater market integration will be associated with increased cooperation.	Somewhat Supported
Group Size	Reduced levels of cooperation in larger groups.	Not Supported
Resource Competition	More cooperation when local resource competition is reduced (lower costs to cooperation).	Supported
Needs-Based Cooperation	Individuals less in need of additional resources will be more cooperative (lower costs to cooperation).	Supported

[a] However, note that lowered levels of cooperation by those with more dependent offspring can be interpreted as kin selection, but towards offspring, rather than the wider camp.

Under conditions of camp instability where individuals gave less to others in the SG, they took more from them in the TG. A lack of giving behaviour in experimental games has previous been interpreted as evidence for a tolerated theft system of food-sharing among the Hadza (Marlowe 2004c). The current analysis extends this by demonstrating that when individuals were not given resources by others, they still acquired resources by taking them. Even when repeated interactions are less likely, resources transfers between individuals still occur, but may do so according to tolerated theft/demand sharing (Blurton Jones 1987; Peterson 1993). This is inconsistent with widespread sharing reflecting costly signalling (Hawkes 1991; Hawkes & Bliege Bird 2002), under which high levels of cooperation would be predicted. However, as there was no potential for signalling in these games this interpretation only holds if game behaviour reflects everyday cooperative behaviour (Rand *et al.* 2014). In contrast, if participants behaved 'rationally', solely within the confines of the game design, then costly signalling was potentially 'untested'. Given that external influences likely influence game behaviour to some extent I find the former interpretation more parsimonious (see also Chapter 8). These results nonetheless suggest a potential continuum of food-sharing practices dependent upon the probability of repeated interactions; from giving to others under conditions of high stability (potentially reciprocity) to demand sharing under conditions of low stability. This possibility will be explored further in the following chapter.

These findings could also be interpreted as evidence that cooperative camps are more stable as a consequence of assortativity or partner choice, whereby cooperative individuals cluster together to the exclusion of non-cooperators (Nowak 2006; Ohtsuki *et al.* 2006; Apicella *et al.* 2012; Barclay 2013; Sylwester & Roberts 2013). However, this pathway is unlikely because: i) it does not explain why camp stability would be correlated with distance to town (see ethnographic chapter and below); and ii) as will be shown in the following chapter, there is little evidence that positive assortativity by cooperativeness occurs. This suggests the causality may flow from stable camps to increased cooperation, rather than from increased cooperation to stable camps.

As camp stability appears to influence cooperation, understanding the causes of this variation is also necessary. There is a significant association between stability and distance from town, with stable camps found closer to town (r=-0.77, n=11, p=0.006). This suggests that integration with recently introduced institutions, such as evangelical church groups, education, health-care availability and labour opportunities, may promote sedentism among the Agta, as these effects are more pronounced nearer town. Although previous studies have used 'distance from town' as a crude proxy for market integration (Gurven 2004b), more recent studies have operationalised market integration as the amount of food acquired by trade (Henrich *et al.* 2010a). However, this is relatively constant among the Agta as all trade foraged goods for rice with their agricultural neighbours, regardless of distance from town. Therefore, although distance to town could be seen as an indirect measure of market integration, given the Agta's reliance on trade for carbohydrates this distance to town effect most likely reflects differences in mobility, rather than exposure to markets. Thus, exposure to markets does not appear to impose exogamous sharing norms on the Agta; rather, increased involvement with outside institutions encourages sedentism, leading to endogenous changes in cooperation and food-sharing practices.

In addition to camp stability, other variables were also found to significantly predict cooperation in these games, such as measures of resource availability and need. Camps engaged in harvesting rice and households with an existing supply of rice have increased resource availability, lowering resource competition and reducing the costs of cooperation, and hence displayed an increase in cooperation in both games. This was remarked upon by one of the Agta, who, after being asked why they gave no rice to anyone else in the games, replied “as it is very hard to find rice”. Previous research with student populations has suggested that increased local resource competition can reduce cooperation (West *et al.* 2006; Barker *et al.* 2012), which may increase demand sharing among foragers. Resource availability may therefore greatly affect cooperation among the Agta.

The association between cooperation and number of dependent offspring may also depend on need, as individuals with more dependent offspring require more resources, raising the cost of giving and consequently decreasing cooperation. The Agta appear aware of this, as one woman with many dependent children who kept the first few tokens for herself in the Sharing Game, said it was because “there are so many [children]! Then, if I have enough, I will give [to others]”. Another man, also with lots of offspring, said that he kept all resources for himself because “he has many children”. Similar patterns regarding cooperation and family size have been found from experimental games conducted in other small-scale populations (Gurven *et al.* 2008; Lamba & Mace 2013; Gwako 2014; Lesorogol 2014; Ziker 2014). These findings correspond well with recent reports of forager food-sharing in which individuals unencumbered with dependent offspring and at a net-surplus provision those with many children who would otherwise be at a net-deficit (Gurven 2004c; Hill & Hurtado 2009; Hooper *et al.* 2015). This is consistent with theoretical accounts of reciprocity, which indicate that reciprocity is more likely to occur when individuals are in surplus and the recipient in deficit, meaning that the benefit of giving to the recipient is higher than the cost to the donor (Trivers 1971; Doebeli & Knowlton 1998). These results may also reflect kin selection, as individuals with more dependent offspring were less cooperative towards the wider camp to provide additional resources for their offspring. Regardless of the specific evolutionary mechanism, in addition to camp-level variation explained by camp stability, cooperation between households appears to be needs-based.

Although the finding that individuals with greater involvement in the cash labour economy were more cooperative in the SG (but not the TG) may be consistent with the market integration hypothesis, it is unclear whether this finding is specifically due to adopting ‘pro-social market norms’ or simply differential costs and benefits to cooperation. For instance, individuals engaged in wage labour are assured of resources each day, while individuals who foraged likely possess increased stochasticity in resource acquisition. This may decrease the costs of cooperation for those participating in wage labour, hence why they were more cooperative. Furthermore, as discussed in the ethnographic chapter, Agta subsistence is highly-flexible to the current opportunities available (Minter 2010), such that individuals who participate in wage labour one week are likely to forage the next week, and vice versa (if the opportunities are available). This weakens the argument that market norms determine cooperative behaviour, as even those Agta not currently engaged in wage labour during fieldwork likely have experience with the cash economy (and, as discussed above, all Agta trade foraged resources for rice, indicating exposure to markets). Rather, this result may also suggest that levels of cooperation are flexible and depend on current socioecological circumstances, although longitudinal studies to assess these ideas in greater details are again required.

Other theoretically-relevant variables were not associated with cooperation. Most noticeably, the presence of kin was not associated with an increase in cooperation. Although consanguineal kin presence did not influence the *amount* given, Agta may preferentially give to kin *when* they distribute resources (Apicella *et al.* 2012; Thomas *et al.* 2015; see the following chapter for a test of this). In fact, in the SG individuals with *less* affinal kinship ties to the camp were more cooperative. This may be a result of increased competition between close affinal kin, analogous to how competition between genetic kin may erode cooperation (Queller 1994; West *et al.* 2002; Wu *et al.* 2015). Alternatively, camp-mates with fewer or more distant affinal ties may be less able to rely upon kin for support, so have to ‘prove their worth’ as sharing partners by giving more to others in order to receive resources. Regardless of the specific mechanism, this suggests that the presence of affinal kin can influence cooperation. This is a topic which is often overlooked in studies of food-sharing, and cooperation more generally, which tend to focus on the effects of consanguineal kin (Gurven 2004b; MacFarlan & Quinlan 2008; Sear 2008; Sear & Mace 2008; although see Alvard 2009). This is likely a significant oversight as cooperation among affines, not just among genetic relatives, can accrue indirect fitness benefits (Chapais 2010), but simultaneously may also result in competition between affinal kin. It is also important to note that this discussion refers to kinship effects *between* households. The decreased cooperation by those with more dependent offspring still likely reflects kin selection, but towards their offspring, rather than the wider camp (Gurven *et al.* 2000b). Thus, while kin selection may influence within-household cooperation, the effect of consanguineal relatedness on levels of between-household cooperation appears weaker and subsidiary to other considerations, such as camp stability and resource availability.

Also unexpected was a lack of camp size effect despite a theoretically increased risk of free-riders (Boyd & Richerson 1988), as larger camps were equally as cooperative as smaller camps. Of the camps tested here, group sizes (minimum=25, maximum=119, average=51.9) fall within the range of other hunter-gatherers (minimum=13, maximum=250, average=37.5; Marlowe 2005), albeit with a slightly higher mean, suggesting that group size may not be a limiting factor to cooperation in hunter-gatherers within the observed range. Thus, ecological and demographic factors based on group stability and varying costs to cooperation are likely to have played a key role in the evolution of cooperation, in what was the dominant human lifestyle up to ~12,000 years ago.

Summary and Next Chapter

In conclusion, I find little evidence for population-wide social norms influencing cooperative behaviour, contrary to expectations based on cultural group selection. Rather, cooperation is highly variable both within and between camps, and depends largely on local socioecological conditions and individual circumstances. The role of repeated interactions and need are found to be particularly important for predicting levels of cooperation, with individuals displaying increased cooperativeness in stable camps and when the costs to cooperation were lower. This supports a behavioural ecological interpretation of cooperation, in which cooperation is flexible and individuals alter their levels of cooperative behaviour in seemingly adaptive ways to the prevailing socioecological context. However, the current chapter only explores the amount of resources that individuals share. In order to further our knowledge of resource transfers and test certain theories of cooperation more directly, such as kin selection, reciprocity and indirect reciprocity, one must explore with whom individuals share these resources when they are transferred. It is this topic which we explore in the next chapter.

Chapter 5 Patterns of Experimental Resource Transfers

This chapter builds upon the results of the previous chapter by exploring who individuals share with, or take from, during experimental resource transfers. Theories of cooperation in which transfers should be targeted to specific recipients can therefore be tested. These include kin selection, direct reciprocity, indirect reciprocity, cooperative homophily and tolerated theft/demand sharing, each of which makes specific predictions regarding patterns of food-sharing. Resource transfers are also expected to vary under differing levels of producer control. Transfers under a low producer control situation, where individuals take resource from others (tolerated theft/demand sharing), are expected to be from those with a greater number of resources, regardless of relationship. Transfers under a high producer control situation, where individuals actively give resource to others, are predicted to be targeted to specific individuals. These resource transfers may be based upon: i) *kin selection:* preferentially sharing with relatives; ii) *direct reciprocity:* sharing with those who also share with ego; iii) *indirect reciprocity:* sharing with cooperative individuals; and iv) *cooperative homophily:* sharing with others of a similar cooperative level. Large differences between resource transfers under conditions of high and low producer control are observed, largely following these theoretical predictions Under conditions of low producer control, the primary determinant of taking behaviour is resource quantity (take from those with more), with little recourse to kinship, reciprocity or cooperativeness. Conversely, under a high producer control situation, transfers occur largely according to reciprocity and kinship. These results demonstrate how differences in producer control can greatly influence patterns of resource transfers among foragers, which may have significant implications for understanding cross-cultural variation in cooperation and food-sharing practices.

Introduction

While the previous chapter investigated the factors predicting variation in how cooperative individuals were, the current chapter explores who individuals share resources with in these games. Cooperation among hunter-gatherers is extensive, and often extends beyond kin to unrelated individuals (Hill *et al.* 2011; Dyble *et al.* 2015). Although several underlying mechanisms have been proposed to explain patterns of food-sharing in forager societies, there remains a lack of consensus as to why individuals share food with the people they do and why this varies across different societies. The majority of previous studies investigating this question have looked at observational food-sharing data to explore individual motivations and adaptive hypotheses regarding resource transfers and cooperation. However, real-world food-sharing might not reflect individual preferences. For example, given the choice, an individual may prefer to share food with their close kin who live on the other side of camp, yet because they live closer to an unrelated individual, this unrelated individual demands a share of their resources. Thus, real-world food transfers may not mirror the *desired* allocation of resources, especially if producer control is low (Gurven 2004d). Marlowe (2004c) compares this situation to mate choice, in which by only observing who individuals are with, and not who they would prefer to be with, one may incorrectly infer that individuals are with their preferred partners. Furthermore, many evolutionary theories make similar predictions regarding distributions of real-world food-sharing, meaning that experimental approaches may be necessary to distinguish between competing theories (more on this below). The present chapter aims to explore these issues by using an experimental methodology to examine who individuals share resources with. Several adaptive hypotheses are tested to understand patterns of resource transfers.

One of the most common hypotheses proposed to explain cooperation in humans is via indirect fitness benefits, or kin selection (Hamilton 1964), in which, all else being equal, individuals preferentially assist close kin over more distant kin or unrelated individuals. This can include those with shared reproductive interests, such as affinal kin, as giving food to a brother-in-law, who in turn will share with ego's kin, will also increase inclusive fitness (Chapais 2010). Some studies report that kin selection does not explain the flow of resource transfers among foragers (Bliege Bird & Bird 1997; Allen-Arave *et al.* 2008), while others find an effect of preferential sharing among kin, but attribute this to proximity rather than kin selection (Gurven *et al.* 2000b). Despite this, meta-analyses comparing across several forager groups have found that relatedness is a significant predictor of food-sharing (Gurven 2004d; Jaeggi & Gurven 2013), although there remains debate over whether this is due to indirect or direct fitness benefits, such as reciprocity among kin (Allen-Arave *et al.* 2008).

The role of reciprocity has been theorised to promote cooperation between unrelated individuals (Trivers 1971), particularly in hunter-gatherer societies where resource variability in hunting returns may lead to reciprocal sharing as a form of risk-reduction. This ensures that, even when an individual returns to camp with no food, they still receive a share from others (Winterhalder 1986; Smith 1988; Hill & Hurtado 2009). Reciprocal cooperation has been documented in several hunter-gatherer populations (Gurven *et al.* 2000b; Gurven 2004c, d; Allen-Arave *et al.* 2008; Nolin 2010), although not in all societies tested (Bliege Bird & Bird 1997; Hawkes *et al.* 2001; Bliege Bird *et al.* 2002; Gurven *et al.* 2002). An alternative approach to resource transfers in foragers relates to tolerated theft, or demand sharing (Blurton Jones 1984, 1987; Peterson 1993; Winterhalder 1996; Lewis *et al.* 2014). Under this system, individuals take food from those with more resources and are not reprimanded for doing so because the costs to the producer of defending the resource are higher than the marginal gains from successfully defending it. Although unlikely to be the sole mechanism explaining food transfers in hunter-gatherers, this hypothesis has been used to explain food-sharing in several societies (Peterson 1993; Bliege Bird & Bird 1997; Hawkes 2000; Jaeggi & Gurven 2013).

The theories discussed above – kin selection, reciprocity and tolerated theft/demand sharing – are often seen as 'traditional' theories for forager cooperation which have been tested since the 1980's (e.g., Kaplan & Hill 1985; for a review see Gurven 2004b). Since this time, however, there have been many advances in the theoretical study of cooperation, suggesting several other mechanisms which can promote the evolution of cooperation. Many of these have not yet been explored in great detail among foragers. Central to many of these theories is the idea of partner choice, or assortment, which emphasises the importance of cooperating with specific phenotypes within the population, rather than interacting randomly (Eshel & Cavalli-Sforza 1982; Nowak 2006; Ohtsuki *et al.* 2006; Pepper 2007; Roberts 2008, 2015; Aktipis 2011). While this assortment is implicit in theories of kin selection and reciprocity, other mechanisms include indirect reciprocity, whereby individuals preferentially cooperate with those possessing a reputation for cooperation, thus excluding defectors and allowing cooperation to evolve (Nowak & Sigmund 1998, 2005; Panchanathan & Boyd 2003; Roberts 2015). A related theory – that of reputation-based partner choice (also known as competitive altruism) – suggests that individuals which display, or have a reputation for, cooperativeness, reap the rewards of their seemingly costly displays in subsequent interactions by attracting cooperative partners. That is, by engaging in costly behaviour to begin with these, individuals ‘compete’ for profitable cooperative partnerships in the future which outweigh the original costs (Roberts 1998; Sylwester & Roberts 2010, 2013). Although the mechanisms by which they promote cooperation are distinct (as described in the introductory chapter), both indirect reciprocity and reputation-based partner choice predict that individuals should preferentially cooperate with cooperative individuals.

Evidence for cooperative assortativity is relatively scarce in hunter-gatherers, although the research discussed in the introductory chapter – such as high-producing Ache being more likely to receive aid in times of illness or injury (Gurven *et al.* 2000a) and generous Martu more likely to be chosen as cooperative hunting partners (Bliege Bird & Power 2015) – suggests that more cooperative individuals may receive direct fitness benefits. However, among the Meriam, skilled foragers were equally as likely to receive resources as non-foraging free-riders (Bliege Bird *et al.* 2002), suggesting little discrimination in terms of food transfers based upon productivity. Although not supporting indirect reciprocity or competitive altruism, as more cooperative individuals were not preferred partners, evidence from the Hadza suggests that assortativity by cooperativeness does occur; individuals of a similar cooperative level clustered together in camp-mate and gift game networks (Apicella *et al.* 2012). This process is known as ‘cooperative homophily’ (see Antal *et al.* (2009) for a model which explores how cooperation can evolve by interactions based on phenotypic similarity). Thus, the role of cooperative assortment, either by indirect reciprocity (or competitive altruism) or cooperative homophily, may potentially underpin several facets of forager food-sharing.

While not an evolutionary explanation for cooperation, several studies have indicated that proximity predicts an increased prevalence of food-sharing among foragers (Gurven *et al.* 2000b; Gurven 2004d; Nolin 2010). As residential decisions are unlikely to be independent of other considerations, food-sharing among neighbours often loses statistical significance once controlling for other variables such as kinship (Patton 2005) or reciprocity (Hames & McCabe 2007), although not in all instances (Gurven *et al.* 2000b, 2002; Nolin 2010). Whether these patterns of distribution among neighbours, controlling for other effects, reflect preferential sharing of resources or instances of tolerated theft – as closer neighbours can spot food easier (Winterhalder 1996) – is currently unclear.

Understanding the mechanisms behind food-sharing is complicated as more than one adaptive process can lead to the same pattern of food-sharing between individuals. For instance, despite seemingly disparate underlying processes, predictions made by reciprocity and demand sharing are often similar in practice (Schnegg 2015), in that both are expected when food packets are large and acquired asynchronously (Winterhalder 1997: 151). As a further example, food transfers from one household with few individuals to another with more dependent offspring could be interpreted as provisioning or as demand sharing, depending on whether there is producer control or not. Many food-sharing theories which require assortativity implicitly assume high producer control, such that producers of the resource can decide who to give resources to (e.g., kin, reciprocal sharing partners, cooperative individuals, etc.). However, low producer control (recipient control) characterises other theories, specifically tolerated theft/demand sharing, where the producer has little say over where food is distributed. Thus, with producer control sharing should be more selective, while in a situation of recipient control resource distribution ought to be less targeted to specific individuals and relate predominantly to resource size (i.e., take from those with more: Blurton Jones 1987; Winterhalder 1996).

Although the magnitude of producer control varies over societies and resource type (Gurven 2004d), it is difficult for observational data to fully determine the amount of control individuals have over distributions. While observations of food-sharing can describe the *patterns* of resources transfers, they have difficultly elucidating the *process* by which food is shared (i.e., high or low producer control). For instance, widespread food-sharing, without recourse to kin selection or reciprocity, could be interpreted as a reputation enhancing device if individuals give resources away (high producer control) or as tolerated theft if resources are taken by others (low producer control). Similarly, when controlling for other factors, proximity effects may either be a consequence of tolerated theft if producer control is low or preferential sharing if producer control is high. Experimental games, such as those designed here which manipulate levels of producer control, can be used to disentangle these mechanisms.

Previous studies have utilised experimental methodologies to examine social relations in forager societies (Rucas *et al.* 2010; Apicella *et al.* 2012; Chaudhary *et al.* 2015), yet none have explicitly tested theories of food-sharing in the context of a social dilemma (where selfish and group motivations compete; Kollock 1998), nor simultaneously explored the roles of producer and recipient control. When given the opportunity to share resources among others, Hadza adults preferentially chose individuals who were closer kin, were more similar to themselves (with respect to cooperativeness, age, height, weight and strength), displayed reciprocity and lived in closer proximity (Apicella *et al.* 2012). However, the Hadza were only able to give resources – three honey-sticks, in this instance – to others, and not keep any for themselves. Thus, this was not a social dilemma as individuals only had the option of sharing. These additional costs to giving may alter the profile of cooperation in terms of selectivity of partners (for instance, costly sharing may be more discriminate than uncostly sharing). Alternatively, although related, costly and uncostly giving may cue different normative contexts (or ‘framing effects’), producing different patterns of cooperation (Cronk 2007; Lesorogol 2007; Gerkey 2013), such that costly giving may cue food-sharing contexts while uncostly giving may not. Although speculative, how, or even if, these contextual cues regarding costly and uncostly giving alter cooperative behaviour has yet to be explored.

Following this, although traditional economic games, such as the Ultimatum Game, Dictator Game and Public Goods Game (Camerer 2003), are social dilemmas, they include only anonymous partners. These games therefore ignore the role that differences in relationship can have on cooperation, so cannot be used to explore *who* individuals preferentially share resources with. The one study to date which has experimentally investigated transfers of goods in a social dilemma situation was conducted with the Tsimane, but concerned bead sharing between women, rather than transfers of food (Rucas *et al.* 2010). Contrary to expectations based on kinship and affiliative closeness, women took more beads from helpers as well as from kin, although there was a trend within kin to take less from those with a higher relatedness coefficient. Individuals also took less from neighbours, enemies and those they wished to be friends with, indicating that additional social factors can influence the distribution of resources (see also Wiessner 2002).

The present study aims to explore individuals’ food-sharing preferences under experimental conditions. It builds upon the previously cited research by combining: i) an exploration of resource transfers under social dilemma conditions (where individuals can either keep resources for self or give to others); with ii) a comparison of food transfers under conditions of both high and low producer control. Given the theories detailed above, one may predict large differences in resource distributions between these two conditions. When individuals give to others in the Sharing Game (where resources are given *to* others; SG) I predict that there will be greater assortativity in resource transfers. In contrast, in the Taking Game (where resources are taken *from* others; TG) these assortative characteristics are likely to play a reduced role, in line with tolerated theft. Given the theories outlined above, several specific hypotheses were formulated. In the game simulating high producer control I test: i) *kin selection*: Individuals should display a preference towards giving to kin or individuals with shared reproductive interests (i.e., affines); ii) *reciprocity*: Individuals should share with those who also share with them; iii) *indirect reciprocity*: Individuals should give to highly cooperative others; iv) c*ooperative homophily*: Individuals should share with individuals of a similar cooperative level; and v) *proximity:* Individuals should share with those they live closer to. In the low producer control condition I explore: vi) *Demand sharing/tolerated theft*: Individuals should take from those who have more resources, regardless of relationship. It is also possible to explore the five above hypotheses relating to assortativity in the low producer control context, to examine whether they also influence whom resources are taken from (i.e., take less from kin; although if present their magnitude may be lower). The one exception is proximity, as if the previously reported effects of proximity on food-sharing reflect tolerated theft, rather than preferential sharing, then taking behaviour may be greater from those living in closer proximity.

I demonstrate that: i) no single theory can explain the totality of resource transfers, meaning that multiple theories must be applied to understand food-sharing in foraging societies; ii) there are significant differences in resource distributions under conditions of low and high producer control; and iii) an experimental approach can provide an answer to questions which observational studies have difficulty distinguishing. Reciprocity and kinship effects were found when producer control was high, while they were absent when producer control was low. Under situations of low producer control the strongest determinant of taking behaviour was resource quantity (take from those with more), consistent with theories of tolerated theft. Assortativity hypotheses regarding indirect reciprocity and cooperative homophily were not supported, as no effects of homophily were found in either game, while in the Sharing Game individuals preferentially gave to *less* cooperative individuals. These results provide a unique insight into the evolutionary mechanisms and individual motivations behind food-sharing in forager societies and support the proposal that demand sharing is particularly important when producer control is low, while reciprocity and kin selection are key when producer control is high.

Methods

As with the previous chapter, games were played with 290 Agta (mean age=37, males=140) over 18 camps, while 324 Agta were included as potential recipients. The experimental methods used are the same as those in the previous chapter (and described in the methods chapter). Only statistical methods will be discussed here.

Statistical Analyses

Response variables were coded in two matrices; for the SG ego giving to alter was coded as ‘1’ while if alter received no gifts this was coded as ‘0’; in the TG ego taking from alter was coded as ‘1’ while if no resources were taken this was coded as ‘0’. Between-camp dyads and within-camp dyads where ego did not have the option of giving to or taking from alter were coded as missing values. Independent variables included: kinship relation between ego and alter, reciprocity, alter level of cooperation, cooperative homophily, proximity and, for the TG, whether alter began the game with 1 or 2 tokens (signifying differences in resource quantity). Effects of age (of ego, alter and age difference) and sex (of ego, alter and sex difference) were also included as control variables. Kin relationships were defined as: primary kin (PK), with a relatedness coefficient of r=0.5 to ego; distant kin (DK), with a relatedness coefficient between r=0.25 and r=0.03125 (second cousins) to ego; spouse; spouse's primary kin/primary kin's spouse (SPK/PKS); spouse's distant kin/other affines (SDK/OA), which includes distant kin of spouse or other affinal relationships up to 5 steps away from ego (e.g., spouse's brother's wife's mother: four steps away); and non-relatives (NR), which includes everyone else without a kinship link to ego (see Dyble *et al.* (2015) for further details). As these are discrete categories, resource distributions towards each of these kinship terms were compared relative to resources given to or taken from non-kin.

The matrix for reciprocity was the transpose of the response variables (i.e., whether alter gave to ego in the SG or took from them in the TG). Each individual possessed a score (between 0% and 100%) indicating the percentage of gifts they kept for themselves in the SG and how many they took from others in the TG. From this, an index of cooperative homophily was constructed reflecting the absolute difference in scores, with '0' meaning both individuals gave the same, and '30' indicating a difference, irrespective of direction, of 30 percentage points between ego and alter. Alter score was also included as a predictor variable to investigate whether individuals gave to cooperative or uncooperative others. This was centred around the mean for each camp, so that between-camp differences in cooperation did not confound within-camp sharing patterns. Individuals with a positive value gave more or took less than others in camp (i.e., they were more cooperative), while individuals with a negative value gave less or took more than others in camp (i.e., they were less cooperative). Proximity was coded from one to four, reflecting increasing distance between ego and alter, with categories of: 1) living in the same house as ego; 2) living in the house next to ego; 3) having a house between ego's and alter's; and 4) living further away. In order to control for differences in the amount given or taken between individuals, ego's cooperative score (% kept for self) was included as a control variable in all models (corresponding to the specific game being analysed). This control ensured that patterns of resource transfers were not confounded with the amount distributed, as without it reciprocity and cooperativeness may be conflated if individuals distribute widely (i.e., mistaking generalised sharing, with no expectations of reciprocation, for actual reciprocity). Although there were 2,752 dyads in total, as a result of the game structure reciprocity was not possible to assess for all individuals in larger camps, resulting in 1,312 dyads which contained data for all predictor variables. Thus, all models contained the same number of dyads (1,312) to ensure that differences in model fit values are not due to differences in sample size.

Analyses were conducted using the statistical software *R* (R Development Core Team 2015). A generalised estimation equation (GEE) approach was utilised to control for repeated data from the same individual (Zeger & Liang 1986). Logistic regressions were conducted on vectors containing dyadic information regarding the relationship between ego and alter. As GEE analyses do not utilise full-likelihood estimates, quasi-likelihood information criterion estimates (QIC; Pan, 2001) were employed to compare model fit. As with the previous chapter, a model averaging approach was used to assess which predictor variables were strongly associated with giving/taking behaviour. For each game, a global model was constructed containing all variables described above. Keeping ego cooperative score and age and sex effects as controls in all models, all possible models containing the theoretically-relevant variables (kinship, reciprocity, proximity, alter cooperativeness, cooperative homophily and (for the TG) starting resource quantity) were constructed and QIC values compared. Models within two QIC values of the top model were subsequently averaged. Thus, 32 and 64 different models were constructed for the SG and TG, respectively.

Continuous input variables were standardised over two standard deviations (SDs) while binary variables were mean-centred (Gelman 2008; Schielzeth 2010). This standardisation allows comparisons of effect sizes between both continuous and binary variables, as well as between continuous variables measured on different scales. Standardised estimates are used in text, while standardised and unstandardised estimates are displayed in tables. However, it is important to remember that only unstandardised coefficients are biologically meaningful. For example, if a two SD increase in proximity is found to significantly influence who individuals cooperate with (a standardised coefficient), the unstandardised coefficient is required to identify how much a one unit increase in proximity increased the odds of receiving a resource. Furthermore, as log-odd coefficients are not necessarily intuitive to interpret, they are converted in to odds ratios (OR) in text to facilitate comprehension of effect sizes (Nolin 2010). Odds ratios for binary variables or factors are compared to the reference, while odds ratios for continuous variables reflect a two SD difference.

Results

Sharing Game

Of the 32 candidate models, those within two QIC values of the top model are displayed in table 5.1. After averaging these top models, it was found that kinship, reciprocity and alter cooperativeness were each associated with sharing resources (table 5.2), suggesting that resource distributions in this game were highly structured. Although all kinship categories appeared more likely to receive resources in the SG from the raw data (figure 5.1), once controlling for other factors only a strong preference towards giving to primary kin (OR=4) and distant kin (OR=1.78) remained. Affinal kin and spouses were not more likely to receive resources than non-kin. Reciprocity was a strong predictor of giving behaviour, with the odds of ego giving to alter increasing by 1.68 times if alter also gave to ego. Although contrary to theoretical expectations, a two SD decrease in alter cooperativeness was associated with a 1.58 times increase in the probability of receiving resources. Less cooperative individuals were therefore *more* likely to receive resources than more cooperative individuals. No effects of proximity or cooperative homophily were reported. Some age and sex effects were also found. Same-sex individuals were nearly twice as likely to receive resources relative to opposite-sex dyads (OR=1.89), while a two SD increase in alter age raised the probability of being given to by ~50% (OR=1.49).

Table 5.1: Comparison of the top models (within two QIC values of the best-fitting model) regarding who individuals gave resources to in the Sharing Game. Keeping age, sex and ego cooperative level control variables constant, 32 potential models were constructed and QIC values compared using all combinations of the variables: kinship, reciprocity, proximity, alter cooperativeness and cooperative homophily.

Model Variables	**QIC**	**ΔQIC**	**Model Weight (w_i)**
Kinship + Reciprocity + Alter Cooperativeness	1086.25	0	0.72
Kinship + Reciprocity + Alter Cooperativeness + Cooperative Homophily	1088.18	1.92	0.28

Table 5.2: Results of the model averaging procedure for sharing resources with camp-mates in the Sharing Game, displaying both standardised and unstandardised coefficients (*n*=290, dyads=1,312). Coefficients are log-odd estimates, with 95% confidence intervals displayed in brackets. Variables in which confidence intervals do not pass through '0' are highlighted in bold. Relative importance denotes the summed Akaike weight (w_i) of each parameter in the top models used in model averaging, with a '1' indicating that this term occurred in all of the top models. Note also that proximity does not appear here as none of the top models contained this variable. All models contain an 'ego cooperative score' variable (not displayed) which controls for differences in amount given by each individual.

Variable	**Std. Parameter Estimate (95% CI)**	**Unstd. Parameter Estimate (95% CI)**	**Relative Import. (w_i)**
Intercept	-1.27 [-0.92; -1.61]	2.36 [1.64; 3.09]	-
Ego Age	-0.08 [-0.36; 0.19]	-0.003 [-0.012; 0.007]	-
Alter Age	**0.4 [0.11; 0.68]**	**0.014 [0.004; 0.024]**	**-**
Age Difference	0.09 [-0.2; 0.38]	0.004 [-0.008; 0.016]	-
Ego Sex (1=M)	0.01 [-0.27; 0.28]	0.01 [-0.27; 0.28]	-
Alter Sex (1=M)	-0.17 [-0.44; 0.1]	-0.17 [-0.44; 0.1]	-
Same Sex (1=No)	**-0.64 [-0.35; -0.92]**	**-0.64 [-0.35; -0.92]**	**-**
PK (Ref.=NR)	**1.39 [0.85; 1.92]**	**1.39 [0.85; 1.92]**	**1**
DK (Ref.=NR)	**0.58 [0.04; 1.11]**	**0.58 [0.04; 1.11]**	**1**
SPK/PKS (Ref.=NR)	0.19 [-0.31; 0.68]	0.19 [-0.31; 0.68]	1
SDK/OA (Ref.=NR)	0.06 [-0.34; 0.45]	0.06 [-0.34; 0.45]	1
Spouse (Ref.=NR)	0.17 [-0.47; 0.8]	0.17 [-0.47; 0.8]	1
Reciprocity	**0.52 [0.21; 0.83]**	**0.52 [0.21; 0.83]**	**1**
Alter Coop.	**-0.46 [-0.16; -0.75]**	**-0.011 [-0.004; -0.018]**	**1**
Coop. Homophily	0.03 [-0.16; 0.22]	0.001 [-0.004; 0.005]	0.28

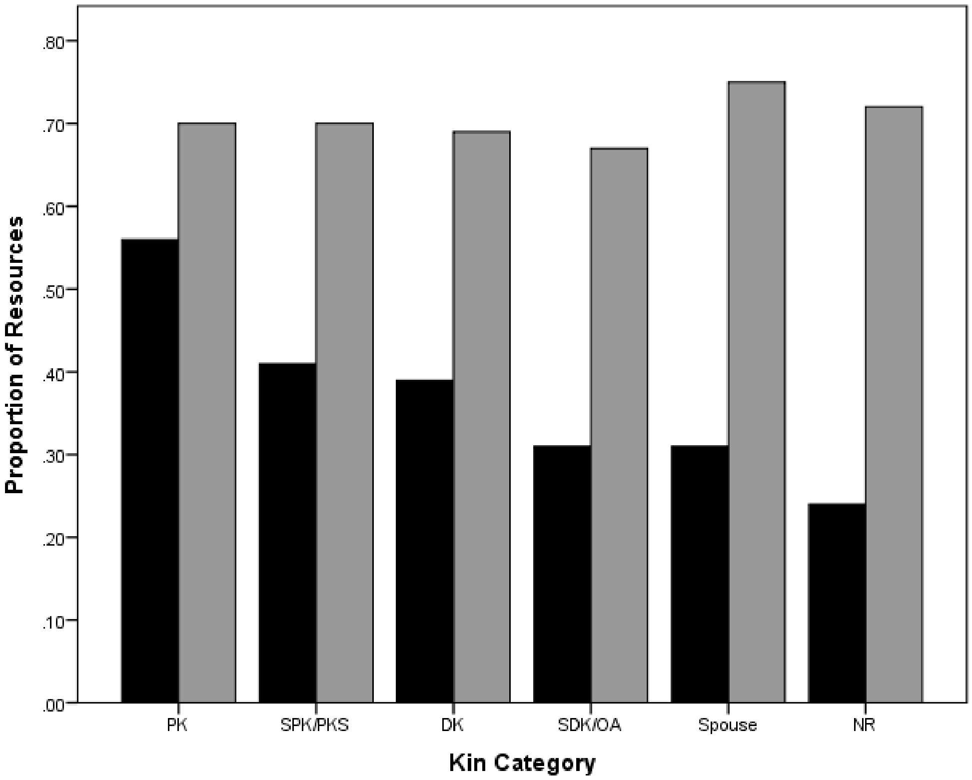

Figure 5.1: Average proportion of resources given to (black; Sharing Game) or taken from (grey; Taking Game) camp-mates as a function of kin category (PK=primary kin; SPK/PKS=spouse's primary kin/primary kin's spouse; DK=distant kin; SDK/OA=spouse's distant kin/other affines; NR=no relation: *n*=290, dyads=2,752).

Reasons for Giving in the Sharing Game

In addition to assessing which camp-mates individuals gave resources to, it was also asked why they gave to these individuals, resulting in a total of 1,001 answers. These answers were then categorised according to various criteria relevant to the evolution of cooperation, such as kinship, personal qualities and reciprocity, among others (see table 5.3 & figure 5.2). The most common reason was genetic relatedness, accounting for over one-quarter of all nominations, while affinal kinship accounted for one-sixth of all nominations. Collectively, nearly half of all reasons given were based on kinship. Around one in ten nominations referred to reciprocity between ego and alter. These results reflect the above analysis, suggesting that both kinship and reciprocity are important reasons why individuals shared food, while also demonstrating, as also shown above, that kinship may carry greater weight than reciprocity. Few individuals mentioned norms of fairness or equality, such as 'need to share' or 'so everybody has some' in deciding who to share with (only 1.3%), while non-kin relationships, such as friend or neighbour, were also relatively infrequent reasons for giving (5.5%). Personal qualities, such as kindness, leadership or generosity, were slightly more likely to be given as reasons (8.4%). After kinship, the second largest reason, comprising one-quarter of all nominations, was needs-based sharing to help others, including reasons such as: old age, pregnancy, many children, weakness, inability to work and having no food. Differences between the sexes appear rather minimal, other than females selecting consanguineal relatedness more often than males (23.9% vs. 23.3%) and males slightly more likely to share based on need (27.8% vs. 23.7%).

Table 5.3: Frequency and percentage of answers given as to why individuals gave resources to camp-mates in the Sharing Game, including male and female answers separately (answers=1,001, male=522, female=479). Note that some answers included two categories (e.g., 'Father' and 'has a kind heart'), in which case half a point was coded as 'genetic kin' and the other half as 'personal qualities'.

Category	**Example Answers**	**Total Freq. (%)**	**Male Freq. (%)**	**Female Freq. (%)**
Genetic Kin	Father, Mother, Son	279 (27.9%)	121.5 (23.3%)	157.5 (32.9%)
Affinal Kin	Father-in-law, Brother-in-law	163 (16.3%)	85.5 (16.4%)	77.5 (16.2%)
Non-Kin	Friend, Neighbour, Companion	55.5 (5.5%)	26.5 (5.1%)	29 (6.1%)
Needs-Based/ Helping	Alter is/has: Old, Pregnant, Many children, Cannot work, No food. To help them	258.5 (25.8%)	145 (27.8%)	113.5 (23.7%)
Reciprocity	When ego needs something alter is there, Alter shares with ego, If ego asks alter gives	94 (9.4%)	47.5 (9.1%)	46.5 (9.7%)
Personal Qualities	Alter is: Good, Has a kind heart, Good in sharing, Chief	84.5 (8.4%)	44.5 (8.5%)	40 (8.4%)
Fairness/ Equality	Need to share, So everybody has some, So they have the same	12.5 (1.3%)	12.5 (2.4%)	0 (0%)
Other	Varied, including: guilt, selfishness, related to the game, 'don't know why'	54 (5.4%)	39 (7.5%)	15 (3.1%)

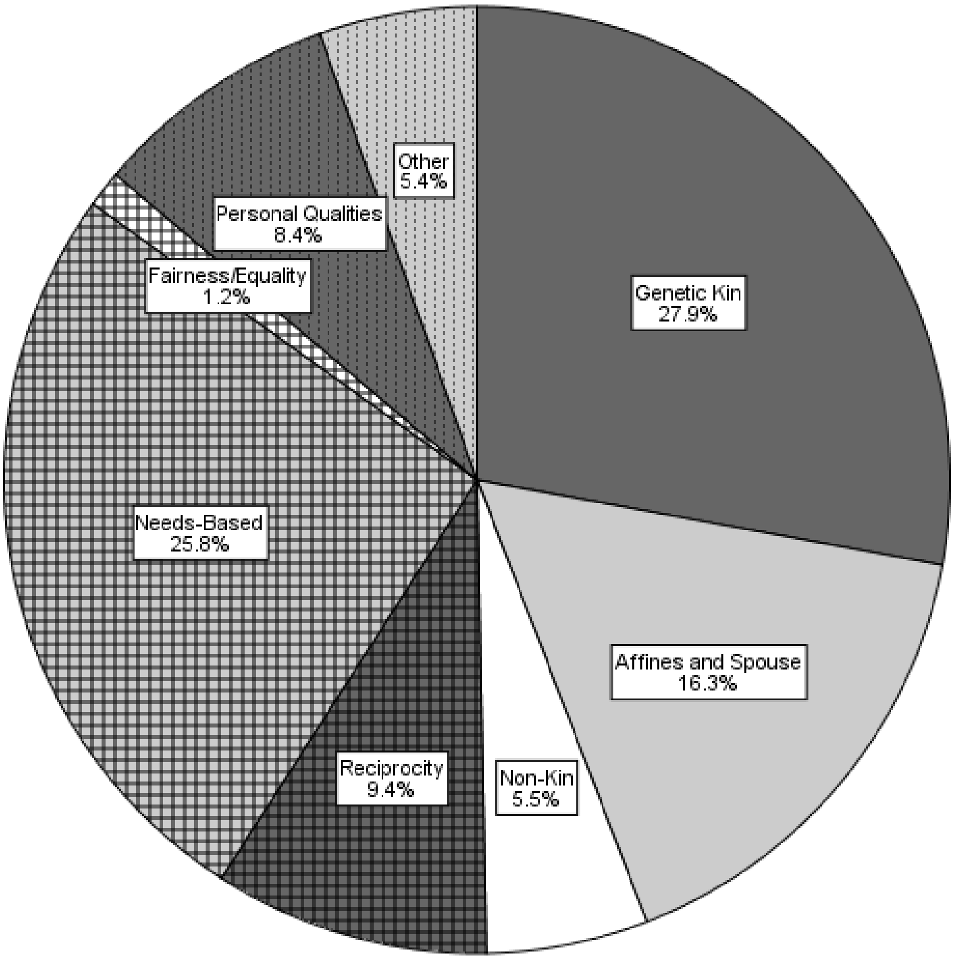

Figure 5.2: Pie chart displaying the proportion of reasons, split by category, for giving to others in the Sharing Game (reasons=1,001).

Taking Game

Of the 64 candidate models in the TG, those within two QIC values of the top model are displayed in table 5.4. After model averaging, the only theoretically-relevant variable which predicted taking behaviour was resource quantity (table 5.5). Individuals who started the game with two resources were 11.1 times more likely to be taken from than those with only one resource. Resource distributions were therefore much less structured in the TG relative to the SG, with no significant effects of kinship (figure 5.1), reciprocity, proximity, alter cooperativeness or cooperative homophily. Even though no overall effect of kinship was reported, an interaction between kinship and resource quantity could be predicted, such that camp-mates with only one resource may be less likely to be taken from if they were kin. However, using the global model as a baseline, model fit decreased when including this interaction term (global QIC=922.76; interaction QIC=923.98), suggesting that kin and non-kin were equally likely to be taken from, regardless of starting resource quantity. Age of ego was also associated with the amount taken from others, with a two SD increase in age increasing the likelihood of taking by 1.62.

Table 5.4: Comparison of the top models (within two QIC values of the best-fitting model) regarding who individuals took from in the Taking Game. Keeping age, sex and ego cooperative level control variables constant, 64 potential models were constructed and QIC values compared using all combinations of the variables: kinship, reciprocity, proximity, alter cooperativeness, cooperative homophily and starting resource quantity.

Model Variables	**QIC**	**ΔQIC**	**Model Weight (w_i)**
Resource Quantity + Proximity	913.01	0	0.43
Resource Quantity	914.24	1.23	0.23
Resource Quantity + Proximity + Alter Cooperativeness	914.84	1.83	0.17
Resource Quantity + Proximity + Reciprocity	914.87	1.85	0.17

Table 5.5: Results of the model averaging procedure for taking resources from camp-mates in the Taking Game, displaying both standardised and unstandardised coefficients (*n*=290, dyads=1,312). Coefficients are log-odd estimates, with 95% confidence intervals displayed in brackets. Variables in which confidence intervals do not pass through '0' are highlighted in bold Relative importance denotes the summed Akaike weight (w_i) of each parameter in the top models used in model averaging, with a '1' indicating that this term occurred in all of the top models. Note also that kinship and cooperative homophily do not appear here as no top models contained either term. All models contain an 'ego cooperative score' variable (not displayed) which controls for differences in amount kept by each individual.

Variable	**Std. Parameter Estimate (95% CI)**	**Unstd. Parameter Estimate (95% CI)**	**Relative Import. (w_i)**
Intercept	1.8 [1.59; 2.01]	-4.31 [-3.37; -5.23]	-
Ego Age	**0.48 [0.16; 0.81]**	**0.017 [0.006; 0.028]**	**-**
Alter Age	-0.01 [-0.33; 0.31]	0.00 [-0.011; 0.011]	-
Age Difference	-0.19 [-0.51; 0.13]	-0.008 [-0.022; 0.006]	-
Ego Sex (1=M)	0.24 [-0.08; 0.56]	0.24 [-0.08; 0.56]	-
Alter Sex (1=M)	0.1 [-0.22; 0.41]	0.1 [-0.22; 0.41]	-
Same Sex (1=No)	-0.03 [-0.35; 0.28]	-0.03 [-0.35; 0.28]	-
Resource Quantity	**2.4 [2.05; 2.76]**	**2.4 [2.05; 2.76]**	**1**
Proximity	-0.24 [-0.61; 0.14]	-0.11 [-0.29; 0.07]	0.77
Alter Coop.	-0.01 [-0.15; 0.13]	0.00 [-0.003; 0.003]	0.17
Reciprocity	-0.02 [-0.18; 0.14]	-0.02 [-0.18; 0.14]	0.17

To summarise these results briefly, I find that there are significant differences in patterns of resources transfers under conditions of high producer control (giving to others; the SG) and low producer control (taking from others; the TG). Resource transfers in the SG were predominantly directed towards specific individuals, in particular kin and reciprocating partners. Resources were also preferentially given to same-sex Agta, as well as to older individuals and to those who were less cooperative. Conversely, in the TG resources were taken less selectively with respect to the relationship between ego and alter, with the main determinant being resource quantity. Those who began the game with two resources were over 10 times more likely to be taken from than those with one resource. No effects of kinship or reciprocity were found regarding taking behaviour, with the only other predictive variable being that older Agta took more from others than younger Agta. The main results of these analyses are summarised in figure 5.3.

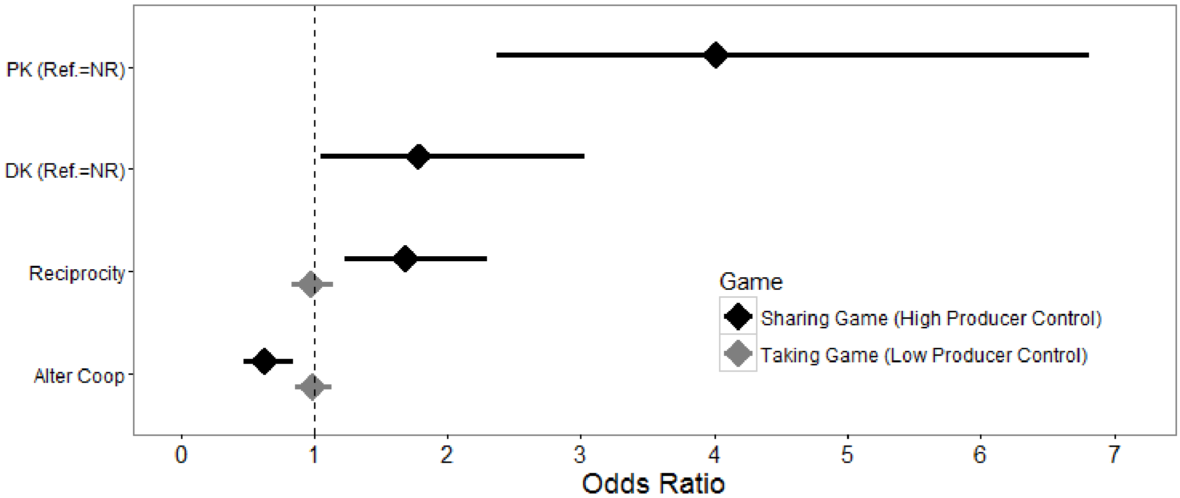

Figure 5.3: Odds ratios, derived from standardised log-odds estimates, of giving to an individual in the Sharing Game (high producer control; black bars; table 5.2) or taking from an individual in the Taking Game (low producer control; grey bars; table 5.5). There is little overlap in behaviour between the games, with who individuals gave to and who they took from associated with a disparate set of variables. Variables relating to age, sex, cooperative homophily and resource quantity are not displayed here (note also that coefficients for 'kinship' in the Taking Game are not displayed as no top models contained this term). Error bars indicate 95% confidence intervals (*n*=290, dyads=1,312).

Discussion

This is the first experimental study specifically investigating food transfers in a hunter-gatherer society, and is particularly significant because it dissociates producer control (giving to others) and recipient control (tolerated theft/demand sharing), which are often confounded in analyses of observational food-sharing (Gurven 2004d; Nolin 2010). Thus, these findings provide a unique insight into the mechanisms and motivations which underlie resource transfers in hunter-gatherers. These results indicate that there are significant differences in sharing behaviour under conditions of high and low producer control (figure 5.3). When producer control is high, individuals predominantly give to kin and reciprocating partners, while when producer control is low resource transfers show little concern for kinship or reciprocity, with resource quantity the largest determinant of taking behaviour.

Although the raw data for the SG (figure 5.1) indicated that all kin categories, including affines, were preferred sharing partners, once controlling for other variables such as reciprocity, only primary and distant kin were given to more than unrelated individuals. While some of the kin selectivity in the SG may be attributed to reciprocal (or other) effects, this nevertheless suggests a strong independent kin-bias regarding the selectivity of sharing partners. Indirect fitness effects therefore appear to be important when deciding with whom to share resources, arguing against recent analyses which suggest that nepotistic resource transfers may solely be due to direct fitness benefits such as reciprocity (Allen-Arave *et al.* 2008). This is reflected in the reasons individuals gave for sharing in the SG, with over one-quarter of all reasons due to consanguineal kinship (figure 5.2). The unique human social structure of long-term pair-bonding and group-living means that both extended consanguineal and affinal kin are known (Chapais 2010), and these shared long-term reproductive interests may promote trust and interdependence which can facilitate cooperation (Roberts 2005). Thus, even if individuals do not gain indirect fitness benefits by cooperating with kin, this interdependence makes them ideal partners to help increase their direct fitness. This is a likely explanation regarding cooperation among affinal kin found here, who appeared more likely to receive resources compared to non-kin from the raw data (figure 5.1), but not in the multivariate analysis once other factors were included. Thus, cooperation among consanguineal kin may be a combination of both direct and indirect fitness benefits, while among affinal kin only direct fitness benefits appear important. Interestingly, however, kin effects were absent in the TG. This suggests that under situations of low resource control kinship affiliation is subsidiary to other considerations, such as resource quantity, when deciding whom to take resources from. Assortative food-sharing – in terms of kin-biased and reciprocal transfers – are therefore more pronounced under conditions of increased producer control, consistent with these mechanisms requiring control over resource distributions.

Consistent with previous studies of food-sharing (Wiessner 2002; Gurven 2004c; Patton 2005; Allen-Arave *et al.* 2008; Nolin 2010), reciprocity was a strong predictor of giving in the SG. This is especially significant as nominations were private, so individuals were unaware of whether others had also given to them. As giving behaviour in the SG was reciprocal, this suggests that individuals gave to others with the expectation that they would also give to ego, while in the TG this expectation of reciprocation was absent. This was again apparent in the reasons individuals gave for sharing, with ten percent of reasons reflecting reciprocal considerations, including "when [ego is] in need, they help" and "they share with ego".

Theories of tolerated theft/demand sharing were also strongly supported. Resource quantity was the most important factor determining from whom to take resources, in line with predictions made by models of tolerated theft which posit that kinship or reciprocal concerns are of less importance under this system (Blurton Jones 1987; Winterhalder 1996). That older individuals took more in the TG than younger individuals also corresponds well with a recent model of demand sharing (Lewis *et al.* 2014). In this model, older individuals (whose production levels fall below consumption levels) in a demand sharing context had significantly longer life-spans than loner individuals, suggesting that older individuals can acquire food by free-riding (taking resources without producing as much) under a demand sharing system. Thus, where older individuals cannot produce much food, they may survive by scrounging – or demanding – resources from others. Additionally, under conditions of high producer control older individuals were more likely to receive resources, suggesting that regardless of the level of producer control, older individuals, who are less able to support themselves, are able to acquire resources.

Although hunter-gatherers may live with many unrelated individuals (Hill *et al.* 2011; Dyble *et al.* 2015), these results suggest that cooperation, at least in terms of giving behaviour in the SG, is not applied indiscriminately to all individuals in camp (*contra* Burkart *et al.* 2014), arguing against theories of 'generalised reciprocity' among foragers (Sahlins 1972). These results also argue against cultural group selection, which posits that, as a consequence of selection between groups, those with stronger norms for cooperation towards the wider community should out-compete less cooperative groups and spread (Henrich 2004a; Boyd & Richerson 2005; Richerson & Boyd 2005). Of all the reasons given for sharing with others in the SG, only 1% of them referred to norms of equality or fairness, irrespective of individual identity. This structuring of cooperative interactions towards kin and reciprocating partners is not consistent with group-level adaptation and altruism towards the wider group, but rather maximising inclusive fitness via direct and indirect fitness benefits (see also Acedo-Carmona & Gomila 2015).

Effects of cooperative assortativity were largely absent, or in the opposite direction to theoretical predictions. In both games there was no evidence of cooperative homophily, suggesting that individuals did not preferentially give to or take from others of a similar cooperative level. In the TG, an individual's cooperativeness was not associated with being taken from, while in the SG less cooperative individuals were given to *more* frequently than highly cooperative individuals. This argues against theories emphasising the importance of cooperative assortativity, such as indirect reciprocity, cooperative homophily and competitive altruism (Nowak & Sigmund 1998; Roberts 1998; Ohtsuki *et al.* 2006; Antal *et al.* 2009; Aktipis 2011; Apicella *et al.* 2012), in explaining patterns of hunter-gatherer cooperation, at least among the Agta. This is in contrast to several lab experiments suggesting that individuals preferentially associate and cooperate with cooperative individuals (Wedekind & Milinski 2000; Nowak & Sigmund 2005; Seinen & Schram 2006; Sylwester & Roberts 2010, 2013; Raihani & Barclay 2016). These lab conditions, however, are highly artificial, as the only information individuals have in many of these experiments when choosing between potential partners is the cooperative level of said partners. Under these conditions it may not be surprising that individuals choose cooperative individuals as future partners, given a lack of other information. In more complex real-world situations there are many other sources of information that one can draw upon when deciding who to cooperate with, such as kinship or past reciprocal encounters, and these appear of greater importance among the Agta. The one other study to date which has explored these factors in another forager group, the Hadza, also found that cooperative individuals were not more likely to be chosen in either gift game or camp-mate networks (Apicella *et al.* 2012). In contrast with the findings here, they did report cooperative homophily, with individuals of a similar cooperative level clustering together. However, their measure of cooperative networks did not incorporate the potential for keeping resources for self, meaning that it was not a social dilemma (Kollock 1998), and this may have altered the network structure as there was no cost to giving to others. How social and cooperative networks are altered by context, such as the presence or absence of a social dilemma, will be discussed in greater detail in the following chapter.

What is particularly striking in the SG is that there appears to be *negative* assortativity by cooperativeness. This suggests that individuals avoided giving resources to cooperative individuals, while they preferentially gave resources to less cooperative individuals. The previous chapter indicated that the total amount kept for self in these games was increased when individuals were in greater need (e.g., they possessed fewer resources or had more dependent offspring). A similar explanation may be in effect here, with individuals preferentially giving to those in greater need of additional resources (Allen-Arave *et al.* 2008; Aktipis *et al.* 2011; Hao *et al.* 2015), as these individuals are likely to be those who kept more for themselves in these games. Indeed, nearly one-quarter of reasons individuals gave for sharing with others in the SG were ostensibly based on need or to help them. Examples of these needs-based reasons include: pregnancy, weakness, many children, inability to find food, no husband, sickness and old age (which may also explain why older individuals were more likely to receive resources in the SG). This is again consistent with recent studies of forager food-sharing, indicating that the ‘haves’ support the ‘have-nots’ (Hill & Hurtado 2009; Hooper *et al.* 2015), and that the best producers of resources do not necessarily receive more shares from others (Bliege Bird *et al.* 2002; Bird & Bliege Bird 2010).

As mentioned in the introduction, however, needs-based sharing is a description of cooperation, not an adaptive hypothesis. Understanding the evolutionary function of this needs-based sharing is therefore essential. The analyses presented here control for kinship, meaning that indirect fitness benefits via kin selection are unlikely to explain this sharing based on need. As there was no possibility of individuals taking resources from others in the SG, tolerated theft cannot explain this pattern of results. One potential functional explanation concerns reciprocity, but on a longer time-scale than assessed here (although note that an immediate effect of reciprocity is reported as well). For instance, by helping those in need now, where the costs to the actor are low and the benefits to the recipient high, if the roles are reversed in the future the former recipient may reciprocate. This may be particularly important in hunter-gatherer contexts where individual stochasticity in resource acquisition is high (Hill & Hurtado 2009). The concept of resource value, rather than resource quantity, is pertinent here as the same quantity of food has greater value for a needy individual compared to a satiated one (Gurven 2006). Taking this value asymmetry into consideration, rather than models where pay-offs are constant, greatly expands the potential for reciprocal cooperation to evolve (Doebeli & Knowlton 1998). This implies that the quantities shared do not need to be equal for reciprocity to occur as long as the long-term resource values are equal (Gurven 2006). Longitudinal research, rather than a cross-sectional approach adopted here, which take variation in need and resource value into consideration are required to explore these dynamics. Delayed reciprocity may therefore provide an adaptive reason for this needs-based sharing, although additional studies exploring these predictions in greater detail are required. Other functional reasons are also possible, such as ‘charitable’ donations to enhance one’s political reputation or social standing (Milinski *et al.* 2002; Bliege Bird & Power 2015; Macfarlan & Lyle 2015) or as a sexually selected costly-signalling strategy to exhibit one’s phenotypic value – by displaying qualities such as care, compassion and generosity – and attract mates (Raihani & Smith 2015). Regardless of the underlying evolutionary explanation, the results presented here demonstrate that needs-based sharing is pervasive among the Agta.

Assortativity via kin-based (Hamilton 1964) and reciprocal (Trivers 1971) considerations may consequently be more important in deciding with whom to cooperate than the general cooperativeness of an individual. Given that cooperation levels vary with life course, socioecological circumstance and relationship to recipient, an individual’s level of cooperation in the present may not necessarily be indicative of cooperative interactions in the future. Among foragers this uncertainty may be exacerbated by stochasticity in foraging returns (Winterhalder 1986; Smith 1988; Hill & Kintigh 2009). Kin and reciprocal partnerships, which are more enduring, may provide a firmer foundation on which to base cooperation. This lack of assortativity by cooperativeness also bolsters the claim made in the previous chapter that camp stability results in cooperation, rather than cooperation resulting in greater stability. If camp stability were a result of cooperative individuals clustering together to the exclusion of non-cooperators, then individuals would be predicted to preferentially share resources with cooperative individuals.

There was also a same-sex bias in the SG, in that individuals preferentially gave to members of the same sex. This pattern was not observed for the TG, again suggesting that taking behaviour is much less discriminate than giving behaviour. As individuals displayed a same-sex bias, this suggests that socio-political factors may underpin some resource transfers in the SG. For example, among the Ju/'hoansi targeted resources transfers are used to alter camp composition with the aim of promoting cooperation and reducing conflict, as well as to trade for childcare in a form of 'not-in-kind' reciprocity (Wiessner 2002). Similarly, food-sharing can be traded for coalitional support (Patton 2005). It is possible that factors similar to these – regarding a social or political, rather than provisioning, function – may underscore this same-sex bias, as well as other instances of resource transfers. For instance, many of reasons given for why individuals shared with others in the SG concerned reciprocity, but many of these were 'not-in-kind', such as for helping with childcare, general assistance or childbirth (table 5.3). Resources were also directed towards others who possessed positive personal attributes, such as kindness, goodness, generosity and leadership, suggesting that individuals who act according to Agta-defined moral standards (i.e., in the interests of others with little self-regard) may be rewarded. Indeed, one individual even shared with another because they "behave like an Agta". These acts of sharing may positively reinforce these other-regarding behaviours, while also acting as a model from which others can learn; by observing that others displaying these unselfish behaviours get rewarded, this may increase the likelihood of others adopting said behaviour. These social and political considerations regarding food transfers deserve further investigation and will be the focus of the subsequent chapter.

These results have significant implications for subsequent analyses of food-sharing data from forager societies as they suggest that the level of producer control can dramatically alter patterns of food transfers. If the patterns observed here are generalisable, they suggest that societies in which resource transfers are kin-biased and/or reciprocal – such as the Lamalera (Nolin 2010), Hiwi (Gurven *et al.* 2000b; Gurven 2004c), reservation-living Ache (Gurven 2004c; Allen-Arave *et al.* 2008) and the Dolgan/Nganasan (Ziker & Schnegg 2005) – may possess high producer control. On the other hand, societies in which distribution is more even among camp-mates, irrespective of kinship or reciprocity – such as forest-dwelling Ache (Kaplan & Hill 1985; Gurven *et al.* 2002), Hadza (Hawkes *et al.* 2001), Martu (Bird & Bliege Bird 2010; Bliege Bird & Power 2015) and Meriam (Bliege Bird & Bird 1997; Bliege Bird *et al.* 2002) – may possess lower producer control. Little research has been conducted into explaining variation in hunter-gatherer food-sharing patterns (although see Gurven *et al.* 2002). I suggest here that some of this variation may be a result of differences in producer control, with reciprocity and kin-biased sharing when producer control is high and demand sharing based predominantly on resource size when producer control is low.

The next question to ask is; what explains differences in producer control between groups? The findings of the previous chapter offer a potential answer; demand sharing (low producer control) was much more prevalent under conditions of low camp stability, while individuals were much more likely to give to others (high producer control) when camps were stable. Taken together, this suggests that stable camps which give resources to others do so with expectations of reciprocity, while unstable camps which engage more in demand sharing predominantly take from those with a greater number of resources, with little concern for reciprocity. Thus, reciprocal cooperation is more prevalent in stable camps while tolerated theft/demand sharing is more prevalent in unstable camps. Both strategies may be adaptive mechanisms to avoid free-riders under differing socioecological conditions;

reciprocity avoids non-sharing free-riders under stable conditions (Trivers 1971) while high mobility avoids non-hunting free-riders under demand sharing conditions (Lewis *et al.* 2014).

Summary and Next Chapter

This chapter has explored differences in resource transfers between conditions of high and low producer control. In the absence of external social pressures, and dissociating the roles of producer and recipient control, these findings shed light on the decisions individuals make regarding with whom to share and take food. These findings therefore represent a controlled test of food-sharing hypotheses which are not confounded by whether *actual* sharing partners (observational data) are *preferred* sharing partners (experimental data, as collected here). For example, proximity effects are often reported in the food-sharing literature (Gurven *et al.* 2000b; Nolin 2010), yet individuals did not preferentially share resources with close neighbours in the SG. Proximity effects in studies of real-life food-sharing may therefore represent opportunity effects of tolerated theft (individuals living closer can spot food more easily), and not necessarily transfers of resources to preferred individuals. These results suggest that many mechanisms proposed to explain food-sharing among foragers are present, although they largely depend on the level of producer control: reciprocity and kin selection when producer control is high, to demand sharing when producer control is low. Mechanisms regarding cooperative assortativity, in terms of predictions made by indirect reciprocity and cooperative homophily, were not supported. More cooperative individuals, or individuals of a similar cooperative level, were not more likely to receive resources. Rather, these findings suggest that many transfers among foragers are needs-based, as less cooperative individuals were more likely to receive resources in the SG, although the specific adaptive hypothesis (or hypotheses) underlying this needs-based sharing remains to be conclusively determined. Furthermore, this patterning of resource transfers mitigates against theories which suggest that humans, and foragers in particular, share widely and indiscriminately according to generalised reciprocity (Sahlins 1972; Pfeiffer *et al.* 2005; Burkart *et al.* 2014) or as a result of a history of cultural group selection (Henrich 2004a; Richerson & Boyd 2005; Richerson *et al.* 2016). When food-sharing is indiscriminate, this appears to be a result of tolerated theft or demand sharing, rather than a desire to share resources with all camp-mates.

This chapter has been predominantly concerned with ‘in-kind’ cooperation: whether patterns of resource transfers by one individual predict transfers received from another. However, recently there has been a shift in focus towards exploring the importance of ‘not-in-kind’ cooperation, where the decision to cooperate is not solely based on the cooperative qualities of an individual in a highly-specified domain (e.g., food-sharing), but rather their wider ‘market value’ as a prospective partner. This topic will be explored in the following chapter.

Chapter 6 The Application of Biological Market Theory to Agta Cooperative and Social Networks

The majority of previous research investigating who individuals should cooperate with has concerned either kin selection or 'in-kind' cooperation, such that individuals who are cooperative, or have a previous history of reciprocal cooperation, should be preferred social partners. However, this overlooks cooperation not returned in-kind, such as trading cooperation for coalitional support, childcare, mating, learning opportunities or other socio-political functions. Individuals with greater competency in these domains may possess greater 'market value' as a partner, making them more likely to be recipients of cooperation, irrespective of their previous cooperative history. I explore this possibility in this chapter by adopting a 'biological market' perspective – where individuals base their decisions regarding who to associate with on the benefits said partner can provide for ego – to investigate how reputation in specific non-food-sharing domains, such as foraging skill, storytelling ability, medicinal knowledge and camp influence, impact the probability of: i) being nominated in a camp-mate network of who individuals wish to live with; and ii) receiving resources in the Sharing Game. I find that camp-mate networks are more influenced by competency valuations than food-sharing networks. Skilled foragers, storytellers and influential individuals are more likely to be chosen as camp-mates relative to individuals who are less skilled in these domains. In contrast, the only competency domain associated with an increased probability of resource transfers was storytelling ability. These findings suggest that a 'biological market' approach may be useful when interpreting hunter-gatherer cooperation, particularly for understanding 'not-in-kind' cooperation, as well as social networks more broadly.

Introduction

Traditional explanations for the evolution of cooperation have generally focused on kin selection (Hamilton 1964) and reciprocity (Trivers 1971). While there is widespread support for kin selection as a mechanism underlying cooperative behaviour (Clutton-Brock 2002; Foster *et al.* 2006; West *et al.* 2007a), despite over thirty years of research the evidence for reciprocity in nature is relatively weak (Clutton-Brock 2009; Leimar & Hammerstein 2010; Hammerstein & Noë 2016), although there are exceptions (Schino & Aureli 2010; Carter & Wilkinson 2013, 2015; Jaeggi & Gurven 2013), especially in humans (Gurven 2004c, d; Patton 2005; Allen-Arave *et al.* 2008; Nolin 2010). Explanations for cooperation based on direct fitness benefits may therefore require additional mechanisms beyond reciprocity (Leimar & Hammerstein 2010; Hammerstein & Noë 2016), many of which have been discussed in previous chapters, such as indirect reciprocity and costly signalling.

One further potential theory is that of ‘biological markets’ (Noë & Hammerstein 1994, 1995; Hammerstein & Noë 2016). Biological market theory is analogous to economic market theory, in that individuals should preferentially interact and cooperate with others who possess the highest ‘market value’ as a social partner. Market value is determined by the goods, resources or services that an individual can offer. These may be returned ‘in-kind’ (such as reciprocal food-sharing), but are especially important when commodities are traded ‘not-in-kind’ and which the focal individual cannot provide (that is, they are complementary rather than substitutional; Kaplan & Lancaster 2003). A central tenet of this theory is that individuals exercise ‘partner choice’ regarding who to interact with. Because individuals receive direct fitness benefits by being cooperated with, as a consequence of partner choice there may be competition between individuals to be chosen, potentially resulting in costly displays, or ‘honest signals’, to out-compete one another.

Despite its generality as a process, biological market theory has traditionally been applied to sexual selection and inter-specific mutualisms (between-species cooperation), rather than *intra*-specific cooperation (Noë & Hammerstein 1994, 1995). For instance, regarding the ‘mating market’ both sexes have different ‘commodities’ (eggs vs. sperm) which are both necessary for reproduction. As the costs of reproduction for females are generally higher (in terms of gamete production, gestation, lactation, etc.), especially in mammals, this means that females should be more selective (Trivers 1972). Males would therefore compete with one another to display their quality to females in order to be chosen as a mating partner, resulting in hard-to-fake signals or handicaps (Zahavi 1975), such as ‘leks’, peacock tails or ‘unconditional’ generosity (Raihani & Smith 2015). Similar considerations regarding the trade of commodities occur in inter-specific mutualisms. One example is between cleaner fish and their hosts, in which cleaner fish receive resources while their hosts benefit from having parasites removed (Bshary & Noë 2003). Among such species partner choice is observed, in that hosts preferentially select more cooperative cleaner fish, consistent with biological market theory (Bshary & Grutter 2006). A further biological example is between plants and arbuscular mychorrhizal fungi, in which the fungi only preferentially share nutrients with roots who provide the fungi with carbohydrates (Kiers *et al.* 2011). In both of these systems more cooperative organisms – those with greater ‘market value’ – are preferentially chosen as cooperative partners. Less research has been conducted using the biological market framework for explaining within-species cooperation, although the same principles apply.

One of the key differences between biological market theory and more traditional theories for cooperation, such as reciprocity, concerns the respective roles of ‘partner control’ and ‘partner choice’ (Noë 2006; Baumard *et al.* 2013; Hammerstein & Noë 2016). In classic models for the evolution of cooperation, different cooperative strategies are randomly pitted against one another over iterated rounds without the possibility of choosing the identity of said partner (e.g., Axelrod & Hamilton 1981). Under this system, mechanisms to control partners, such as reciprocal cooperation, are essential. However, recently there has been an increasing appreciation that individuals do not interact with others randomly, but rather structure interactions with specific individuals. This partner choice, or assortativity, is central to biological market theory and greatly expands the conditions under which cooperation can evolve (Pepper & Smuts 2002; Ohtsuki *et al.* 2006; Fu *et al.* 2008; Antal *et al.* 2009; Rankin & Taborsky 2009; Aktipis 2011; Debove *et al.* 2015; Roberts 2015). Experimental evidence suggests that individuals do preferentially interact and cooperate with certain individuals, specifically cooperative individuals, over others (Wedekind & Milinski 2000; Seinen & Schram 2006; Barclay & Willer 2007; Sylwester & Roberts 2010, 2013; Apicella *et al.* 2012; Cuesta *et al.* 2015; Gallo & Yan 2015; Raihani & Barclay 2016).

These studies suggest that partner choice can have a significant impact on cooperation, yet they have rarely been explicitly linked to biological market theory, but rather to other mechanisms such as indirect reciprocity (Roberts 2015). When combined with partner choice, mechanisms such as indirect reciprocity, direct reciprocity, costly signalling (Zahavi 1975; Hawkes & Bliege Bird 2002) and competitive altruism (Roberts 1998) can be incorporated within biological market theory as each increases the market value of an individual as a cooperative partner.

Thus, biological markets can provide a more general framework for understanding the evolution of cooperation, within which several existing theories can be encompassed. Thinking of cooperation in terms of markets also extends previous theories which focus on ‘in-kind’ cooperation – for instance, cooperate with others who previously cooperated with self, or preferentially cooperate with those possessing a reputation for cooperation – by including ‘not-in-kind’ cooperation, such as trading cooperation for other commodities (such as mating opportunities, learning experiences, knowledge, cooperation in other currencies, etc.).

Although biological market theory has been less studied regarding intra-species cooperation (Noë & Hammerstein 1995), one area where it has been applied concerns cooperative acts between non-human primates. Many studies have shown that individuals trade one commodity for another, including; males grooming females in return for sex in long-tailed macaques (Gumert 2007); chimpanzees trading meat for sex and coalitional support (Gomes & Boesch 2011); and chamca baboons trading grooming for infant handling (Henzi & Barrett 2002). There has been considerably less focus on the application of biological market theory to human cooperation (although see Barclay 2013, 2016; Macfarlan & Lyle 2015).

This may be a significant oversight, as, in common with economic markets, biological markets are particularly prevalent when there are multiple valued commodities which can be traded (Noë & Hammerstein 1994, 1995; Hammerstein & Noë 2016), and when there is significant variation between individuals in terms of skill and competency (McNamara & Leimar 2010; Barta 2016). These conditions are met in humans with great aplomb; in human societies there is a division of labour, not just among the sexes, but in terms of skills and niche specialisation more generally. Some individuals are better foragers, politicians, story-tellers, craftsmen, healers, etc., all of which are integral to living and thriving in all human societies, including among hunter-gatherers (Sugiyama & Chacon 2000; Sugiyama & Scalise Sugyiama 2003). Individuals displaying these qualities may possess greater 'market value' and be cooperated with because, even though resources may not be returned 'in-kind', they may hold value in other domains. For instance, an individual may give resources to a skilled or competent individual in return for an opportunity to learn these skills (Henrich & Gil-White 2001). Alternatively, good foragers may receive more cooperation as an incentive to stay with that group and continue supplying them with resources (Smith & Bliege Bird 2000). Similarly, skilled negotiators or individuals with greater influence may receive additional resources as they quell disputes, promoting trust and facilitating collective action (Glowacki & von Rueden 2015; Smith *et al.* 2016b). Despite this potential for market models, compared to studies on non-human primates, the majority of studies regarding human cooperation focus on 'in-kind' cooperation (Koster *et al.* 2015), rather than the wider 'market value' of individuals as cooperative and social partners.

Some real-world studies of foragers are consistent with biological market theory, such as Ecuadorian forager-horticulturalists trading meat for coalitional support (Patton 2005). Among the Tsimane, individuals were found to reciprocally trade cooperation in one domain for cooperation in another, such as trading labour for childcare (Jaeggi *et al.* 2016). Focussing more specifically on the effects of reputation as a proxy for market value, a few studies have explored how generosity may influence subsequent cooperative interactions. For instance, skilled Ache hunters were more likely to receive resources when they were ill or injured (Gurven *et al.* 2000a), while generous Martu who shared more resources were more central in cooperative hunting networks (Bliege Bird & Power 2015). However, in these studies concerning food-sharing it is difficult to separate economic competency (i.e., foraging skill) from generosity (i.e., willingness to provision others), as better hunters share more widely as a simple consequence of having more resources (Kaplan & Hill 1985; Bliege Bird & Power 2015). Thus, the two are highly correlated when using observational food-sharing data. The Martu study (Bliege Bird & Power 2015) attempted to separate these effects, as generosity was measured by the total 'foraging income' shared. However, foraging income included not only the amount produced by the hunter, but also the amount given to them by others prior to distribution. This means that generosity in subsequent distributions would still be confounded by the amount of 'foraging income' they possessed, as those who were given more by others to begin with prior to the recorded distribution would have more to give. This makes it unclear whether generosity was independent of resource size. In both of these forager cases it is therefore ambiguous whether individuals respond to competency or generosity when deciding who to cooperate or interact with.

The one study to date in a small-scale society which dissociated these factors by using reputational ratings of others found that, among Dominican bay oil manufacturers and Peruvian agro-pastoralists, competency may be more important regarding who to interact and cooperate with than generosity (Macfarlan & Lyle 2015). Individuals with a reputation for labour skill were more likely to receive a bay oil labour contract in Dominica, while those with a reputation for hard-work or competence possessed a larger support network in Peru. Among the Hadza, individuals preferentially gave to others of a similar cooperative level, rather than the most cooperative individuals (Apicella *et al.* 2012), although no effects of reputation in other domains were assessed. These results, in addition to the results of the previous chapter, suggest that individuals may not necessarily preferentially cooperate or interact with the most cooperative individuals. Rather, market value in other domains may be as, and potentially more, important.

An individual's market value is unlikely to be constant for all individuals in a society, however. Evaluations of market value may especially differ by age and sex. For instance, an individual possessing a trait such as 'good hunting ability' may be more valued by men than women. While good hunters may be preferred partners by both sexes, as these individuals bring more resources back to camp, they may hold greater value for males as a pedagogic tool from which they too can learn to be a good hunter. Conversely, some males – particularly young males looking for a mate – may see skilled foragers as potential rivals in the mating market, so may wish to avoid living with them in order to make themselves look better by comparison (Wood & Hill 2000; Wood 2006). Furthermore, as mating effort decreases with age, especially among foragers (Vinicius & Migliano 2016), and the need to provision multiple dependent offspring to maximise inclusive fitness increases, it could be hypothesised that older adults would be more likely to cooperate and interact with kin in an attempt to maximise inclusive fitness relative to younger adults. Additionally, as a result of a supposed evolutionary history of male-bonded groups, social networks among men may be more diffuse than female networks, which may be more dyadic (David-Barrett *et al.* 2015), although this sex difference is not always observed (Dunbar & Spoors 1995). Although age and sex influences are likely to influence perceptions of market value, it is difficult to make firm predictions regarding the direction of these effects as they may differ by social and ecological conditions. As given in the example above, it could be predicted that males may either be drawn to good hunters or to avoid them, depending on the respective strengths of the need to learn foraging skills and the potential rivalry for mating opportunities. Therefore, a more exploratory analysis will be conducted to investigate how age and sex influence decisions surrounding an individual's market value.

This chapter aims to be the first exploration of the utility of a biological market approach to explaining patterns of hunter-gatherer cooperation and social networks. Previous studies which have used a market approach have not explored cooperative dynamics among foragers (Macfarlan & Lyle 2015), while the few studies which have explored the effects of skill and cooperativeness on subsequent cooperation among foragers have difficultly dissociating these two factors (Gurven *et al.* 2000a; Bliege Bird & Power 2015). The experimental approach adopted here, when combined with competency reputations assessed in various relevant domains, allows these factors to be considered separately; the amount given in the games reflects an individual's level of cooperativeness, while their reputational rating reflects their skill level or competency. Several reputational domains are explored here, including: hunting skill, fishing ability, tuber-gathering competence, storytelling ability, medicinal knowledge and camp decision-making influence.

In line with biological market theory, I predict that individuals with greater market value – those with reputations for competency and cooperativeness – will possess a higher probability of being selected as a future partner and more likely to receive resources. As partner choice is central to biological market theory, I use camp-mate networks (Apicella *et al.* 2012) to explore who individuals preferentially want to live and interact with. Patterns of giving behaviour in the Sharing Game are used as a measure of assortative cooperation. I find that individuals of higher competence, but not cooperativeness, are preferred recipients of cooperation and preferred living partners, with storytellers held in particularly high regard. This suggests that individuals may use competency, rather than their cooperativeness, when deciding with whom to interact and cooperate. The social roles these competent individuals play, such as coordinating collective action problems and transmitting fitness-relevant information, appear especially important factors in determining an individual's desirability as a social partner among foragers, irrespective of their cooperative tendencies. These competency-based decisions are largely unaffected by ego's age or sex, suggesting that these traits may be important to all individuals. Nonetheless, some age and sex effects are reported, specifically concerning the intensity of social network ties; both younger and male Agta are more likely to reciprocate camp-mate nominations, relative to older or female Agta. These results suggest that market models may be of great utility in explaining patterns of human interactions, especially regarding commodities not returned 'in-kind'.

Methods

The data collection methods have been described elsewhere (see methods chapter). I focus here on issues regarding data preparation and statistical analysis.

Statistical Analyses

The analyses presented in this chapter employ the same GEE logistic regression methods used in the previous chapter, but applied to a new data-set (the 'camp-mate network'). Data preparation methods regarding the Sharing Game (referred to here as the 'sharing network') have been described in the previous chapter, so will not be discussed at length again. As part of a semi-structured interview, 291 Agta (mean age=37.3, males=138) were asked to name five individuals they would most like to live with. Individuals were given no prior specifications regarding camp-mate choice, so were free to choose whoever they liked (camp-mate or non-camp-mate, Agta or non-Agta, etc.). The majority of individuals selected five others (~90%), although some selected fewer – or even zero – individuals as future camp-mates (mean number of nominations=4.8). Genealogical interviews were conducted previously, so interviewers were familiar with the names of most people chosen. When names were not recognised, individuals were asked if that person went by any other names, or to specify kinship relations of the target individual (e.g., brother of sister's husband). Some Agta also practice a taboo against mentioning the names of in-laws (Headland 1987a), so these often had to be inferred indirectly (e.g., spouse's brother who is married to *x*). Using these methods, only 2 of the 1,391 named individuals could not be identified (both of whom were from distant camps that had not been visited by the research group).

Although individuals were free to nominate anyone, individuals overwhelmingly selected others from the same camp (1,074 of 1,391: 77.2%), with only 196 (14.1%) Agta chosen from other camps and 121 (8.7%) non-Agta selected. Therefore, to explore within-camp proximity effects, and not confound within-camp variation in cooperation with between-camp differences in cooperation, analyses focused on within-camp selections of preferred living partners. Of these 1,074 within-camp choices, 161 (15%) were for young individuals or transient Agta who only briefly visited the camp. Data concerning cooperation and reputation were not possible to collect for these individuals, so they were removed. The remaining data used for the final analyses contained 913 camp-mate selections out of a possible 7,177 dyads.

For the response variable, a matrix was constructed containing a '1' if ego selected alter to live with or a '0' if not. Between-camp dyads were coded as missing values. A 324 by 324 matrix was constructed (the same as used for the game analyses). Many of the same predictor variables used in the game analysis in the previous chapter were employed again, including: kinship, reciprocity (if alter chose to live with ego), proximity, alter cooperativeness, cooperative homophily, as well as age (of ego, alter, and age difference) and sex (of ego, alter, and whether ego and alter were of the same or different sex). Camp size (number of adult individuals) was also included for analyses on the camp-mate network to control for larger camps possessing a greater number of potential recipients to nominate.

A final set of predictor variables concerned reputational measures aimed to assess competency and reputation. In an interview conducted after the games had been played, each individual was asked to name the camp-mates they believed were the best at various activities. These included: hunting, fishing, tuber-gathering, storytelling, medicinal knowledge and camp decision-making influence. These questions were conducted in a separate interview to the one asking them to name who they would like to live with to forestall cross-over effects (i.e., choosing to live with someone and then selecting them as a good hunter as their name was primed). Individuals were free to name as many people as they wished. The proportion of nominations for each camp-mate (nominations for non-camp-mates were disregarded) were then transformed into *z*-scores to permit comparisons between camps of different sizes. *Z*-scores for sex-specific domains, such as hunting and fishing for men, or tuber-gathering for women, were calculated only for the relevant sex, to prevent the lack of nominations for the opposite sex skewing *z*-scores (e.g., a poor male fisher may obtain an inflated *z*-score if females, who would also receive few nominations, were included). Even though there were no restrictions against naming females as hunters or fishers, or males as tuber-gatherers, these were incredibly rare, so all instances were removed prior to analysis.

Although difficult to validate these measures against total foraging returns, because hunting and tuber-gathering were relatively rare occurrences during our fieldwork, it was possible to assess a small sample of fishers from one particularly well-studied camp for which enough trips were recorded to permit comparisons between individuals (this foraging data was collected by Mark Dyble). In this camp, perceived skill in fishing was significantly correlated with both fishing returns per hour (r=0.606, n=16, p=0.013) and total calories obtained from fishing (r=0.802, n=16, p<0.001), indicating that these nominations likely reflect a combination of both effort and skill, and are therefore valid and can be used as a proxy for competence. Further verifying this methodology, comparable protocols on Hadza hunting skill indicated a similar profile, with those perceived as possessing greater hunting skill having greater overall return rates and returns per hour (Marlowe 1999). As the z-score values for these skill measures are left-skewed (there are many poorly skilled individuals and few that are highly-skilled) these were converted into binary variables. Individuals with a positive z-score were given a value of ‘1’, while those with a negative z-score were given a value of ‘0’. To allow all skill measures to be compared in the same model, all women were given a ‘0’ for hunting and fishing, while all men were given a ‘0’ for tuber-gathering (any sex differences resulting from this would be controlled for by including ‘sex’ as a covariate in the model).

As with the previous chapter, GEE regressions were used to control for the non-independence of data points, as repeated nominations were elicited from the same individual. Three multivariate models were constructed: a control model containing only age, sex and camp size variables; a second model containing additional kinship, reciprocity and proximity variables; and a final full model including competency and cooperativeness measures. QIC values and model weights were compared between models to assess improvements in model fit. All multivariate models contained the same number of dyads (6,140), meaning that differing QIC estimates between models were not a result of differences in sample size. Three equivalent multivariate models were also constructed for the sharing network, with the only difference that the ‘camp size’ control was replaced by an ‘ego cooperative score’ control (see previous chapter). In order to make meaningful comparison between parameter estimates of differently-scaled variables, as well as between continuous and binary variables, continuous input variables were standardised over two standard deviations (Gelman 2008; Schielzeth 2010). Standardised estimates are used in text, while standardised and unstandardised estimates are displayed in tables. Analyses for both the camp-mate network and sharing network contained the same set of predictor variables. For the SG, this consisted of the same variables used in the analysis from the previous chapter, but now also including the reputational measures discussed above. To explore the effects of age and sex on valuations of market value each independent variable (kinship, reciprocity, hunting ability, etc.) was entered into four different interaction models, using the full model (with no interactions) as the baseline model. These four interaction models were: i) ego age by target variable; ii) ego sex by target variable; iii) ego age by target variable and ego sex by target variable; and iv) a three-way interaction between ego age, ego sex and the target variable. Each of these were compared against the QIC value of the baseline (full) model to assess whether taking age or sex interaction effects into consideration increased model fit.

Results

Camp-Mate Networks

Comparison of QIC values indicated that the inclusion of kinship, reciprocity and proximity resulted in a better model compared to the control (QIC control model=3810.24; QIC second model=3672.31). Compared to these models, the full model also increased model fit (QIC full model=3578.82), demonstrating that individuals use evaluations of competency and cooperativeness when making residential decisions. Comparison of model weights revealed overwhelming support for the full model relative to the other models (table 6.1). These results suggest that there are several independent factors which influence who individuals choose to live with (tables 6.2 & 6.3). Focusing initially on reputational variables, the largest effect was found to be for storytelling; accomplished storytellers were twice as likely to be chosen as future camp-mates compared to poorer storytellers (OR=1.99). Fishing skill possessed the second largest effect size (OR=1.47), with good fishers ~50% more likely to be chosen than poor fishers. Agta also preferred to live with influential individuals (OR=1.34) and others of a similar cooperative level to self (OR=1.29). Weak effects for living with good hunters (OR=1.34), good tuber-gatherers (OR=1.28) and less cooperative individuals (OR=1.18) were also found. Medicinal knowledge did not appear to influence who individuals chose to live with. The effect of storytelling was particularly pronounced, with skilled storytellers estimated to be twice as likely to be selected as skilled fishers, three times more likely than influential individuals and good hunters, and nearly four times more likely than proficient tuber-gatherers. Although effects of alter cooperativeness were reported in the full model, this was in the opposite direction to that predicted; cooperative individuals were *less* likely to be selected as camp-mates, with a two SD increase in cooperativeness reducing the likelihood of being nominated by ~20%. Cooperative homophily was also reported, with individuals preferring to live with others of a similar cooperative level. A two SD increase in cooperative similarity increased the probability of being nominated by ~30%.

Table 6.1: Comparison of QIC values and model weights for each of the three camp-mate network models (n=291, dyads=6,140) regarding who individuals chose to live with. All models also contain camp size as a control.

Model Variables	**QIC**	**ΔQIC**	**Model Weight (w_i)**
Control Model: Age and Sex Variables	3810.24	231.42	0
Model 2: Age and Sex Variables + Kinship + Reciprocity + Proximity	3672.31	93.49	0
Full Model: Age and Sex Variables + Kinship + Reciprocity + Proximity + Competency and Cooperativeness Variables (Alter Coop., Coop. Homophily, Hunting Skill, Fishing Skill, Tuber-Gathering Skill, Storytelling Ability, Medicinal Knowledge and Camp Influence)	3578.82	0	1

Similar to the analysis of the Sharing Game in the previous chapter, kinship was a major predictor of camp-mate choice, with all kinship categories other than spouses more likely to be selected (primary kin OR=2.15; distant kin OR=1.92; spouse's primary kin/primary kin's spouse OR=1.88; spouse's distant kin/other affines OR=1.39). Both reciprocity and proximity were also important; individuals were nearly twice as likely to nominate those who also nominated them (OR=1.84) and there was a strong preference for selecting closer neighbours (OR=2). Regarding age, Agta were more likely to nominate younger individuals (OR=1.59), as well as those of a similar age to themselves (OR=1.81). Individuals were also more likely to select an individual of the same sex (OR=11.48), while males were less likely to nominate adult camp-mates than females (OR=1.51). A summary of the main results is displayed in figure 6.1.

These results regarding reputation effects are unlikely to be a result of a general 'halo effect' (where evaluations of an individual competent in one domain are extended to other domains, such that skilled hunters may also be perceived as good fishers, irrespective of whether they actually are skilled fishers; Nisbett & Wilson 1977). Although there is some correlation between different reputational domains (see table A8 in Appendix 7), these are generally quite weak (i.e., r<0.3). Although collinearity diagnostics cannot be conducted when using GEE analyses, a similar approach employing multiple regression using aggregate popularity for each individual indicated that collinearity between these reputational domains is relatively weak and is therefore unlikely to bias these results (see table A9 in Appendix 7).

Table 6.2: Models for the camp-mate network demonstrating who individuals chose to live with using standardised log-odds estimates. Three models are displayed: a control model containing just age and sex variables; a second model containing additional kin, reciprocity and proximity variables; and a final full model containing reputational variables. 95% confidence intervals are displayed in brackets. Variables in which confidence intervals do not pass through ‘0’ (or do so only marginally) are highlighted in bold and QIC values comparing model fit are displayed at the bottom of the table (*n*=291, dyads=6,140). All models contain a ‘camp size’ variable (not displayed) which controls for differences in camp size.

Variable	**Control Model (Age and Sex)**	**Model 2 (Kinship, Reciprocity and Proximity)**	**Full Model (Competency and Cooperativeness)**
Ego Age	0.05 [-0.13; 0.23]	0.06 [-0.13; 0.24]	0.04 [-0.15; 0.23]
Alter Age	0.04 [-0.14; 0.23]	0.05 [-0.15; 0.25]	**-0.46 [-0.19; -0.73]**
Age Difference	**-0.66 [-0.46; -0.86]**	**-0.67 [-0.46; -0.89]**	**-0.6 [-0.38; -0.82]**
Ego Sex (1=M)	**-0.4 [-0.11; -0.68]**	**-0.41 [-0.12; -0.69]**	**-0.42 [-0.13; -0.7]**
Alter Sex (1=M)	0.25 [-0.08; 0.59]	0.28 [-0.07; 0.62]	0.25 [-0.14; 0.65]
Same Sex (1=No)	**-2.47 [-2.23; -2.82]**	**-2.37 [-2; -2.74]**	**-2.44 [-2.07; -2.82]**
PK (Ref.=NR)	-	**0.82 [0.42; 1.22]**	**0.77 [0.35; 1.18]**
DK (Ref.=NR)	-	**0.67 [0.36; 0.99]**	**0.65 [0.33; 0.97]**
SPK/PKS (Ref.=NR)	-	**0.68 [0.33; 1.03]**	**0.63 [0.27; 1]**
SDK/OA (Ref.=NR)	-	**0.36 [0.09; 0.62]**	**0.33 [0.06; 0.59]**
Spouse (Ref.=NR)	-	-0.29 [-1.06; 0.48]	-0.33 [-1.1; 0.44]
Reciprocity	-	**0.6 [0.38; 0.81]**	**0.61 [0.39; 0.83]**
Proximity	-	**-0.67 [-0.45; -0.89]**	**-0.69 [-0.46; -0.92]**
Alter Coop.	-	-	**-0.17 [0; -0.34]**
Coop. Homophily	-	-	**-0.26 [-0.04; -0.47]**
Hunting Skill (1=High)	-	-	**0.29 [0; 0.58]**
Fishing Skill (1=High)	-	-	**0.38 [0.11; 0.66]**
Tuber-Gathering Skill (1=High)	-	-	**0.25 [-0.05; 0.54]**
Storytelling Ability (1=High)	-	-	**0.69 [0.48; 0.89]**
Medicinal Knowledge (1=High)	-	-	0.16 [-0.08; 0.4]
Camp Influence (1=High)	-	-	**0.3 [0.04; 0.55]**
Intercept	**-2.08 [-1.93; -2.22]**	**-2.65 [-2.37; -2.93]**	**-2.77 [-2.48; -3.06]**
QIC Value	**3810.24**	**3672.31**	**3578.82**

Table 6.3: Models for the camp-mate network demonstrating who individuals chose to live with using unstandardised log-odds estimates. Three models are displayed: a control model containing just age and sex variables; a second model containing additional kin, reciprocity and proximity variables; and a final full model containing reputational variables. 95% confidence intervals are displayed in brackets. Variables in which confidence intervals do not pass through ‘0’ (or do so only marginally) are highlighted in bold and QIC values comparing model fit are displayed at the bottom of the table (*n*=291, dyads=6,140). All models contain a ‘camp size’ variable (not displayed) which controls for differences in camp size.

Variable	**Control Model (Age and Sex)**	**Model 2 (Kinship, Reciprocity and Proximity)**	**Full Model (Competency and Cooperativeness)**
Ego Age	0.002 [-0.005; 0.008]	0.002 [-0.005; 0.009]	0.002 [-0.005; 0.007]
Alter Age	0.001 [-0.005; 0.008]	0.002 [-0.005; 0.009]	**-0.016 [-0.007; -0.026]**
Age Difference	**-0.028 [-0.019; -0.037]**	**-0.029 [-0.02; -0.038]**	**-0.025 [-0.016; -0.035]**
Ego Sex (1=M)	**-0.4 [-0.11; -0.68]**	**-0.41 [-0.12; -0.69]**	**-0.42 [-0.13; -0.7]**
Alter Sex (1=M)	0.25 [-0.08; 0.59]	0.28 [-0.07; 0.62]	0.25 [-0.14; 0.65]
Same Sex (1=No)	**-2.47 [-2.23; -2.82]**	**-2.37 [-2; -2.74]**	**-2.44 [-2.07; -2.82]**
PK (Ref.=NR)	-	**0.82 [0.42; 1.22]**	**0.77 [0.35; 1.18]**
DK (Ref.=NR)	-	**0.67 [0.36; 0.99]**	**0.65 [0.33; 0.97]**
SPK/PKS (Ref.=NR)	-	**0.68 [0.33; 1.03]**	**0.63 [0.27; 1]**
SDK/OA (Ref.=NR)	-	**0.36 [0.09; 0.62]**	**0.33 [0.06; 0.59]**
Spouse (Ref.=NR)	-	-0.29 [-1.06; 0.48]	-0.33 [-1.1; 0.44]
Reciprocity	-	**0.6 [0.38; 0.81]**	**0.61 [0.39; 0.83]**
Proximity	-	**-0.35 [-0.23; -0.47]**	**-0.36 [-0.24; -0.48]**
Alter Coop.	-	-	**-0.004 [0; -0.007]**
Coop. Homophily	-	-	**-0.005 [-0.001; -0.009]**
Hunting Skill (1=High)	-	-	**0.29 [0; 0.58]**
Fishing Skill (1=High)	-	-	**0.38 [0.11; 0.66]**
Tuber-Gathering Skill (1=High)	-	-	**0.25 [-0.05; 0.54]**
Storytelling Ability (1=High)	-	-	**0.69 [0.48; 0.89]**
Medicinal Knowledge (1=High)	-	-	0.16 [-0.08; 0.4]
Camp Influence (1=High)	-	-	**0.3 [0.04; 0.55]**
Intercept	**0.85 [0.48; 1.23]**	**0.95 [0.37; 1.52]**	**1 [0.4; 1.6]**
QIC Value	**3810.24**	**3672.31**	**3578.82**

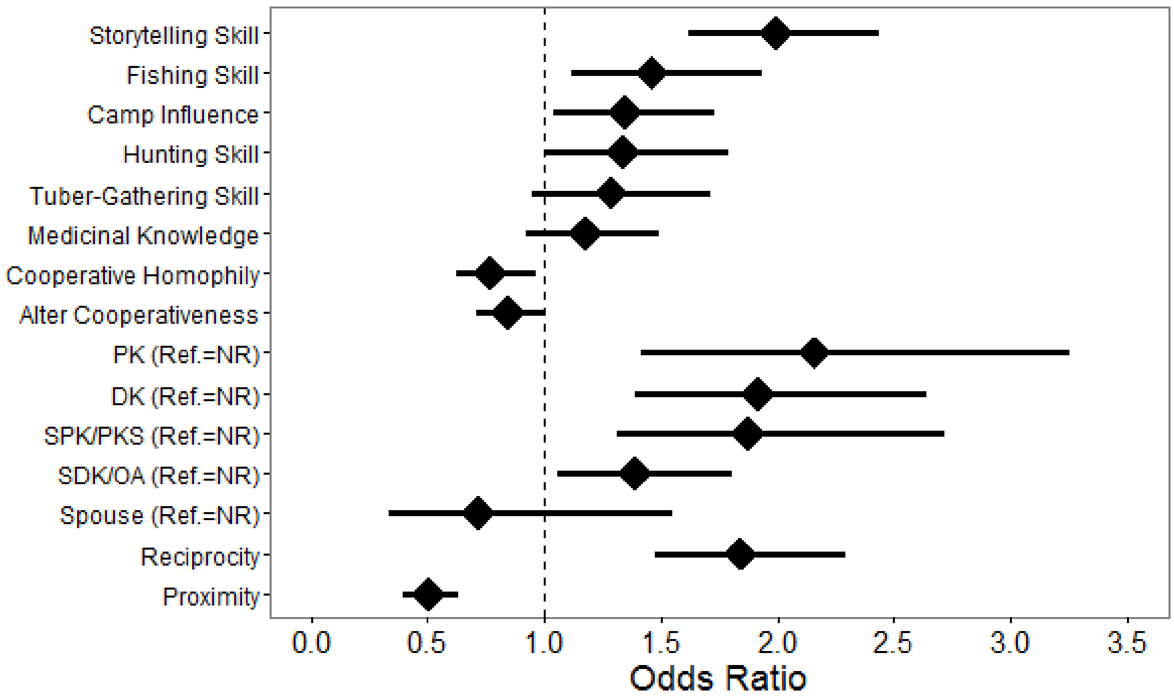

Figure 6.1: Odds ratios, derived from standardised log-odds estimates in the full model (table 6.2), of nominating to live with an individual in the camp-mate network. Note that effects relating to reputation are more pronounced than those of cooperativeness, especially regarding storytelling ability. Variables relating to age and sex are not displayed. Error bars indicate 95% confidence intervals (*n*=291, dyads=6,140).

The results of the interaction models, to explore if age or sex influenced evaluations of market value, indicated that for the majority of variables there was little observable effect of age or sex on camp-mate nominations (table A14 in Appendix 7; other than preferring individuals of a similar age and sex as indicated from the models above). For instance, patterns of nominating kin were unaffected by differences in age or sex. Only two strong effects emerged, concerning reciprocity and fishing skill (although a marginal effect for proximity was also noted). Both age and sex effects were reported for reciprocal nominations, with this model receiving overwhelming support relative to the full model without interactions (full model QIC=3578.82; w_i=0: age and sex by reciprocity interaction model QIC=3559.86; w_i=1). Younger Agta were more likely to nominate those who also chose them (i.e., nominations by younger Agta were more reciprocal), while nominations by older individuals were less dependent upon contingency (age; *b*=0.008, 95% CI: [0; 0.016]: reciprocity; *b*=1.41, 95% CI: [0.76; 2.06]: interaction term; *b*=-0.03, 95% CI: [0.014; 0.046]: figure 6.2 upper). Regarding sex effects, while both males and females were equally as likely to nominate those who also nominated them, males were less likely to select others who did not nominate them; that is, male nominations were more contingent upon reciprocity than female nominations (sex; *b*=-0.55, 95% CI: [-0.29; -0.84]: reciprocity; *b*=1.41, 95% CI: [0.76; 2.06]: interaction term; *b*=0.7, 95% CI: [0.27; 1.31]: figure 6.2 lower).

Sex effects were also found for fishing reputation, with this model receiving greater support than the baseline full model (full model QIC=3578.82; w_i=0.02: sex by fishing skill interaction model QIC=3571.12; w_i=0.98). The interaction indicated that males were more likely to nominate good fishers than females (sex; *b*=-0.63, 95% CI: [-0.33; -0.92]: fishing skill; *b*=-0.38, 95% CI: [-0.99; 0.23]: interaction term; *b*=1, 95% CI: [0.33; 1.67]). This is unlikely to be just a sex effect of males and females nominating same-sex individuals, as this model controlled for sex similarity. Additionally, if this was solely an effect of sex, one would expect to see similar interactions emerging for other sex-biased skills, such as hunting or tuber-gathering, yet these are not present. A weaker interaction was also found between age and proximity (age, *b*=-0.018, 95% CI: [-0.042; 0.006]: proximity, *b*=-0.6, 95% CI: [-0.29; -0.91]: interaction term, *b*=0.006, 95% CI: [-0.002; 0.014]). Individuals of all ages preferentially chose closer-living Agta, but as age increased there was a slight decrease in the probability of selecting closer-living individuals. However, although the QIC value of the interaction model improved slightly relative to the full model, Akaike weights suggest that the models were of a similar fit (full model QIC=3578.82; w_i=0.48: age by proximity interaction model QIC=3578.67; w_i=0.52).

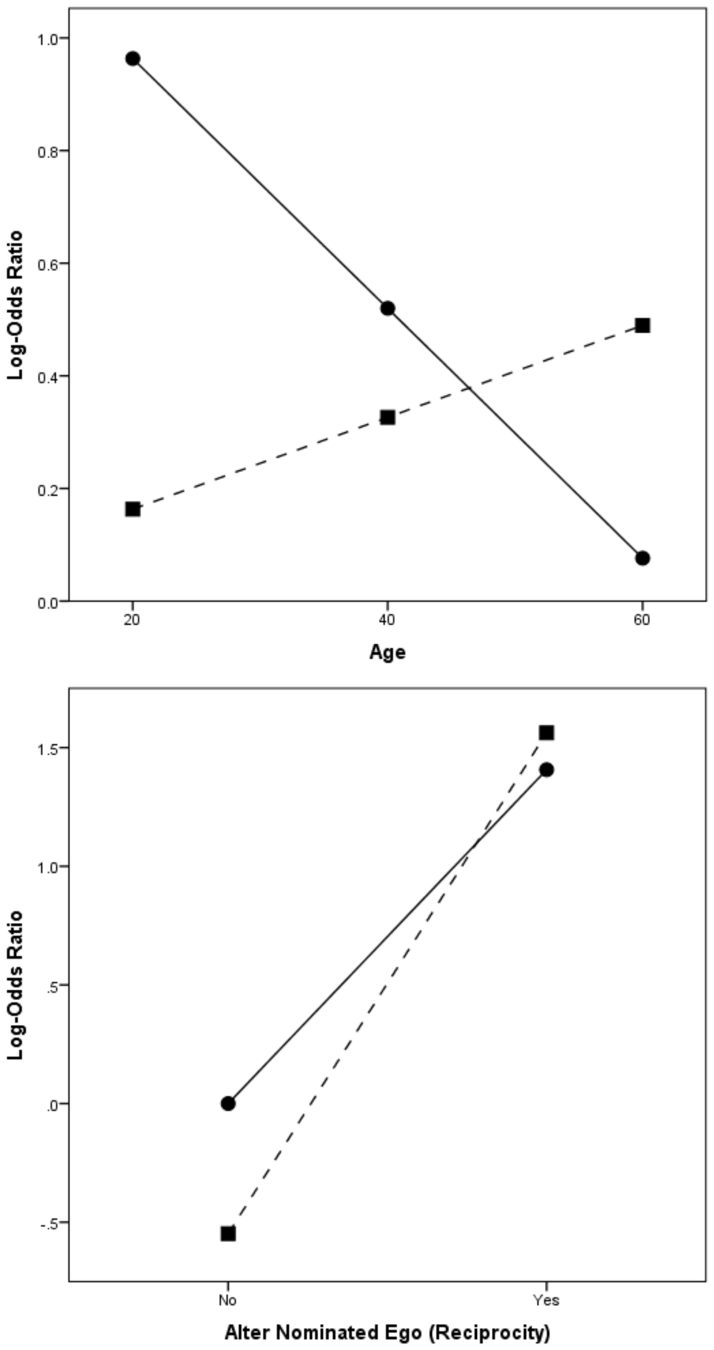

Figure 6.2: Interactions between age and reciprocity (upper) and sex and reciprocity (lower) in the camp-mate network. *Upper*: Alter nominating ego is the solid line with circular symbols, while alter not selecting ego is the dashed line with square markers. The figure demonstrates that younger individuals were more likely to select those who nominated them, while the probability of selecting an alter who did not nominate ego increased slightly with age. *Lower*: Females are the solid line with circular symbols, while males are the dashed line with square markers. The figure demonstrates that both sexes were more likely to select those who nominated them, while the probability of selecting an alter who did not nominate ego was greater in females compared to males. Log-odds ratios were estimated using coefficients derived from the relevant interaction models.

Sharing Game

Comparable analyses were conducted using data from the Sharing Game to explore whether reputational factors predicted who individuals shared resources with. As with the camp-mate network, three multivariate analyses were conducted: a control model (age and sex effects, as well as ego cooperative score as a control); a second model (with additional kinship, reciprocity and proximity variables); and a full model (with additional competency and cooperativeness variables). Compared to the control model (QIC=1113.53), model fit was improved in the second model (QIC=1093.13). In contrast to the camp-mate network above, the inclusion of reputational and cooperativeness variables did not increase the predictive value of the model (QIC=1098.06). However, as the QIC penalises more complex models, when the competency and cooperative variables which were seemingly not associated with receiving gifts were omitted, leaving just alter cooperative score and storytelling reputation, model fit increased relative to the second model (QIC=1087.39). Comparison of model weights revealed overwhelming support for the reduced full model relative to the other models (table 6.4).

Table 6.4: Comparison of QIC values and model weights for each of the four Sharing Game network models regarding who individuals chose to share resources with (*n*=290, dyads=1,312). All models also contain ego cooperative score as a control.

Model Variables	**QIC**	**ΔQIC**	**Model Weight (w_i)**
Control Model: Age and Sex Variables	1113.53	26.94	0
Model 2: Age and Sex Variables + Kinship + Reciprocity + Proximity	1093.13	6.55	0.036
Full Model: Age and Sex Variables + Kinship + Reciprocity + Proximity + Competency and Cooperativeness Variables	1098.06	10.53	0.005
Reduced Model: Age and Sex Variables + Kinship + Reciprocity + Proximity + Reduced Competency and Cooperativeness Variables (Alter Cooperativeness and Storytelling Ability)	1087.39	0	0.959

As with the previous chapter, I find that relatedness and reciprocity are significant determinants of who individuals shared resources with, no little effect of proximity (tables 6.5 & 6.6). Additional effects included giving to less cooperative individuals, a same-sex bias and a weak preference towards giving to older individuals (each of which were reported in the previous chapter). A novel finding of this analysis is that storytelling ability is also a predictor of receiving resources. Skilled storytellers were nearly 40% more likely to be given rice than unskilled individuals (OR=1.39). No other reputational domains were associated with receiving resources.

Interaction models were also performed on the sharing network to explore whether any effects of age or sex on resource allocations emerged. In 10 of the 11 variables tested, the null model possessed the best fit (see table A11 in Appendix 7). This demonstrates that there are very few differences in resource allocation decisions regarding differences in age or sex of ego. The one variable in which an interaction was reported was between storytelling ability and age, although model weights suggest do not provide overwhelming support for the interaction model relative to the full model (full model QIC=1098.06; w_i=0.27: age by storytelling ability interaction model QIC=1096.06; w_i=0.73). The interaction indicates that younger Agta were more likely to share resources with skilled storytellers relative to older individuals (age; *b*=0.008, 95% CI: [-0.006; 0.022]: storytelling ability; *b*=1.12, 95% CI: [0.63; 1.61]: interaction term; *b*=-0.023, 95% CI: [-0.001; -0.045]: figure 6.3). No effects of age similarity were apparent, although Agta did preferentially give to others of the same sex (table 6.5).

Table 6.5: Models for the Sharing Game network displaying who individuals shared resources with, using standardised log-odds estimates. Four models are displayed: a control model containing just age and sex variables; a second model containing additional kin, reciprocity and proximity variables; a full model containing reputational variables; and a reduced full model containing only those reputational variables which were associated with sharing resources. 95% confidence intervals are displayed in brackets. Variables in which confidence intervals do not pass through '0' (or do so only marginally) are highlighted in bold and QIC values comparing model fit are displayed at the bottom of the table (*n*=290, dyads=1,312). All models contain an 'ego cooperative score' variable (not displayed) which controls for differences in amount given by each individual.

Variable	**Control Model (Age and Sex)**	**Model 2 (Kinship, Reciprocity and Proximity)**	**Full Model (Competency and Cooperation)**	**Reduced Model (Storytelling and Alter Cooperation)**
Ego Age	-0.1 [-0.34; 0.13]	-0.05 [-0.3; 0.2]	-0.06 [-0.32; 0.19]	-0.08 [-0.33; 0.17]
Alter Age	**0.29 [-0.02; 0.6]**	**0.36 [0.04; 0.69]**	0.24 [-0.18; 0.66]	**0.32 [-0.04; 0.67]**
Age Difference	0.18 [-0.16; 0.51]	0.07 [-0.27; 0.41]	0.11 [-0.22; 0.45]	0.12 [-0.22; 0.46]
Ego Sex (1=M)	-0.07 [-0.31; 0.17]	0 [-0.26; 0.27]	0.02 [-0.25; 0.29]	0.01 [-0.26; 0.28]
Alter Sex (1=M)	-0.19 [-0.52; 0.14]	-0.2 [-0.54; 0.14]	-0.3 [-0.82; 0.22]	-0.11 [-0.46; 0.22]
Same Sex (1=No)	**-0.65 [-0.31; -0.98]**	**-0.64 [-0.28; -1]**	**-0.67 [-0.31; -1.04]**	**-0.65 [-0.29; -1.01]**
PK (Ref.=NR)	-	**1.29 [0.65; 1.93]**	**1.32 [0.69; 1.95]**	**1.34 [0.71; 1.97]**
DK (Ref.=NR)	-	**0.57 [0; 1.15]**	**0.56 [-0.03; 1.15]**	**0.58 [0; 1.16]**
SPK/PKS (Ref.=NR)	-	0.17 [-0.43; 0.78]	0.1 [-0.51; 0.72]	0.14 [-0.47; 0.75]
SDK/OA (Ref.=NR)	-	0.03 [-0.41; 0.47]	0.04 [-0.4; 0.48]	0.04 [-0.4; 0.48]
Spouse (Ref.=NR)	-	-0.02 [-0.93; 0.9]	0 [-0.92; 0.92]	0.04 [-0.88; 0.96]
Reciprocity	-	**0.3 [-0.01; 0.6]**	**0.49 [0.14; 0.85]**	**0.52 [0.15; 0.86]**
Proximity	-	-0.14 [-0.49; 0.21]	-0.1 [-0.46; 0.27]	-0.09 [-0.44; 0.26]
Alter Coop.	-	-	**-0.41 [-0.04; -0.78]**	**-0.43 [-0.06; -0.8]**
Coop. Homophily	-	-	0.21 [-0.18; 0.59]	-
Hunting Skill (1=High)	-	-	0.22 [-0.28; 0.72]	-
Fishing Skill (1=High)	-	-	0.27 [-0.19; 0.74]	-
Tuber-Gathering Skill (1=High)	-	-	0.13 [-0.4; 0.67]	-
Storytelling Ability (1=High)	-	-	**0.3 [-0.05; 0.65]**	**0.33 [-0.01; 0.66]**
Medicinal Knowledge (1=High)	-	-	-0.09 [-0.54; 0.36]	-
Camp Influence (1=High)	-	-	0.15 [-0.34; 0.63]	-
Intercept	**-1.03 [-0.9; -1.16]**	**-1.35 [-0.99; -1.71]**	**-1.33 [-0.95; -1.7]**	**-1.38 [-1.02; -1.73]**
QIC Value	**1113.53**	**1093.13**	**1098.06**	**1087.39**

Table 6.6: Models for the Sharing Game network displaying who individuals shared resources with, using unstandardised log-odds estimates. Four models are displayed: a control model containing just age and sex variables; a second model containing additional kin, reciprocity and proximity variables; a full model containing reputational variables; and a reduced full model containing only those reputational variables which were associated with sharing resources. 95% confidence intervals are displayed in brackets. Variables in which confidence intervals do not pass through '0' (or do so only marginally) are highlighted in bold and QIC values comparing model fit are displayed at the bottom of the table (*n*=290, dyads=1,312). All models contain an 'ego cooperative score' variable (not displayed) which controls for differences in amount given by each individual.

Variable	**Control Model (Age and Sex)**	**Model 2 (Kinship, Reciprocity and Proximity)**	**Full Model (Competency and Cooperation)**	**Reduced Model (Storytelling and Alter Cooperation)**
Ego Age	-0.004 [-0.012; 0.005]	-0.002 [-0.011; 0.007]	-0.002 [-0.011; 0.007]	-0.003 [-0.012; 0.006]
Alter Age	**0.01 [-0.001; 0.021]**	**0.013 [0.001; 0.024]**	0.009 [-0.006; 0.024]	**0.011 [-0.001; 0.024]**
Age Difference	0.008 [-0.007; 0.022]	0.003 [-0.012; 0.018]	0.005 [-0.01; 0.019]	0.005 [-0.009; 0.02]
Ego Sex (1=M)	-0.07 [-0.31; 0.17]	0 [-0.26; 0.27]	0.02 [-0.25; 0.29]	0.01 [-0.26; 0.28]
Alter Sex (1=M)	-0.19 [-0.52; 0.14]	-0.2 [-0.54; 0.14]	-0.3 [-0.82; 0.22]	-0.11 [-0.46; 0.22]
Same Sex (1=No)	**-0.65 [-0.31; -0.98]**	**-0.64 [-0.28; -1]**	**-0.67 [-0.31; -1.04]**	**-0.65 [-0.29; -1.01]**
PK (Ref.=NR)	-	**1.29 [0.65; 1.93]**	**1.32 [0.69; 1.95]**	**1.34 [0.71; 1.97]**
DK (Ref.=NR)	-	**0.57 [0; 1.15]**	**0.56 [-0.03; 1.15]**	**0.58 [0; 1.16]**
SPK/PKS (Ref.=NR)	-	0.17 [-0.43; 0.78]	0.1 [-0.51; 0.72]	0.14 [-0.47; 0.75]
SDK/OA (Ref.=NR)	-	0.03 [-0.41; 0.47]	0.04 [-0.4; 0.48]	0.04 [-0.4; 0.48]
Spouse (Ref.=NR)	-	-0.02 [-0.93; 0.9]	0 [-0.92; 0.92]	0.04 [-0.88; 0.96]
Reciprocity	-	**0.3 [-0.01; 0.6]**	**0.49 [0.14; 0.85]**	**0.52 [0.15; 0.86]**
Proximity	-	-0.08 [-0.26; 0.11]	-0.05 [-0.24; 0.14]	-0.05 [-0.23; 0.14]
Alter Coop.	-	-	**-0.009 [-0.001; -0.017]**	**-0.009 [-0.001; -0.017]**
Coop. Homophily	-	-	0.004 [-0.003; 0.011]	-
Hunting Skill (1=High)	-	-	0.22 [-0.28; 0.72]	-
Fishing Skill (1=High)	-	-	0.27 [-0.19; 0.74]	-
Tuber-Gathering Skill (1=High)	-	-	0.13 [-0.4; 0.67]	-
Storytelling Ability (1=High)	-	-	**0.3 [-0.05; 0.65]**	**0.33 [-0.01; 0.66]**
Medicinal Knowledge (1=High)	-	-	-0.09 [-0.54; 0.36]	-
Camp Influence (1=High)	-	-	0.15 [-0.34; 0.63]	-
Intercept	**-1.03 [-0.9; -1.16]**	**-1.35 [-0.99; -1.71]**	**-1.33 [-0.95; -1.7]**	**-1.38 [-1.02; -1.73]**
QIC Value	**1113.53**	**1093.13**	**1098.06**	**1087.39**

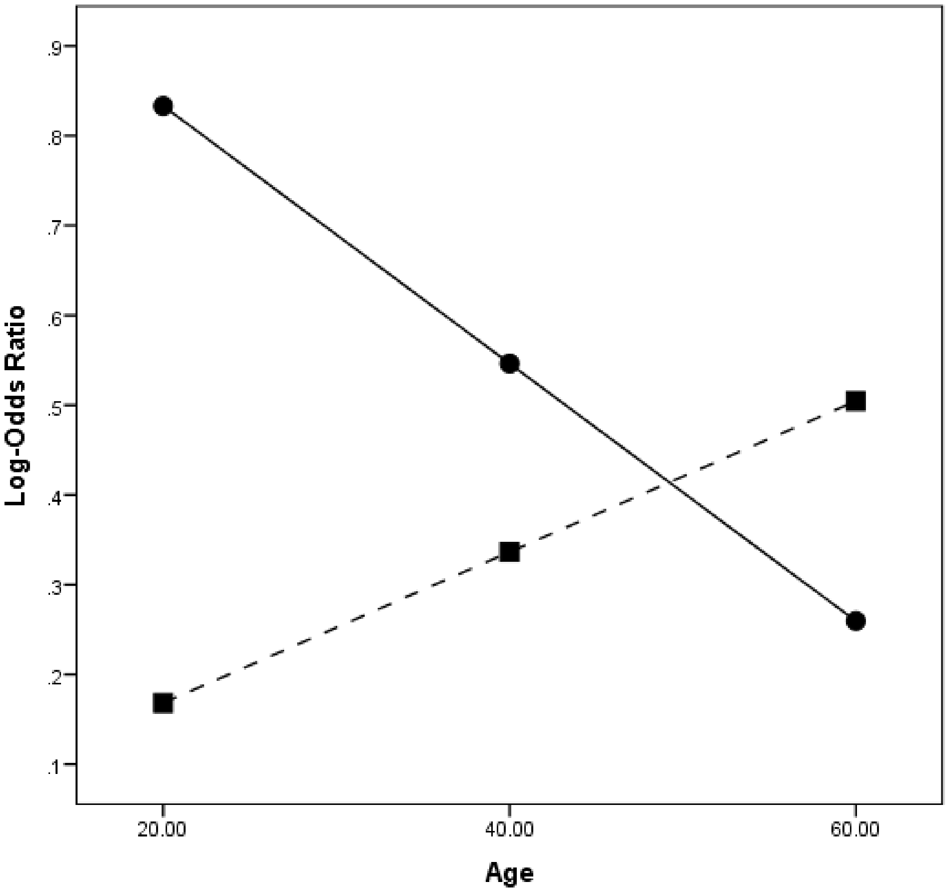

Figure 6.3: Interaction between age and storytelling ability regarding the likelihood of allocating resources to others in the Sharing Game. Skilled storytellers are the solid line with circular symbols, while unskilled storytellers are the dashed line with square markers. The figure demonstrates that younger individuals are more likely to share resources with skilled storytellers relative to older individuals. Log-odd ratios were estimated using coefficients derived from the age by storytelling skill interaction model.

Discussion

Traditional explanations for cooperation have generally been explored as either a result of kin selection or reciprocity (Leimar & Hammerstein 2010; Hammerstein & Noë 2016). I find evidence for both of these effects in the sharing network and the camp-mate network, suggesting that many interactions are based upon these considerations. However, other direct benefits also appear to be important, including the skill-level and competency of individuals. In the camp-mate network, Agta preferentially selected to live with skilled storytellers, fishers, influential individuals and, to a lesser extent, competent hunters and tuber-gatherers. Although these effects were less pronounced in the SG, individuals still preferentially gave resources to skilled storytellers. In contrast, in neither network were more cooperative individuals preferentially given resources or selected as camp-mates. Under both conditions those displaying higher cooperativeness were *less* likely to be nominated. This suggests that an individual's 'market value' is greatly dependent upon multiple reputational domains, not merely their cooperativeness (Macfarlan & Lyle 2015). These results indicate that biological market theory, with its emphasis on partner choice and 'not-in-kind' exchanges, may be a useful framework for investigating the evolution of cooperation (Noë & Hammerstein 1994, 1995; Hammerstein & Noë 2016) and understanding social networks.

This study provides a novel exploration of biological market theory, as in the majority of experimental games conducted in industrial societies players are anonymous and do not know one another, let alone their reputations, beyond their cooperativeness when this is made public (e.g., Wedekind & Milinski 2000; Seinen & Schram 2006; Barclay & Willer 2007; Sylwester & Roberts 2010, 2013; Cuesta *et al.* 2015; Gallo & Yan 2015). Although these studies reporting preferential partner choice between cooperative individuals in the lab are highly replicable, as discussed in the previous chapter, they may be less generalisable when exploring cooperative dynamics in real-world populations (that is, they have low external validity). With no other information to draw upon in these lab experiments individuals appear to use cooperativeness as a cue on which to base further interactions. However, reality is unsurprisingly more complex and when players are known to one another and multiple other sources of information upon which to make judgements are available, cooperativeness appears to be of lesser importance (see also Apicella *et al.* 2012; Macfarlan & Lyle 2015). While it may be understandable that individuals in the SG gave to less cooperative individuals as a result of needs-based sharing (see previous chapter), it is less clear why individuals would avoid living with cooperative individuals. One potential – and admittedly speculative and post-hoc – explanation could be that the Agta avoid overly-cooperative individuals as these camp-mates may have ulterior motives, such as sharing resources to create debt obligations (comparable to companies giving away free samples to induce guilt or mafia extortion rackets), although this requires additional studies to replicate these effects.

There is also the possibility that there are different domains of cooperative behaviour, with cooperativeness in a food-sharing domain, as assessed experimentally here, less important regarding who to live with than cooperative behaviour in other contexts (e.g., cooperative hunting, allocare, social support, etc.). Cooperative behaviour is often seen as a single relatively stable phenomenon across different contexts (Henrich *et al.* 2005; Peysakhovich *et al.* 2014), yet research, particularly in small-scale societies, has rarely compared cooperativeness over different domains (although see Jaeggi *et al.* 2016). When multiple cooperative domains are explored they are often grouped together, rather than investigated separately (e.g., Kasper & Borgerhoff Mulder 2015). An exploration of how social networks in different cooperative domains relate to one another – for instance, comparing food-sharing networks to childcare networks – would be extremely enlightening.

While predictions derived from indirect reciprocity and competitive altruism were not supported, evidence for cooperative homophily was found in the camp-mate network (although not the sharing network). This indicates that individuals of a similar cooperative level clustered together; that is, cooperative individuals selected to live with other cooperative individuals while uncooperative individuals chose other uncooperative individuals. Similar results among the Hadza have been interpreted as evidence that cooperators preferentially assort and cooperate with other cooperators, which may facilitate the evolution of cooperation (Apicella *et al.* 2012). However, the inverse also applies: non-cooperators preferentially assorted with non-cooperators. Given the choice, why would non-cooperators choose to live with other non-cooperators? One reason may be that they knew cooperative individuals would not cooperate with them, via a process of network reciprocity (Nowak 2006), where non-cooperative individuals are excluded from interacting with cooperative others (Rand *et al.* 2011). Cooperative similarity did not influence who individuals shared food with, however, suggesting that exclusion from cooperative food-sharing networks is an unlikely reason underlying decisions regarding resources transfers in this game. It is possible that the observed cooperative homophily may reflect similarity in other domains or an unspecified underlying latent variable. Age and sex similarity strongly predicted nominations in the camp-mate network, while these effects were weaker (in the case of sex) or non-existent (in the case of age) in the SG. The effect of cooperative homophily in the camp-mate network may therefore represent other kinds of similarity, such as number of offspring, which also impacts cooperativeness. For instance, parents with lots of kids, who are less cooperative (Chapter 4), may cluster together, as may those with fewer kids, who are more cooperative. Although including 'number of offspring similarity' in the full camp-mate model did not increase model fit (full QIC=3578.82; offspring similarity QIC=3581.47) or negate the effect of cooperative homophily (*b*=-0.005, 95% CI: [-0.001; -0.009]), suggesting that cooperative homophily cannot be explained by this factor, other latent variables may still underpin this result. Nonetheless, these findings suggest that cooperative homophily may occur, but it only applies to who individuals want to live with, not the sharing of resources. This effect was also rather weak compared to other variables such as kinship, reciprocity and storytelling ability (figure 6.1). This indicates that the relative impact of cooperative homophily on human cooperative evolution, if not an artefact, may not be particularly strong compared to these other factors.

From this dataset it is difficult to know the exact reasons why individuals chose to live with certain competent individuals, although several answers are possible. Regarding selecting to live with skilled foragers, this could be due to a ‘copy-the-successful’ transmission bias, where individuals learn foraging skills from skilled individuals (Mesoudi & O’Brien 2008). Alternatively, individuals may want to live with skilled foragers because they produce more resources (Smith & Bliege Bird 2000). While difficult to distinguish between these alternatives here, it is possible to test between these hypotheses by assessing whether skilled foragers are preferred foraging partners. If this preference is a consequence of learning foraging skills then individuals should preferentially forage with these skilled individuals, while if they live in the same camp only because these competent individuals acquire more resources then patterns of co-foraging should not be biased towards skilled individuals. This remains a test for future research (although see below for a tentative answer regarding living with skilled fishers).

For social roles, such as storytelling and camp influence, wanting to live with these individuals is less likely to concern acquiring skills or receiving resources, but rather facilitating social life, transmitting fitness-relevant information and solving collective action problems. Storytellers in particular appear to be held in great esteem by the Agta, and comparison of the role of storytellers in other subsistence populations suggests that they are important for many reasons. These include transmitting fitness-relevant information about hunting techniques, social roles, geography and other details crucial for survival, among numerous other domains (Scalise Sugiyama 2001). Storytelling is a way of learning from events without having to experience them first-hand, which could potentially be fatal. It is also a mechanism to coordinate behaviour (Biesele 1986), one which can only be achieved through language and hence not possible in other animals (Smith 2010). A distinction in the collective action literature (where individuals work together to achieve a common goal) is often made between problems of cooperation (pay-offs regarding cooperation and defection) and problems of coordination (knowing the behaviour of others), such that a group of organisms may be motivated to cooperate, but because of a lack of coordination they do not solve the collective action problem (Smith 2010; Cronk & Leech 2013). Storytellers may coordinate behaviour by transmitting to others expectations regarding certain behaviour – the 'rules of the game' – such as correct behaviour regarding marriage, interactions with in-laws, food-sharing and hunting norms (Wiessner 2014), which facilitates collective action. It is also possible that storytellers may also be favoured in less formalised circumstances, such as everyday conversation or 'gossip' (Dunbar 1998, 2004). Much conversation, both in Western societies (Dunbar *et al.* 1997) and in hunter-gatherers (Wiessner 2014), concerns transmitting information regarding the actions and reputations of third parties, which may in turn influence how others interact and cooperate with them. For instance, the threat of gossip can increase cooperation in experimental games (Piazza & Bering 2008; Wu *et al.* 2016a, b), while among the Pimbwe horticulturalists accusations of witchcraft against parents are associated with increased child mortality (Borgerhoff Mulder & Beheim 2011). When asking Agta to name the best storytellers, the specifics of 'storytelling' were left intentionally open, so it may be that many, or all, of these potential functions were at play when individuals decided to live with skilled storytellers.

Influential individuals also appear important when deciding who to live with. Although hunter-gatherer societies tend to be egalitarian, there are often certain – generally older – individuals whose opinions are listened to the most and carry more weight than others (Sugiyama & Chacon 2000; Sugiyama & Scalise Sugyiama 2003; Wiessner 2005). Their role may be comparable to that of leaders who assist in facilitating and coordinating collective action problems (von Rueden *et al.* 2014; Glowacki & von Rueden 2015; Smith *et al.* 2016b). For instance, 'strong' Ju/'hoansi individuals engage in norm enforcement to maintain cooperation and cohesion among camp-mates (Wiessner 2005). From observations and interviews with the Agta, these influential individuals tend to adopt a similar role in mediating disputes and coordinating group behaviour. Thus, while skilled foragers are preferred living partners to some extent, individuals possessing social competence appear in even greater demand. The effect size for living with skilled storytellers is similar in magnitude to that of close kin, reciprocity and proximity effects, highlighting the value afforded to these individuals (figure 6.1). This suggests that individuals who perform socio-political functions, such as transmitting fitness-relevant information and coordinating group behaviour, are particularly valuable camp-mates, even more so than expert foragers.

In addition, these results highlight the influence that partner choice may play regarding the evolution of cooperation among unrelated individuals. This partner choice is consistent with a process of 'social selection', whereby differential phenotypic fitness is determined by interactions with conspecifics, rather than the environment, as with more traditional forms of natural selection (Nesse 2007). The Agta appear to preferentially cooperate and interact with storytellers and other individuals who perform important social functions, such as foragers or leaders, in what may be trade-like relationships. That is, a skilled storyteller may receive resources or social support in return for transmitting fitness-relevant information or promoting cooperation by coordinating group behaviour. Niche specialisation and the associated complementarity in trade of expertise necessary for survival in human societies (Sugiyama & Scalise Sugyiama 2003) increases interdependence among individuals, facilitating cooperation (Roberts 2005). As with Adam Smith's 'invisible hand' (Smith 1776), specialisation and trade between otherwise self-interested agents can result in indirect societal benefits, such as large-scale non-kin cooperation, without requiring group-selected altruism towards the wider community.

However, it is also possible that interaction networks may be exploitative or asymmetric, rather than solely cooperative. In contrast to the sharing network, where sharing is costly, in the camp-mate network there are no costs to nominating others. This means that individuals can theoretically free-ride on the skills and competencies of others, without needing to cooperate with them. For instance, individuals may have preferred to live with skilled foragers as they are likely to supply the camp with more resources, even if the individual does not provide the skilled forager with any direct benefit in return. As long as the skilled forager increases their inclusive fitness in other ways – perhaps they invest more in foraging as they need to provision many dependent offspring, or display foraging prowess as a costly signal for access to the mating market – these asymmetric relationships may be evolutionarily stable. This perspective suggests that social networks may not solely reflect cooperative interactions but may also be exploitative (Connor 2010), analogous to how resource transfers may reflect tolerated theft (Blurton Jones 1987; Winterhalder 1996), rather than cooperation which evolved to benefit others (West *et al.* 2007b; Clutton-Brock 2009). In part, this may explain the differences between the two networks. Focusing just on reputational domains, in the sharing network individuals only cooperated with skilled storytellers, potentially in trade-like relationships (trading cooperation for knowledge or coordinating group behaviour; see above). In contrast, in the camp-mate network skilled foragers were also nominated as they may possess increased market value as social partners, but the relationship may be asymmetric, or exploitative, rather than solely cooperative.

There are also other potential explanations for the differences between these two networks. In the camp-mate network several factors predicted residential decision-making, while for the SG fewer variables predicted who individuals gave resources to. One possibility is that this may just be a result of differences in sample size, as the camp-mate network contained 6,140 dyads, while the SG contained 1,312 (over four times fewer data points). While this may explain some of the differences, behaviour in both networks appears quite different regardless of this sample size effect, although there are some similarities. These differences and similarities are summarised in table 6.7 and displayed graphically in figure 6.4. For instance: cooperative homophily was reported for the camp-mate network but not the sharing network; proximity was an important determinant of living with individuals but not sharing resources with them; while in the camp-mate network individuals chose to live with younger individuals while in the SG they gave to older individuals. These differences may reflect the necessity of different networks to solve different adaptive problems: the individuals it is optimal to live with may not be the individuals it is optimal to share food with. Deciding who to live with may, to a greater extent than food-sharing, reflect the necessity of resource acquisition and solving collective action problems, resulting in a preference for skilled foragers, competent storytellers and younger, fitter, individuals. This is in addition to those who are well-known and trusted, such as kin, reciprocal partners and those living in closer proximity. In contrast, food-sharing, while also relying on trust, kinship and reciprocation, has a much stronger needs-based component (Hill & Hurtado 2009; Hooper *et al.* 2015), reflected in preferential giving to older and less cooperative individuals.

Table 6.7: Differences and similarities in predictor variables between the camp-mate and Sharing Game networks. Note that not all variables related to age or sex are presented here.

Variable	Similarity or Difference	Description
Consanguineal Kin	Same	Preferred primary and distant consanguineal kin in both networks
Affinal Kin	Different	Only preferred to live with affinal kin, not give to them
Reciprocity	Same	Preferentially selected others who also chose ego in both networks
Storytelling Ability	Same	Preferred skilled story-tellers in both (although stronger in the camp-mate network)
Hunting Skill	Different	Only preferred to live with good hunters, not give to them
Fishing Skill	Different	Only preferred to live with good fishers, not give to them
Tuber-Gathering Skill	Different	Only preferred to live with good tuber-gatherers, not give to them
Medicinal Knowledge	Same	No preference for those with medicinal knowledge in either network
Camp Influence	Different	Only preferred to live with influential individuals, not give to them
Cooperativeness	Same	Give to and live with less cooperative individuals (although effect is stronger in sharing network)
Cooperative Homophily	Different	Only preferred to live with individuals of a similar cooperative level, not give to them
Proximity	Different	Only preferred to live with neighbours, not give to them
Same Sex Bias	Same	Same sex preference in both (although stronger in the camp-mate network)
Age Difference	Different	Only preferred to live with similar aged individuals, not give to them
Age of Alter	Different	Preferred to live with younger individuals but give to older individuals

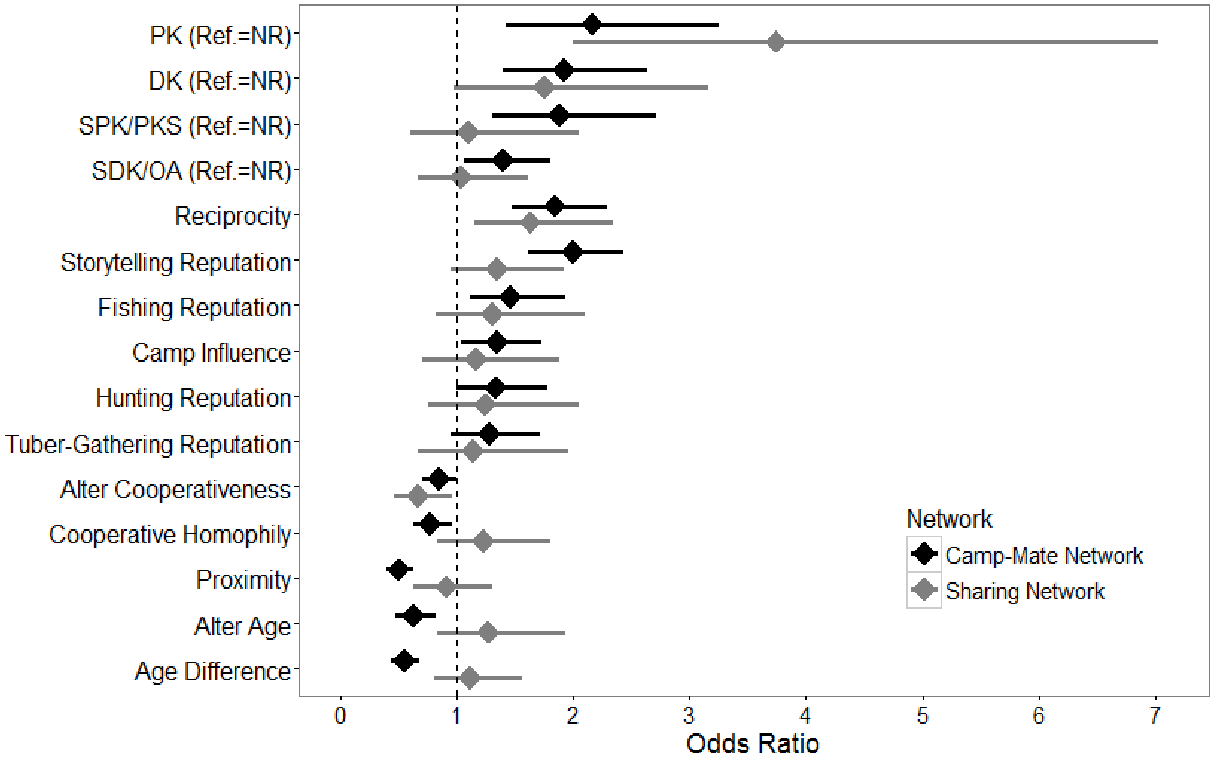

Figure 6.4: Odds ratios, derived from standardised log-odds estimates from the full models (tables 6.2 & 6.5), of nominating to give resources to others in the Sharing Game (dark grey bars) compared to selecting to live with others in the camp-mate network (light grey bars). Note that not all variables included in the full models are displayed here. Error bars indicate 95% confidence intervals (camp-mate network; *n*=291, dyads=6,140: sharing network; *n*=290, dyads=1,312).

To assess whether popularity in one domain (food-sharing) predicted popularity in another (camp-mate choice), a linear regression was conducted with SG popularity *z*-scores as the response variable and camp-mate popularity *z*-scores as the predictor variable. Although individuals who received more nominations in the SG also received more camp-mate nominations (b=0.25, SE=0.05, n=304, p<0.001), the effect size was relatively small (adjusted R^2=0.061), with only ~6% of the variation in SG popularity explained by camp-mate popularity. This suggests that different social networks may be used for different purposes, such that a food-sharing network is unlikely to be identical to a camp-mate or interaction network, although there is some degree of overlap. A comparable result was found among the Lamalera, with cooperative whaling networks distinct from food-sharing networks. In the former, lineage – belonging to a certain ‘descent’ clan – rather than genetic relatedness, predicted the composition of cooperative whaling groups, while genetic relatedness, rather than lineage, predicted patterns of inter-household food-sharing (Nolin 2011). This pattern was interpreted in terms of coordinating whale hunts, as lineage is a dichotomous ‘either/or’ phenomenon, while relatedness is a matter of degree. The norm that only members of a single lineage can hunt together therefore coordinates collective action and forestalls competition between males to hunt together. Food-sharing, meanwhile, can proceed according to genetic relatedness as it requires less coordination. This research highlights the importance of understanding the adaptive function of different networks within a society, rather than assuming one social network performs the same function as other networks.

These results have important implications when compared against a recent study conducted with the Hadza using camp-mate and gift game networks (Apicella *et al.* 2012). The gift game is similar to the SG played here, but without the opportunity to keep any resources for self (individuals just had three honey-sticks that they had to give to others). In their study both networks were similar, such as both indicating cooperative homophily. In the current study, the camp-mate network is broadly similar to those networks reported with the Hadza, while the SG network appears somewhat different. Any reason hypothesising why the results of the SG here are different to the gift game with the Hadza, despite their superficial similarities, will be speculative, but it may be that the two conditions cue different contexts, similar to the effects of framing reported in other cooperative games (Cronk 2007; Lesorogol 2007; Gerkey 2013). The SG may cue norms regarding food-sharing to a stronger extent than that of the gift game as individuals were not obligated to give to others in the

SG. These contextual cues regarding food-sharing may therefore not have been present in the gift game, in which case sharing potentially reflected alliances between individuals of a similar age or cooperativeness, similar to a camp-mate network. As discussed above, as both camp-mate and gift game decisions among the Hadza were cost-free, these networks may, to some extent, represent exploitative interactions, rather than solely cooperation. Alternatively, the divergence in results may be due to methodological differences; if both the camp-mate network and gift game were asked sequentially, the Hadza may have used their response from the first question to answer the second (it is unclear from their methods whether this was controlled for or not). These cross-over effects are less likely in the current study as camp-mate nominations and the SG were conducted during different interviews. Further research exploring how resource distributions are affected by contextual differences, such as costly versus uncostly sharing, is required.

Despite these open questions, the results of this study indicate that not all networks possess the same properties. This may hamper comparisons between studies which use different measures to assess social networks. Few studies, other than Nolin (2011) above, have explored properties of different cooperative networks. Previous studies have tended to either examine single networks (such as food-sharing or cooperative hunting; Nolin 2010; Koster & Leckie 2014; Bliege Bird & Power 2015), group various networks together (Kasper & Borgerhoff Mulder 2015) or produce a single ‘interaction network’ which likely contains many different activities combined (Koster *et al.* 2015; Migliano *et al.* 2017). Different networks are likely to be adaptive responses to different challenges and constraints, even if they are in a broad sense ‘cooperative’. Further exploration of the adaptive function of different networks would be extremely enlightening.

The results of the interaction models indicate that valuations of market value tend to vary little among individuals of a different age or sex. In the camp-mate network only three of the eleven variables explored indicated that age or sex influenced residential decision-making (and in one of these cases the effect was marginal). In the SG only one of the eleven variables possessed a strong interaction. The largest interaction effect in the camp-mate network concerned that of reciprocity, which displayed both age and sex interactions with young and male Agta more likely to nominate reciprocally. This sex difference is particularly interesting because it is counter to a recent finding suggesting that females prefer dyadic relationships while males prefer more diffuse 'clubs' (David-Barrett *et al.* 2015). Here the opposite pattern is observed, with dyadic ties stronger between males than females, demonstrating that these sex differences are not cross-culturally invariant and are likely to vary with ecological conditions. For instance, as resource acquisition and sharing is generally more stochastic among hunter-gatherer males than females (e.g., males often hunt or fish in groups and pool their catch due to high resource variability: Gurven 2004d), this may require detailed knowledge of others' behaviour to ensure no free-riding occurs. Females, in contrast, tend to target less variable resources and are subsequently less dependent on others for acquiring resources (Bliege Bird 2007). Additionally, females are generally more involved in childcare than males. Although requiring assistance from others, childcare is likely to be lower-cost and less susceptible to free-riding than high-variance foraging. Long-term partnerships may therefore be less essential for women's activities compared to men's, hence fewer reciprocal nominations. A similar explanation may also explain why males were more likely to select non-camp-mates than females. Again, as female livelihoods are predominantly child-based, allomothering is essential, but depends upon help in the present, hence choosing camp-mates more often. For males, however, resource acquisition may be a greater adaptive challenge. This may require a more diffuse inter-camp network for access to distant foraging grounds, receiving shares of large game from other camps and acquiring information regarding game location. Thus, male interaction networks are structured to be more reciprocal within-camps than female networks, but also possess more between-camp connections, potentially as a consequence of the demands of resource acquisition, while female networks are predominantly within-camp but more diffuse, reflecting the increased importance of childcare considerations. This explanation is highly speculative, however, and requires further empirical investigation.

Male Agta were also more likely to nominate skilled fishers as potential camp-mates than women. This suggests that resource acquisition is unlikely to be the only reason that individuals nominated good fishers, otherwise it would be expected that both males and females would value them equally. Similarly, these results make it unlikely that males avoid skilled fishers in order to make themselves appear of higher-quality by comparison, and consequently more attractive as a potential mate (Wood & Hill 2000; Wood 2006). One interpretation of this finding may be that males nominated competent fishers in order to learn from them and improve their own skills. Regarding interaction effects in the sharing network, the only strong effect was that of age and storytelling ability, with younger individuals more likely to give resources to skilled storytellers than older Agta. This may be because younger individuals possess less knowledge and therefore trade cooperation for information, although the lack of an interaction between age and storytelling ability in the camp-mate network weakens the case for this argument. Nonetheless, despite some differences, by and large age and sex effects do not appear to greatly influence valuations of market value. One notable exception is that of same sex relationships, as Agta were overwhelmingly more likely to nominate individuals of the same sex in both the camp-mate and sharing networks. This suggests that same-sex relationships are vastly more important that opposite-sex relationships among the Agta, and potentially hunter-gatherers more generally.

Summary and Next Chapter

This is the first analysis exploring social and cooperative dynamics among a hunter-gather population explicitly using a biological market approach. According to this approach, individuals should interact and cooperate with those of the highest market value in order to receive the most benefits, even if these are not returned ‘in-kind’. This study moves beyond previous similar research exploring forager social networks, which has been largely descriptive in nature (Apicella *et al.* 2012), by attempting to explain the adaptive decisions individuals make regarding with whom to cooperate and interact. Here, I suggest that cooperativeness is not the most valued trait among the Agta. Rather, other competency factors increase an individual’s market value, such as storytelling ability or foraging skill (alongside more traditional factors such as kinship and reciprocity). These individuals may be particularly valued not just for their resource acquisition capabilities, but also for their role in transmitting fitness-relevant information, coordinating group behaviour and promoting cooperation. I also find that there are significant differences between food-sharing and camp-mate networks, likely reflecting different adaptive pressures regarding who to share resources with and who to live with.

This chapter raises many more questions than it answers. An extremely pertinent question requiring empirical research concerns how different cooperative domains (e.g., resource transfers, allocare, social support, etc.) relate to one another and how ‘domain general’ cooperative behaviour is. For instance, cooperative food-sharing behaviour may (or may not) be unrelated to cooperation in terms of social support. Following this, it is also important to understand how these different cooperative domains relate to different social networks (e.g., camp-mate, food-sharing, cooperative hunting, etc.). Cooperativeness in one domain may predict patterns of interaction in one network but not others, which may be why cooperative behaviour regarding resource transfers was not strongly associated with selection in a camp-mate network here. Additionally, the importance of exploitative relationships in purportedly cooperative networks ought to be explored in greater depth, such that interactions may benefit one partner but not the other, and therefore may not strictly reflect cooperative behaviour. Nonetheless, there appears to be great potential in advocating a biological market approach to the study of cooperation, and social networks more broadly.

While these past chapters have explored cooperative decision-making by adults, the next chapter takes an ontogenetic perspective and asks: how does cooperative behaviour develop in forager children, both in terms of the amount they give and who they give to?

Chapter 7 The Ontogeny of Cooperation and Partner Choice among the Agta

Previous chapters have explored cooperative behaviour and social networks among adult Agta. In the present chapter I investigate the development of these behaviours among Agta children. Exploring cooperative behaviour in children is relevant for a number of reasons. Firstly, it provides an ontogenetic perspective to understand how cooperative behaviours displayed in adulthood develop over the lifespan. This research can provide a developmental perspective as to how individuals, groups and species differ in cooperativeness, an approach which is essential for a complete understanding of behaviour. Secondly, this ontogenetic approach permits an exploration of how evolution has shaped children's cooperative behaviour and how variation in the development of cooperation may reflect evolved processes. A simple resource allocation game – analogous to that played with adults – was conducted with 179 children between the ages of 3 and 18. Children were given five resources (candies) and asked, for each one, whether they would like to keep it for themselves or to give it to somebody else, and if so, to who. This design permitted both a measure of cooperativeness (how many resources children gave to others) and an index of their social network (who they gave to). The only significant predictor of the amount children gave was the average amount given by adults in camp, demonstrating that levels of cooperation were analogous between children and adults in the same camp. No age effects were observed, as young children were equally as cooperative as older children. Stronger age-specific effects emerged regarding who children shared with, corresponding to hunter-gatherer childhood interaction networks. Older children were more likely to give to less

related individuals than younger children, while older children (particularly females) increasingly gave to others younger than themselves. Findings are discussed in terms of their implications for understanding variation in cooperative behaviour among children, as well as broader implications regarding human life history and the evolution of extended childhood.

Introduction

Despite much debate over the years surrounding the nature of cooperation in adult hunter-gatherers, specifically regarding food-sharing (Smith & Bliege Bird 2000; Bliege Bird *et al.* 2002; Hawkes & Bliege Bird 2002; Gurven & Hill 2009; Wood & Marlowe 2013) and behaviour in experimental games (Henrich *et al.* 2004b, 2005, 2010a; Ensminger & Henrich 2014), little attention has been given to the role of ontogeny in shaping cooperative behaviour (although see Crittenden & Zes 2015 and House et al. 2013). Indeed, despite the obvious continuity between childhood and adulthood – “the child is father of the man” – studies investigating developmental trends in forager societies are largely absent. When children are studied it is often in terms of their economic cost to others, rather than as agents in and of themselves (Bird-David 2005; Kramer 2011). This is a significant oversight, as children are not merely burdens to adults, but rather are actively engaged in useful activities such as allocare (looking after others in camp; Hrdy, 2005; Ivey Henry, Morelli, & Tronick, 2005; Meehan, Quinlan, & Malcom, 2013) and foraging (Bird & Bliege Bird 2005; Tucker & Young 2005; Kramer 2011; Crittenden *et al.* 2013), despite being somewhat dependent on provisioning until adulthood (Kaplan *et al.* 2000).

In addition to being autonomous agents, the evolved nature of children’s behaviour is often overlooked. Studies of children’s cooperative behaviour tend to interpret results from a developmental perspective, such as ‘learning to be adult’, rather than from an evolutionary fitness-maximising perspective. Although development is undoubtedly a constraint for performing certain behaviours, being evolved organisms children should still strive, consciously or not, to maximise their inclusive fitness. Childhood behavioural strategies are therefore likely to have been shaped by evolution in an attempt to maximise inclusive fitness, both in the present and for future survival and reproductive success (Belsky *et al.* 1991; Bjorklund & Pellegrini 2000; Machluf *et al.* 2014). For instance, parent-offspring conflict can be understood as children, or even neonates, attempting to maximise their individual fitness. Examples include offspring manipulating the *in utero* environment to promote foetal growth, even if this lowers the mother's fitness, and conflict over when to wean (Trivers 1974; Moore & Haig 1991; Crespi & Semeniuk 2004; Haig 2010). Children also possess evolved mechanisms such as social learning and phenotypic plasticity to adapt to local conditions (Belsky *et al.* 1991; O'Brien 2014). This fitness-maximising perspective is often absent in studies investigating the ontogeny of cooperative behaviour.

Nonetheless, in recent years there has been much research on the development of cooperative behaviour in children, predominantly using simple experimental games (see Gummerum, Hanoch, and Keller (2008) and Tomasello and Vaish (2013) for reviews). However, most of this work has been confined to Western societies, with a few notable exceptions (Rochat *et al.* 2009; House *et al.* 2013; Blake *et al.* 2015). Behaviour in these populations is often atypical compared to small-scale subsistence populations, such as pastoralists, horticulturalists and hunter-gatherers (Henrich *et al.* 2010b). Cross-cultural work is therefore necessary to understand the social and ecological factors which influence the development of cooperative behaviour.

In studies focusing on small-scale societies, cooperativeness has usually been found to increase with age, although not necessarily monotonically (Rochat *et al.* 2009; House *et al.* 2013; Blake *et al.* 2015). For instance, when assessing costly giving across six diverse societies, House *et al.* (2013) found that cooperative behaviour was similar in all societies until middle childhood (~6-8 years old), after which societies diverged to approximate population-specific adult levels. Comparable patterns were found among juvenile Hadza food-sharing, with the amount of food shared by children increasing with age (Crittenden & Zes 2015). The authors interpreted these results as indicating that culturally-transmitted society-specific norms influence costly cooperative behaviour from middle childhood onwards, as it is around this age that children tend to become more integrated into the wider society (Lancy & Grove 2011). While plausible, these and similar studies (Fehr *et al.* 2008; Blake *et al.* 2015) overlook how this behaviour may be functional in a given socioecological context. Social learning is a proximate mechanism and does not answer why said behaviour is adaptive in a particular environment, which is an ultimate explanation (Mace & Jordan 2011; Scott-Phillips *et al.* 2011; Mace 2014). These studies also overlook the role of individual-level phenotypic plasticity in response to local conditions, which also provides a potential proximate explanation for variation in cooperative behaviour, both developmentally and cross-culturally (Belsky *et al.* 1991; Bjorklund & Pellegrini 2000; O'Brien 2014).

Related to these issues, previous studies have only compared one group per population. This may conflate population-level differences in cooperative norms with differences in socioecology (Lamba & Mace 2011). When multiple groups are sampled from the same society, high levels of variation in adult cooperative behaviour are often found (Gurven *et al.* 2008; Lamba & Mace 2011), which may match or exceed variation found between societies (Lamba & Mace 2013; see also Chapter 4 in this thesis). Importantly, this within-society variation is not random, but likely represents adaptive responses to differences in socioecology, such as kinship, need and the probability of repeated interactions. The extent of within-society variation in the development of cooperative behaviour, and whether this variation conforms to adaptive expectations, has not previously been explored.

A further consideration to be taken into account when assessing the development of cooperative behaviour is ‘partner choice’ (Noë & Hammerstein 1995; Barclay 2013; Barclay & Raihani 2016; Hammerstein & Noë 2016). In many previous developmental studies, recipients of resources were either anonymous (Fehr *et al.* 2008) or the player had no choice over who they could share with (House *et al.* 2012, 2013). Furthermore, in the majority of cases only dyadic interactions were studied. Social networks in children (Cairns *et al.* 1995), hunter-gatherers (Apicella *et al.* 2012) and juvenile non-human primates (Barale *et al.* 2015) display non-random assortativity, as individuals interact and cooperate in a non-uniform manner with others in their social group based on factors such as age, sex, relatedness and reciprocity. By modelling merely dyadic interactions previous methodologies implicitly assume that cooperation is equivalent across all recipients. Yet when multiple recipients are included children preferentially give to kin and friends over strangers (Olson & Spelke 2008), indicating that cooperation is targeted to specific individuals and not merely generalised to all (see also Moore 2009). A recent study of real-world food-sharing among Hadza hunter-gatherer children found that individuals preferentially shared food with kin and reciprocating partners (Crittenden & Zes 2015). This partner choice is increasingly being recognised as fundamental to the evolution of cooperation (Sylwester & Roberts 2010; Barclay 2013; Baumard *et* *al.* 2013; Roberts 2015). Both the pre-selection of partners and an over-representation of dyadic interactions are unrealistic assumptions of child (and adult) cooperation; individuals not only choose with whom to interact, but can also interact and cooperate differently with multiple individuals. This may be especially true in hunter-gatherer societies where children are given much more autonomy than in large-scale industrial societies (Konner 2005).

An exploration of how cooperation develops in forager societies is of particular interest for several related reasons. Firstly, the majority of our evolutionary history has been as hunter-gatherers (Lee & Daly 1999), and is therefore the best model for understanding the context in which our unique suite of adaptations, such as extended childhood, cooperative breeding and cumulative culture, evolved (Kaplan *et al.* 2000, 2009; Hill *et al.* 2011; Chaudhary *et al.* 2015; Dyble *et al.* 2015). Although modern-day hunter-gatherers are not pristine relics of the Pleistocene past and display great variation in behaviour both within and between populations, understanding how cooperation develops in present day forager societies provides the best opportunity available for inferring the evolutionary and ecological roots of this behaviour. For example, children born in agricultural societies, which tend to be patrilocal, would interact more often with paternally-related kin and less often with unrelated individuals, compared to children from hunter-gatherer societies (Dyble *et al.* 2015). Children's cooperative partners would therefore be expected to differ between the two societies. Additionally, although often grouped under the umbrella term 'small-scale societies', child-rearing practices between hunter-gatherer and agricultural societies are markedly different, with the latter engaging in more physical punishment, enhanced sibling conflict, an increased preference for females as babysitters and a reduced focus on individual autonomy, compared to foragers

(Hewlett & Lamb 2005; Konner 2005). Development is therefore unlikely to be homogeneous across all small-scale societies, meaning that broad cross-cultural comparisons of childhood in small-scale societies which do not distinguish between different socioecological conditions (e.g., Lancy & Grove, 2011) may overlook diversity specific to hunter-gatherers.

Secondly, little is actually known about how cooperation and social networks develop throughout childhood in hunter-gatherers. There is evidence that children from forager societies are involved in cooperative breeding, in terms of looking after younger children, assisting in household tasks and foraging (Bird & Bliege Bird 2005; Tucker & Young 2005; Kramer 2010, 2011; Crittenden *et al.* 2013; Meehan *et al.* 2013), indicating that children do cooperate with others and contribute to subsistence. This role may explain, in part, aspects of our derived life-history, such as high fertility and short inter-birth intervals (Kramer 2005, 2011). One study which investigated experimental cooperative behaviour among foragers, the Aka from the Central African Republic, reported that willingness to give to others at a cost to self began high in early childhood (3-5 years), decreased in middle childhood (6-8 years), then increased again in later childhood (9-11 years) to reach adult levels (House *et al.* 2013). However, individuals could not choose who to interact with, and recipients were not immediate family members, which may have influenced levels of cooperation (Olson & Spelke 2008; Moore 2009). The Hadza study examining observed food-sharing among children found that quantities of food-sharing increased with age (Crittenden & Zes 2015). Although this suggests that cooperative behaviour increases with age, this study did not explore motivations for cooperation; younger children may be willing to share with others, but as they are less-skilled at foraging they acquire less resources, so share less. An experimental approach can separate these effects of motivation to share and foraging skill.

The theoretical links between partner choice and the ontogeny of cooperative behaviour have yet to be formalised in to a set of testable hypotheses and there is little quantitative research assessing with whom forager children interact. I present a broad sketch now based upon theories for the evolution of cooperation and using the available evidence regarding the development of social and cooperative networks among hunter-gatherer children. A central theory is kin selection (Hamilton 1964), where cooperation is directed towards related individuals for indirect fitness benefits. Many hunter-gatherer children engage in allocare of younger children in their camp, particularly siblings, potentially to increase their inclusive fitness (Kramer 2005, 2011; Crittenden & Marlowe 2008). Age and sex effects may also modulate the strength of kin selection. Sisters tend to allomother more frequently than brothers (Kramer 2010), suggesting that the importance of kin selection in shaping cooperative behaviour throughout childhood may be greater for females. Additionally, interactions with non-kin increase throughout childhood (Migliano *et al.* 2017), likely reflecting the need for extensive non-kin cooperation in adulthood (Hill *et al.* 2011; Dyble *et al.* 2015), meaning that the influence of kin selection in shaping children’s behaviour may decrease with age.

Direct fitness benefits are also likely to be important in deciding who to cooperate with. These can be broadly categorised as either ‘immediate direct fitness benefits’ or ‘delayed direct fitness benefits’ (which broadly correspond to the distinction between ‘ontogenetic adaptations’ and ‘deferred adaptations’ posited by others; Machluf *et al.* 2014). Immediate direct fitness benefits are those which benefit the individual in the present (or short-term). These theories are also used to explain cooperation among adults. One example is reciprocal cooperation (Trivers 1971), which has been found to predict resource transfers among Hadza children (Crittenden & Zes 2015). A further immediate direct fitness benefit may be via sexual selection, which might also play a role in adolescence if individuals cooperative with members of the opposite sex as a potential strategy to attract and acquire mates (Bliege Bird *et al.* 2001; Smith *et al.* 2003; Raihani & Smith 2015). Other direct fitness benefits discussed in previous chapters, such as indirect reciprocity, competitive altruism and ‘not-in-kind’ reciprocity, may also influence childhood cooperation, but will not be discussed further in this chapter.

Alternatively, children may interact and cooperate with specific individuals to learn relevant skills necessary for adulthood. As the pay-offs to these cooperative behaviours would occur later in life, these can be categorised as delayed direct fitness benefits (although the division between immediate and delayed fitness benefits is likely to be less clear-cut than presented here). Learning foraging skills may be a particularly salient delayed fitness benefit (Kaplan *et al.* 2000). Analysis of Baka children’s play activities suggests some sex segregation in foraging societies, with boys more involved in hunting and physical play and girls in domestic play (Kamei 2005). Similarly, Hadza juveniles initially forage for tubers with adult females and other children in early childhood, but around the ages of 10-12 males begin to hunt game while females of this age continue to forage for tubers (Blurton Jones & Marlowe 2002; Crittenden *et al.* 2013). The sexual division of labour regarding foraging may become particularly apparent at this age. As male foraging is generally more skill-intensive than female foraging (hunting/fishing vs. gathering; or high vs. low variance returns: Bliege Bird 2007), males may need to invest more time and effort in cooperating with other males to gain proficiency and learn these techniques

(Kaplan *et al.* 2000; Gurven *et al.* 2006). Older female children, while also foraging, do so in less skill-intensive tasks such as gathering (Crittenden *et al.* 2013), and may therefore continue to invest more heavily in allocare of younger children compared to males. This investment in allocare may be for indirect fitness benefits, as discussed above, but may also be for other delayed direct fitness benefits, in terms of 'learning to mother' (Lancaster 1971; Hrdy 1976). In several species, individuals with experience of mothering during childhood were more competent adult mothers (Fairbanks 1990; Margulis *et al.* 2005; Stone *et al.* 2010), although there has been a suggestion that some instances of allocare among foragers may be coercive, rather than voluntary (Crittenden & Marlowe 2008). Thus, as childhood progresses sex differences may become increasingly apparent, with females continuing to invest more in allocare while males begin to cooperatively forage more frequently with other males of a similar age. Given these differences, divergent patterns of cooperation ought to become apparent. In addition to foraging and care-giving skills, childhood may also be a period of developing general social skills necessary for successfully navigating the complexities of social life in peer groups (Harris 1995; Flinn & Ward 2005; Del Giudice *et al.* 2009). From this perspective, same-age and same-sex relationships may be particularly salient for both juvenile males and females as adult social and cooperative networks among hunter-gatherers are also predominantly same-sex (Apicella *et al.* 2012; see also Chapters 5 and 6 in this thesis), while similar age-mates may be necessary as a 'scaffold' to develop increasingly-complex social skills.

This is a preliminary sketch based on scant data and this general picture is likely to vary by socioecological conditions. For instance, although juvenile females tend to allomother more frequently than males (Kramer 2010), few sex differences were found among the Efe (Ivey Henry *et al.* 2005). Involvement in subsistence over childhood also varies across populations (Kramer 2005), which is likely to influence who children interact and cooperate with. Nevertheless, this broad outline is a useful tool from which to make predictions and test data against for the purposes of the present study, and does indicate that partner choice is likely to vary considerably throughout ontogeny based on inclusive fitness considerations.

The present chapter aims to investigate variation in cooperative behaviour among Agta children, utilising a non-anonymous experimental game methodology in which children divide resources between themselves and multiple potential recipients. This design permits an examination not only of how much children share with others, but also with whom they cooperate. Several camps are tested to explore between-camp variability in cooperative behaviour. Analogous games conducted with Agta adults (see previous chapters) are used to investigate whether the observed ontogenetic trends continue into adulthood. Two main topics are explored: i) how do levels of cooperation develop in forager children? and ii) how does partner choice change throughout ontogeny? Regarding the first question, as children's cooperative behaviour should be sensitive to the costs and benefits of cooperation, I predict that children's behaviour will correspond to that of adults (which does respond to differential costs and benefits; Chapter 4). As previous cross-cultural research has reported that cooperativeness is relatively similar between societies in early childhood while diverging to approach adult levels with increasing age (House *et al.* 2013; Blake *et al.* 2015), between-camp cooperative behaviour among the Agta may follow a similar pattern. Regarding who children give to in these games, I predict that partner choice will vary across childhood as children engage in different social roles and cooperate with different individuals in ways which may maximise their inclusive fitness. Specifically, I explore the respective roles of: i) *kin selection*: individuals will preferentially share with kin, but older individuals may increasingly cooperate with non-relatives as they integrate into the wider society; ii) *reciprocity*: individuals will share with others who share with them; iii) *sexual selection*: adolescents, particularly males, will give to others of the opposite sex in an attempt to attract mates; and iv) *learning skills*: if males learn complex foraging skills they will cooperate with others of the same age (or older) and same sex, especially as they approach adulthood. Meanwhile, if females learn care-giving skills then younger children, regardless of sex, will be more likely to receive resources from females. Additionally, if childhood is where general social competence regarding interactions with peers is acquired then sex differences may be less apparent, although same-age and same-sex relationships may be equally salient for both sexes.

Contrary to previous research, results indicate that age has little effect on levels of cooperation, while adult levels of cooperation in camp are the best predictor of children’s cooperativeness. This suggests that similar socioecological factors may influence both children’s and adult’s cooperative behaviour. Findings also demonstrate that partner choice changes significantly over childhood. Kin are more likely to receive resources than non-kin, but the frequency of sharing with non-kin increases with age. Additionally, results indicate that: i) individuals preferentially share with recipients of a similar age (an effect which is stronger in males); ii) the age difference between giver and recipient also increases with age, such that older individuals increasingly share with others younger than themselves (an effect which is stronger in females); and iii) children preferentially give to same-sex individuals. Hypotheses for children’s sharing based upon kin selection were therefore strongly supported, while support for immediate direct fitness benefits, such as reciprocal cooperation and sexual selection, were not supported. Predictions regarding delayed direct fitness benefits, such as learning skills necessary for adulthood, were somewhat supported but difficult to evaluate conclusively. These results suggest that partner choice may display a more pronounced ontogenetic trajectory than overall levels of cooperation. Findings are discussed in terms of their implications for understanding variation in cooperative behaviour among children, as well as broader implications regarding human life-history and cumulative cultural evolution.

Methods

Games were conducted on 179 children between the ages of 3 and 18 (Mean=8.86, SD=3.16), of which 87 were male. A total of 14 camps were sampled. However, to increase sample sizes some camps with few children and in close proximity to one another were pooled together, producing 11 camps used in the final analysis. Differences in cooperative behaviour between the pooled camps were minimal, as these camps were similar both behaviourally and ecologically, meaning that this procedure is unlikely to qualitatively alter the conclusions below (see table A12 and figure A3 in Appendix 7 for verification). The experimental methods used in this chapter have been discussed in the methods chapter, so will not be repeated again here. Only statistical methods will be discussed in this section.

Statistical Analyses

Analyses were conducted using the statistical program *R* (R Development Core Team 2015). Two sets of analyses were conducted, one exploring how much children gave to others and the other exploring who they gave to. The ‘amount given’ analysis will be described first. Data for the response variable were coded so that each participant was given a score between 0% and 100%, depending of the number of resources (candies) kept for themselves. A score of 0% meant that all candies were given to others while 100% meant all candies were kept for self. As there were 5 candies this measure increased in 20% intervals (percentages were chosen so that adult and child measures of cooperative behaviour were on the same scale). Independent variables were age (for descriptive statistics regarding sample sizes for different age groups see table 7.1), sex, number of siblings and relative birth order (a measure of birth order controlling for size of sib-set, ranging from ‘0’ (first born) to ‘1’ (youngest)). Sex and sibling effects were included as previous developmental research has indicated that these may influence childhood cooperation (Fehr *et al.* 2008; Gummerum *et al.* 2008b; House *et al.* 2012). As analogous games were conducted with adults (Chapter 4), comparisons between child and adult levels of cooperation were also explored. Three indices from the adult games were used: father’s score, mother’s score and adult camp average (the average percentage of resources given by adults in said camp). Three interactions were also explored. Two concerned the interaction between parent’s score and sex (to investigate if, for instance, daughters were more similar to their mother or sons to their father). The other interaction term involved age and adult camp average, as it may be that children learn camp-specific cooperative behaviour (if indeed they do) gradually over time, in which case an interaction may be expected. Alternatively, children may acquire camp-specific behaviour (again, assuming that they do) from a young age, in which case no such interaction would be predicted.

Table 7.1: Sample sizes for the number of children in different age cohorts (*n*=179).

Age Cohort	Sample Size
Early Childhood (3-5)	35
Middle Childhood (6-8)	61
Late Childhood (9-11)	46
Adolescence (12+)	37

Analyses were predominantly conducted using an Information-Theoretic approach (Burnham & Anderson 2002) in which various models were constructed and their goodness-of-fit compared using the Akaike Information Criterion (AIC; Akaike, 1998), followed by a model averaging approach to identify significant predictor variables over a set of the best-fitting models (Grueber *et al.* 2011). As a consequence of missing data for certain variables (namely amount given by a child's mother and father, as not all parents participated in the adult games), and the need for valid comparisons between AIC values of different models to possess an equal number of cases (Nakagawa & Freckleton 2011), a 'multiple imputation' procedure was utilised using the package *Amelia* (Honaker *et al.* 2011). This creates *M* number of datasets (five, in this instance) while imputing missing values. The amount of missing data was relatively small, with only 66 data points missing out of a total of 1,432 (4.6%). Analyses were then conducted on each imputed dataset, and the results subsequently pooled. All analyses employed a multi-level modelling approach using the package *lme4* (Bates *et al.* 2015), which controled for the hierarchical nature of the data (individuals nested within camps; Kreft & de Leeuw 1998). Due to interaction terms potentially masking the effects of their constituent variables (Engqvist 2005), continuous variables in all models were standardised over two standard deviations while binary variables were mean-centred (Gelman 2008). This permits main effects and interaction terms to be interpreted simultaneously (Schielzeth 2010). This standardisation also allows direct comparison of effect sizes between continuous and binary variables, as well as between continuous variables on different scales (Gelman 2008). Prior to this model averaging analysis, a preliminary analysis to explore associations between age and cooperative behaviour will be conducted for comparison with a recent publication exploring the ontogeny of cooperation over multiple small-scale societies (House *et al.* 2013).

For the analysis of who children gave to, response variables depended on the analysis conducted. To explore the effects of kin on cooperative behaviour the coefficent of relatedness between giver and receiver was calculated. The first analysis assessed whether the relatedness between ego and alter was greater than expected by chance, based on background levels of relatedness between children in camp. Secondly, age effects were explored to determine whether ego's age or sex influenced nominations towards relatives. Five models were constructed ('null', 'ego age', 'ego sex', 'ego age and ego sex', and 'ego age by ego sex interaction') and model averaging performed to identify strongly-predictive terms. Further analyses explored how ego's age, sex and relatedness to recipient were associated with: i) alter's age; ii) the age difference between ego and alter (calculated by subtracting ego age from alter age, so that negative values meant alter was younger than ego); iii) alter's sex; and iv) whether ego and alter were of the same sex. For each of these analyses multiple models were constructed with all possible models (including interaction effects) tested using ego's age, ego's sex and relatedness between ego and alter as independent variables. Again, model averaging was conducted to identify the predictor variables possessing the strongest association with the dependent variable. All analyses used mixed-effect models to control for multiple nominations by the same individual (with each individual as a random effect). Logistic regressions were used when sex was the dependent variable. As above, continuous response variables were standardised over 2 standard deviations, while binary response variables were mean-centred, permitting comparison of relative effect sizes and simultaneous interpretation of main effects and interaction terms.

Reciprocal nominations were also assessed, but employing qualitative methods due to the nature of the data.

Results

The mean amount of resources kept by children was 64.1% (SD=29), with large variation in behaviour at the camp level (minimum camp average=44.4%, SD=16.7: maximum camp average=100%, SD=0). A null multi-level model possessed a lower AIC value (AIC=1696.41) than the corresponding non-multi-level model (AIC=1713.83), and comparison of model weights provoide overwhelming support that the multi-level formulation was a better fit to the data (w_i=1). The null multi-level model found that 23% of the variance in giving behaviour occurred at the camp level, while 77% was found at the residual, or individual, level.

To explore the effect of age on amount given four models were created to explore different potential relationships between age and cooperativeness (see House et al. 2013): i) a monotonic relationship between age and amount given across all camps; ii) a monotonic relationship between age and amount given, but with a different trajectory for each camp; iii) a non-monotonic relationship regarding age across all camps; and iv) a non-monotonic relationship with age, but with a different trajectory for each camp. The only model which indicated an increased model fit compared to the null model was model 1 (table 7.2), suggesting a 1.15% point increase in amount given for every additional year in age (95% CI: [-0.11; 2.42]). However, the 95% confidence interval passes through zero and comparison of Akaike weights do not provide strong support that this model is a better fit to the data than the null model (table 7.2). It is worth noting here that although age may not have strongly predicted the *amount* given by children, it did predict the *number* of recipients that children gave to (null AIC=595.8, w_i=0.01; number of recipients AIC=585.7, w_i=0.99). Each additional year in age was associated with giving to 0.1 more individuals (95% CI: [0.05; 0.16]). This suggests that although older children may not have given substantially larger amounts, they did share with a greater number of individuals (put another way, younger children were more likely to give to the same individual).

Table 7.2: Model comparison of different trajectories regarding age and cooperative behaviour (FE=fixed effect, RE=random effect: *n*=179, camps=11). Note that centred age squared is a transformation of age to detect non-monotonic developmental trajectories, calculated by squaring age after standardising over two standard deviations.

Model	Description	AIC	ΔAIC	Weight (w_i)
FE: N/A **RE: Camp**	Null model (no age effects)	1696.41	1.2	0.236
FE: Age **RE: Camp**	1 monotonic age trajectory across all camps	1695.21	0	0.432
FE: Age **RE: Age|Camp**	Different monotonic age trajectories for each camp	1697.14	1.93	0.164
FE: Age + Centred Age^2 **RE: Camp**	1 non-monotonic age trajectory across all camps	1697.15	1.94	0.164
FE: Age + Centred Age^2 **RE: Age + Centred Age^2|Camp**	Different non-monotonic age trajectories for each camp	1704.94	9.73	0.003

A model averaging approach was subsequently utilised to compare predictor variables by examining all possible combinations of variables and averaging across a set of the best models for all independent variables (age, sex, birth order, etc.). As mentioned above, due to missing data a multiple imputation procedure was employed, whereby the model averaging approach was conducted on five imputed datasets and the results subsequently pooled (see table A13 in Appendix for AICc values and model weights for each of the five imputed datasets). None of the variables entered into the model averaging approach displayed high collinearity (see table A14 in Appendix 7). Results are summarised in table 7.3, and indicate that the only variable which was found in all candidate models and strongly predicted children's cooperative behaviour was adult camp average amount given. A two SD increase in adult camp average was associated with a 26.3% point increase in the amount kept by children. Entering adult camp average into a null model reduced the amount of variance at the camp level from 23% to 4.6%, explaining ~80% of the camp-level variance. Validating this result, at the camp level a significant correlation was found between child camp average and adult camp average (figure 7.1; n=11, r=0.81, p=0.002), with an adjusted R^2 value of 0.62. None of the other variables, including age or an age by adult camp average interaction, were observed to have a strong association with the amount children gave.

Table 7.3: Results of the model averaging approach displaying the factors associated with children's cooperative behaviour, using standardised coefficients (n=179, camps=11). Positive parameter estimates indicate an increase in the amount of resources kept for self. Results displayed are pooled across each of the five imputed datasets. 95% confidence intervals are displayed in brackets. Relative importance denotes the summed Akaike weight (w_i) of each parameter in the top models used in model averaging, with a '1' indicating that this term occurred in all of the top models.

Variable	**Level**	**Standardised Parameter Estimate (95% CI)**	**Relative Importance (w_i)**
Intercept	-	65.04 [59.48; 70.6]	-
Adult Camp Average	Camp	26.3 [14.72; 37.87]	1
Father Score	Individual	-8.95 [-18.9; 1]	0.87
Age	Individual	-5.02 [-13.57; 3.52]	0.79
Sex	Individual	-2.15 [-8.67; 4.37]	0.47
Mother Score	Individual	1.27 [-4.9; 8.09]	0.18
Birth Order	Individual	-0.38 [-3.58; 2.83]	0.11
Size of Sibset	Individual	-0.13 [-2.52; 2.83]	0.05
Adult Camp Average*Age	NA	7.27 [-12.72; 27.26]	0.46
Father Score*Sex	NA	-3.48 [-12.01; 5.04]	0.22
Mother Score*Sex	NA	-0.2 [-7.77; 7.37]	0.02

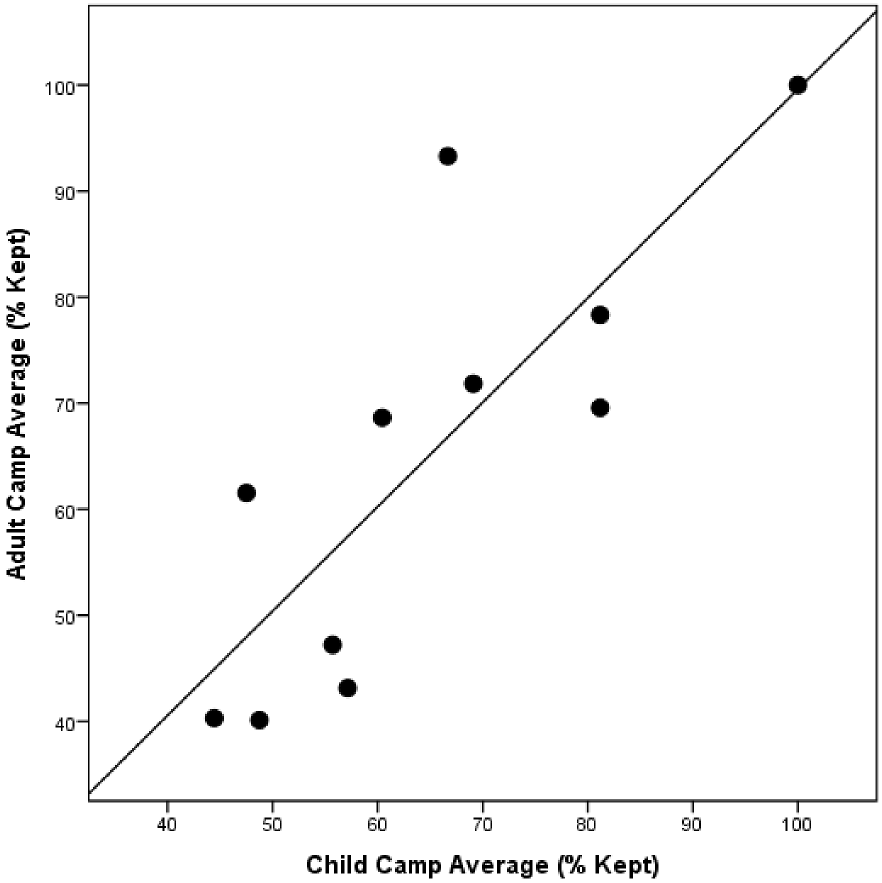

Figure 7.1: Scatterplot displaying the relationship between the child camp average amount kept (%) and the adult camp average amount kept (%; *n*=11).

Figure A4 in Appendix 7 displays the residuals from the null model using Q-Q plots. Although this plot somewhat follows a normal distribution, a Shapiro-Wilk test reported that this model violated the assumption of normality (*p*=0.014). As with the analysis of adult's games, I also analyse children's behaviour using ordinal logistic regression methods (cumulative link models), and demonstrate that the results of this analysis is qualitatively identical to that presented above, providing confidence that these findings are not a statistical artifact of the methods used (see tables A15 and A16 in Appendix 7).

Recipients of Gifts

Of the 320 gifts given by children to others, 12 were to adults over the age of 20 (3.8% of all gifts). In order to compare interactions between just children, in addition to removing outliers, all recipients over the age of 20 were omitted, resulting in 308 gifts from 125 children. Firstly, to test whether individuals selectively gave to kin, the relatedness coefficient between alter and ego for each nomination was compared against the average camp relatedness to all children for each child. The average relatedness between nominees was 0.3, while the average relatedness to all child camp-mates was 0.09. A linear mixed-effects model, with each individual as a random effect, found that relatedness between ego and alter was significantly higher than expected by chance, with recipients possessing a relatedness coefficient 0.21 greater than the average camp relatedness (95% CI [0.19; 0.23]). This model receiving overwhelming support relative to the null model (AICc=-617, w_i=1; null AICc=-324.8, w_i=0). Next, associations between relatedness and ego age and sex were explored. AICc values and model weights are presented in table 7.4. After model averaging, the only strongly predictive variable was ego age. A two SD increase in ego age was associated with a decrease in recipient relatedness by 0.015 (95% CI: [-0.005; -0.025]), demonstrating that older children gave to less-related individuals. This pattern is displayed in figure 7.2.

Table 7.4: Comparison of AICc values and model weights derived from different models regarding the effect of ego's age and sex on the relatedness between ego and alter. All models are mixed-effects models which control for repeated nominations by individuals (*n*=125, nominations=308).

Model	AICc Value	ΔAICc	Weight (w_i)
Ego Age + Ego Sex	-202.53	0	0.519
Ego Age	-201.06	1.47	0.248
Ego Age*Ego Sex	-200.62	1.91	0.2
Ego Sex	-196.31	6.22	0.023
Null	-194.51	8.02	0.009

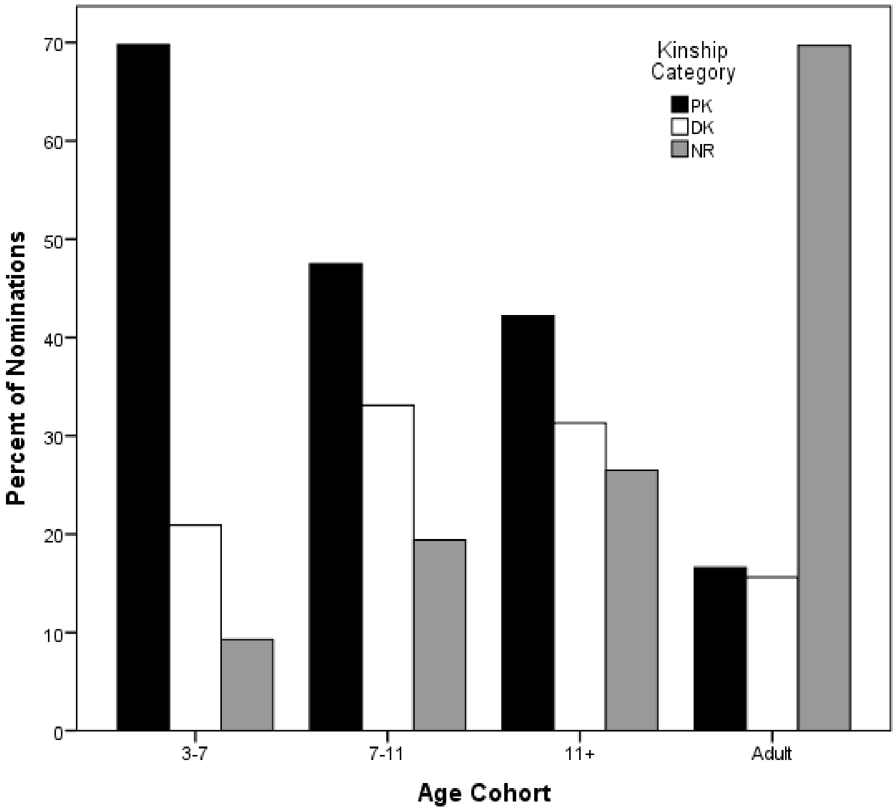

Figure 7.2: Proportion of gifts given to either primary kin (PK: $r=0.5$), distant kin (DK: $r<0.5$ but ≥ 0.03125; that is, all kin more closely related than second cousins, excluding primary kin) or non-relatives (NR: $r<0.03125$) as a function of age group. Adult behaviour is also displayed alongside children's behaviour, to show that the trend of giving to less related individuals with age continues into adulthood.

Regarding age of recipient, model values and Akaike weights for models within two AICc values of the top model are displayed in table 7.5 and model averaged parameters are in table 7.6. Two strong main effects of ego age and relatedness were reported. Taking age effects first, a positive association between ego age and alter age was reported, with a 2 SD increase in ego's age associated with a 1.5 year increase in alter's age, indicating that older children gave to older recipients. A main effect of kinship was also reported, with older recipients more likely to be non-kin than younger recipients. Unrelated recipients were therefore older than related recipients. No main effect of sex on alter age was found. A weak interaction between ego age and sex was also observed. Although this interaction was not strongly predictive using the ‘zero method’ of model averaging (table 7.6), using the less-stringent ‘conditional method’ of model averaging (in which terms absent in a given candidate model are ignored, rather than given a value of ‘0’) an interaction was present (*b*=2.18, 95% CI: [0.003; 4.35]). This suggests that older males gave to older individuals, while recipient age was less dependent on ego’s age for females (figure 7.3). However, as this interaction was absent using the ‘zero method’ of model averaging, this effect is weaker than the main effects of age and relatedness.

Table 7.5: Comparison of AICc values and Akaike weights for models within two AICc values of the top model derived from different models comparing the effect of ego’s age, sex and relatedness on age of alter, age difference between ego and alter, sex of alter and whether ego and alter are the same sex (*n*=125; nominations=308). All models are mixed-effects models which control for repeated nominations by individuals.

Model	**AICc Value**	**ΔAICc**	**Weight (w_i)**
Age of Alter Models			
Ego Age + Ego Sex + Relatedness + Ego Age*Ego Sex + Ego Sex*Relatedness	1646.65	0	0.33
Ego Age + Relatedness	1647.17	0.52	0.25
Ego Age + Ego Sex + Relatedness + Ego Age*Ego Sex + Ego Sex*Relatedness + Ego Age*Relatedness	1648	1.35	0.17
Ego Age + Ego Sex + Relatedness + Ego Age*Ego Sex	1648.58	1.93	0.13
Ego Age + Ego Sex + Relatedness + Ego Sex*Relatedness	1648.64	1.99	0.12
Age Difference Models			
Ego Age + Ego Sex + Relatedness + Ego Age*Ego Sex + Ego Sex*Relatedness	1646.65	0	0.33
Ego Age + Relatedness	1647.17	0.52	0.25
Ego Age + Ego Sex + Relatedness + Ego Age*Ego Sex + Ego Sex*Relatedness + Ego Age*Relatedness	1648	1.35	0.17
Ego Age + Ego Sex + Relatedness + Ego Age*Ego Sex	1648.58	1.93	0.13
Ego Age + Ego Sex + Relatedness + Ego Sex*Relatedness	1648.64	1.99	0.12
Sex of Alter Models			
Ego Age + Ego Sex + Relatedness + Ego Age*Relatedness	397.82	0	0.4
Ego Sex + Relatedness	398.6	0.78	0.27
Ego Sex	399.43	1.6	0.18
Ego Age + Ego Sex + Relatedness + Ego Sex*Relatedness + Ego Age*Relatedness	399.77	1.94	0.15
Same Sex Models			
Null	398.75	0	0.38
Ego Sex	399.43	0.67	0.27
Ego Age	400.22	1.47	0.18
Ego Sex + Relatedness + Ego Sex*Relatedness	400.48	1.72	0.16

Table 7.6: Coefficients and 95% confidence intervals of model averaged parameters from the models in table 7.5 (*n*=125; nominations=308). All models are mixed-effects models which control for repeated nominations by individuals. Note that 'sex of alter' and 'same sex' are logistic regressions, so estimates are log-odds ratios. Relative importance denotes the summed Akaike weight (w_i) of each parameter in the top models used in model averaging, with a '1' indicating that this term occurred in all of the top models.

Variable	**Age of Alter**	**Rel. Imp. (w_i)**	**Age Difference**	**Rel. Imp. (w_i)**	**Sex of Alter**	**Rel. Imp. (w_i)**	**Same Sex**	**Rel. Imp. (w_i)**
Intercept	6.72 [6.19; 7.25]	-	-2.41 [-1.88; -2.94]	-	0.2 [-0.21; 0.62]	-	0.64 [0.23; 1.06]	-
Ego Age	1.5 [0.42; 2.58]	1.00	-4.86 [-3.78; -5.94]	1.00	0.02 [-0.59; 0.63]	0.55	-0.05 [-0.44; 0.34]	0.43
Ego Sex	0.03 [-0.87; 0.93]	0.75	0.03 [-0.87; 0.93]	0.75	1.4 [0.52; 2.27]	1.00	0.21 [-0.49; 0.9]	0.18
Relatedness	-1.66 [-0.72; -2.61]	1.00	-1.66 [-0.72; -2.61]	1.00	-0.46 [-1.29; 0.36]	0.82	-0.03 [-0.36; 0.3]	0.16
Age* Sex	1.36 [-1.33; 4.04]	0.62	1.36 [-1.33; 4.04]	0.62	-	0	-	0
Sex* Rel	1.16 [-1.16; 3.49]	0.62	1.16 [-1.16; 3.49]	0.62	-0.05 [-0.68; 0.59]	0.15	-0.21 [-1.32; 0.91]	0.16
Age* Rel	-0.14 [-1.12; 0.84]	0.17	-0.14 [-1.12; 0.84]	0.17	-0.94 [-2.99; 1.11]	0.55	-	0

Similar effects were found for models examining the age difference between ego and alter. When including age as a predictor in these models the AICc values are identical to the previous set of models investigating alter's age (table 7.5). This is because age difference is a product of both ego's and alter's age, so the models produce analogous results. Parameter estimates for sex and relatedness main effects and the interaction terms are therefore identical for these models. What this analysis does show, however, which the previous one did not, is that the age difference between ego and alter is negatively associated with ego's age; as ego's age increases, the age difference between ego and alter's age also increases (figure 7.4). This suggests that individuals increasingly gave to younger children, relative to ego, with increasing age. A 2 SD increase in ego age was associated with a 4.9 year increase in the age difference between ego and alter. To some extent this finding may reflect 'floor effects', as young children could not give to those more than a few years younger than themselves. However, as recipient age increased with ego age (figure 7.3), this suggests that giving to the youngest individuals was not the sole aim of these resource transfers. As with the previous result regarding alter's age, the age difference was reduced if the recipient was a non-relative, while a weak interaction between ego age and sex suggested that the age difference increased more strongly with age for females than for males (figure 7.4).

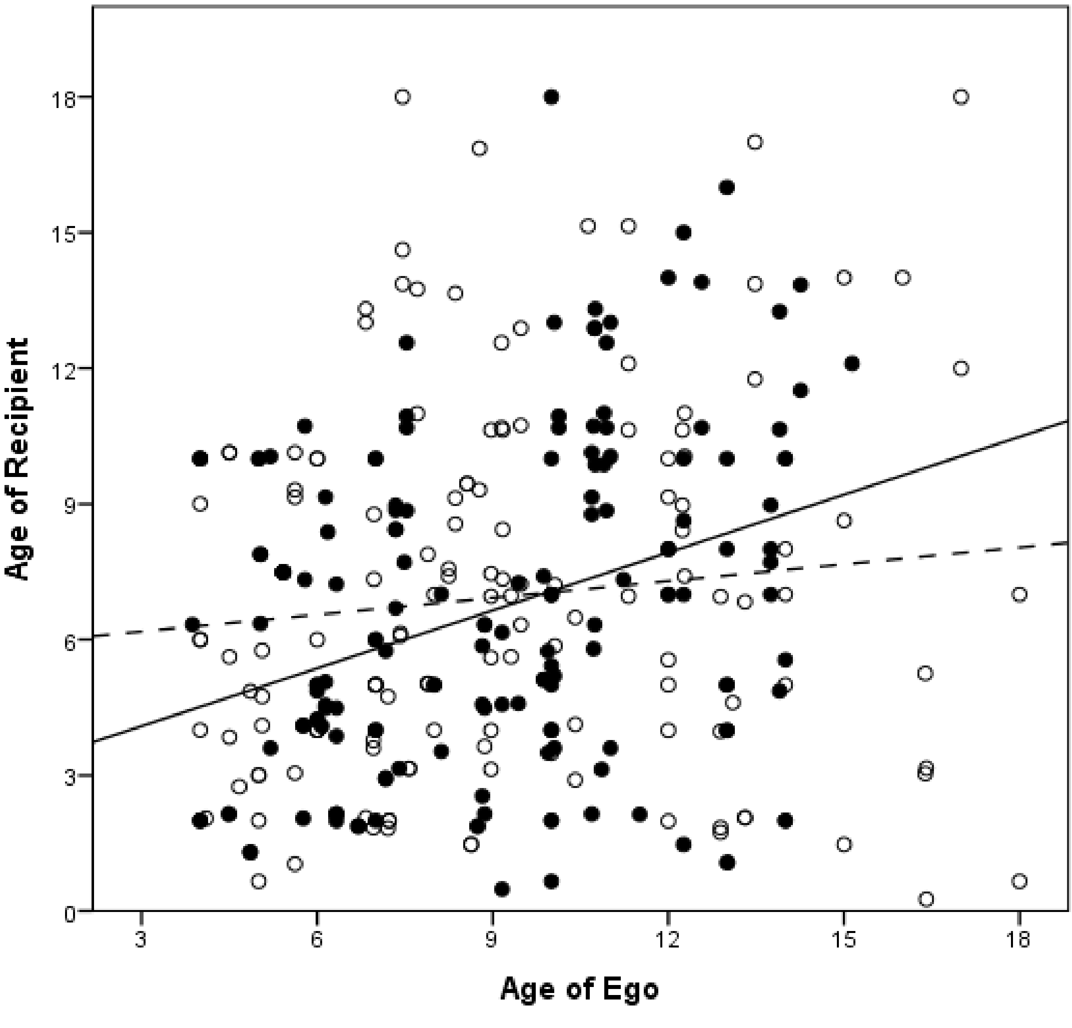

Figure 7.3: Interaction between age and sex of ego regarding the age of recipient (*n*=125; nominations=308). Female data points are denoted by hollow circles and are associated with the dashed line, while filled circles are male data points and are associated with the continuous line. This plot indicates that the effect of individuals giving to older children as they age is stronger in males, while for females the age of recipient co-varies less strongly with ego's age. Note that this figure does not control for repeated nominations by the same individual.

Taken together, these results indicate that there was a positive association between age of ego and age of recipient, which was potentially stronger in males (figure 7.3), and also that older children increasingly gave to recipients younger than themselves, particularly in females (figure 7.4). Although this may seem slightly counter-intuitive, if on average 5-year-olds gave to other 5-year-olds while 15-year-olds gave to 8-year-olds, then both the age of recipient (from 5 to 8) and the age difference (from 0 to negative 7) would increase with ego's age.

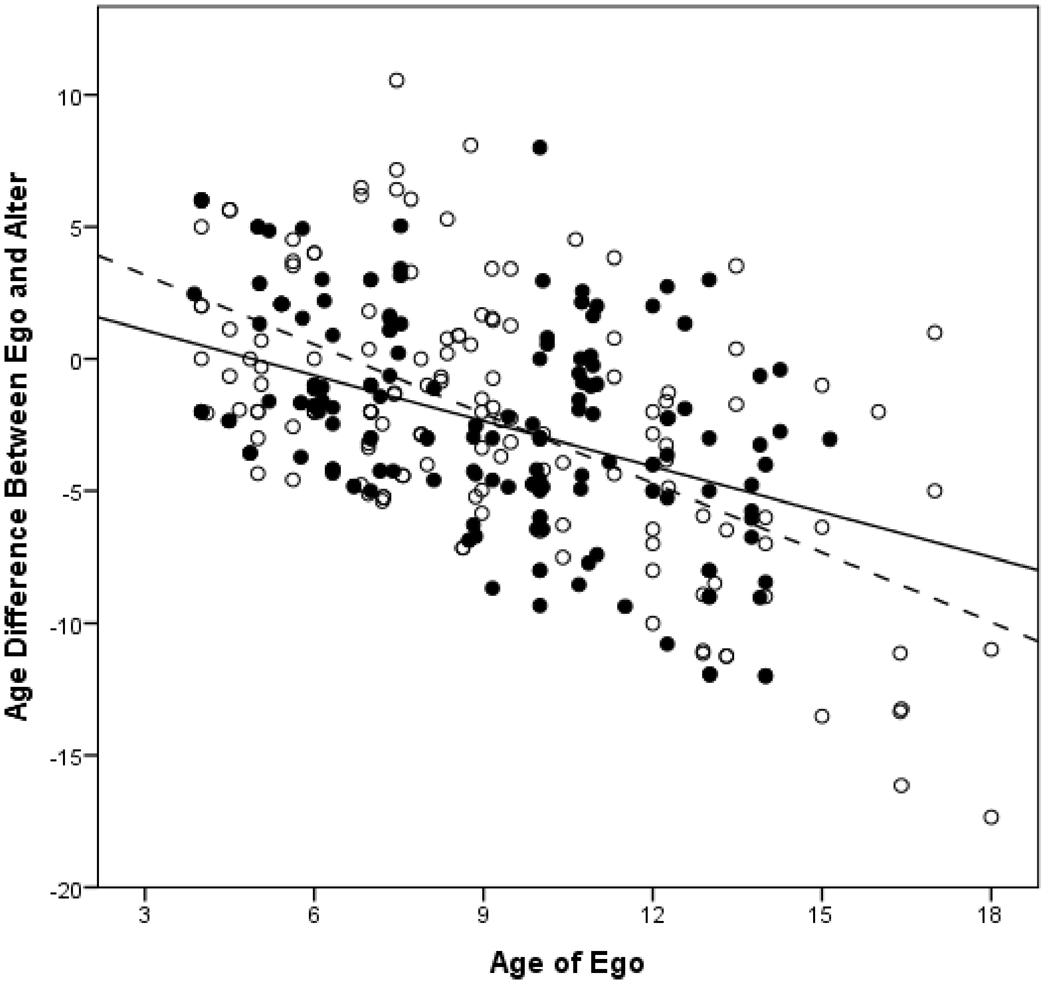

Figure 7.4: Interaction between age and sex of ego regarding the age difference between ego and recipient (*n*=125; nominations=308). Female data points are denoted by hollow circles and are associated with the dashed line, while filled circles are male data points and are associated with the continuous line. This plot indicates that the effect of individuals giving to others younger than self as they age is present in both sexes, but stronger in females. Note that this figure does not control for repeated nominations by the same individual.

Sex of recipient was most strongly associated with sex of ego, with individuals around four times more likely to give to same-sex recipients (table 7.6; for candidate model used in model averaging, see table 7.5). Males gave to other males 64% of the time (100 of 157 nominations) while 58% of female nominations were to other females (87 of 151 nominations; figure 7.5). No interactions or main effects of ego age or relatedness were reported regarding the sex of recipient. Although males were slightly more likely to nominate same sex individuals than females, the null model possessed the lowest AIC value regarding the probability of nominating same-sex individuals (table 7.5) and model averaging indicated that no terms were associated with an increased likelihood of giving to same-sex others (table 7.6).

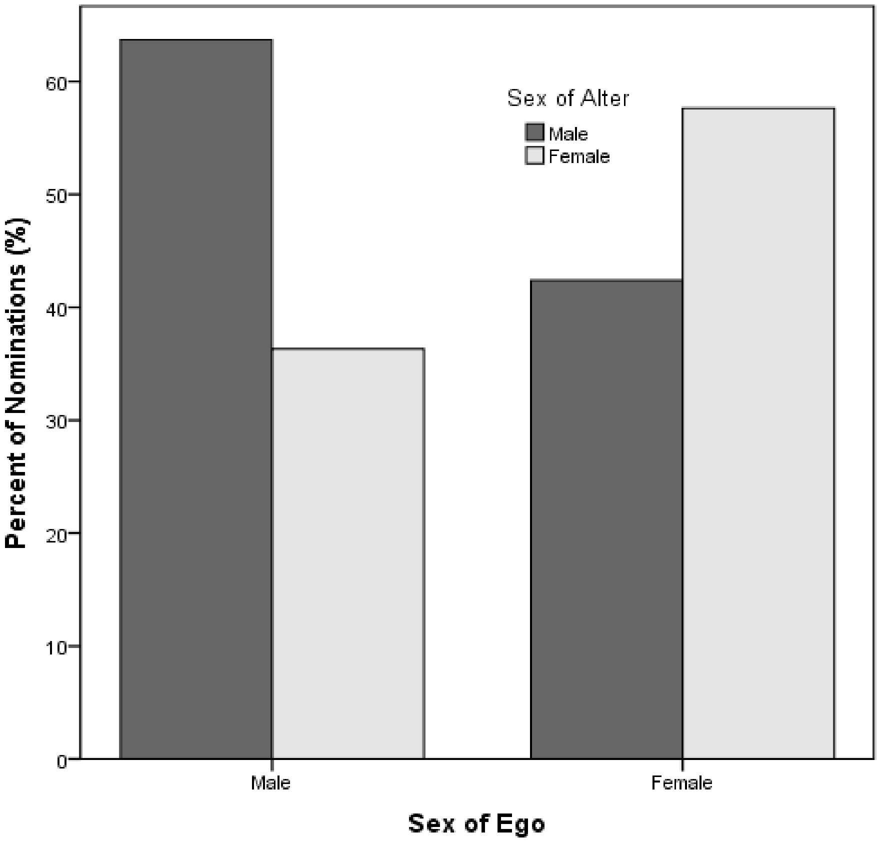

Figure 7.5: Percent of children's nominations divided by sex of ego (*x*-axis) and sex of recipient (males=dark grey; females=light grey: *n*=125; nominations=308: total male nominations=157, total female nominations=151). Both sexes preferentially nominated others of the same sex. Note that this figure does not control for repeated nominations by the same individual.

Of the 308 resources given to others, only 28 were reciprocated (9.1%). Many of these were between primary kin (19 of 28), meaning that kinship rather than reciprocity may have motivated these nominations. Only nine resources were shared reciprocally between non-primary kin (2.9% of all nominations), consisting of only four dyads. Of these, five resources were shared reciprocally between distant kin, meaning that only four resources were shared reciprocally between non-kin (1.3% of all nominations). That is, only two unrelated dyads shared resources reciprocally. These figures may slightly underestimate the level of reciprocity due to many individuals who received resources not having played the game. Even if only recipients who played the games are included, resulting in 186 nominations, levels of reciprocity still appear low, especially after controlling for kinship (table 7.7). Although difficult to assess definitively due to the small sample size and high collinearity with relatedness, these results suggest that much cooperation among children is independent of reciprocal concerns. It may also be instructive to compare these frequencies against those of adults; of 492 resources given to others in the adult Sharing Game, 266 were reciprocated (54.1%), a much higher frequency than observed among children.

Table 7.7: Frequency and percentage of reciprocal nominations, split by relatedness, for both the full sample of nominations (*n*=125, nominations=308) and the sub-sample of nominations for recipients who also played the game (nominations=186).

Relationship	Number of Reciprocal Nominations	Number of Reciprocal Dyads	% of Reciprocal Nominations (full sample)	% of Reciprocal Nominations (of recipients who played the game)
Primary Kin	19	7	6.2%	10.2%
Distant Kin	5	2	1.6%	2.7%
Non-Kin	4	2	1.3%	2.2%
Total	28	11	9.1%	15.1%

Discussion

These results have several implications for the ontogeny of cooperative behaviour, both specific to hunter-gatherers and more generally. Findings are initially discussed in terms of children's levels of cooperation, then subsequently by who they chose to share with. Firstly, and similar to findings regarding adult levels of cooperation (Chapter 4), children displayed a great amount of variability in cooperative behaviour, especially at the camp level. Some camps averagely gave more than half of all gifts to others, while in other camps every child kept all resources for themselves. Interestingly, this was also the camp in which every adult kept all resources for themselves. The only strongly significant predictor of children's giving behaviour was the average adult camp level of cooperativeness, which explained ~80% of the camp-level variance in children's behaviour. Researchers should therefore be wary about cross-cultural comparisons which only explore one (or few) groups from each society, as they may be detecting local, rather than population-wide, differences in cooperation (Lamba & Mace 2011), even among children.

Compared to previous studies investigating the ontogeny of cooperative behaviour in small-scale societies, the results here both somewhat corroborate and somewhat differ from their findings. The present study supports the conclusion that childhood cooperativeness corresponds to adult levels, although in this instance at an inter-camp level, as opposed to an inter-society level (House *et al.* 2013). However, rather than develop these camp-specific profiles of cooperativeness over time, Agta children appear to possess them from early childhood, with little effect of age. This demonstrates that group-level cooperative profiles are performed by even the youngest children, arguing against theories that middle-childhood is a particularly important period for children to acquire group-specific cooperative behaviour (House *et al.* 2013). This also suggests that the lowered levels of food-sharing among young Hadza children, relative to older Hadza children, may reflect constraints on foraging and resource acquisition, rather than a lack of motivation to share (Crittenden & Zes 2015). Although no age effects regarding overall levels of cooperation were reported, the total number of recipients given to did increase with age. The number of sharing partners, but not necessarily the amount shared, may therefore increase with age. Other variables previously reported as influencing cooperative behaviour, such as sex (Gummerum *et al.* 2008b; House *et al.* 2012) and siblings effects (Fehr *et al.* 2008; House *et al.* 2012), were not replicated among the Agta. There was also no evidence for the vertical transmission (from parent to offspring) of cooperative behaviour.

When interpreting these results a distinction needs to be made regarding proximate mechanisms and ultimate explanations for behaviour (Mayr 1961; Tinbergen 1963). Ultimate explanations concern the fitness consequences of behaviour (*why* organisms perform that behaviour), while proximate mechanisms relate to how said behaviour is achieved (*how* organisms perform that behaviour; Scott-Phillips, Dickins, & West, 2011). As adult cooperation levels depend largely on socioecological factors (Chapter 4), Agta cooperative behaviour conforms to theoretical expectations, such as cooperation requiring repeated interactions (Trivers 1971; Axelrod & Hamilton 1981; Pfeiffer *et al.* 2005) or increased costs decreasing levels of cooperation (West *et al.* 2006). As children's cooperative behaviour is solely and strongly predicted by that of adults (figure 7.1), children's levels of cooperation therefore also appear to conform to adaptive expectations based on maximising inclusive fitness (an ultimate explanation). Children may therefore be sensitive to the varying costs and benefits of cooperation under different environmental conditions and adapt their behaviour accordingly. The proximate mechanisms are more difficult to assess, as several different mechanisms could underlie these results. For instance, the similarity between children and adults from the same camp could be a result of social learning, individual learning, reaction norms based on environmental cues, genetic predispositions, or any combination thereof. Although a solely genetic explanation is unlikely and it is possible to rule out vertical transmission, it is impossible to assess the relative value of each of the other approaches from the data here (and it is likely that each of them has some merit).

A theoretical point relating to this concerns the fields of cultural evolution and human behavioural ecology, which are often seen as competing hypotheses as explanations for human behaviour (Mathew & Perreault 2015). Proponents of a ‘cultural evolution’ approach claim that cultural transmission can explain much of the variation in human behaviour (Boyd & Richerson 1985; Richerson & Boyd 2005; Mathew & Perreault 2015), while tending to overlook or disregard hypotheses derived from behavioural ecology based on maximising individual fitness (Mace 2014). Meanwhile, human behavioural ecologists are often charged with ignoring the role that cultural transmission can play in their models of human behaviour (Borgerhoff Mulder 2013; Mathew & Perreault 2015). As human behavioural ecology explores the ultimate fitness consequences of behaviour (Winterhalder & Smith 2000; Borgerhoff Mulder & Schacht 2012; Nettle *et al.* 2013a), the actual proximate mechanisms, be they social learning, individual learning or genetically programmed, are largely irrelevant to whether behaviour maximises fitness or not (this is not to disregard the importance of understanding proximate mechanisms, however). Culture and cultural transmission are mechanisms which are often – although not inevitably – used to increase inclusive fitness. Cultural evolution is not therefore opposed to a human behavioural ecology approach (and vice versa), but rather answer different questions and can be difficult to separate in practice (Mace 2014).

Contrary to the amount given to others discussed above, a significant ontogenetic trend emerged regarding the recipients of cooperative behaviour. Firstly, resources were predominantly given towards kin, suggesting that kin selection may play a strong role in shaping patterns of children's cooperation. Additionally, as children aged they increasingly gave resources to less related individuals. This is especially relevant in the context of extensive cooperation between unrelated individuals, as is common among forager societies (Hill *et al.* 2011; Chaudhary *et al.* 2015; Dyble *et al.* 2015). These findings dovetail well with interaction data from the same population indicating that children spend increasing amounts of time with less related individuals as they age (Migliano *et al.* 2017). In contrast to patterns of sharing among adult Agta in these games (Chapter 5), children appeared to have little concern regarding reciprocity. Removing any potential confound of kinship, only four gifts (between two dyads) were given reciprocally among children. These results also do not conform to predictions made by a sexual selection argument for cooperation as adolescents were not more likely to give to members of the opposite sex than younger children. Therefore, while kin selection appears to significantly predict children's resource transfers, immediate direct fitness benefits, at least regarding reciprocity and sexual selection, seem to be of lesser importance.

I also find evidence consistent with other hypotheses regarding cooperating for delayed direct fitness benefits, such as learning foraging, childcare or general social skills. Strong ontogenetic changes were found regarding the age of recipient and the age difference between ego and alter. A positive association between age of ego and age of recipient was reported, while, simultaneously, older individuals also preferentially gave to children increasingly younger than themselves. Children of both sexes gave resources to same-sex individuals, with no change in this bias over childhood. These same-age and same-sex effects may reflect the need for children to learn social skills with their peers and form same-sex relationships (Flinn & Ward 2005), as in adulthood foragers spend much of their time in same-sex groups and cooperate with same-sex individuals (Apicella *et al.* 2012; see also Chapters 5 and 6 in this thesis). Children also gave to increasingly younger children relative to their own age as they developed, likely reflecting allocare of young camp-mates. Kinship effects also mediated recipient age, with close kin who received resources younger than non-kin recipients. This is consistent with cooperation towards kin, who were younger, reflecting indirect fitness benefits, and cooperation towards less-related children, who were older, reflecting cooperation with peers for direct fitness benefits (potentially including learning skills necessary for adulthood).

Some age-sex interaction effects were also reported, indicating that the association between giving to individuals of a similar age was stronger in males than females (figure 7.3), while older females were more likely to give to younger children than older males (figure 7.4), although these interaction effects were relatively weak. Same-age relationships may be more important in juvenile males potentially due to either the need to learn foraging skills from peers (Kaplan *et al.* 2000) or because same-age relationships, for reasons other than learning to forage, are more important for males than females. Such explanations may include higher benefits to male coalition formation, potentially reflecting group defence, warfare, cooperative foraging, or other adaptive challenges requiring male cooperation (Wrangham 1999;

Macfarlan *et al.* 2014; David-Barrett *et al.* 2015). While it is difficult to distinguish between these competing hypotheses from the current data, if juvenile males cooperated just as a consequence of learning to forage, then cooperating and interacting with older or more experienced partners would be a better strategy to learn these skills. Despite a positive association between age of ego and age of recipient, juvenile males still preferentially shared with others younger than themselves, which may weaken the argument that these sharing networks reflect the need to learn complex foraging skills. I therefore tentatively suggest that forming social bonds and learning social skills may be more important determinants of male children's cooperative networks than learning to forage, although this requires much more extensive empirical research.

Giving to younger children may be more important for adolescent females, relative to adolescent males, potentially due to either indirect fitness benefits (kin selection) or direct benefits, such as learning to mother. It is probable that these results reflect a combination of the two. This sharing, particularly among unrelated children, may reflect the need for females to learn skills necessary to become competent mothers. Experience with care-giving during development has been associated with heightened mothering ability among several non-human species (Fairbanks 1990; Margulis *et al.* 2005; Stone *et al.* 2010), although this relationship is not found in all studies (Paul & Kuester 1996; Silk 1999) and little research in this area has been conducted on humans (but see Leerkes & Burney 2007). However, as a same-sex bias is observed among juvenile females this suggests that cooperation among female children may also be a result of learning general social skills and not just learning to mother. These sex differences likely reflect greater engagement in sex-specific adult roles throughout adolescence, with males beginning to participate in all-male groups, while females increasingly prepare for a care-giving role (Kaplan *et al.* 2009). These findings are consistent with children cooperating with specific others for delayed direct fitness benefits, in addition to cooperation with kin for indirect fitness benefits discussed above. While sex differences in cooperative networks are present, these should not obscure a main effect of these analyses which suggests that all children, regardless of sex, engage in significant levels of allocare of young camp-mates, particularly of kin.

Regardless of the specific underlying mechanisms, these results suggest a development shift, not in terms of how cooperative children are, but rather with whom children cooperate. On a broader theoretical level these results indicate that partner choice is present as children display discriminative cooperative behaviour. Partner choice is central to several theories for the evolution of cooperation (Barclay 2013; Baumard *et al.* 2013; Roberts 2015), yet these have rarely been explored in ontogenetic studies of cooperation in children (although see Moore 2009; Olson & Spelke 2008). These findings demonstrate the importance of considering assortativity and partner selectivity in explaining patterns of cooperation not just among adults, but also among children, and observing how these develop over the lifespan and serve an individual's adaptive needs.

This developmental trend towards giving more to unrelated individuals as childhood progresses may also explain why the results of the present study differ from that of other studies which do report age effects (Fehr *et al.* 2008; House *et al.* 2013; Blake *et al.* 2015). In these studies, immediate family members were excluded as recipients, meaning that younger children may have appeared more selfish because at this age they would normally preferentially cooperate with kin rather than unrelated individuals. These ontogenetic shifts in partner choice may explain why an increase in cooperativeness over childhood was not observed in the present study (this does not account for why the youngest children in the House et al. (2013) study were particularly cooperative, though). However, human behaviour is nothing if not adaptable, meaning that these patterns of cooperation may vary given different socioecological circumstances. For instance, kin may be of less importance in 'WEIRD' (Western, Educated, Industrialised, Rich, and Democratic: Henrich, Heine, & Norenzayan, 2010) societies as kinship ties are generally much weaker. The ontogeny of partner choice and how this varies with socioecological conditions is an area in need of further research.

The findings presented here have important implications for human's derived life history. In order for reproductive-aged women to maintain their high fertility rate, allomaternal help is necessary to supplement care and help provision children. This has traditionally assumed to have been by fathers (Kaplan *et al.* 2000), grandmothers (Hawkes *et al.* 1998) or other extended kin (Sear & Mace 2008). The role of older siblings, or other children, in caring for these dependants has generally been overlooked, although recently several papers exploring the role of children in subsistence and aiding offspring survival have been published (Kramer 2005, 2011; Sear & Mace 2008; Crittenden *et al.* 2013). The results here provide evidence for the importance of allocare by children, as they appear willing to engage in costly giving to assist other, especially younger and related, children. Young children in particular provision siblings, with ~70% of all resources shared by 3-7 year olds given to siblings (figure 7.2). This also indicates that children are motivated to invest in helping others and are not necessarily coerced into caring (Crittenden & Marlowe, 2008; although the variation in cooperativeness between camps suggests that children in some camps may be more willing to invest in allocare, at least regarding resource sharing, than others). These results demonstrate that children possess a motivation to provision and care for other children, particularly siblings, which may contribute to the high fertility rate and demographic success of humans (Kramer 2010).

These results also have a significant bearing on human's derived cumulative cultural capabilities, which are much more extensive than other animals, including great apes (Marshall-Pescini & Whiten 2008; Tennie *et al.* 2009; Dean *et al.* 2012). A larger group of potential cultural models, combined with increasingly cooperative and friendly interactions with conspecifics, have been theorised to increase the rate of cumulative cultural evolution (Burkart *et al.* 2009; Powell *et al.* 2009; Hill *et al.* 2011; Derex & Boyd 2016). Previous studies have indicated that the range of potential models in hunter-gatherers is large, as a result of high mobility between camps as part of a meta-group (Hill *et al.* 2014). The present study augments this argument by investigating the developmental trajectory of cooperative behaviour and with whom individuals cooperate. Results suggest that interactions and cooperation between unrelated individuals increase in frequency with age, potentially enhancing the pool of cultural models to learn from, which may facilitate cumulative cultural evolution (see also Migliano *et al.* 2017). As older children were also found to share with a greater number of camp-mates, this also suggests that network size increases with age, again potentially increasing the rate of information transfer.

Summary and Next Chapter

The main points of this chapter can be summarised as follows: i) within-society variation in the ontogeny of cooperative behaviour is high, suggesting that cross-cultural developmental research needs to examine more than one group per population, as otherwise one may mistake local differences in socioecology for wider differences between cultures; ii) the only significant predictor of childhood cooperativeness was the adult camp level of cooperation. This indicates that cooperative behaviour, at least in this highly-simplified task, does not necessarily increase with age, but rather depends on similar socioecological factors to those influencing adult levels of cooperation; and iii) ontogenetic trends did, however, emerge regarding who individuals gave to, with closely-related children more likely to receive resources than non-kin. Older children were also increasingly likely to give to more individuals, share with less related camp-mates and cooperate with both similar-aged individuals as well as those increasingly younger than themselves. These findings support the perspective that children's cooperative behaviour can be understood from a functional evolutionary perspective, and not interpreted solely as 'learning to become adult', as implied by the results of several previous studies which stress the importance of 'socialisation' (House *et al.* 2013; Blake *et al.* 2015). Rather, the ontogenetic trajectory of cooperative behaviour can also be explored from the perspective that children are decision-making agents in their own right (taking physical and cognitive developmental constraints into consideration), navigating a complex social world which, in order to maximise inclusive fitness, may require different adaptive solutions from that of adults, as well as from other children of a different age or sex. The next chapter summarises the main findings and conclusions of this thesis, integrates them with the wider literature on the evolution of cooperation and details avenues for further research.

Chapter 8 Summary and Conclusions

The aim of this thesis has been to use experimental protocols to explore theories for the evolution of cooperation in humans, with a specific focus on understanding hunter-gatherer cooperation and food-sharing. As described in the introductory chapter, a number of experimental games to investigate cooperation exist and have been applied in several small-scale societies. However, these methods often suffer from a lack of convergent validity (different games seem to measure different aspects of cooperation) and external validity (it is unclear the extent to which behaviour in these games is representative of real-world cooperative behaviour). Many previous methodologies are also insufficient to test various existing theories for the evolution of cooperation and food-sharing among hunter-gatherers. For instance, games such as the Dictator or Ultimatum Game, which employ anonymous partners, cannot directly explore effects of kinship or reciprocity, even though these are central to cooperative evolution. In addition to exploring cooperative dynamics among hunter-gatherers, this thesis is also an attempt to overcome these limitations by designing ecologically valid experimental methods which bridge the gap between experimental game behaviour and evolutionary theories of cooperation and forager food-sharing. I begin by summarising the main findings, followed by the wider theoretical significance of these results and end on recommendations for future experimental game research in forager and other small-scale societies, as well as experimental studies on human cooperation more generally.

Summary of Main Findings

I find considerable variation in cooperative behaviour between Agta camps, with some camps giving on average nearly three-quarters of resources to others, while in other camps every individual kept all resources for themselves. Indeed, ~30% of the variance in cooperative behaviour in the Sharing Game was at the camp level. This within-society variation is nearly three times greater than the between-society variation found across 15 different small-scale societies, in which ~12% of the variation in Ultimatum Game behaviour was found at the population level (Henrich *et al.* 2005). This within-society variation is difficult to reconcile with cultural group selection (CGS) approaches to the evolution of cooperation (Henrich 2004a; Boyd & Richerson 2005; Richerson & Boyd 2005; Richerson *et al.* 2016). In order for CGS to occur, cooperative behaviour within ethnolinguistic groups must to be uniform to reduce within-group competition and increase the magnitude of between-group selection. The findings reported here, in addition to those of other societies displaying substantial levels of within-society variation (Gurven *et al.* 2008; Lamba & Mace 2011, 2013; Nettle *et al.* 2011; Holland *et al.* 2012; Silva & Mace 2014), argue against CGS as an explanation for much of human cooperative behaviour, particularly prior to the advent of large-scale societies.

Rather, the results of this thesis and other studies have indicated that differences in socioecology appear to predict a significant amount of variation in cooperative behaviour. For instance, I find that measures of need and resource availability predict cooperativeness, with individuals in greater need or with fewer resources (i.e., having more dependent offspring or fewer rice supplies) displaying a reduction in cooperative behaviour. This can be explained by a simple difference in the costs and benefits to cooperation. For individuals in greater need the costs to cooperation are higher as resources would hold greater value for them compared to others less in need. The socioecological variable which explained the most variation in cooperative behaviour among the Agta, though, was camp stability, with individuals in more stable camps displaying greater levels of cooperative behaviour. This is consistent with theories positing that repeated interactions aid the evolution of cooperation (Trivers 1971; Axelrod & Hamilton 1981; Pfeiffer *et al.* 2005).

The semi-anonymous design of these experimental games permitted not only an analysis of how much individuals cooperated, but also who they cooperated with. This allowed analyses similar to numerous food-sharing studies among hunter-gatherers investigating which individuals foragers are most likely to share resources with (Hawkes *et al.* 2001; Bliege Bird *et al.* 2002; Gurven 2004c, d; Ziker & Schnegg 2005; Allen-Arave *et al.* 2008; Nolin 2010). This moves beyond previous experimental games which pair anonymous partners, meaning that the present design permits an exploration of the respective roles of kin selection, reciprocity, indirect reciprocity, and other theories relevant to the evolution of cooperation which posit partner choice. The two games were designed to explore patterns of food-sharing under two conditions which are often difficult to assess via observational data: high vs. low levels of producer control. To recap briefly, high producer control refers to situations where the acquirer of the resources has control over distribution, while under conditions of low producer control recipients take resources from the producer, regardless of the producer's wishes. Patterns of resource transfers were dramatically different under the two conditions. In the Sharing Game (high producer control) resources were predominantly given to consanguineal kin and reciprocating partners, whereas in the Taking Game (low producer control) resources were predominantly taken from those with more resources, with no consideration for kinship or reciprocity. The role of producer control therefore appears to exert an enormous influence on subsequent resource distributions.

Taken together with the results regarding camp stability, these findings suggest that giving behaviour is more prevalent in stable camps, and that this giving behaviour is associated with both kin-biased and reciprocal sharing. In contrast, taking behaviour is more common in unstable camps, and individuals take from those who possess more resources, regardless of reciprocal or kinship considerations. These results indicate that a high frequency of repeated interactions, increased levels of producer control and reciprocity (in addition to kin selection) may form an adaptive suite of traits. These are likely to be adaptive because reciprocity avoids non-sharing free-riders (Trivers 1971; Axelrod & Hamilton 1981), but requires repeated interactions and high levels of producer control in order to distribute resources to known reciprocating partners. Kin selection may also be associated with these traits as it too requires high levels of producer control to distribute resources to kin. In contrast, increased residential mobility, reduced producer control and demand sharing also appear to form an alternative adaptive suite of traits. Under situations where interactions are less likely to be repeated, reciprocity is a less viable mechanism to avoid free-riders. However, a recent model exploring the evolution of demand sharing found that, in order for demand sharing to be viable, high levels of mobility were required to avoid non-hunting free-riders (Lewis *et al.* 2014). Thus, hunter-gatherer food-sharing may form a continuum: from demand sharing and low producer control where camp stability is low and mobility high, to reciprocity (and kin selection) and high producer control where camp stability is high and mobility low. Both may be adaptive strategies under different socioecological conditions.

Despite the great amount of variation in patterns of food-sharing among forager societies, with kin selection, reciprocity and tolerated theft explaining distributions in some societies but not others (for a review see Gurven 2004d), little research has examined the cause(s) of this variation (although see Gurven *et al.* 2002). The results of the present thesis suggest that mobility and camp stability may play a particularly important role in explaining this variation. For instance, among the highly-mobile forest-living Ache, food transfers were neither reciprocal nor kin-based, but rather based on proximity, indicative of a demand sharing system. In contrast, among the settled reservation-living Ache, both kinship and reciprocity were significant predictors of distributions, indicative of increased levels of producer control (Gurven *et al.* 2002). Similarly, among the highly-mobile Hadza food-sharing was not reciprocal (Hawkes *et al.* 2001), while among the settled Lamalera (Nolin 2010) and Dolgan/Nganasan (Ziker & Schnegg 2005) reciprocity and kin selection were both significant predictors of food-sharing. Rather fortuitously, the Ultimatum Game has also been conducted in these four populations: reservation-living Ache and the Lamalera were the two most cooperative societies studied in Phase I of the *Roots of Human Sociality Project*, offering 48% and 57% of the stake, respectively. Meanwhile, the Hadza were one of the least cooperative populations, offering only 33% of the stake in Phase I (Henrich *et al.* 2005) and 26% in Phase II (Henrich *et al.* 2010a). The Dolgan/Nganasan from Phase II of the project were also extremely cooperative in the Ultimatum Game, offering an average of 48% of the stake (Ziker 2014). Thus, it appears that groups with reduced mobility which engage in reciprocal and kin-biased sharing were also more cooperative in these experimental games.

Similar patterns are found among the Agta. Food-sharing data were collected in six camps (by fellow project member Mark Dyble), and in three of these camps significant levels of reciprocity were found, while in the other three reciprocity was a non-significant predictor of resource transfers (Smith *et al.* 2016a). The reciprocal camps were found to have greater camp stability and also gave more to others in the Sharing Game, while the non-reciprocal camps possessed lower camp stability and took more from others in the Taking Game, consistent with a demand sharing system of food-transfers. Some of the observed variation in food-sharing practices, as well as experimental game behaviour, may therefore be explained by differences in mobility and camp stability, although future research, particularly cross-cultural work, is required to assess this putative link further.

The majority of research on cooperation and food-sharing has concerned 'in-kind' transfers, such as like-for-like reciprocal sharing or those with a reputation for food-sharing receiving more resources via indirect reciprocity (Nowak & Sigmund 1998, 2005) or competitive altruism (Roberts 1998). However, 'not-in-kind' transfers, such as trading meat for coalitional support (Patton 2005) or resources for mating opportunities (Bliege Bird *et al.* 2001; Hawkes & Bliege Bird 2002), are being increasingly recognised as important to forager food-sharing and cooperation more widely (Jaeggi *et al.* 2016). These different approaches can be subsumed within a wider 'biological market' framework, in which individuals interact and cooperate with those who hold the greatest 'market value' for them as potential partners, be it in terms of reciprocity, mating opportunities, information transfer, resource procurement, or other considerations (Noë & Hammerstein 1995; Barclay 2013; Hammerstein & Noë 2016). I find that skilled storytellers appear to possess high value among the Agta, as these individuals were both more likely to be nominated in a camp-mate network and to receive resources in the Sharing Game. There was no evidence for indirect reciprocity in either network, as more cooperative individuals (as inferred from behaviour in the Sharing Game) were less likely both to receive resources and be nominated as a future camp-mate. Competency, in terms of information transfer and facilitating group cohesion, as performed by storytellers, may therefore be held in greater esteem by the Agta than an individual's level of cooperativeness. This 'biological market' approach therefore has the potential to greatly increase our understanding of cooperative and interaction networks. Although the sharing and camp-mate networks were broadly similar in some respects, such as a preference for kin and reciprocating partners in both, there were also several noticeable differences. For instance, age, sex and cooperative homophily effects were much stronger in the camp-mate network, while individuals preferentially shared resources with older individuals but wished to live with younger camp-mates. This suggests that different social networks may serve different adaptive functions, although work on this topic is largely in its infancy.

This thesis also explored cooperative behaviour among Agta children using a similar experimental game to the Sharing Game conducted with adults. In contrast to previous studies investigating the ontogeny of cooperative behaviour in small-scale societies (Rochat *et al.* 2009; House *et al.* 2013; Blake *et al.* 2015), I find no effect of age on levels of cooperation, indicating that young children were equally as cooperative as older children. The only strongly predictive effect was that child levels of cooperation corresponded with the adult average level of cooperation in said camp. This demonstrates that group-specific cooperative behaviour may be internalised and stable throughout childhood, arguing against theories suggesting that ontogenetic changes in cooperative behaviour are equivalent between different populations prior to middle-childhood (House *et al.* 2013; Blake *et al.* 2015). Instead, these results indicate that camp-level patterns of cooperation may have a pervasive influence throughout the entirety of childhood. Ontogenetic changes are, however, found regarding who children share resources with. The probability of giving to non-kin was greater in older children, indicating that the importance of cooperating with unrelated individuals increased with age, likely reflecting integration beyond the immediate family and with the wider social community. Age effects were also reported, with individuals more likely to give to older children as they aged, an effect which was more pronounced in males. This may highlight the significance of similar-aged peer groups among hunter-gatherer children. Simultaneously, older children were also more likely to give to children increasingly younger than themselves, an effect which was stronger in older female children. These results emphasise the importance of allocare and cooperative breeding in understanding forager children's cooperation, which may have implications for understanding the evolution of human life history.

Together, these results demonstrate how experimental approaches can help understand patterns of hunter-gatherer cooperation. I next turn to some of the wider theoretical and conceptual issues surrounding these results.

Wider Theoretical and Conceptual Issues

There is a disparity, despite similar subject matter, in how research on food-sharing and research on experimental games in small-scales societies has been interpreted. Studies of hunter-gatherer food-sharing are often interpreted from a human behavioural ecology (HBE) perspective of individuals attempting to maximise their inclusive fitness (Kaplan & Hill 1985; Hawkes *et al.* 2001; Gurven 2004d; Nolin 2010). Yet when experimental games have been conducted in small-scale societies this approach is often neglected in favour of a 'cultural evolution' approach (Henrich *et al.* 2004b, 2005, 2010a; Ensminger & Henrich 2014). That is, cross-cultural variation in experimental cooperative behaviour has tended to be interpreted as cultural adaptations, such as market or religious norms, which evolved via CGS.

One of the aims of this thesis has been to use a HBE approach to explore and understand variation in cooperative game behaviour. In many studies, between-group variation is only explored from a CGS perspective (Henrich *et al.* 2005, 2010a; Richerson *et al.* 2016), with little attempt at explaining it from an individual fitness-maximising perspective. Although group-level variation in behaviour is often ascribed to CGS, HBE makes similar predictions if there are differences in socioecology which require different behavioural strategies in order to maximise fitness. As demonstrated in this thesis and in other previous publications (Lamba & Mace 2011, 2013; Holland *et al.* 2012; Silva & Mace 2014), when variation in cooperative behaviour is explored from an inclusive fitness framework it appears to have significant predictive power. This perspective also predicts within-group variation which cannot be explained by CGS. HBE is often overlooked as a theoretical framework for understanding the evolution of cooperative behaviour (see, for instance, Henrich *et al.* 2005, 2014; Tomasello *et al.* 2012; Chudek *et al.* 2013; Zefferman 2014; Richerson *et al.* 2016), yet this may be a significant oversight as HBE appears a powerful approach for understanding human cooperation.

A related topic, also discussed in the previous chapter, concerns whether cultural evolutionary perspectives and HBE approaches based on maximising inclusive fitness to the local socioecological conditions are competing or consilient approaches to understanding human behavioural diversity (this discussion excludes CGS, which *is* a competing approach to an inclusive fitness perspective for understanding human behaviour from an evolutionary perspective). Some studies pit these as competing approaches, for example, assessing whether cultural history or local ecology better predict behaviour (Guglielmino *et al.* 1995; Mathew & Perreault 2015). Others see these as consilient explanations for human behaviour, with culture (a proximate mechanism) used to maximising inclusive fitness (an ultimate explanation) given current socioecological circumstances (Mace 2014). Under this latter perspective there is no conflict between these two approaches as they answer different questions; ultimate explanations based on maximising fitness answer *why* said behaviour is adaptive in the current context, while cultural transmission offers one answer of *how* said behaviour is achieved (Scott-Phillips *et al.* 2011). This is not to imply that cultural transmission mechanisms are infallible and always result in optimally-adapted behaviour. All proximate mechanisms may 'misfire' when placed in novel or unusual circumstances (West *et al.* 2011) and the importance of history should not be ignored (Guglielmino *et al.* 1995; Mathew & Perreault 2015), but cultural transmission – like all proximate mechanisms – should align with promoting inclusive fitness in many contexts (otherwise it would be selected against if it reduced fitness).

The next question to ask is: what *are* the proximate mechanisms involved in explaining variation in human cooperative behaviour? The HBE approach adopted here is largely 'mechanism neutral', in that it is concerned with ultimate explanations rather than proximate mechanisms (it assumes a 'phenotypic gambit' where the precise proximate mechanisms are often left unspecified; Winterhalder & Smith 2000; Brown *et al.* 2011; Borgerhoff Mulder & Schacht 2012; Nettle *et al.* 2013a). A full understanding of human behaviour, however, requires knowledge of the proximate mechanisms involved, which are often difficult to assess. Differences between groups or populations are often interpreted as a result of cultural transmission and a shared cultural history (Richerson & Boyd 2005; Mesoudi 2015; Richerson *et al.* 2016). This is likely to be a reasonable assumption for complex cultural traits such as technology (Henrich 2004b; Powell *et al.* 2009; Kline & Boyd

2010), institutional complexity (Currie & Mace 2009, 2011; Currie *et al.* 2010) and folktales or religions (Watts *et al.* 2015, 2016; Graça da Silva & Tehrani 2016), as these could not be conceived of by individuals without cumulative cultural learning. Problems occur, however, concerning individual behaviours such as cooperation which can emerge by several mechanisms, including genetic predispositions, evolved reaction norms, individual learning or social learning (or combinations thereof). Unlike complex technology which is absent in other species, many other species display variability and plasticity in cooperative behaviour, from bacteria (Kümmerli *et al.* 2009) to long-tailed tits (Adams *et al.* 2015). This cooperation evolved in the absence of cultural transmission, meaning that there are multiple pathways to developing cooperative behaviour. Many of these make similar predictions regarding the distribution of cooperative behaviour, making them difficult to differentiate. For instance, both reaction norms and biased cultural transmission (e.g., conformism) predict that, given different environments, behaviour within groups will be more similar than behaviour between groups, irrespective of differences in genetics.

As discussed in the previous chapter regarding children's cooperative game behaviour (and which also applies to adults), the available evidence does not allow us to differentiate between these alternatives. It is often assumed that cooperative behaviour, in both children (Fehr *et al.* 2008; House *et al.* 2013; Blake *et al.* 2015) and adults (Henrich *et al.* 2005, 2010a; Richerson *et al.* 2016), is socially learned, yet without additional research this largely remains an untested assumption (Lamba 2014). In the absence of social information individuals change their cooperative behaviour according to cues of anonymity (Ernest-Jones *et al.* 2011; Nettle *et al.* 2013b), whether competition is within- or between-groups (West *et al.* 2006), as well as whether there are repeated interactions or not (Dal Bo 2005; Kanagaretnam *et al.* 2010). This variation can all be explained by individual-level adaptive decision-making, without the need for socially learned cooperative norms. In fact, even when individuals are explicitly given social information in an experimental cooperative game, they tend to display neither conformity nor pay-off biased transmission, indicating a lack of utilising social information when performing cooperative behaviour (Lamba 2014). This is not to say that cultural transmission is unimportant for acquiring cooperative behaviour, but at the moment this is a largely untested assumption and likely occurs in combination with other processes such as individual learning, reaction norms and genetic predispositions. Understanding the proximate mechanisms underlying variation in cooperative behaviour is therefore currently an open question in need of further research. Determining these proximate mechanisms may be a more complex undertaking than understanding whether behaviour is adaptive in a given environment.

Irrespective of the proximate mechanisms involved, these findings highlight the importance of socioecology as a determinant of cooperative behaviour. When the costs to cooperation are higher, such as for those in need due to low resource availability or a high number of dependent offspring, a decrease in cooperation is reported. This is consistent with cooperative behaviour being sensitive to differential costs and benefits, in line with adaptive evolutionary expectations. That camp stability significantly predicted patterns of cooperation is also consistent with several theoretical models demonstrating the importance of repeated interactions (Trivers 1971; Axelrod & Hamilton 1981; Pfeiffer *et al.* 2005). Despite its long-standing theoretical basis, the influence of repeated interactions on cooperative behaviour has often been overlooked in real-world studies. Camp stability was the largest predictor of cooperation among the Agta, suggesting that its omission in previous research may have been a significant oversight. While relatively few in number, some previous studies assessing the benefits of group stability in other societies and species have found analogous results. For instance, among US cities lower levels of migration were associated with decreased crime rates (Crutchfield *et al.* 1982), while among degus (cooperatively breeding south American rodents) group stability was associated with increased female fitness (Ebensperger *et al.* 2016).

Although repeated interactions are essential to many theories of cooperative evolution, such as generalised reciprocity (Pfeiffer *et al.* 2005), they may be most relevant for understanding direct reciprocity (Trivers 1971; Axelrod & Hamilton 1981). Repeated interactions are essential for reciprocal cooperation as the long-term benefits of iterated cooperative interactions outweigh the short-term benefits to defection. Among the Agta stability does appear linked to reciprocity, as those who gave to others, which was more frequent in stable camps, shared resources reciprocally. These results demonstrate how stability may modulate producer control (the amount of control individuals have over resource distributions), which in turn influences sharing patterns, as producer control is necessary for partner choice to occur. As detailed above, this variation in cooperative behaviour may be adaptive, with high producer control permitting reciprocity to avoid non-sharing free-riders in stable camps, while under a demand sharing system (low producer control) high mobility may assist in the avoidance of non-hunting free-riders. This flexibility demonstrates the resilient nature of hunter-gatherer cooperation as these populations can adapt sharing patterns to the prevailing socioecological conditions. If foragers were reliant on just one cooperative system it would greatly limit the number of possible environments pre-agricultural humans could inhabit. The capacity to adapt cooperative behaviour to changing environments may be one of the reasons humans have been so successful and colonised every habitat on earth.

This thesis has also demonstrated that partner choice is central to the evolution of cooperation, in terms of individuals preferentially cooperating with specific partners. In contrast to many experimental studies with university students (Barclay & Willer 2007; Sylwester & Roberts 2010, 2013; Cuesta *et al.* 2015), among the Agta cooperative individuals were not actively sought out as partners, nor did cooperators preferentially associate with other cooperators (Apicella *et al.* 2012). Therefore, mechanisms of cooperative assortativity (indirect reciprocity, competitive altruism or cooperative homophily) may not have universal application as explanations for the evolution of human cooperation. However, there are several types of assortativity which prioritise specific partners over others, not just by cooperativeness. Cooperation in the Sharing Game is predominantly associated with assortativity by kinship and direct reciprocity, but in different contexts other assortative mechanisms may take precedence. For instance, in many post-industrial societies kinship ties are weaker and interactions repeated less frequently, meaning that kin selection and direct reciprocity may be weaker mechanisms in these contexts. Under these circumstances, mechanisms of cooperative assortment may become more important (as a case in point see the proliferation of review systems on Internet shopping sites). This requires further empirical cross-cultural research exploring how cooperative mechanisms vary depending on socioecological context.

In addition to kin and reciprocating partners, the Agta preferentially selected to live and share resources with skilled storytellers. The role of storytellers is often overlooked in small-scale societies, yet the results here indicate that individuals were twice as likely to choose to live with a skilled storyteller relative to a skilled forager.

Storytellers may be especially favoured for their role in coordinating group behaviour and promoting cooperation, as well as transmitting fitness-relevant information (Biesele 1986; Scalise Sugiyama 2001; Wiessner 2014). Achieving a consensus on group behaviour, such as cooperation, movement, foraging or mating, is important in social species; these behaviours are intimately tied to individual fitness as coordination reduces competition and facilitates cooperation (Conradt & Roper 2005). The importance of coordinating behaviour to achieve cooperation is often under-appreciated in humans (Smith 2010; Cronk & Leech 2013), yet simply allowing participants to talk in Public Goods Games significantly increases levels of cooperation (Bochet *et al.* 2006). This suggests that many breakdowns in cooperation may be due to a failure in coordinating behaviour, highlighting the importance of mechanisms such as storytelling to broadcast shared cooperative norms. I also find that the Agta preferentially share resources with those in need, although the ultimate adaptive reason for this needs-based sharing remains unclear. Although little evidence for partner choice based on cooperative assortment was reported, partner choice in other domains does appear to influence Agta cooperative dynamics, suggesting that the ability to choose specific partners may be central to understanding human cooperation. As detailed in Chapter 6, biological market theory may provide a broad conceptual framework from which to understand the evolution of cooperation and social networks via partner choice (Noë & Hammerstein 1995; Leimar & Hammerstein 2010; Barclay 2013; Hammerstein & Noë 2016).

An important caveat to be recognised here is that cooperative networks, and social networks more broadly, are likely to vary by domain. That is, a cooperative network in one domain (say, food-sharing) may not represent cooperative networks more widely or in other domains (say, childcare or political coalitions). Despite some broad similarity, the sharing and camp-mate networks were markedly different in several ways. For instance, the importance of age, sex and cooperative homophily in the camp-mate network may potentially reflect the demands of everyday interactions, such as resource acquisition among males and sharing childcare responsibilities among females. These pressures may be weaker regarding resource transfers, hence why homophily was of less importance in the Sharing Game. Put simply, the individuals it may be optimal to share food with may not be the same individuals it is optimal to interact and cooperate with more broadly. This highlights the importance of different networks for solving different adaptive challenges (Nolin 2011). In many studies 'cooperation' appears to be theorised as a unitary construct, which to some extent it may be (Peysakhovich *et al.* 2014), yet greater attention should be given to understanding how and why individuals differ in the amount they cooperate in different domains and with whom.

This thesis also explored the ontogeny of cooperation among the Agta, both in terms of the amount they share and with whom. In contrast to several recent studies exploring the development of cooperative behaviour in small-scale societies which have focused on proximate mechanisms of social learning (House *et al.* 2013; Blake *et al.* 2015), here I have advocated understanding children's behaviour from an ultimate fitness-maximising perspective. As children's cooperative behaviour displays great between-camp variability and corresponds to adult levels of cooperation in camp, with little effect of age, this suggests that: i) similar socioecological factors may influence both child and adult cooperative behaviour; and ii) previous findings that cooperative behaviour follows a common trajectory of low between-group variation in early childhood to high between-group variation in later childhood (House *et al.* 2013; Blake *et al.* 2015) cannot be generalised to all populations. These results highlight how children's behaviour can be understood through a functional evolutionary lens, a perspective which is often absent from developmental literature. The disparity between the present study and previous findings may be due to the effects of partner choice among children. Among the Agta, young children preferentially gave resources to kin, while cooperation with non-kin increased with age. However, in previous experiments close kin were excluded as cooperative partners. The lower levels of cooperation by younger children in previous studies may therefore reflect a tendency to cooperate with kin over non-kin, rather than low levels of cooperativeness more generally.

These results – here from an ontogenetic perspective – again demonstrate the importance of partner choice for cooperation. Although there was a strong overall trend for sharing with closer kin, as children aged they were more likely to share with distant kin and unrelated individuals. Indirect fitness benefits may determine young children's patterns of cooperation, while for older children direct fitness benefits, such as those gained from forming peer-to-peer relationships, appear to begin to increase in significance. A strong kin-bias in children's cooperative behaviour suggests that kin selection may play an important role in determining patterns of children's cooperation, especially at young ages. This may have important implications for the evolution of human life history, especially regarding extended childhood, supporting multiple dependent offspring and increased fertility rates. Due to the high energetic demands of these traits on mothers, human life history requires a cooperative breeding system where individuals other than the mother assist in raising offspring (Kaplan *et al.* 2000; Hrdy 2009). The role of children fulfilling this role is often overlooked, yet the results here demonstrate that children possess a motivation to cooperate and care for other children, particularly younger siblings.

This behaviour may, in part, help to explain the unique social structure and life history present in humans.

A final conceptual topic to be addressed in this section concerns whether the cooperative behaviour observed in these games is the behaviour of 'rational' actors who understand the experimental context and display altruistic other-regarding preferences (the CGS interpretation: e.g., Chudek *et al.* 2013; Henrich *et al.* 2014; Zefferman 2014) or whether game behaviour reflects a 'misfiring' of mechanisms, such as reciprocity or reputation, which would be adaptive outside of the artificial game context (Hagen & Hammerstein 2006; Delton *et al.* 2011; West *et al.* 2011; Rand *et al.* 2014). There is currently little consensus on this matter, but the present results suggest that the latter may be a more parsimonious interpretation. When compared against actual food-sharing data (Smith *et al.* 2016a), Agta camps which gave more resources to others and did so reciprocally in the Sharing Game were more likely to engage in real-world reciprocal food-sharing. In contrast, camps which gave less resources to (and took more resources from) others in the games did not engage in real-world reciprocal food-sharing. Reciprocity requires high levels of producer control to avoid sharing with non-reciprocators, necessitating that resources be given to others, as found in these games. A similar profile of results is found across other societies when comparing patterns of food-sharing against Ultimatum Game behaviour (see above). Populations engaged in reciprocal food-sharing, such as the Lamalera (Nolin 2010), Dolgan/Nganasan (Ziker & Schnegg 2005) and reservation-living Ache (Gurven *et al.* 2002; Allen-Arave *et al.* 2008) displayed high levels of cooperation in the Ultimatum Game (Henrich *et al.* 2005; Ziker 2014), while societies with non-reciprocal food-sharing, such as the Hadza (Hawkes *et al.* 2001) displayed low levels of game cooperation (Henrich *et al.* 2005).

This suggests that the cooperative strategies used in actual food-sharing may have been applied in these games. In the absence of other cues on how to behave in these experimental games individuals seemingly employ previously successful ‘heuristics’ from similar everyday situations (Peysakhovich & Rand 2016). Only after previous experience with the experimental protocol do individuals, at least in more westernised societies, begin to act more ‘rationally’ based on maximising individual pay-offs (Rand *et al.* 2014; Burton-Chellew *et al.* 2015). The seemingly ‘altruistic’ behaviour by some may therefore be understood as a potential misapplication of otherwise adaptive cooperative strategies outside of the experimental game context, and not evidence for self-sacrificial group-beneficial behaviour which evolved via CGS.

This interpretation rests on the assumption that similar contextual cues are activated in both game and real-world cooperation (Hagen & Hammerstein 2006). Given the correspondence between Agta game and actual food-sharing behaviour (Smith *et al.* 2016a) this interpretation may be valid here. Although the association between Ultimatum Game behaviour and real-world reciprocal food-sharing in certain foraging societies is suggestive, it is far from clear whether the same contextual cues regarding game and real-world behaviour are activated in all societies in which games have been conducted. Several studies in small-scale societies have reported a lack of external validity between indices of game and real-world cooperation (Hill & Gurven 2004; Gurven & Winking 2008; Wiessner 2009), while others have found that framing these experimental games in relevant real-world contexts greatly alters levels of cooperation (Cronk 2007; Lesorogol 2007; Gerkey 2013). The extent to which experimental games cue real-life contexts therefore appears highly variable across different populations and methodologies.

Reconciling these findings with an understanding of how individuals actually play these games and the contextual cues participants bring with them remains one of the fundamental challenges in the study of experimental game research. In the final section I aim to provide some suggestions on how this may be achieved and discuss potential recommendations for future studies which utilise experimental games, specifically in small-scale societies, but also more widely.

Recommendations and the Future of Experimental Games

The main recommendation for future experimental games is to make sure that they are relevant to the social context and to tailor methods to specific research questions (see also Gurven & Winking 2008). Although the same abstract game played in multiple societies allows control over study design, it is very difficult to know if all societies interpret the game identically, meaning that differences in behaviour may instead reflect differences in understanding or interpretation. Whether any contextual association between the game and real-world cooperation is present has the potential to greatly influence behaviour (Cronk 2007; Lesorogol 2007; Gerkey 2013; Bolyanatz 2014). Designing experimental protocols to investigate specific questions, such as food-sharing behaviour explored here, makes these games more ecologically valid as they are relevant to the cooperative context of the specific society. It also reduces the potential for individuals or societies to interpret the games in different ways (for instance, when a contextualised Dictator Game was conducted among Samburu pastoralists lower levels of behavioural variation were reported compared to a decontextualised version; Lesorogol 2007). One limitation of this approach is that it makes between-society comparisons more difficult if populations do not share the same cooperative context. For instance, while similar methodologies to those employed here could easily be conducted in other societies which share food, applying these games in societies less reliant on food-sharing may be problematic as the contexts are different (although this requires further empirical corroboration). A trade-off therefore exists regarding generality, using uncontextualised methods but with the potential for different societies to interpret and play the games differently, and specificity, using contextualised games but with the potential that certain contexts only apply to specific societies. Within-society studies such as this one (see also Gurven *et al.* 2008; Lamba & Mace 2011, 2012; Silva & Mace 2014) somewhat overcome this trade-off as many different groups can be assessed within a single ethnolinguistic population, meaning that contextualised games can explore behavioural variation over different groups but with the relevant context held constant.

A further reason for tailoring these games to answer specific research questions concerns issues of validity. Previous studies using 'traditional' experimental games (such as the Dictator Game, Ultimatum Game and Public Goods Game) have tended to assume that cooperation is a unitary construct (Henrich *et al.* 2005). Yet convergent validity between different cooperative games is relatively low (see introductory chapter) and a general lack of external validity to real-world cooperative dynamics (Hill & Gurven 2004; Gurven & Winking 2008; Wiessner 2009) questions this assumption. The games designed in the present thesis display both convergent validity, as Sharing and Taking Game behaviour significantly correlate with one another, as well as external validity, as patterns of experimental cooperative behaviour corresponded to real-world food-sharing (Smith *et al.* 2016a: as a tangential aside, the correspondence between game and real-world food-sharing also suggests that these patterns of experimental cooperation may be generalisable to other resources, not just specific to rice). Designing experimental games to test specific research questions may therefore increase both convergent and external validity. Without an understanding of which contexts experimental games cue, is it difficult to know whether different games should elicit similar behaviour or whether game behaviour should correspond to specific patterns of real-world behaviour. This again suggests that cooperation may not be a unitary construct, but rather is context-specific, with different cooperative domains reflecting different adaptive challenges. While this may make the study of cooperation more complex, as it may be erroneous to use one index of cooperation and say that this individual or society is more or less cooperative than another, ultimately this perspective will provide a deeper insight into how humans actually do cooperate and why.

A further recommendation is that, depending on the research question, future games should be non-anonymous and include multiple partners, similar to those employed here (see also Rucas *et al.* 2010). This non-anonymity increases ecological validity, as individuals rarely act anonymously with others and often have the choice to interact with one of a number of individuals. This would also allow direct testing of theories relevant to the evolution of cooperation, such as kin selection (Hamilton 1964), reciprocity (Trivers 1971; Axelrod & Hamilton 1981) and reputational effects (Nowak & Sigmund 1998, 2005; Roberts 1998). Each of these theories highlights the importance of partner choice in understanding the evolution of cooperation (Noë & Hammerstein 1994; Bshary & Noë 2003; Barclay 2013, 2016; Baumard *et al.* 2013; Roberts 2015) and suggests that cooperation is not uniform across all group members as implied by ‘traditional’ experimental games (Camerer 2003; Camerer & Fehr 2004; Henrich *et al.* 2005).

Although only touched upon briefly in this thesis (Chapter 6), an additional recommendation is that future studies should explore ‘not-in-kind’ cooperation in greater detail (Macfarlan & Lyle 2015). This may include cooperation returned in other currencies such as mating opportunities (Hawkes 1991; Hawkes & Bliege Bird 2002), coalitional support (Patton 2005), recruitment for cooperative breeding (Wiessner 2002), information transfer (Henrich & Gil-White 2001) and group-beneficial social roles, such as storytellers. These and future findings may benefit from a 'biological market' approach to understanding cooperative and interaction networks (Noë & Hammerstein 1994, 1995; Barclay 2013, 2016; Hammerstein & Noë 2016).

One of the main take-home messages from this thesis is that it is difficult, if not impossible, to understand cooperation without context. Individuals do not just 'cooperate'; they display cooperative behaviour in specified domains, such as food-sharing, coalitions, cooperative hunting and allocare, and this cooperative behaviour is often targeted to specific individuals, such as kin, reciprocating partners and storytellers. Stripping experimental games of context means that many assumptions regarding individual decision-making have to be made, many of which do not stand up to empirical scrutiny. These include: game behaviour reflecting 'ephemeral interactions' (Henrich *et al.* 2014: 91) rather than wider everyday social dynamics; individuals cooperating equally with all group members; and individuals from different societies playing the game identically (Rai & Fiske 2010; Shweder 2010). A contextualised approach, as adopted here, overcomes many of these assumptions by linking game behaviour to a specific cooperative domain (food-sharing, in this instance). As discussed above, unlike many previous uncontextualised games this design possesses both convergent and external validity among the Agta (Smith *et al.* 2016a).

Regarding the future of experimental games in small-scale societies, I predict that these traditional anonymous games will be replaced by contextualised experimental methods which test particular hypotheses in specific cooperative contexts. The factors predicting competitive interactions among Tsimane women is one example where a similar approach has already been employed using a non-anonymous game with multiple potential partners (Rucas *et al.* 2010). These network-based approaches to cooperation (see also Apicella *et al.* 2012; Chaudhary *et al.* 2015; Thomas *et al.* 2015) bridge the gap between experimental games and theories for the evolution of cooperation which depend on partner choice, such as kin selection and reciprocity, which have often been overlooked in past research on experimental games. I expect future studies to develop further methodologies, perhaps specific to each study population, to explore these cooperative dynamics. I also predict that future research will be conducted more closely between experimental and field researchers to explore and validate the efficacy and validity of experimental approaches, such as by linking game and real-world behaviour in a more quantitative manner. Recent examples of similar approaches which test specific research questions and draw more heavily upon ethnographic data include: the association between moralistic high-gods and cooperation with distant co-religionists (Purzycki *et al.* 2016); the social and economic factors influencing cooperative interactions with out-groups (Pisor & Gurven 2016); and exploring the nature of cooperative interactions between spouses (Stieglitz *et al.* 2017).

As a final thought: if one aims to explore actual cooperative behaviour, what is the benefit of measuring this behaviour experimentally – which requires many assumptions about game behaviour – rather than observationally? One answer concerns simple time constraints; it is simply not possible to collect observational data as quickly as experimental data. If a project is time-limited, as many are, then experiments are a useful method for collecting data in a relatively short space of time (compared to food-sharing data which may require weeks of observations at each location). This then leads to a catch-22 situation though, as in order to validate the experimental methods real-world data are necessary. The real benefit to an experimental approach, however, concerns the ability to manipulate conditions and detect patterns which would otherwise be difficult or impossible to assess via observational methods. Only an experimental approach can dissociate the respective roles of producer and recipient control regarding resource distributions, as it may be difficult to differentiate the two from observational patterns of food-sharing. For instance, food-sharing may not be reciprocal because an individual may share widely, without recourse to reciprocity, to obtain a reputation for cooperativeness and receive more resources (or returns in another currency) from others in the future. Alternatively, rather than share widely, distributions may not be reciprocal as a result of tolerated theft/demand sharing, where resources are taken, rather than given. The *pattern* of resource transfers is the same in both scenarios, yet the *process* (high vs. low producer control), and the underlying evolutionary mechanisms (costly signalling vs. demand sharing), are different. As another example, experimental methods can also explore whether observed patterns of cooperation and interaction are *preferred* patterns of cooperation and interaction. That is, experimental methods can investigate the *motivations* individuals have, which again may be difficult using observation-based methods. Two examples from this thesis can be given to support this. Firstly, in many studies of food-sharing proximity predicts transfers (Gurven *et al.* 2000b, 2002; Nolin 2010; Schnegg 2015), yet the results of Chapter 5 suggest that when individuals possess full control over distributions no effects of distance are present after controlling for other factors such as kinship and reciprocity. Distance effects in real-world food-sharing may therefore represent instances of tolerated theft/demand sharing, rather than preferred sharing partners. Secondly, younger children have been found to share less food with others than older children (Crittenden & Zes 2015). However, this appears to be a result of developmental constraints on foraging, rather than reflecting differences in intrinsic motivations to share, as in the experimental games conducted here young children were equally as cooperative as older children. The ‘added value’ of an experimental approach is that it can differentiate between scenarios such as these which are difficult to separate using other methods. It is answering these types of questions, as demonstrated in this thesis, which I believe experimental approaches will be most beneficial in helping researchers understand the evolution of human cooperation.

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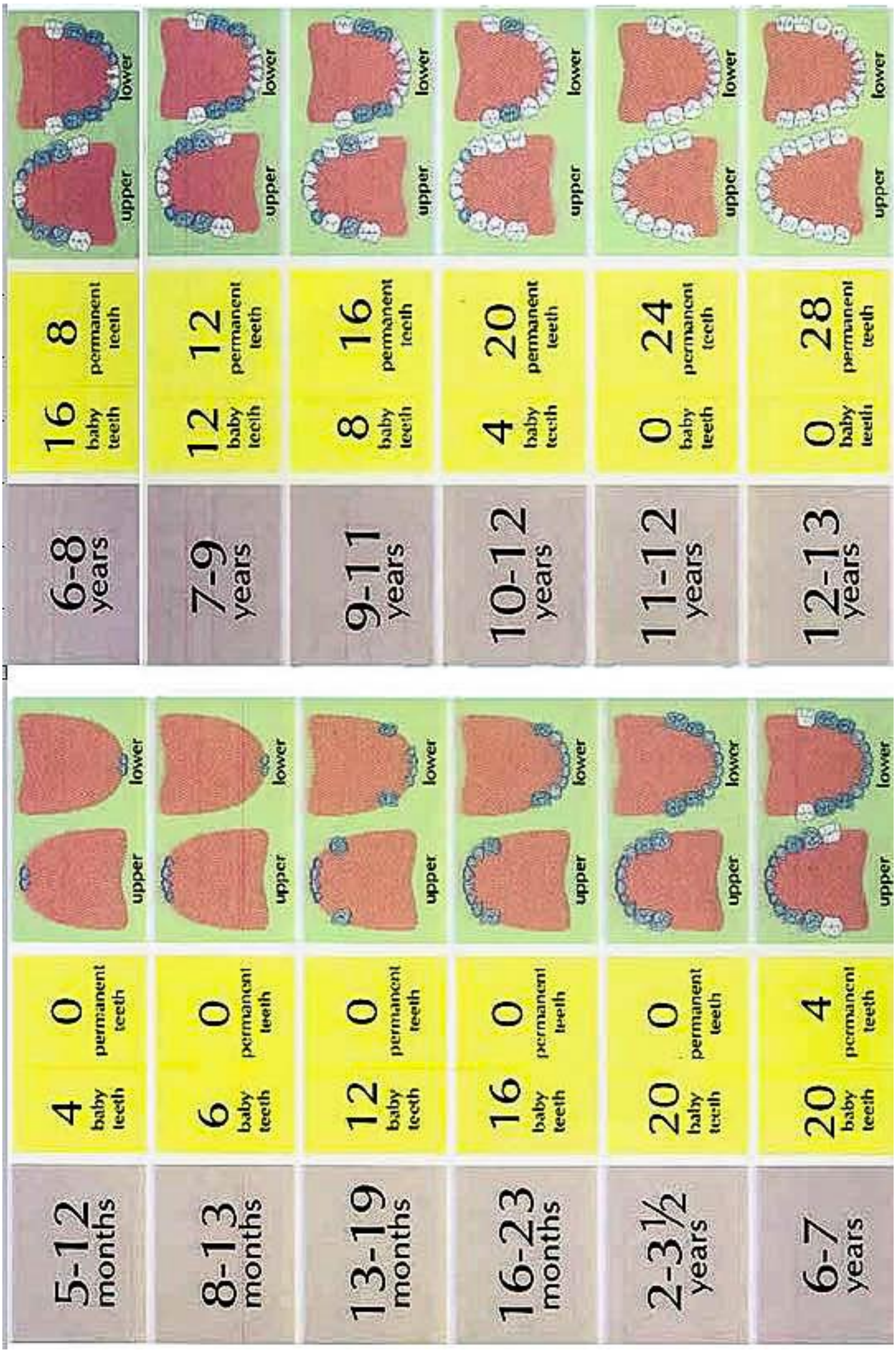
Appendix 1: Dental Development Chart



5-12 months	4 baby teeth	0 permanent teeth
8-13 months	6 baby teeth	0 permanent teeth
13-19 months	12 baby teeth	0 permanent teeth
16-23 months	16 baby teeth	0 permanent teeth
2-3½ years	20 baby teeth	0 permanent teeth
6-7 years	20 baby teeth	4 permanent teeth
6-8 years	16 baby teeth	8 permanent teeth
7-9 years	12 baby teeth	12 permanent teeth
9-11 years	8 baby teeth	16 permanent teeth
10-12 years	4 baby teeth	20 permanent teeth
11-12 years	0 baby teeth	24 permanent teeth
12-13 years	0 baby teeth	28 permanent teeth

Appendix 2: Anthropometrics

Based upon protocols used by Jed Stevenson, Jimma Child Development Study
(2007 / 2008)

1. Head circumference (for children)

1. Ask the mother to hold the child (if young) so that they are sitting sideways on her lap.
    a. Position yourself in front of the mother, and to the side of the child, so that you are looking at the side of their head.

2. Place the measuring tape around the child's head.

3. Position the tape correctly:
    a. At the front of the head, the tape should be immediately **above the eyebrows**
    b. At the back of the head, the tape should go over the bulge (**occiput**), so that you get the maximum circumference

4. Record the measurement to the nearest 0.1cm

2. Weight

1. Put the scale on a flat place on the floor and turn the scale on (if electric).

2. Ask the individual to stand on the scale.

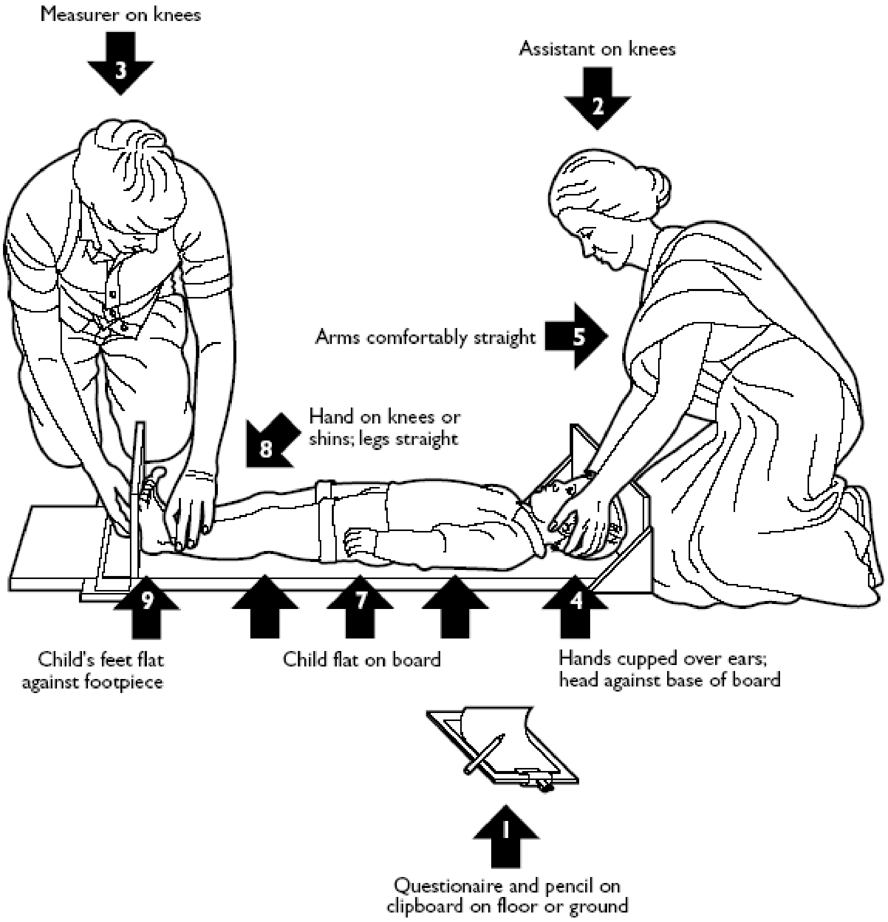
3. For infants, weigh the Mother alone, then Mother with child, and subtract the two to get infant’s weight

3. Length (for infants)

1. Lay the infant flat on the ground (flat bit of ground, wooden board, etc.).

2. Position the child correctly:
    a. One person should hold the child's head against the one end of the anthropometer.
        i. The child should look directly upward, and the crown of his/her head should touch the tip of the anthropometer.
    b. Another person should straighten the child's legs.
        i. The child's toes should point directly upwards.

3. Record the measurement in centimetres to the nearest 0.1 cm using the anthropometer.



4. Height

1. Put the anthropometer on a flat place on the ground.

2. Tell the individual to stand with the rod to his / her back.

3. Position the individual correctly:
   a. One person should check the person’s position:
      i. The individual should look directly forward.
      ii. The individual’s toes should point directly forwards.
      iii. Their back should be straight.

4. Another person should take the measurement:
   a. Ask the person to breathe in, and move the gauge on the anthropometer down until level with the crown of their head.
      i. Another person makes sure that the anthropometer is straight, and not tilted forwards or backwards.

5. Record the measurement in centimetres to the nearest 0.1 cm.

5. Hip Width

1. Find the widest part of the individual's hip bone (at the crest of the bone) on both sides.

2. Hold the anthropometer in place on one side (getting another person to do this may be easier), and extend until reached the other hip.

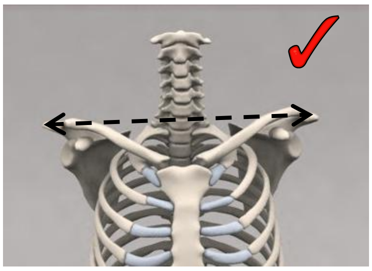
3. Record the measurement in centimetres to the nearest 0.1 cm.

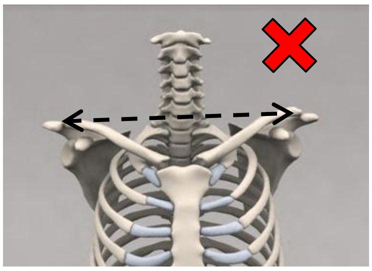
6. Shoulder Width

1. Find the end of the individual's shoulder bone (You may find a protruding clavicle which is similar, but this is not the end of the bone; see diagram below) on both sides.

2. Hold the anthropometer in place on one side (getting another person to do this may be easier), and extend until reached the other shoulder.

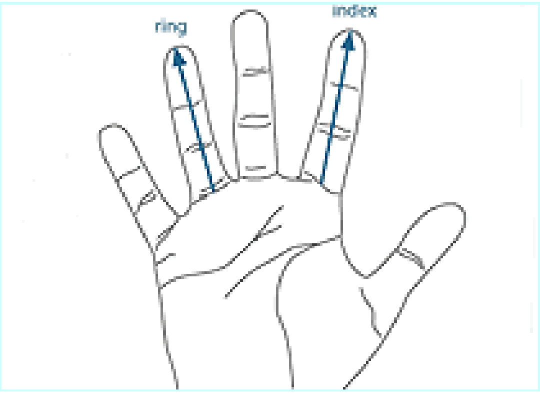
3. Record the measurement in centimetres to the nearest 0.1 cm.





7. 2D:4D Ratio

1. Using calipers/tape-measure, measure from lowest crease on index finger to tip
2. Repeat for ring finger, but as has 2 low creases, take from lower crease.
3. Repeat for other hand
4. Divide the second finger measurement by the fourth finger measurement to obtain the 2D:4D ratio



8. Hand-Grip Strength

1. Reset the dynamometer for each trial
2. The handle of the dynamometer is adjusted if required - the base should rest on first metacarpal (heel of palm), while the handle should rest on middle of four fingers.
3. Position: The arm hanging by the side of the body
4. When ready the subject squeezes the dynamometer with maximum isometric effort, which is maintained for 5 seconds. No other body movement is allowed. The subject should be strongly encouraged to give a maximum effort.
5. Perform the test on 3 successive occasions for each hand. Allow at least 15 seconds recovery between each effort.
6. Record the best value for each hand (in Kgs).

Appendix 3: Camp Scan Data Collection Sheet

A) Domestic Activities	**B) Childcare**	**C) Out of Camp**	**D) Non-Work**
A1 - Cooking **A2** - Food processing **A3** - Fetching water **A4** - Collecting firewood **A4** - Cleaning **A5** - Washing clothes **A6** - Preparing medicines **A7** - Constructing/repairing dwelling **A8** - Manufacturing goods/repairing tools (specify) **A9** - Walking with light load (<10kg) **A10** - Walking with heavy load (10 kg – 35kg) *For A1 and A2 state who obtained the food?*	**B1** – Breastfeeding **B2** - Holding children **B3** - Feeding children (not breast-feeding) **B4** - Medical/hygiene care **B5** - Play/Affectionate Activities **B6** - Keeping an eye on children (without direct contact) **B7** - Other touching behaviours **B8** - Proximity (less than 3 meters) **B9 -** Vocalising	**C1** - Hunting **C2** - Fishing **C3** - Gathering wild foods **C4** - Collecting honey **C5** - Collecting items for trade (specify shells, orchids, etc.) **C6** - Agricultural work on own land **C7** - Wage labour (specify which) **C8** - Visiting nearby camps (specify which) **C9** - Trade with non-Agta (specify where and item traded) **C10** - At school or accompanying child to school **C11** - Logging *(specify trade/own use for C1, C2, A8)*	**D1** - Resting (state reason; tired/injured/ill/pregnant/ bad weather) **D2** - Relaxing/Socialising **D3** - Participating in religious ceremony **D4** – Drinking **D5** - Playing **D6** - Sleeping

ID	**Name**	**Time:**			**Time:**			**Time:**			**Time:**		
		Activ	**Grp**	**Whose**	**Activ.**	**Grp**	**Whose**	**Activ.**	**Grp**	**Whose**	**Activ.**	**Grp**	**Whose**

Camp: **Dates:**

Appendix 4: Household Questionnaire

1. **Do you own any land? If yes, approximately how large, what do you grow there, and do you have a title for the land?**

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2. **Do you have any food stored? If yes, what type and weight/cash value**

………

………

………

To the following questions please answer always, sometimes or never true - *ask the mother*

Question	Always	Sometimes	Never
3. **How often do you have food in your household for more than the next day?**			
4. **We did not have enough to eat**			
5. **I was worried our food would run out**			
6. **I was not eating enough**			
7. **The children were not eating enough**			
8. **The children did not eat for one day**			
9. **I did not eat for one day**			
10. **I had to eat less/miss meals so my children could eat**			
11. **I am hungry but didn't eat because there was not enough food**			
12. **The children are hungry but didn't eat because there was not enough food**			

13. **Housing type:**

Description	Score 0 if	Score 1 if	Score
House type	Lean-to (end here)	Hut/House	
Roof	Palm leaves	Metal	
Walls	Absent	present	
Wall type (if present)	Rattan	Planks	
Floor (if present)	Rattan	Planks	
Size (ranked variable)	Smallest	Largest	
Ownership	Shared home	Family home	
Number of Houses	One house	Two or more houses	

14. **Family education and vaccination history** (***write children's names in beforehand to ensure coverage)***

Family member	Highest education level	Vaccinations received
Mother		
Father		
Child 1		
Child 2		
Child 3		
Child 4		
Child 5		
Child 6		
Child 7		
Child 8		
Child 9		

15. **Do you have any cash savings? If yes, how much and what are you saving for**

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16. **Do you go to church?**

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17. **MOTHER: Name 5 individuals you would most like to live with**

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18. **FATHER: Name 5 individuals you would most like to live with**

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19. **MOTHER: What camp were you born in? What camp did you move to next, approximately how old were you, why did you move, and who did you move with (parents, consanguineal kin, affinal kin, etc.)? Repeat until present camp.**

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20. **FATHER: What camp were you born in? What camp did you move to next, approximately how old were you, why did you move, and who did you move with (parents, consanguineal kin, affinal kin, etc.)? Repeat until present camp.**

....

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....

21. **MOTHER: Order the following in terms of which you do the most and explain how often per week (use cards to show activities)**

Activity	Order	How often per week
Hunting		
Foraging		
Gardening/planting crops/fieldwork		
Fishing		
Collecting/making things for trade		
Cash labour		

22. **FATHER: Order the following in terms of which you do the most and explain how often per week (use cards to show activities)**

Activity	Order	How often per week
Hunting		
Foraging		
Gardening/planting crops/fieldwork		
Fishing		
Collecting/making things for trade		
Cash labour		

23. ***How many of the following items do you own?***

Item	*Number*	*Item*	*Number*	*Item*	*Number*	*Item*	*Number*
Cooking Pot		***Spoons***		***Speargun***		***Goggles***	
Cups		***Forks***		***Fishing Net***		***Mat***	
Radio		***Machete***		***Gun***		***Blanket***	
Plates		***Kettle***		***Bow & Arrow***		***Necklaces***	

24. ***Which of these are the most important to you?***

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25. ***Are you happy with the amount of possessions you own or do you wish you had more?***

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26. ***Other comments/observations***

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Appendix 5: Adult Game Script

Note: Actions to be performed by the experimenter are indicated in brackets.

"We are going to play two simple games where you can win rice both for yourself and for your camp-mates. Here is a picture of yourself, along with *x* other camp-mates [place ego's picture, along with all other camp-mates in a row behind ego. Shuffle the order of photos each time the game is played]. We will be playing with small tokens [show tokens], each of which represents one-eighth of a kilo of rice, about the size of a small cup. Any rice for you put on your picture, you will get to keep. Any rice you put on a camp-mate's picture, they will get to keep. We will give this rice out after we have played the games with everyone in camp. There are no correct answers in this game, so you can give as many or as few tokens as you want, to whichever camp-mates you want. No-one else in camp will know of your decisions.

Do you understand? Do you have any questions?

Sharing Game (randomise the game order):
For this game, you will be given *x* tokens. For each token, you have to decide first if you would like to keep it for yourself, or if you would like to give it to a camp-mate. Secondly, if you decide to give it to a camp-mate, which camp-mate [show token and place on ego's picture, then move the token over pictures of other camp-mates].

For the first token [show token], would you like to keep it for yourself, or give it to a camp-mate? [If chooses self, then put token on their picture. If chooses a camp-mate, ask:] Which camp-mate would you like to give this token to? [Place token on the camp-mate they choose. Write decision in notebook]. Why did you give to this person? [Write answer in notebook].

For the next token [show token], would you like to keep it for yourself, or give it to a camp-mate? [If chooses self, then put token on their picture. If chooses a camp-mate, ask:] Which camp-mate would you like to give this token to? [Place token on the camp-mate they choose. Write decision in notebook]. Why did you give to this person? [Write answer in notebook].

[Repeat until only one token left]

For the last token [show token], would you like to keep it for yourself, or give it to a camp-mate? [If chooses self, then put token on their picture. If chooses a camp-mate, ask:] Which camp-mate would you like to give this token to? [Place token on the camp-mate they choose. Write decision in notebook]. Why did you give to this person? [Write answer in notebook].

Taking Game:

For this game, each of your camp-mates will begin with either one or two tokens [place tokens on camp-mates and write down which camp-mates began with each number of tokens]. In order for you to receive tokens, you must move these tokens off of your camp-mates and put them on to your picture [simulate this action]. Okay, go!

[Wait until they seem to have finished moving tokens, then ask:] Are you finished? [If yes, then note down how many tokens each camp-mate finished with and how many ego took. If no, then wait until they seem to have finished moving tokens and ask again until they have finished].

Okay, that's it! The rice will be given out soon once we have played games with all people in camp. It is also very important that you do not tell anyone else how you played in this game – *Secreto!* [The Tagalog word for 'secret'].

Thank you again for taking part!"

Appendix 6: Child Game Script

Note: Actions to be performed by the experimenter are indicated in brackets.

“We are going to play a simple game where you can win candy both for yourself and for your camp-mates. Here are five candies [show candies]. For each candy, you have to decide first if you would like to keep it for yourself, or if you would like to give it to a camp-mate [with the candy, motion towards ego and then towards the wider camp]. Secondly, if you decide to give it to a camp-mate, which camp-mate? Any candies you keep for yourself, you will get to keep. Any candies you give to others, they will get to keep. We will give these candies out after we have played the games with everyone in camp. There are no correct answers in this game, so you can give as many or as few candies as you want, to whichever camp-mates you want. No-one else in camp will know how many you kept or who you gave to.

Do you understand? Do you have any questions?

For the first candy [show candy], would you like to keep it for yourself, or give it to a camp-mate? [If chooses a camp-mate, ask:] Which camp-mate would you like to give this candy to? [Write decision in notebook].

For the next candy [show candy], would you like to keep it for yourself, or give it to a camp-mate? [If chooses a camp-mate, ask:] Which camp-mate would you like to give this candy to? [Write decision in notebook].

[Repeat until only one token left]

For the last candy [show candy], would you like to keep it for yourself, or give it to a camp-mate? [If chooses a camp-mate, ask:] Which camp-mate would you like to give this candy to? [Write decision in notebook].

Okay, that’s it! The candies will be given out soon once we have played games with all children in camp. It is also very important that you do not tell anyone else how you played in this game – *Secreto!* [The Tagalog word for ‘secret’].

Thank you again for taking part!”

Appendix 7: Supplementary Data Analysis

Table A1: Delta AICc values and model weights for each model within two AICc values of the top model for the Sharing Game using a multi-level linear regression approach. Due to the multiple imputation procedure estimating missing values, raw AICc values are not comparable across each imputed dataset so are not displayed here. The values presented are therefore delta AICc values and model weights for each of the five datasets separately, while a final column averages the model weights for each model over all imputed datasets.

Model Parameters	**Imputation 1**		**Imputation 2**		**Imputation 3**		**Imputation 4**		**Imputation 5**		**Averaged Model Weight (w_i)**
	ΔAICc	**w_i**	**ΔAICc**	**w_i**	**ΔAICc**	**w_i**	**ΔAICc**	**w_i**	**ΔAICc**	**w_i**	
# Dependent Offspring + Affinal Closeness + Harvesting Rice + Stored Rice + Camp Stability + Cash Labour Involvement	0	1	0	1	0	1	0	1	0	0.52	0.904
# Dependent Offspring + Affinal Closeness + Harvesting Rice + Stored Rice + Camp Stability	NA	0	NA	0	NA	0	NA	0	1.19	0.28	0.056
# Dependent Offspring + Affinal Closeness + Harvesting Rice + Stored Rice + Camp Stability + Cash Labour Involvement + Camp Size	NA	0	NA	0	NA	0	NA	0	1.92	0.2	0.04

Table A2: Delta AICc values and model weights for each model within two AICc values of the top model for the Taking Game using a multi-level linear regression approach. Due to the multiple imputation procedure estimating missing values, raw AICc values are not comparable across each imputed dataset so are not displayed here. The values presented are therefore delta AICc values and model weights for each of the five datasets separately, while a final column averages the model weights for each model over all imputed datasets.

Model Parameters	**Imputation 1**		**Imputation 2**		**Imputation 3**		**Imputation 4**		**Imputation 5**		**Avgd Model Weight (w_i)**
	ΔAICc	**w_i**	**ΔAICc**	**w_i**	**ΔAICc**	**w_i**	**ΔAICc**	**w_i**	**ΔAICc**	**w_i**	
# Dependent Offspring + Harvesting Rice + Stored Rice + Camp Stability + Consanguineal Relatedness	0	0.14	0	0.16	0	0.16	0	0.17	0	0.16	0.158
# Dependent Offspring + Harvesting Rice + Stored Rice + Camp Stability + Affinal Closeness	0.01	0.14	0.01	0.16	0.01	0.16	0.05	0.16	0.01	0.16	0.156
# Dependent Offspring + Harvesting Rice + Stored Rice + Camp Stability	0.29	0.12	0.29	0.14	0.29	0.14	0.3	0.14	0.29	0.14	0.136
# Dependent Offspring + Harvesting Rice + Stored Rice + Camp Stability + Affinal Closeness + Camp Size	0.38	0.12	0.38	0.13	0.38	0.13	0.64	0.12	0.38	0.13	0.126
# Dependent Offspring + Harvesting Rice + Stored Rice + Camp Stability + Consanguineal Relatedness + Camp Size	0.5	0.11	0.5	0.12	0.5	0.12	0.7	0.12	0.5	0.12	0.118
# Dependent Offspring + Harvesting Rice + Stored Rice + Camp Stability + Camp Size	0.7	0.1	0.7	0.11	0.7	0.11	0.93	0.1	0.7	0.11	0.106
# Dependent Offspring + Harvesting Rice + Stored Rice + Camp Stability + Consanguineal Relatedness + Affinal Closeness	0.85	0.09	0.85	0.1	0.85	0.1	0.87	0.11	0.85	0.1	0.1
# Dependent Offspring + Harvesting Rice + Stored Rice + Camp Stability + Consanguineal Relatedness + Affinal Closeness + Camp Size	1.32	0.07	1.32	0.08	1.32	0.08	1.56	0.08	1.32	0.08	0.078
# Dependent Offspring + Harvesting Rice + Stored Rice + Camp Stability + Consanguineal Relatedness + Cash Labour Involvement	1.92	0.05	NA	0	NA	0	NA	0	NA	0	0.01
# Dependent Offspring + Harvesting Rice + Stored Rice + Camp Stability + Consanguineal Relatedness + Camp Size + Cash Labour Involvement	1.94	0.05	NA	0	NA	0	NA	0	NA	0	0.01

Table A3: Correlation of fixed effects from the global model for the Sharing and Taking Games, averaged over five imputed datasets, showing no evidence for strong collinearity in predictor variables (a correlation coefficient greater than 0.6 or 0.7 is generally regarded as highly collinear (Tabachnick & Fidell 2006), and none of the comparisons here reach this level).

	# Dependent Offspring	**Relatedness to Sample**	**Affinal Closeness**	**Harvesting Rice**	**Stored Rice**	**Camp Size**	**Camp Stability**	**Cash Labour Involvement**
# Dependent Offspring	-	0.112	0.208	0.121	0.203	-0.04	0.036	0.053
Relatedness to Sample	-	-	0.317	0.015	-0.048	0.011	0.044	-0.063
Affinal Closeness	-	-	-	0.01	0.03	-0.116	0178	-0.117
Harvesting Rice	-	-	-	-	0.128	-0.555	0.418	0.117
Stored Rice	-	-	-	-	-	-0.164	0.125	0.002
Camp Size	-	-	-	-	-	-	-0.539	0.265
Camp Stability	-	-	-	-	-	-	-	-0.273
Cash Labour Involvement	-	-	-	-	-	-	-	-

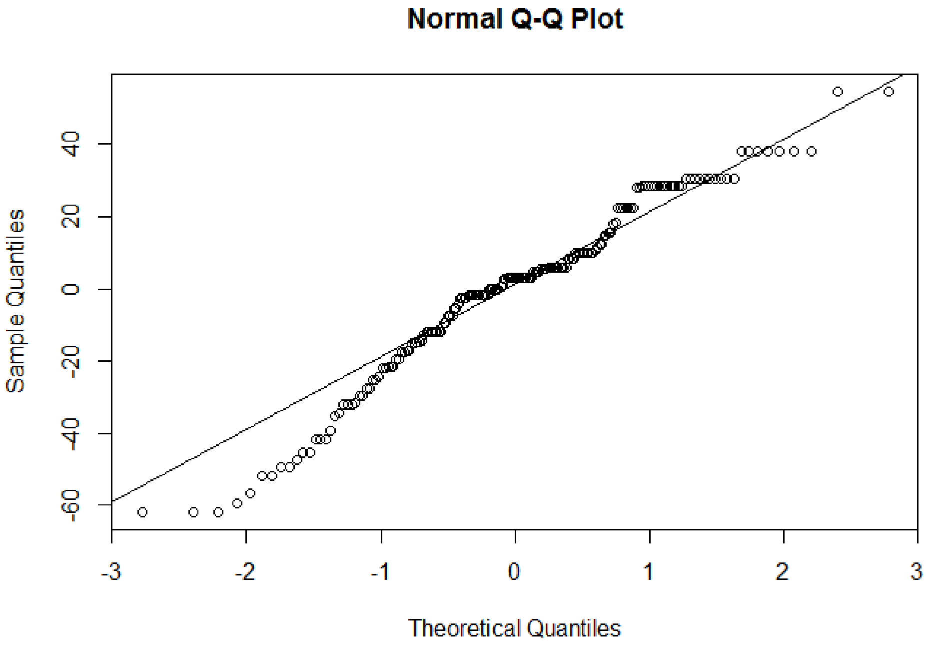

Figure A1: Q-Q plot for the null multi-level Sharing Game model. Although residuals somewhat differ from a normal distribution, results of the analyses are likely to be robust as: i) linear regression models are generally robust to violations of normality, and ii) ordinal logistic regression models, which do not require normally distributed response variables, indicate a qualitatively similar pattern of results (table A5).

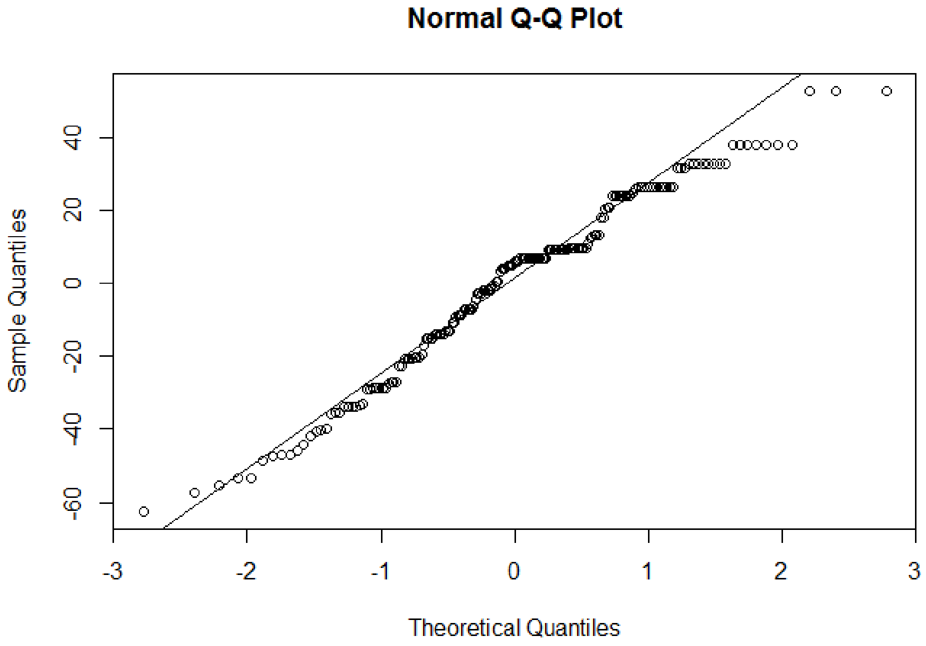

Figure A2: Q-Q plot for the null multi-level Taking Game model. Although residuals somewhat differ from a normal distribution, results of the analyses are likely to be robust as: i) linear regression models are generally robust to violations of normality, and ii) ordinal logistic regression models, which do not require normally distributed response variables, indicate a qualitatively similar pattern of results (table A7).

Table A4: Delta AICc values and model weights for each model within two AICc values of the top model for the Sharing Game using an ordinal logistic regression approach. Analyses utilise cumulative link mixed-models from the r package 'ordinal' (Christensen 2015). Due to the multiple imputation procedure estimating missing values, raw AICc values are not comparable across each imputed dataset so are not displayed here. The values presented are therefore delta AICc values and model weights for each of the five datasets separately, while a final column averages the model weights for each model over all imputed datasets.

Model Parameters	**Imputation 1**		**Imputation 2**		**Imputation 3**		**Imputation 4**		**Imputation 5**		**Averaged Model Weight (w_i)**
	ΔAICc	**w_i**	**ΔAICc**	**w_i**	**ΔAICc**	**w_i**	**ΔAICc**	**w_i**	**ΔAICc**	**w_i**	
# Dependent Offspring + Affinal Closeness + Harvesting Rice + Stored Rice + Camp Stability + Cash Labour Involvement	0	0.43	0	0.64	0	0.41	0	0.38	0	0.41	0.454
# Dependent Offspring + Affinal Closeness + Harvesting Rice + Camp Stability + Cash Labour Involvement	1.17	0.24	1.17	0.36	1.41	0.2	0.8	0.25	1.36	0.21	0.252
Affinal Closeness + Harvesting Rice + Stored Rice + Camp Stability + Cash Labour Involvement	1.85	0.17	NA	0	1.32	0.21	1.58	0.17	1.91	0.16	0.142
Affinal Closeness + Harvesting Rice + Camp Stability + Cash Labour Involvement	1.9	0.17	NA	0	1.6	0.18	1.27	0.2	NA	0	0.11
# Dependent Offspring + Affinal Closeness + Harvesting Rice + Stored Rice + Camp Stability	NA	0	NA	0	NA	0	NA	0	1.21	0.22	0.044

Table A5: Results of the model averaging analysis, pooled across five imputed datasets, for the Sharing Game using ordinal regression methods on standardised data (*n*=183, camps=11). Analyses utilise cumulative link mixed-models from the r package 'ordinal' (Christensen 2015). Raw percentages of amount kept have been collapsed into discrete categories (<10%=0; 10-19%=1, 20-29%=2 […] 100%=10). Coefficients are log-odd estimates of the association between the predictor variable and a one unit increase in the ordinal scale of amount of rice taken from others. 95% confidence intervals are displayed in brackets. Relative importance denotes the summed Akaike weight (w_i) of each parameter in the top models used in model averaging, with a '1' indicating that this term occurred in all of the top models. Predictive variables are analogous to those from the linear multi-level model in the main text (table 4.4), although here number of dependent offspring and supplies of stored rice lose some of their predictive power, relative to the linear multi-level model in the main text (although these effects are still in the same direction). Note that when random effects are added to ordinal logistic regression models there can be issues of convergence (Agresti *et al.* 2000), meaning that accurate standard errors could not be obtained for all models used in model averaging. While this is unlikely to greatly influence the overall pattern of results, the estimates presented here should be interpreted as approximations, rather than precise estimates, of the effect sizes. Note also that consanguineal relatedness to sample and camp size do not appear here as none of the top models contained either of these variables.

Variable	**Level**	**Standardised Parameter Estimate (95% CI)**	**Relative Importance (w_i)**
Camp Stability	Camp	-2.26 [-1.55; -2.98]	1.00
Harvesting Rice (1=No)	Camp	1.43 [0.61; 2.26]	1.00
Affinal Closeness	Individual	-0.87 [-0.29; -1.46]	1.00
Cash Labour Involvement	Individual	-0.72 [-0.11; -1.34]	0.956
# Dependent Offspring	Individual	0.43 [-0.25; 1.18]	0.75
Stored Rice (1=No)	Individual	0.34 [-0.33; 1.01]	0.638

Table A6: Delta AICc values and model weights for each model within two AICc values of the top model for the Taking Game using an ordinal logistic regression approach. Analyses utilise cumulative link mixed-models from the r package 'ordinal' (Christensen 2015). Due to the multiple imputation procedure estimating missing values, raw AICc values are not comparable across each imputed dataset so are not displayed here. The values presented are therefore delta AICc values and model weights for each of the five datasets separately, while a final column averages the model weights for each model over all imputed datasets.

Model Parameters	Imputation 1		Imputation 2		Imputation 3		Imputation 4		Imputation 5		Averaged Model Weight (w_i)
	ΔAICc	w_i	**ΔAICc**	w_i	**ΔAICc**	w_i	**ΔAICc**	w_i	**ΔAICc**	w_i	
# Dependent Offspring + Affinal Closeness + Harvesting Rice + Stored Rice + Camp Stability	0	0.36	0	0.36	0	0.36	0	0.45	0	0.36	0.378
# Dependent Offspring + Affinal Closeness + Harvesting Rice + Stored Rice + Camp Stability + Camp Size	0.15	0.34	0.15	0.34	0.15	0.34	0.4	0.37	0.15	0.34	0.346
# Dependent Offspring + Affinal Closeness + Harvesting Rice + Stored Rice + Camp Stability + Consanguineal Relatedness	1.75	0.15	1.75	0.15	1.75	0.15	1.72	0.19	1.75	0.15	0.158
# Dependent Offspring + Affinal Closeness + Harvesting Rice + Stored Rice + Camp Stability + Camp Size + Consanguineal Relatedness	1.85	0.15	1.85	0.15	1.85	0.15	NA	0	1.85	0.15	0.12

Table A7: Results of the model averaging analysis, pooled across five imputed datasets, for the Taking Game using ordinal logistic regression methods on standardised data (*n*=183, camps=11). Analyses utilise cumulative link mixed-models from the r package 'ordinal' (Christensen 2015). Raw percentages of amount kept have been collapsed into discrete categories (<10%=0; 10-19%=1, 20-29%=2 […] 100%=10). Coefficients are log-odd estimates of the association between the predictor variable and a one unit increase in the ordinal scale of amount of rice kept for self. 95% confidence intervals are displayed in brackets. Relative importance denotes the summed Akaike weight (w_i) of each parameter in the top models used in model averaging, with a '1' indicating that this term occurred in all of the top models. Predictive variables are analogous to those from the linear multi-level model in the main text (table 4.5), although here affinal closeness gains predictive power, with individuals sharing weaker affinal kinship ties to the sample taking less from others. Note that when random effects are added to ordinal logistic regression models there can be issues of convergence (Agresti *et al.* 2000), meaning that accurate standard errors could not be obtained for all models used in model averaging. While this is unlikely to greatly influence the overall pattern of results, the estimates presented here should be interpreted as approximations, rather than precise estimates, of the effect sizes. Note also that cash labour involvement does not appear here as none of the top models contained this variable.

Variable	**Level**	**Standardised Parameter Estimate (95% CI)**	**Relative Importance (w_i)**
Camp Stability	Camp	-2.31 [-1.45; -3.18]	1.00
Harvesting Rice (1=No)	Camp	1.47 [0.52; 2.43]	1.00
# Dependent Offspring	Individual	0.98 [0.37; 1.59]	1.00
Stored Rice (1=No)	Individual	0.79 [0.2; 1.39]	1.00
Affinal Closeness	Individual	-0.71 [-0.08; -1.34]	1.00
Camp Size	Camp	-0.28 [-0.81; 0.26]	0.458
Consanguineal Relatedness	Individual	0.07 [-0.25; 0.4]	0.278

Table A8: Correlation matrix displaying the association between each of the reputational domains (*n*=324). Although some correlations are significant, the effect sizes are relatively weak (all bar one are *r*≤0.3). Reputation is measured as a binary variable, with ‘1’ indicating skill in said domain (a *z*-score above ‘0’), and less-skilled individuals given a ‘0’ (a *z*-score equal or lower than ‘0’). *p*-value codes: ˙ <.1, * <.05, ** <.01, *** <.001

	Hunting Skill	**Fishing Skill**	**Tuber-Gathering Skill**	**Story-Telling Ability**	**Medicinal Knowledge**	**Camp Influence**
Hunting Skill	-	**0.274*** **	**-0.241*** **	0.06	-0.05	**0.254*** **
Fishing Skill		-	**-0.256*** **	-0.011	**-0.181*** **	**0.221*** **
Tuber-Gathering Skill	-	-	-	**0.292*** **	**-0.401*** **	-0.084
Storytelling Ability	-	-	-	-	**0.3*** **	**0.276*** **
Medicinal Knowledge	-	-	-	-	-	**0.255*** **
Camp Influence	-	-	-	-	-	-

Table A9: Collinearity diagnostics (variance inflation factors; VIFs) regarding reputational domains with aggregate popularity in the camp-mate network as the dependent variable (*n*=304). Aggregate popularity was calculated by transforming the proportion of nominations for each individual in a camp into *z*-scores (thus controlling for different camps sizes). A VIF above 3 is indicative of severe collinearity which may bias parameter estimates (Zuur *et al.* 2010). None of the VIFs here are greater than 1.42, indicating little evidence for collinearity between these reputational variables.

Reputational Domain	**VIF**
Hunting Skill	1.17
Fishing Skill	1.18
Tuber-Gathering Skill	1.42
Storytelling Ability	1.22
Medicinal Knowledge	1.38
Camp Influence	1.33

Table A10: Camp-mate networks comparing interactions with age and sex, using the full model as the null model. Other than for reciprocity, fishing skill, and (more weakly) proximity, the null model has the best fit, indicating that age and sex effects do not appear to greatly influence residential decisions. Model fit is compared using quasi-likelihood information criterion (QIC) estimates. The model with the lowest QIC value is highlighted in bold.

Model	Kinship	Reciprocity	Alter Coop.	Coop. Homophily	Proximity	Hunting Skill	Fishing Skill	Tuber Skill	Story-Telling	Med. Know.	Camp Inf.
Null	**3578.82**	3578.82	**3578.82**	**3578.82**	3578.82	**3578.82**	3578.82	**3578.82**	**3578.82**	**3578.82**	**3578.82**
Age	3584.4	3573.32	3581.02	3579.86	**3578.67**	3581.57	3583.1	3581.8	3580.67	3579.08	3579.67
Sex	3586.58	3569.76	3580.87	3581.32	3580.85	3580.98	**3571.12**	3579.57	3581.45	3580.55	3581.55
Age + Sex	3592.75	**3559.86**	3582.21	3582.19	3580.33	3583.69	3575.8	3582.69	3583.33	3580.5	3582.55
Age*Sex	3597.82	3564.07	3587.87	3585.66	3582.61	3588.35	3580.92	3589.76	3588.21	3583.09	3587.67

Table A11: Sharing Game comparing interactions with age and sex, using the full model as the null model. Other than for storytelling, the null model has the best fit, indicating that age and sex effects do not appear to greatly influence resource allocation decisions. Model fit is compared using quasi-likelihood information criterion (QIC) estimates. The model with the lowest QIC value is highlighted in bold.

Model	Kinship	Reciprocity	Alter Coop.	Coop. Homophily	Proximity	Hunting Skill	Fishing Skill	Tuber Skill	Story-Telling	Med. Know.	Camp Inf.
Null	**1098.06**	**1098.06**	**1098.06**	**1098.06**	**1098.06**	**1098.06**	**1098.06**	**1098.06**	1098.06	**1098.06**	**1098.06**
Age	1105.86	1099.17	1100.66	1100.19	1101.16	1100.5	1098.14	1100.68	**1096.06**	1100.26	1101.74
Sex	1108.64	1100.48	1100.09	1099.96	1100.09	1100.28	1099.7	1100.43	1100.25	1099.36	1099.84
Age + Sex	1116.57	1101.6	1102.7	1102.27	1103.17	1102.77	1099.62	1103.64	1097.94	1101.65	1103.39
Age*Sex	1125.33	1102.64	1106.47	1103.64	1107.31	1106.92	1101.42	1106.14	1101.1	1105.82	1109.23

Table A12: Differences in adult and child cooperative behaviour in pooled and unpooled camps. Sample sizes are displayed in brackets next to the camp average. High values indicate increased amount of resources kept for self. Compared to the large amount of variation between other camps, the differences between the pooled camps are low, reducing the potential for this procedure to influence the conclusions presented above. A statistically significant relationship between child and adult camp average scores is still reported (n=14, r=.744, p=.002), with an adjusted r^2 value of .517 (figure A3), indicating that pooling camps is unlikely to significantly alter the conclusions derived in the main text regarding the association between child cooperativeness and adult camp average scores.

Unpooled Camp	Unpooled Adult Score	Unpooled Child Score	Pooled Camp	Comprised of Camps	Pooled Adult Score	Pooled Child Score
54	40.816 (7)	53.333 (3)	**84**	54 + 84	40.924 (17)	44.444 (9)
84	41 (10)	40 (6)				
M1	30.667 (15)	63.333 (6)	**M**	M1 + M2 + M3.1	40.11 (37)	48.75 (16)
M2	50.714 (14)	42.857 (7)				
M3.1	39.286 (8)	33.333 (3)				

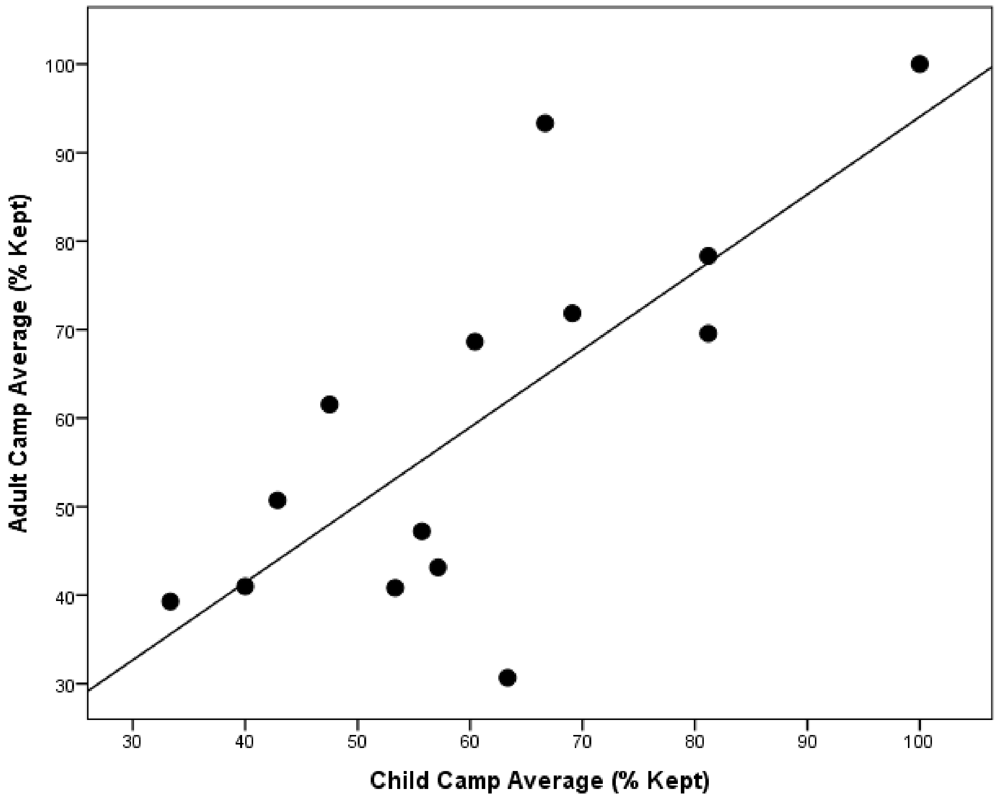

Figure A3: Scatterplot displaying the relationship between child and adult camp average amount of gifts kept using unpooled camp data (n=14). Compared to figure 7.1, which uses pooled camp data, the results are qualitatively identical.

Table A13: Delta AICc values and model weights for each model within two AICc values of the top model for the children's cooperative game using a multi-level linear regression approach. Due to the multiple imputation procedure estimating missing values, raw AICc values are not comparable across each imputed dataset so are not displayed here. The values presented are therefore delta AICc values and model weights for each of the five datasets separately, while a final column averages the model weights for each model over all imputed datasets.

Model Parameters	**Imputation 1**		**Imputation 2**		**Imputation 3**		**Imputation 4**		**Imputation 5**		**Avgd Model Weight (w_i)**
	ΔAICc	**w_i**	**ΔAICc**	**w_i**	**ΔAICc**	**w_i**	**ΔAICc**	**w_i**	**ΔAICc**	**w_i**	
Adult Camp Average + Age + Father Score + Adult Camp Average*Age	0	0.12	0.31	0.06	0	0.14	1.37	0.09	0	0.16	0.114
Adult Camp Average + Father Score	0.5	0.09	0.54	0.05	0.77	0.1	NA	0	0.92	0.1	0.068
Adult Camp Average + Age + Father Score	0.6	0.09	0.42	0.06	0.84	0.09	NA	0	0.98	0.1	0.068
Adult Camp Average + Age + Adult Camp Average*Age	0.92	0.08	1.22	0.04	NA	0	NA	0	1.14	0.09	0.042
Adult Camp Average + Age + Father Score + Sex + Adult Camp Average*Age	0.97	0.07	0.97	0.04	0.62	0.11	NA	0	0.9	0.1	0.064
Adult Camp Average	1.27	0.06	1.56	0.03	NA	0	NA	0	1.48	0.08	0.034
Adult Camp Average + Age + Father Score + Sex	1.28	0.06	0.77	0.05	1.13	0.08	NA	0	1.57	0.07	0.052
Adult Camp Average + Father Score + Sex	1.29	0.06	1.02	0.04	1.19	0.08	NA	0	1.62	0.07	0.05
Adult Camp Average + Age	1.29	0.06	1.59	0.03			NA	0	1.51	0.08	0.043
Adult Camp Average + Age + Father Score + Birth Order + Adult Camp Average*Age	1.61	0.05	NA	0	1.35	0.07	NA	0	1.68	0.07	0.038
Adult Camp Average + Age + Father Score + # Siblings + Adult Camp Average*Age	1.83	0.05	NA	0	NA	0	NA	0	NA	0	0.01
Adult Camp Average + Age + Father Score + Sex + Father Score*Sex	1.87	0.05	NA	0	NA	0	0.08	0.17	NA	0	0.044
Adult Camp Average + Age + Sex + Adult Camp Average*Age	1.88	0.05	NA	0	NA	0	NA	0	NA	0	0.01
Adult Camp Average + Age + Father Score + Sex + Adult Camp Average*Age + Father Score*Sex	1.88	0.05	NA	0	1.64	0.06	0	0.17	NA	0	0.056
Adult Camp Average + Age + Sex	1.98	0.04	NA	0			NA	0	NA	0	0.01

Adult Camp Average + Age + Father Score + Mother Score	NA	0	0	0.07	1.73	0.06	NA	0	NA	0	0.026
Adult Camp Average + Age + Father Score + Mother Score + Adult Camp Average*Age	NA	0	0.37	0.06	1.03	0.09	NA	0	1.87	0.06	0.042
Adult Camp Average + Age + Father Score + Mother Score + Sex	NA	0	0.62	0.05	NA	0	NA	0	NA	0	0.01
Adult Camp Average + Father Score + Mother Score	NA	0	0.64	0.05	1.89	0.06	NA	0	NA	0	0.022
Adult Camp Average + Age + Father Score + Mother Score + Sex + Mother Score*Sex	NA	0	1.21	0.04	NA	0	NA	0	NA	0	0.008
Adult Camp Average + Age + Father Score + Mother Score + Sex + Adult Camp Average*Age	NA	0	1.23	0.04	NA	0	NA	0	NA	0	0.008
Adult Camp Average + Father Score + Mother Score + Sex	NA	0	1.36	0.04	NA	0	NA	0	NA	0	0.008
Adult Camp Average + Age + Father Score + Mother Score + Birth Order	NA	0	1.55	0.03	NA	0	NA	0	NA	0	0.006
Adult Camp Average + Age + Father Score + Mother Score + Sex + Adult Camp Average*Age Mother Score*Sex	NA	0	1.7	0.03	NA	0	NA	0	NA	0	0.006
Adult Camp Average + Age + Mother Score + Birth Order + Adult Camp Average*Age	NA	0	1.73	0.03	NA	0	NA	0	NA	0	0.006
Adult Camp Average + Age + Father Score + Mother Score + Sex + Father Score*Sex	NA	0	1.77	0.03	NA	0	NA	0	NA	0	0.006
Adult Camp Average + Age + Father Score + Birth Order	NA	0	1.79	0.03	NA	0	NA	0	NA	0	0.006
Adult Camp Average + Father Score + Mother Score + Sex + Father Score*Sex + Mother Score*Sex	NA	0	1.82	0.03	NA	0	NA	0	NA	0	0.006
Adult Camp Average + Age + Father Score + Mother Score + # Siblings	NA	0	1.84	0.03	NA	0	NA	0	NA	0	0.006
Adult Camp Average + Age + Father Score + Mother Score + Birth Order + Adult Camp Average*Age	NA	0	1.94	0.03	NA	0	NA	0	NA	0	0.006
Adult Camp Average + Age + Father Score + Sex + Birth Order + Adult Camp Average*Age	NA	0	NA	0	1.92	0.06	NA	0	NA	0	0.012
Adult Camp Average + Father Score + Sex + Father Score*Sex	NA	0	NA	0	NA	0	0.8	0.12	NA	0	0.024

Adult Camp Average + Age + Father Score + Sex + Birth Order + Father Score*Sex	NA	0	NA	0	NA	0	1.32	0.09	NA	0	0.018
Adult Camp Average + Age + Father Score + Sex + Birth Order + Adult Camp Average*Age + Father Score*Sex	NA	0	NA	0	NA	0	1.37	0.09	NA	0	0.018
Adult Camp Average + Age + Father Score + Sex + # Siblings + Adult Camp Average*Age + Father Score*Sex	NA	0	NA	0	NA	0	1.68	0.07	NA	0	0.014
Adult Camp Average + Age + Father Score + Sex + # Siblings + Father Score*Sex	NA	0	NA	0	NA	0	1.73	0.07	NA	0	0.014
Adult Camp Average + Age + Father Score + Mother Score + Sex + Father Score*Sex	NA	0	NA	0	NA	0	1.93	0.07	NA	0	0.014
Adult Camp Average + Age + Father Score + Mother Score + Sex + Adult Camp Average*Age Father Score*Sex	NA	0	NA	0	NA	0	1.97	0.06	NA	0	0.012

Table A14: Correlation of fixed effects for the global models of the children's sharing game, averaged over five imputed datasets, showing no evidence for strong collinearity in predictor variables (a correlation coefficient greater than 0.6 or 0.7 is generally regarded as highly collinear (Tabachnick & Fidell 2006), and none of the comparisons here reaches this level).

	Age	**Sex**	**# Sibs**	**Birth Order**	**Adult Camp Ave.**	**Mother Score**	**Father Score**
Age	-	0.025	-0.168	0.151	0.068	-0.058	0.049
Sex	-	-	-0.051	0.04	-0.044	0.116	-0.013
# Sibs	-	-	-	-0.462	0.102	-0.242	-0.009
Birth Order	-	-	-	-	-0.163	0.134	0.063
Adult Camp Ave.	-	-	-	-	-	-0.428	-0.206
Mother Score	-	-	-	-	-	-	-0.352
Father Score	-	-	-	-	-	-	-

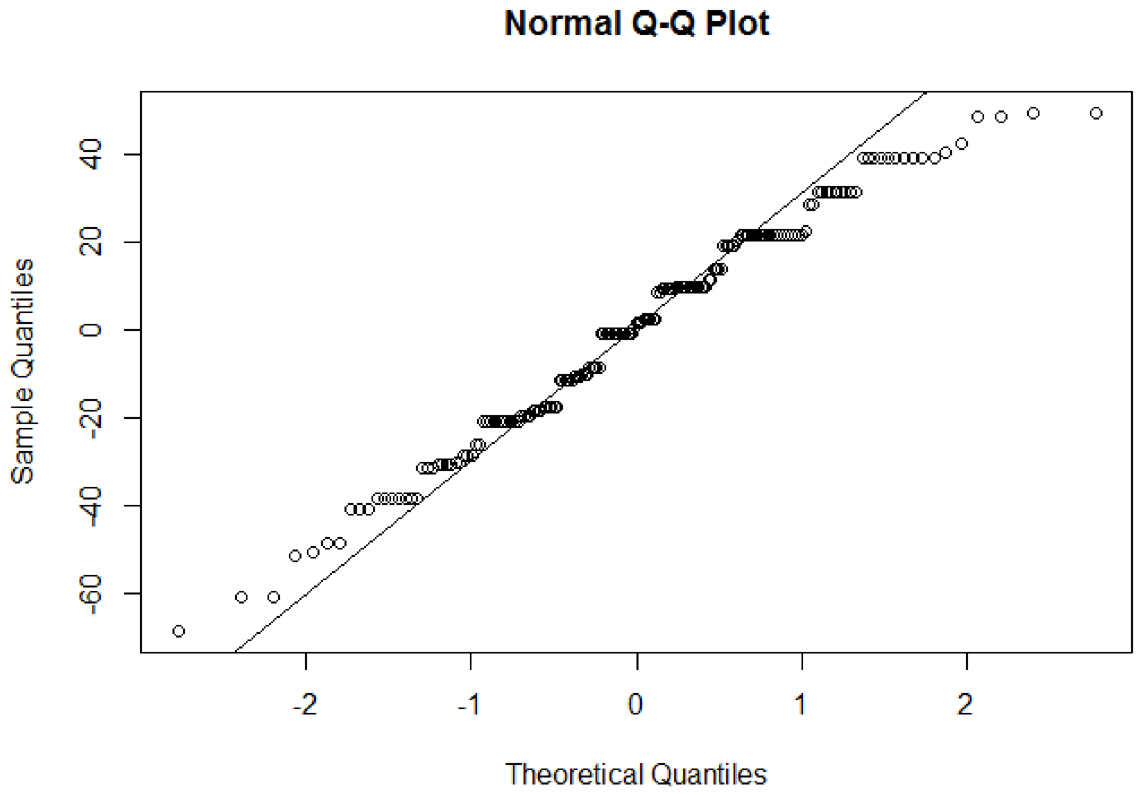

Figure A4: Q-Q plot for the null multi-level model for the children's Sharing Game. Although residuals somewhat differ from a normal distribution, results of the analyses are likely to be robust as: i) linear regression models are generally robust to violations of normality, and ii) ordinal logistic regression models, which do not require normally distributed response variables, indicate a qualitatively similar pattern of results (table A16).

Table A15: Delta AICc values and model weights for each model within two AICc values of the top model for the children's sharing game using an ordinal logistic regression approach. Analyses utilise cumulative link mixed-models from the r package 'ordinal' (Christensen 2015). Due to the multiple imputation procedure estimating missing values, raw AICc values are not comparable across each imputed dataset so are not displayed here. The values presented are therefore delta AICc values and model weights for each of the five datasets separately, while a final column averages the model weights for each model over all imputed datasets.

Model Parameters	**Imputation 1**		**Imputation 2**		**Imputation 3**		**Imputation 4**		**Imputation 5**		**Avgd Model Weight (w_i)**
	ΔAICc	**w_i**	**ΔAICc**	**w_i**	**ΔAICc**	**w_i**	**ΔAICc**	**w_i**	**ΔAICc**	**w_i**	
Adult Camp Average + Age + Father Score + Adult Camp Average*Age	0	0.24	0	0.14	0	0.27	1.63	0.19	0	0.33	0.234
Adult Camp Average + Age + Adult Camp Average*Age	0.67	0.17	0.84	0.09	NA	0	NA	0	1.33	0.17	0.086
Adult Camp Average + Age + Father Score + Sex + Adult Camp Average*Age	0.78	0.16	0.65	0.1	0.39	0.22	NA	0	0.69	0.23	0.142
Adult Camp Average + Age + Sex + Adult Camp Average*Age	1.52	0.11	1.7	0.06	NA	0	NA	0	NA	0	0.034
Adult Camp Average + Age + Father Score + Sex + Adult Camp Average*Age + Father Score*Sex	1.66	0.11	NA	0	NA	0	NA	0	NA	0	0.022
Adult Camp Average + Age + Father Score + Birth Order + Adult Camp Average*Age	1.74	0.1	1.41	0.07	1.4	0.13	NA	0	1.84	0.13	0.086
Adult Camp Average + Age + Father Score	1.86	0.1	1.14	0.08	NA	0	NA	0	NA	0	0.036
Adult Camp Average + Age + Father Score + Mother Score + Adult Camp Average*Age	NA	0	0.75	0.09	1.31	0.14	NA	0	NA	0	0.046
Adult Camp Average + Age + Father Score + Mother Score	NA	0	1.31	0.07	NA	0	NA	0	NA	0	0.014
Adult Camp Average + Age + Father Score + Sex	NA	0	1.36	0.07	NA	0	NA	0	NA	0	0.014
Adult Camp Average + Age + Father Score + Sex + Adult Camp Average*Age	NA	0	1.49	0.07	NA	0	NA	0	NA	0	0.014
Adult Camp Average + Father Score	NA	0	1.65	0.06	NA	0	NA	0	NA	0	0.012
Adult Camp Average + Age + Father Score + Mother Score + Sex	NA	0	1.72	0.06	NA	0	NA	0	NA	0	0.012
Adult Camp Average + Age + Father Score + Birth Order + Sex + Adult Camp Average*Age	NA	0	1.98	0.05	1.73	0.11	NA	0	NA	0	0.032

Adult Camp Average + Age + Father Score + Sex + Adult Camp Average*Age + Father Score*Sex	NA	0	NA	0	1.55	0.12	0	0.42	1.87	0.13	0.134
Adult Camp Average + Age + Father Score + Sex + Father Score*Sex	NA	0	NA	0	NA	0	1.36	0.21	NA	0	0.042
Adult Camp Average + Age + Father Score + Birth Order + Sex + Adult Camp Average*Age + Father Score*Sex	NA	0	NA	0	NA	0	1.64	0.18	NA	0	0.036

Table A16: Results of the model averaging analysis, pooled across five imputed datasets, for the children's sharing game using ordinal logistic regression methods on standardised data (*n*=179, camps=11). Analyses utilise cumulative link mixed-models from the r package 'ordinal' (Christensen 2015). Rather than percent of resources kept, response data were simply the number of resource ego kept for self, ranging from 0 to 5. Coefficients are log-odd estimates of the association between the predictor variable and a one unit increase in the ordinal scale of number of resources kept for self. 95% confidence intervals are displayed in brackets. Relative importance denotes the summed Akaike weight (w_i) of each parameter in the top models used in model averaging, with a '1' indicating that this term occurred in all of the top models. Predictive variables are qualitatively identical to those from the linear multi-level model in the main text (table 7.3). Note that when random effects are added to ordinal logistic regression models there can be issues of convergence (Agresti *et al.* 2000), meaning that accurate standard errors could not be obtained for all models used in model averaging. While this is unlikely to greatly influence the overall pattern of results, the estimates presented here should be interpreted as approximations, rather than precise estimates, of the effect sizes. Note also that number of siblings and the sex by mother's cooperative score interaction do not appear here as none of the top models contained either of these terms.

Variable	**Level**	**Standardised Parameter Estimate (95% CI)**	**Relative Importance (w_i)**
Adult Camp Average	Camp	2.07 [1.17; 3.02]	1.00
Father Score	Individual	-0.7 [-1.43; 0.07]	0.878
Age	Individual	-0.49 [-1.07; 0.09]	0.988
Sex	Individual	-0.18 [-0.69; 0.33]	0.484
Mother Score	Individual	0.04 [-0.49; 0.58]	0.086
Birth Order	Individual	-0.04 [-0.32; 0.24]	0.156
Adult Camp Average*Age	NA	1.26 [-0.31; 2.84]	0.87
Father Score*Sex	NA	-0.26 [-1.06; 0.54]	0.234