On Trade-offs and Communal Breeding

The Behavioural Ecology of Agta Foragers

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I, Abigail E. Page 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

Time is finite and no organism can avoid the allocation dilemma that this necessarily entails. A quintessential trade-off is that between parental investment and reproduction, otherwise known as the quality-quantity trade-off. However, humans may be exceptional among apes given our high quantity production of high quality offspring. This success has been argued only to be possible by breeding communally. In this thesis I explore questions surrounding trade-offs, communal breeding and their fitness consequences in a small-scale foraging society, the Agta. The first analysis examines the composition of Agta childcare using an innovative form of data collection to maximise sample sizes, previously a major limitation in hunter-gatherer research. The Agta, like many small-scale societies are prolific communal breeders. However, *contra* previous conclusions, juveniles and non-kin appeared to provide more allocare than grandmothers. Interactions with non-kin were associated with significant decreases in maternal workload, while interactions with siblings and grandmothers were not. The next analysis explores why both kin and non-kin behave cooperatively, finding support for kin selection among close kin and reciprocity for distant kin and non-kin allocare. Communal breeding appears to be an important mechanism to ensure enough childcare was received in the absence of other strategies to counter shortfalls in household energy budgets. The next analysis asks, what are the fitness consequences of maternal social networks and allocare? Mothers' network centrality positively correlated with non-kin allocare as well as reproductive success, revealing the adaptive value of communal breeding. These results highlight the optimising nature of hunter-gatherer cooperation and life history strategies.

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1 INTRODUCTIONS

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Chapter One

Introductions: Human Behavioural Ecology and Hunter-Gatherers

"Feign illness, feign fatigue, go to the limit of all lies and feign frigidity. But no more children, hiccoughed to conception. Four were enough. But how she loved them when she held them first, heavy-lidded, helpless, the head out of all proportion…Given security she'd bear a dozen, but not as things were. No paupers for the parish". Daphne Du Maurier, *Mary Anne: 70*

Awareness of reproductive trade-offs is not limited to the realms of academia or the evolutionary study of human behaviour. Each mother faces the decisions that define the study of life history, such as how many children to have, when to have the next child, how much to invest in which child and when to start and when to stop reproducing. Like all organisms our time, and hence our energy, is finite (Charnov 1993). Thus, we all face an allocation dilemma; too many children and we will not be able to provide for them all. Life history theory is a theoretical approach within behavioural ecology which takes for granted that reproductive behaviours and decision-making, such as expressed by the fictional character Mary-Anne above, are fitness maximising (Hill & Hurtado 1996). This by no means requires an conscious break down of calorific energy expenditure versus proportion of genetic representation in future generations – this laborious task is left to human behavioural ecologists – but rather, natural selection favours behaviours which increase fitness regardless of whether they are couched in cultural or social emic explanations (Davies *et al.* 2012).

Humans, like several gregarious mammals do not raise their children in isolation but are commonly defined as cooperative breeders (Hrdy 2005). Cooperative breeding is, in its simplest form, when non-mothers provide childcare and provisioning to offspring, a theory predominately developed to explain the extreme cooperation in co-nesting birds (Koenig & Dickinson 2004), or reproductive suppression in mammals such as naked mole rats (*Heterocephalus glaber,* (Solomon & French 1997)) and eusocial insects (Wilson 2008). When mothers have access to additional assistance in childrearing, trade-offs are altered; earlier weaning and a quicker resumption of ovulation is possible when someone else can take an infant off your hands. That human someone has often been argued to be grandmothers, and consequentially, our exceptional survival post-reproduction has been associated with grandmaternal importance in the successful production of multiple offspring (Hawkes *et al.* 1997; Hrdy 2005).

This thesis investigates cooperative breeding, life history and their adaptive values. This research is firmly grounded in behavioural ecology and seeks the ultimate explanation of behaviour in its given ecological context (Nettle *et al.* 2012). Hypotheses are developed following key life history predictions, focusing on parental investment and inclusive fitness explanations of cooperation. In conducting this research with the Agta – a Philippine foraging group – I aim to further the understanding of life history, reproduction and cooperation in a natural fertility (individuals who do not use modern contraceptives, but may of course use natural means of limiting their fertility such as avoidance and prolonged breastfeeding) population which spends the majority of subsistence activities foraging. However, significant variability exists within the Agta, as with any population, allowing the exploration of the 'reactive norms' of behaviour in different contexts. Foragers face a unique situation among humans (but not animals) in which they survive without maternal wealth, leading many to argue that the origins of cooperation and sociality lie in the importance of relational wealth buffering inherent risks and shortfalls in foraging niches (Winterhalder 1986). I aim to explore the variability in wealth, cooperation and reproduction among the Agta to shed light on the adaptive role of human social networks.

1.1 Who are the hunter-gatherers?

The definition of hunter-gatherers is fraught with difficulties and contention. Their very name implies that the distinction is an economic one. Thus, hunter-gatherers are those without domesticated plants and livestock (Kelly 2013). However, this excludes the majority of ethnographically known foraging populations since most are involved in some form of market exchange and a diversification of subsistence (Hitchcock & Biesele 2000). Given that hunter-gatherers could not be defined as 'Pleistocene economies' in 1968 during the first symposium on foraging societies since "such a definition would effectively eliminate most, if not all, of the peoples reported…" (Lee & DeVore 1968: 4), this is certainly not possible today. Attempts to define hunter-gatherer groups in this way is reflective of nostalgia for

Jean-Jacques Rousseau's concept of the Noble Savage and of Sahlins' 'original affluent society' (Sahlins 1968). This harps back to early thought in anthropology of hunter-gatherers as primitive, uncultured fossils who had yet to evolve 'civilisation' (Kelly 2013). Yet, such topological definitions are unnecessary, and predictably hide more variability that exists between the remaining hunter-gatherers today. Here, I am in complete agreement with Kelly (2013) who argues that the term hunter-gatherer has no explanatory weight; however there are aspects of hunter-gatherer lifeways which the Agta share with other foraging groups that poses specific constraints, pressures and contextual influence, which (I expect to) condition human behaviour. The exact percentage of time spent in foraging is meaningless[1] as a taxonomic division between 'foragers' and 'non-foragers'. However, foraging modes of subsistence poses a unique set of behavioural challenges which individuals are expected to meet. Consequentially, it is the variability among hunter-gatherers that can inform our understanding of behaviour.

A division is commonly draw between 'complex' or 'delayed-return' hunter-gatherers and 'primitive' or 'immediate-return foraging[2] societies. The former labels are problematically value ridden. As a result I will use Woodburn's (1982) 'return' terminology here. Delayed return foragers are those epitomised by North West American hunter-gatherers, who were more sedentarised, practiced mixed methods of food production, produced surplus requiring storage, leading to the accumulation of wealth, social status and hierarchy (Kelly 2013). In contrast, immediate-return foragers, as the name suggests, produce and consume food on a daily basis; there is no food storage and individuals move freely throughout the environment as there is little concept of property, territoriality and belongings are rare. Thus, the distinction between these groups is based on degree of egalitarianism associated with key features of mobility and wealth (Woodburn 1982). The Agta fall into the latter, allowing me to draw parallels between other egalitarian groups such as the Aka, BaYaka, Hadza, !Kung and Batak (to name a few). Over the next section I will introduce the theoretical framework underpinning this research and discuss humans' key life history traits.

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[1] For instance, what is exactly the 'right' amount of foraging? More than 50%, 75% or 95% of subsistence activities? Who sets this threshold and what is the model for comparison?

[2] I use both terms 'hunter-gatherers' and 'foragers' interchangeably throughout this thesis for linguistic variance only.

1.2 Theoretical approaches

1.2.1 Evolutionary perspectives

Evolution can be defined as descent with modification, often driven by natural selection which itself is the product of three observable aspects of traits: *(i)* heritability; *(ii)* variability; and *(iii)* competition resulting in differential reproductive outcomes (Darwin 1859). There is no sense of progression here. Instead, adaptation by natural selection will simply favour the propagation of traits which maximises individuals reproductive success or lifetime fitness, i.e. the number of genetic copies present in future generations (Gross 2005; West *et al.* 2011). It is through behaviour that most animals interact with the environment. Consequently, behavioural strategies have a large influence on fitness, and thus, a target of evolution (Kappeler *et al.* 2013). For instance, a South African brown fur seal (*Arctocephalus pusillus*) who, rather than swim in a large mobbing group, goes for a solitary dip on a regular basis would soon find herself face-to-teeth with a great white (*Carcharodon carcharias*). In other words, antipredatory behaviours are a key survival strategy. The evolutionary analysis of behaviour falls under the discipline of behavioural ecology which seeks to understand how and why behaviours are optimal in fitness terms given their ecological context (Davies *et al.* 2012; Winterhalder & Smith 2000). At the heart of this is the assumption that individuals tend to be fitness maximising due to the evolution of reactive norms which increase lifetime reproductive success (Grafen 2002; Nettle *et al.* 2013). A reactive norm is simply the evolved ability to respond adaptively to differential circumstances. This means that there is no need for behaviour to be rigorously under the control of genes (Sear 2015) but it is the *ability to respond* which is under selective pressure. This reactive norm is expected to result in a fitness payoff. However, this is tempered by a series of phylogenetic, developmental, morphological and genetic constraints (Kappeler *et al.* 2013; Hill & Hurtado 1996). Therefore, the underlying assumption in behavioural ecology predictions and hypotheses is that "phenotypes should be approximately optimal (i.e. fitness maximizing)" (Hill & Hurtado 1996: 13).

1.2.2 Human behavioural ecology

Human behavioural ecology is an offshoot of behavioural ecology specifically dealing with humans. In complete agreement with Nettle's *et al.* (2013) recent review of the field, there is no fundamental difference in approach between the study of human or other animal behaviour; humans are expected to have evolved behavioural strategies which increase their genetic representation in future generations, given ecological context and constraints. This starting point generates hypothesis for further analysis to explore both ultimate and proximate explanations about the evolution of behaviour. As originally laid out by Tinbergen (1963), ultimate explanations are those which ask the evolutionary *why* question, which can be answered in terms of phylogeny - which marine bird species have evolved cooperative breeding – or functionality – do mothers increase their reproductive success by breeding cooperatively? Proximate questions are those that ask *how,* and include ontological investigations – how do children learn to cooperate – and mechanistic questions – what maintains an individual's cooperative behaviour? The boundaries between whether an explanation is casual or mechanistic can become blurred, especially in the study of cooperation (Barrett & Stulp 2013). Here, I focus on ultimate explanations for behaviour as I seek to directly quantify the fitness consequences of reproductive trade-offs and cooperative breeding, as well as understanding the roles of kin selection and reciprocity in cooperation. However, the measurement of fitness is difficult given the long life of human subjects (Orr 2009). Therefore, as a proxy for lifetime fitness, similar to many human behavioural ecologists, I use age-controlled fertility and survivorship to maturity rates to explore the fitness consequences of life history trade-offs among the Agta (Sear 2015).

1.2.3 Life history theory

Life history schedules are the outcome of individuals' allocation of time and energy to maximise inclusive fitness, given extrinsic mortality rates (Charnov 1993). The production of offspring requires energy, the harvesting of which takes time. Time is also required to grow and develop, the longer time spent in which, the greater the amount of energy can be extracted from the environment (Hill & Kaplan 1999). Organisms face a trade-off between time spent in reproduction (shortened by time spent in growth) and adult reproductive rate (increased due to growth and somatic investment), or otherwise put, a trade-off between current and future reproduction (Stearns 1992; Kaplan *et al.* 2000a). The solution to this dilemma is represented in a number of predictable life history traits across species, such as: size at birth, age at maturity, size at maturity and length of life (Stearns 1992).

The longer an organism survives for, the more energy can be devoted to growth and the accumulation of resources and skills. This is somatic effort and it is crucial for fitness as height, body mass index (BMI) and resources are commonly positively correlated with reproductive success (Gibson & Mace 2003; Allal et al. 2004; Lawson & Mace 2011; Kaplan,

K. Hill, et al. 2000a; but not consistently Sear 2010)However, the future is not certain, and the amount of time invested in somatic effort is dictated by extrinsic mortality risks. Hence, in an environment in which mortality is higher, we would expect less investment in growth and life history schedules to be speeded up (Charnov 1993). Yet too early reproduction can result in diminishing returns as intrinsic mortality increases (Charnov & Berrigan 1993; Stearns 1992). The distinction between intrinsic and extrinsic mortality is thus crucial in life history theory, the former being influenced by the allocation decisions of organisms and the latter being uninfluenced by trade-offs (Stearns 1992). However, this distinction can be difficult to make (Promislow 1991) as many forms of mortality could be arguably be influenced by investment at some points but not at others; a child of better nutritional condition may fight influenza, however nutritional condition may do little in the face of a highly virulent zoonotic pathogen. Ultimately then age at maturity and cessation of growth is dependent on the costs and benefits of maturation of different ages and sizes. If individuals are facing high extrinsic mortality risks it follows that early maturing individuals will be more likely to survive and thus reproduce, maximising their reproductive success (Stearns 1992). However, this simultaneously reduces time spent in growth and development. As a result extrinsic risks in the environment can be considered to result in either 'fast' (develop fast, reproduce lots, die young) or 'slow' (develop slowly, invest in offspring, live long) life history traits as organisms attempt to optimise allocations given constraints (Nettle 2010; Promislow & Harvey 1990).

Fast life history strategies are not only represented by features like earlier maturation and smaller body size (Migliano *et al.* 2007), but also by the trade-off between the number and quality of offspring, otherwise referred to as the quantity-quality trade off. The quantity-quality premise states that the optimal level of fertility is that which balances the number of offspring produced against their survival and future reproductive success (Borgerhoff Mulder 2000; Lack 1954). A parent cannot invest excessively in multiple offspring, and thus must choose between fewer high quality offspring or multiple low quality offspring (Hill & Hurtado 1996). While some evidence is supportive of natural fertility populations acting 'optimally' in this regard (Borgerhoff Mulder 2000; Strassmann & Gillespie 2002; Lawson *et al.* 2012), the evidence is inconclusive as data from the Ache and !Kung reveal that women would have achieved higher fitness by exhibiting higher fertility (Pennington & Harpending 1988; Hill & Hurtado 1996).

One cause may be unmeasured heterogeneity among women or in their environments (Lawson & Mace 2011). For instance, a mother's allocation of effort is dependent on the degree of risk in the environment. In high mortality environments mothers are expected to invest in quantity rather than quality. Quinlan (2007) demonstrated that maternal care shows a quadratic relationship with pathogen load. Maternal investment occurs for as long as an offspring's survival is responsive to care. Once the mother starts to receive diminishing returns from this investment due to unalterable environmental assaults, her care drops dramatically. At this time, a mother increases her fitness by investing elsewhere. This demonstrates the blur between intrinsic and extrinsic risk, revealing the usefulness of thinking of risk as a continuum. Desai (1995) compared child outcomes with sibship size, finding that in resource poor contexts sibling quantity had little influence of child quality. This indicates that parental ability to influence child outcomes plays an important role in life history strategies, potentially obscuring quantity-quality trade-offs if left unmeasured (Lawson & Mace 2011). Unlike the Dogon and Kipsigis (agropastoralists) for whom quality-quantity trade-offs have been demonstrated (Strassmann & Gillespie 2002; Borgerhoff Mulder 2000) variance in reproductive success of the Ache is more dependent on fertility than it is mortality (Hill & Hurtado 1996; Strassmann & Gillespie 2002). Thus, in environments where there is little variance in mortality (i.e. childhood and juvenile mortality occurs regardless of parental interventions) fitness is maximised by fertility, suggesting that the point of diminishing returns for higher fertility may be at a substantially higher threshold than in lower mortality environments, in which mortality has a larger relative influence of reproductive success.

The quality-quantity trade-off is part of the subset of life history theory that falls under 'parental investment'. Trivers (1972: 139) defines parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring". A mother's reproductive success is not only the result of the production, survival and future reproductive value of one offspring, but a combination of all her current offspring's survival and expected reproductive value plus all her future offspring's survival and expected reproductive success (Gross 2005). However, this equation is further influenced by the fact that not all children are born equal. Due to differential mortality and skewed sex ratios, the reproductive value of different offspring, often dependent on age and sex, varies. As a result, in some scenarios males have significantly higher reproductive value than their sisters, and thus are favoured in terms of parental investment (Mace 1996). Ultimately then, the art of reproduction is one of the optimal allocation of time following expectations of reproductive value given estimated extrinsic mortality risks. So how in general do humans solve this allocation problem?

1.3 Human life history traits and cooperative breeding

Humans have been noted for their combination of 'fast' and 'slow' life history traits defined by long lives, late maturation and prolonged growth as well as early weaning, shorter interbirth intervals and high fertility (Charnov & Berrigan 1993; Robson & Wood 2008). Compared to other great apes we manage quite a feat by producing and simultaneously raising, on average, six to eight highly dependent offspring (Table 1.1, (Campbell and Wood, 1988)). This extreme dependency of infants stems from our energetically expensive brains (Aiello & Wheeler 1995) as gestation and lactation both significantly increase the energetic demands on the mother (by 25% and 39%, respectively (Aiello & Key 2002)). Furthermore, given our prolonged juvenile period and arguably minimal productive ability, offspring remain dependent on parents for many years as they, like many animals with slow life histories, invest in growth, development and skills (Kaplan *et al.* 2003). This is possible because of the doubling of adult life expectancy between humans and chimpanzees (Hill *et al.* 2001; Kaplan *et al.* 2000a), setting humans on a slow life history path.

Table 1.1: Life history variables for human foragers and non-human great apes.

	Human foragers	**Orangutans**	**Gorillas**	**Chimpanzees**
Mean age at first reproduction	19.7	15.6	10	14.3
Mean age at last reproduction	39	38	-	27.7
Mean inter-birth interval (IBI)	3.72	8.1	4.4	5.5
Age at weaning	2.8	7	4.1	4.5
Expected age of death at 15	54.1	39	-	29.7
Total fertility rate (TFR)	6.1	-	3	2

Human forager data is the average of Ache, Hadza, Hiwi, and !Kung data reported in (Marlowe 2010; Howell 1979; Hill & Hurtado 1996; Kaplan *et al.* 2000a). The chimpanzee (*Pan sp.*) data is the average for Bossou, Gombe, Kibale, Mahale, and Tai reported also reported in (Kaplan *et al.* 2000), except for age at weaning which is taken from (Alvarez 2000). Data for Orangutans (*Pongo sp.*) is reported in (Alvarez 2000) for age at weaning and IBI, and in (Wich *et al.* 2004) for age at first and last reproduction and life span. Age at weaning for gorillas (*Gorilla spp.*) is the mean reported for *G. beringei* (3.6 years (Fletcher 2001)) and *G. gorilla* (4.6 years (Nowell & Fletcher 2007)), TFR as reported by (Kaplan *et al.* 2000a) and IBI and age at weaning as reported by (Alvarez 2000).

However, unlike other species with late maturation and extended life span, humans wean infants at a younger age resulting in shorter interbirth intervals and high fertility. Across mammals infants are weaned when they reach a third of the mother's body weight or at the eruption of the first permanent molar (Charnov & Berrigan 1993). For humans this suggests we should wean our offspring at around 6 years of age, closer to the Orangutan (*Pongo spp.*) pattern. However, human populations average at around half this at 2.8 years (Lee *et al.* 1991; Alvarez 2000), significantly earlier than all other apes. Consequently humans have combined strategies and invest in a high number of high quality offspring, made possible, according to the cooperative breeding hypothesis, by allomaternal assistance (Hrdy 2011; Kennedy 2005).

Allomothering[3] refers to care from any individual other than the mother (Tecot *et al.* 2012) and is assumed critical for the successful rearing of multiple dependents as they provide the additional investment required by mothers (Snopkowski & Sear 2013; Hrdy 2005). As a result, 'allocare' can be defined as childcare from anyone other than the mother. However, in terms of cooperative breeding literature the key function of allocare is to reduce the energetic burden from the mother, allowing her to invest in both quality and quantity. As a result 'allocare' should not be considered to be only be high-quality, active childcare (such as carrying for instance), as low-quality, passive childcare has the same ability to reduce maternal energetic burden (discussed in more detail in chapter 5). Mothers with assistance have additional energy to invest in subsistence labour, childcare or their own somatic condition and fertility. Thus, in the ultimate sense, cooperative breeding is expected to be associated with increases in either fertility or child survivorship and quality (dependent on environmental risks). Such evidence is apparent among callitrichids in which allocarer presence increased the amount of time mothers spent feeding (Mitani & Watts 1997) and their foraging efficiency (Tardif 1997) as well as pup weight gain and survivorship in Kalahari meerkats (*Suricata suricatta* (Clutton-Brock *et al.* 2001)). Not wishing to cherry pick examples, some studies do fail to demonstrate fitness consequences of cooperative breeding, however overall among both birds (Dickinson & Hatchwell 2004) and mammals there appears a consensus that allocare is associated with reductions in parental investment and load lighting, leading to increases in recipient fitness (Solomon & French 1997; Russell 2004), a trend matched in the human literature (Sear & Mace 2008).

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[3] Alloparent on the other hand refers to care from any individual who is not the parent, the distinction being whether male or bi-parental care is of theoretical interest.

1.4 Hypotheses and objectives

Given the above I developed three major hypotheses which guide the analyses within this thesis. Firstly, based on our understanding of humans' combination of fast and slow life history strategies, I hypothesised that allocare is an important form for childcare among the Agta, particularly due to their reliance of relational wealth. However, rather than an 'ace in the hole' allocarer that does it all, I hypothesised that mothers would have large flexible networks to maintain cooperative breeding in a diverse and unpredictable environment (both socially and naturally). Finally, following the cooperative breeding hypothesis I predicted that patterns in allocare would have implications for child and material health and/or material fertility. These hypotheses are explored in analysis chapters 6, 7 and 8.

1.5 Overview of thesis structure

This thesis explores and brings together these different aspects of human life history – cooperative breeding, reproductive trade-offs and parental investment – in a population of hunter-gatherers living in the Philippine rainforest. My intention is to offer unique insights to the complexities around cooperative behaviour, parental investment and fitness outcomes in a foraging group which continues to be largely reliant on mobility and foraging modes of subsistence. However, the Agta, like many hunter-gatherers today, also exhibit significant variability in terms of degree of foraging, cultivation, sedentism and wealth accumulation. Rather than sweep this variability under the carpet, this thesis seeks to explore the relationship variability has with different behavioural strategies and demographic consequences.

After an introduction to my data collection, methodology and the Agta themselves I examine several interrelated questions across four analysis chapters. The literature review found in chapter two and analyses in chapters five and six focuses on the explanation of the occurrence of cooperative breeding from an inclusive fitness standpoint. I ask firstly, who provides allocare among the Agta (chapter five), and secondly what causes apparently selfish individuals to provide costly allocare (chapter six). Chapter seven also deals with cooperative breeding, but this time asks, what is its adaptive value? In this analysis I explore the fitness consequences of allocare and maternal social networks. The analysis in chapter eight deals with quality-quantity trade-offs and explores how mothers maximise their reproductive success. Here, I ask what is the adaptive function of behavioural change towards increased settlement and cultivation, and what hypothesises can be put forward to understand the paradox of Neolithic health deterioration alongside population growth. Finally, chapter nine brings together these analysis and comments on the overarching themes of this work in the context of the wider literature. I focus on the implications of these research findings for perspectives of human cooperation, life history as well as the role of hunter-gatherers studies in human behavioural ecology.

Chapter Two

The Agta: Resilient Foragers Under Transition?

The Agta are one of several Negrito populations residing in the Philippines. Negrito refers to a phenotypically similar group – dark skinned, short statured and curly haired - of hunter-gatherers in Southeast Asia, ranging from the western Andaman Islanders in India, to the Semang of Malaysia and ending at the north-eastern Agta of the Philippines (Omoto 1984; Endicott 2013). Other hunter-gatherer groups in the Philippines include the Batak from Palawan, the Aeta of western Luzon and the Ata from Negros. Some have rejected the term Negrito as derogatory as it means 'little black person' (Minter 2010). However, it remains a useful terminology to refer to a genetically similar population dispersed throughout the region, separating populations like the Aeta and Agta from the other 'indigenous peoples' (IPs) of the Philippines who arrived in later population migrations (Scholes *et al.* 2011).

Archaeological and genetic data suggests that anatomically modern hunter-gatherers reached Southeast Asia around 50,000 years ago and resided in Luzon for the last 45-40,000 years based on radiocarbon and luminescence dating (Bellwood 2010; Higham 2013). Investigations into the genetic diversity of the Aeta and Agta reveal long-term settlement of the region due to high levels of autosomal differentiation (Heyer *et al.* 2013). Interestingly, however, recent evidence reveals that there is no significant Y-chromosome differentiation between Negritos and non-Negrito Philippine populations (Delfin *et al.* 2011), supported by mtDNA and Y-chromosome genetic variation from the Batak revealing a lack of a common Negrito ancestor which excludes non-Negritos (Scholes *et al.* 2011). Finally, Philippine Negritos have been found to be more genetically similar to non-Negrito neighbours than one another (Migliano *et al.* 2013). Thus, while some of the 'Negrito' phenotypes, such as dark skin colour, are likely due to deep ancestry and survival of isolated populations, other phenotypes, such as short stature, may occur due to convergent evolution (Migliano *et al.* 2013; Scholes *et al.* 2011; Endicott 2013).

From around 5-4,000 years ago systemic agriculture arose in the region as a later wave of migration of Austronesian-speaking farmers spread from Taiwan throughout the Philippines

(Lipson *et al.* 2014). Linguistic evidence suggests heavy interaction at this point as the 'original' Agta languages were replaced by the Austronesian languages (Diamond 2014; Bellwood 2010; Reid 2013). Despite this significant interaction, hunter-gatherer groups remain in some of the Philippines most isolated regions, maintaining lifestyles that match many of the features of other immediate-return foragers.

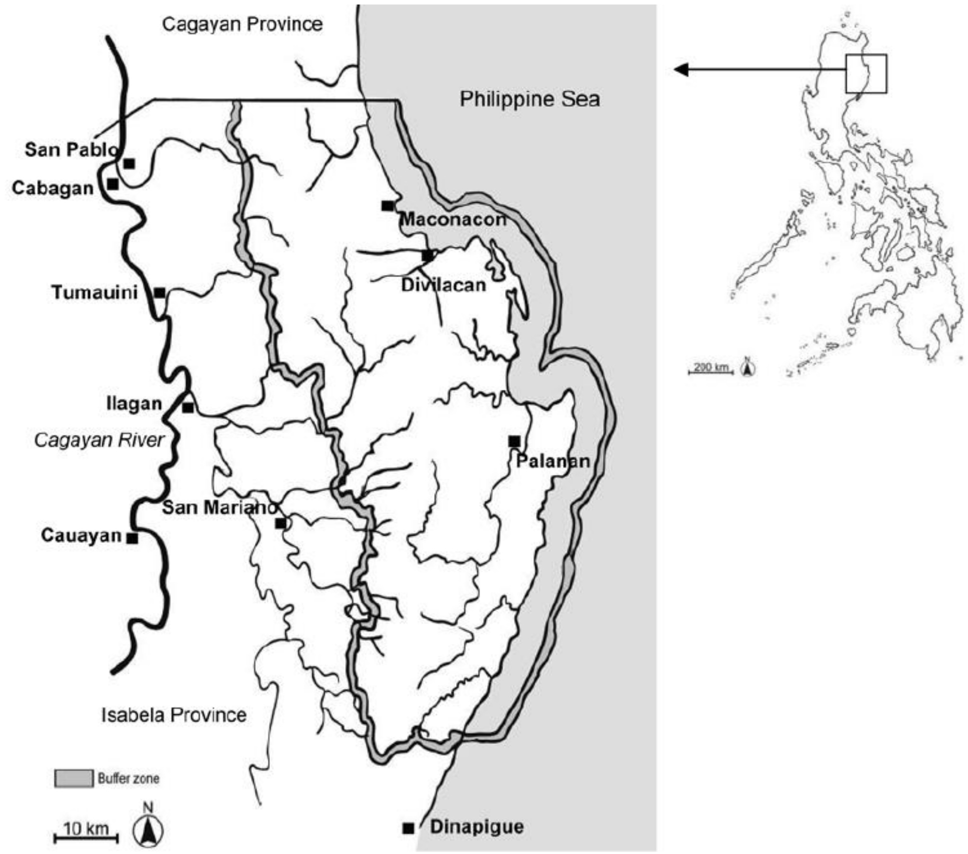

Figure 2.1: Map of the Sierra Madre, Isabela. Thick line represents the National Park boundaries (NSMNP). The Palanan Agta reside within its boundaries. From Minter (2010: 2).

There are around 1,800 Agta living within the Northern Sierra Madre Natural Park (NSMNP) found in Isabela Province, the second largest administrative district located in the north east of Luzon (Figure 2.1). The NSMNP is a the largest protected zone in the Philippines, covering around 360,000 hectares and includes mountainous tropical rainforest, river watersheds and the beaches, coral reefs and diverse marine eco-system of the Pacific Ocean (Minter 2010). This study focuses on a population of 914 Agta living within Palanan. During 2013-2014 we (Mark Dyble, Sylvain Viguier, Daniel Smith and I, please see section

4.1 for further discussion about the hunter-gatherer resilience team and data collection) met 914 of these Agta residing in a total of 20 mobile camps (Figure 2.2). As discussed by Rai (1990) the Agta throughout the region form distinct linguistic groups, broadly adhering to municipal lines. Thus, there is in fact limited interaction between the Agta living in San Mariano (Rai 1990), Cagayan (Griffin & Griffin 1992), Maconacon (Griffin & Griffin 1997) and Casiguran (Early & Headland 1998; Headland *et al.* 1989; Headland 1989). From our own records, we find that marriage between these groups is rare. This perhaps is not surprising since many Agta do not know Tagalog, the national language of the Philippines, making communication difficult between linguistic groups.

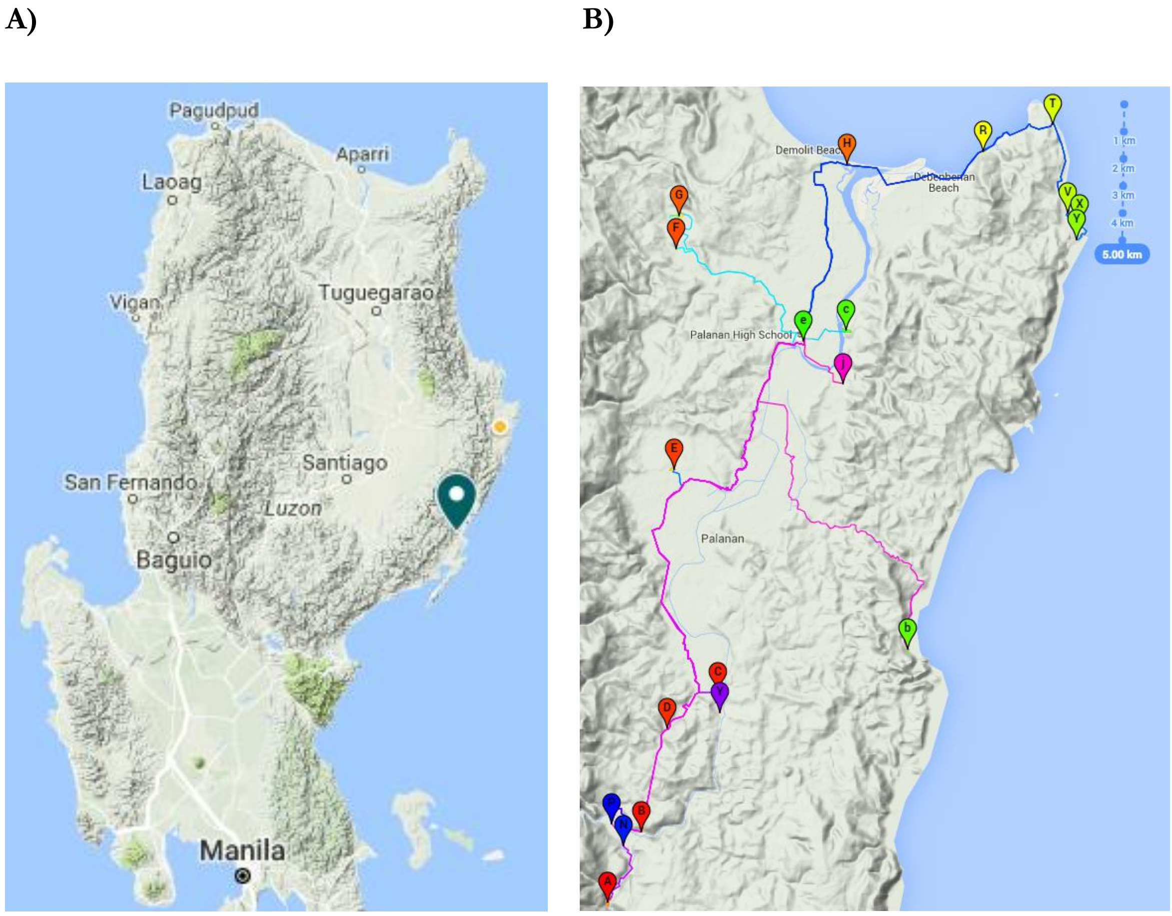

Figure 2.2: A) The location of Dilasag (Aurora province) is marked by the green icon, Palanan (Isabela province) is marked by the yellow pot. The road from Manila ends at Dilasag. B) Close up of Palanan and Agta camps. Markers are each camp we visited during our fieldwork. The lines are the major routes taken from these camps to Palanan.

Some of the best-known literature on the Agta stems from groups living in Casiguran, to the south of Palanan and the NSMNP. Early and Headland (1998) and Headland (1989) demographic data reveals the Casiguran Agta to be at the extremes of known rates of infant mortality, homicide and life span, revealing a rapidly declining population (1.2% per year between 1936 to 1976). In part, Headland argues that this is the result of external forces in the area with the rise of migrants, logging, mining and other extractive exploits (Headland 1984). These events were related to the construction of a road in 1977 to Dilasag, bringing an influx of violence, alcoholism, homicide and environmental and subsistence loss (caused by land grabbing, fishing with poisons and dynamite as well as land clearing (Early & Headland 1998)). Comparatively, the Agta of Palanan avoided this turmoil and social upheaval. No road joins Palanan to 'the mainland', as locals refer to the rest of Luzon (Figure 2.2). The only access to the interior of the NSMNP remains an irregular boat service from Dilasag (depending on weather conditions) or an expensive light-air craft journey across the mountains (also dependent on the weather and pilot availability). Therefore, the area has remained undeveloped, and there remains a minimal presence of logging and mining in the area (Minter, Personal communication).

The Palanan Agta have been comparatively less well studied, as previous researchers have focused on Agta groups to the south (Casiguran) and to the North (Cagayan and Maconacon) as well as those living in the mountainous area of San Mario. However, Tessa Minter from Lieden University has worked extensively with the Agta from the NSMNP since 2002, including the Agta communities in Palanan. Her research has primarily been demographic and applied in its nature, focusing on the Agta's resilience to changing economic and subsistence contexts and the interaction between the Agta and the state. Her PhD thesis provides a significant amount of ethnographic detail found in this chapter, and we have since worked in close collaboration with her to produce applied research focused on the well-being of the Agta.

2.1 Demographics

There are 914 Agta living in Palanan at the time of this study in 2013-2014. The sex ratio appears significantly skewed at 117.6 (one-side proportion test $x^2 = 5.8$, $p = 0.02$, 95% CI [0.51, 0.57]). The population pyramid below (Figure 2.3) reveals that this skew is mainly caused by a higher proportion of males in the under-five age category that has a sex ratio of 141.3 ($n = 222$, $x^2 = 6.2$, $p = 0.01$, 95% CI [0.52, 0.65]). Accordingly, if the under-fives are removed from the sample, males no longer out number females ($n = 692$, $x^2 = 1.8$, $p = 0.2$, 95% CI [0.49, 0.56]). Any remaining skew is the product of more males surviving beyond 55 than females (ratio of 250). Thus, during the reproductive years (16 – 55) the sex ratio is in fact 1:1. Similarly, male skewed ratios from birth have been reported among the Ache (125, Hill and Hurtado, 1996) and the Hiwi at 117 (Hurtado & Hill 1987) which may be influenced by male-specific mortality rates. If, as Fisher's (1930) observation states, more males die before reaching maturity, the males who actually survive to reproduce experience significantly higher reproductive success given the lack of competition. As a result, there would exist selective pressure on producing more males than girls at birth. Thus, male biased sex ratios during infancy, as evident among the Agta, may be the result of a compensation for higher male mortality rates, a hypothesis supported by the absence of a biased sex ratio after the 1 – 5 age group.

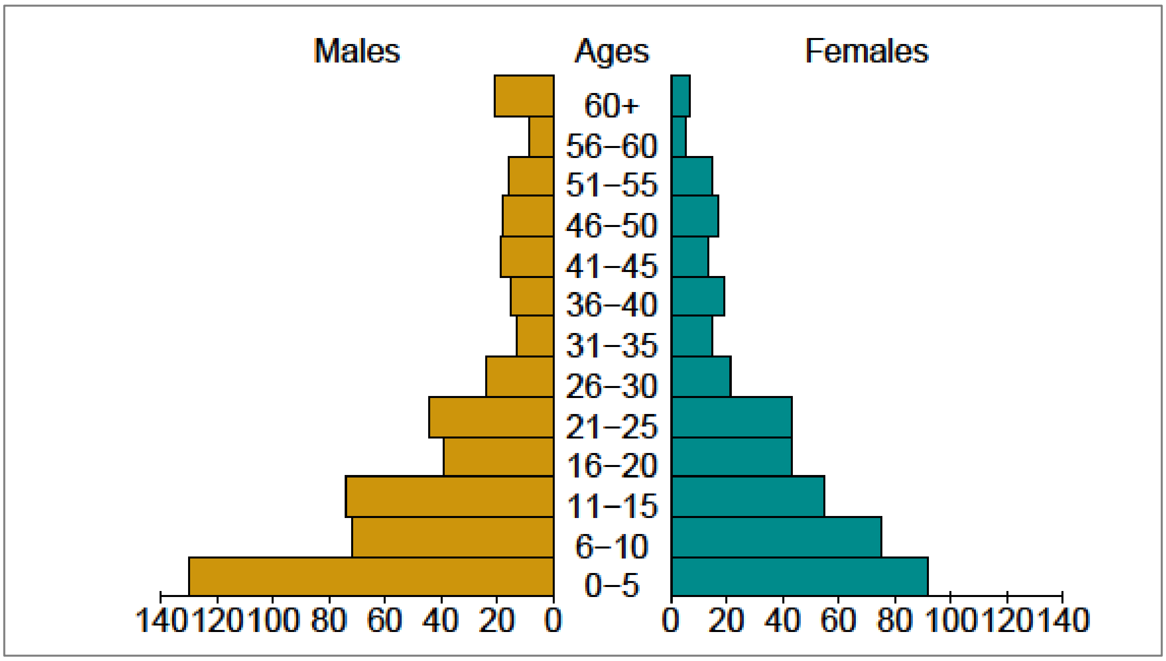

Figure 2.3: Population pyramid for 914 Agta censured during 2013-2014 separated by sex and 5 year age groups.

2.1.1 Marriage and fertility

Minter (2010) finds that marriage normally occurs at age 22 for men and 19 for women. Early and Headland (1998) argue this occurs soon after menarche at age 17, however our preliminary data suggests that 50% of Agta teens have reached menarche at age 13.8, indicative of a significantly earlier entry into reproduction. Nonetheless, the mean age at first birth is 20.4 among the Casiguran Agta, similar to our own figure at 20.2 years.

Previous estimates of Agta fertility has placed them at the higher end of the foraging fertility spectrum, for instance, Headland (1988) finds a total fertility rate (TFR) of 6.3 among the Agta from Casiguran and 5.9 from Agta of Palanan. Similarly Early and Headland (1998) report a TFR of 7 for the San Ifendo Pensiula Agta, while Goodman *et al.* (1985) find a TFR of 6.5 among the Cagayan Agta to the North. This is high compared to estimates for the Batek (5.2), Batak (3.7), Efe (2.6), Mbuti (5.0) and !Kung (4.1-4.7), however it is important to note that the TFR rates of the !Kung and Efe are likely negatively impacted by the high prevalence of sexually transmitted infection in Africa (Kelly 2013; Harpending 1994; Pennington & Harpending 1991). Accordingly, we find a period TFR of 7.7 based on births occurring during 2013-2014, one of the highest reported for hunter-gatherers (Kramer (2008) reports a TFR for the Pumé of 7.8 while Hill and Hurtado (1996) report a TFR of 8 for Ache still residing in the forest). Our sample contains 27 post-reproductive females (aged 50 or over), and their completed family sizes are significantly lower than the TFR at 6.13. This may be the consequence of under-reporting by older women, or perhaps indicates a more recent increase in fertility, driven perhaps by recent emphasis on reducing mobility; the TFR for women living in a settled camp was significantly higher than the TRF for women living in a mobile camp, 7.7 versus 6.6, respectively.

2.1.2 Life expectancy and Mortality

Minter (2010) finds life expectancy from birth to be 25 years, due in part to extremely high childhood mortality rates: 283 per 1000 live births based on reproductive histories with 159 households. Headland finds infant mortality rates of 34-37%, and childhood mortality (under 15 years) at 49-50% of all live births in Agta from Casiguran (Headland 1988; Early & Headland 1998). Comparing these results with our data, it appears the infant and child mortality rates are lower. Out of 520 reported live births during reproductive histories with 124 women, 19% children were reported to die before age one, 13.9% between the ages one to five and 6% between five to fifteen years. This means the Agta experience a childhood mortality rate of 388.5 per 1000 live births. Including later term miscarriages and stillbirths reveals that 17.9% of 592 conceptions do not result in a live birth, increasing the total mortality rate to 15 years to 520.3 per 1000 live births. Thus, whilst lower than previously reported the Agta can still be considered a high mortality population.

2.1.3 Causes of mortality

The major causes of mortality among the Agta are similar to those reported in other foraging groups (Hill & Hurtado 1996; Hill *et al.* 2007; Gurven *et al.* 2007; Howell 1979; Headland 1989; Early & Headland 1998; Minter 2010; Froment 2014) and include several respiratory diseases such as tuberculosis (TB) and pneumonia, as well as gastrointestinal infections and malaria. In our full sample of 427 deaths reported during family histories from direct family members, infectious disease accounted for 86% of cases. A full breakdown of causes of mortality are reported in Table 2.1, and match reports from both Minter (2010) and Early and Headland (1998) in neighbouring Agta populations.

Table 2.1: Major causes of mortality for 427 cases reported during family histories. RTI stands for respiratory tract infection, GID for gastrointestinal disease, neonatal for all cases of infant mortality soon after birth for unknown reasons.

Cause of death	*n*	%	Cum
Unknown	71	0.17	0.17
Violence	10	0.02	0.19
Malaria	26	0.06	0.25
Tuberculosis	35	0.08	0.33
Accident	21	0.05	0.38
Old Age	23	0.05	0.44
RTI	36	0.08	0.52
Childbirth	51	0.12	0.64
GID	35	0.08	0.72
Other disease	56	0.13	0.85
Measles	13	0.03	0.88
Neonatal	31	0.07	0.96
Alcoholism	19	0.04	1.00

The distribution of causes of death varies significantly according to the age of the individual. If we take the 202 childhood deaths, we see that accidents (15%) become an increasingly important cause of mortality in children aged one to fifteen years while RTI (20%) and nutritional conditions such as 'subi-subi' (17%) are major causes of mortality in the under one's (Table 2.2). Subi-subi is caused by a thiamine deficiency, and otherwise known as beri-beri (Minter, 2010). Malnutrition has a role to play in many of these deaths. In a nutritional study among Casiguran Agta, De Souza (2006) found that 34% of Agta adults were undernourished while 10% were extremely malnourished. This suggests that chronic under nutrition is a significant secondary factor in infectious disease mortality.

Table 2.2: Major causes of childhood mortality for 202 cases broken down by age. RTI stands for respiratory tract infection, GID for gastrointestinal disease, neonatal for all cases of infant mortality soon after birth for unknown reasons.

	< 1 year old		**1 - 15 years**		**< 15 years**	
	n	**%**	***n***	**%**	***n***	**%**
Malaria	9	0.09	15	0.15	24	0.12
Hepatitis	0	0.00	5	0.05	5	0.02
RTI	20	0.20	13	0.13	33	0.16
GID	8	0.08	16	0.16	24	0.12
Other disease	0	0.00	14	0.14	3	0.01
Measles	10	0.10	22	0.21	32	0.16
Subi-subi	17	0.17	3	0.03	20	0.10
Accident	4	0.04	15	0.15	19	0.09
Infection	6	0.06	0	0.00	6	0.03
Neonatal/Unknown	25	0.25	0	0.00	36	0.18

2.1.3.1 Skewed mortality sex ratios

One possible explanation for the extreme male-bias in the 1-5 year category above is the occurrence of sex-specific mortality rates in the under-fives. Looking at only infant (aged under one) mortality figures, there is no significant sex bias in the mortality results, as females account for 54% of deaths. However, there is a significant bias in the 1-5 age category, with a mortality sex ratio of 170.6 (Table 2.3), substantially higher than the 1-5 sex ratio (141.3). This reduces slightly during the 5 - 15 ages to 118.8. In adulthood, mortality becomes skewed towards females with a ratio of 0.8, likely due to the risks associated with childbirth, explaining why substantially fewer women survive to age 55 and beyond. A significantly higher proportion of male mortality is associated with accidents (mortality sex ratio 5), and virulent infectious diseases (malaria: 4, hepatitis: 2, RTI: 3 and measles: 4). Otherwise there seems to a significant nutritional element to female dominated causes of death (subi-subi: 0.33 and GID: 0.5). Therefore, these results indicate that accidents are a far greater cause of mortality for boys, likely due to their early adventures in the sea, river and trees. It also indicates they are either more likely to catch infectious diseases, are more susceptible to them or receive differential care from parents. However, the mortality skews are likely affected by the small sample sizes per cause of mortality in the 1-5 age group. Nonetheless, for all causes of mortality the sample is larger (*n* = 144), suggesting that males are far more likely to die during the ages 1-15 years, as such this may indicate an adaptive reason for such an extremely skewed sex ratio from birth.

Table 2.3: Sex ratio of mortality rates by cause of death, $n = 144$.

Cause of death	1 - 5 years	n	0 - 15 years	n
Malaria	4.0	5	1.43	17
Hepatitis	2.0	3	0.67	5
RTI	3.0	4	0.75	21
GID	0.5	6	1.17	13
Other	1.0	5	0.81	29
Measles	4.0	10	2.0	21
Subi-subi	0.33	4	0.7	17
Accident	5.0	6	2.67	11
Unknown	2.0	3	2.0	9
Total	1.71	46	1.15	144

In our whole sample, other 'social' causes of death such as violence (2.3%) and alcoholism (4.4%) appear much less important than infectious disease or accidents. If we take the adult only sample ($n = 108$) we find 6 cases of death associated with alcoholism (5.5%) and 8 cases associated with violence (7.4%). Demographic data on 2,953 individuals included in the Agta genealogy (ranging from roughly 1920 to today) reveal that only 10 homicides have occurred over the last 90 years, producing an effective homicide rate of 3.39. This is significantly lower than the rates reported for both the San Ildefonso Agta (129 per 1000 or 11 homicide since 1950 (Early & Headland 1998) and 326 in the Casiguran Agta (Headland 1989)). Similarly, Minter (2010) finds the influence of violence to be 'less manifest' among the Agta of the NSMNP. This is likely linked to the isolation of Palanan from the negative influences of logging and mining, and external population pressures (such as land grabbing). This rate puts the Palanan Agta to a violence level much closer to that found in the Batek (Endicott & Endicott 2008) and Hadza (Marlowe 2010).

In his 1989 paper on 'population decline' Headland argues that the majority of Agta adults from Casiguran are alcoholics. We did not witness such extreme rates of drinking during our fieldwork in Palanan. Alcohol consumption was limited to a few households, never the majority. Nonetheless, the Agta attribute 4% of deaths to alcohol-related causes, not too far from the 6% Headland found in Casiguran. This mismatch between the witnessed levels of alcohol consumption and reported causes of alcohol-related deaths could stem from either *(i)* the Agta citing alcohol as the cause of death when they do not know and/or felt an individual was of poor 'moral' character or *(ii)* as our mortality records data back 90 years, perhaps alcohol consumption was higher historically when Headland was conducting his fieldwork. However, the difference in social cohesion between the two populations at Casiguran and Palanan suggests that the Palanan Agta have never experienced such high rates of alcoholism, and I believe scenario *(i)* to be much more likely.

2.2 Kinship and Residence Patterns

Most authors portray the Agta as following a bilateral or cognatic descent system, in which ego gives equal weight to both lines of descent (i.e. matrilineal or patrilineal, Headland 1987; Rai 1990; Griffin 1996; Minter 2010)). Having a large but flexible kin base is important as it allows access to collectively held land (Minter 2010), a common feature in many immediate-return foraging societies (Kelly 2013).

On average, households move once every 10 days, but this varies according to the camp. This figure was established from individuals' presence in daily camp scans; each day households were recorded as there or away. Some households moved regularly between nearby sites (a trend noted by Peterson 1978), while some never moved. When data is transformed into a binary variable of either "moved once" or "never moved" we find that 27.5% out of 444 households were witnessed to move camp at least once. Rai (1990) finds among the Disabungan Agta that households moved once every 18 days in the late 1970's, while during the summer months Minter (2010) witnessed households to change camp as much as once every couple of days. Families cited a number of reasons for their move, often involving visiting missed relatives, seasonal fishing grounds, increasing social tensions and a dislike of the camp they were in. Often, individuals would make short distance moves because their previous location was dirty or smelly or families moved just because they liked to be mobile. The most mobile of individuals were teenagers, who would often go further afield visiting relatives without their immediate family. This trend is likely related to seeking out suitable marriage partners. Marriage is prohibited within an individual's own specific area (often referring to three to five camps spanning a relatively short distance) as the Agta are exogenous and avoid marriage with close kin. Marriage partners are most commonly found in neighbouring areas that have a few, but significantly less distant kin links (Minter 2010).

Marriages are monogamous and they appear highly stable. Marriages more commonly end due to death than divorce. Headland (1987) discusses a period of brideservice occurring in

Casiguran Agta that resulted in a period of matrilocal residence, after which the young family reverts to patrilocality. However, Peterson (1978) and Rai (1990) both argue that there is a matrilineal preference, leading to families joining the wife's family. This debate is a common one in anthropology, as the traditional view, that foragers are often patrilocal to best facilitate cooperative hunting, defence or warfare, appears hard to support given the cross-cultural evidence (Marlowe 2004). In part, the lack of clarity on this topic is due to hunter-gatherers ambilocal or bilocal residence pattern. As they are highly mobile and do not follow a unilineal descent system they do not need one set residence rule. Rather, they live with both the maternal and paternal kin depending on their needs (i.e. childcare early in life might simulate a matrilocal bias) and environmental conditions (i.e. good fishing where paternal kin might cause patrilocality). Therefore, it is more accurate to examine residence systems across a whole life course which demonstrate the majority of warm-climate foragers (68.8%) are bilocal (Marlowe 2004). This trend is found in the Palanan Agta, who live with both matrilineal and patrilineal kin without particular bias (Dyble *et al.* 2015). This has important implications for the flexibility of social networks: as individuals move between camps and reside with different relatives, having large and broad networks of contacts is important. As a consequence, who is included in an individual's social network is likely to change on a regular basis, which has implications for the discussion of social networks in chapter 8.

2.3 Camps and their mobility

The nature of camps varies according to location and degree of acculturalisation and cultivation. The Agta reside in broadly three types of camps. The most mobile of these are comprised of lean-tos, temporary housing which are constructed in less than an hour, and frequently moved according to rain, wind and sun (Figure 2.4). These shelters are made of crossed poles and palm leaves for roofing, thus are commonly abandoned (Rai 1990; Peterson 1978). Temporary camps do not have a church or water pump, but rather are based around a fresh water source (stream or river). The composition of these camps changes frequently, both in terms of the number, position and location of structures and the individuals residing within the camp. New individuals arrive and leave every couple of days.

Figure 2.4: Temporary Agta camp with lean-tos

A semi-permanent camp often contains a mixture of lean-tos and more permanent buildings, perhaps with a water pump. The water pumps and other infrastructure such as a church are the product of interventions from either the local government or the evangelical church organised by the Summer Institute of Linguistics. The more permanent type of Agta shelters are still built over a matter of days, consisting of natural materials. However, these are moved less often and commonly expanded or altered rather than abandoned. Finally, permanent camps have often been built around a church, garden or water pump and mainly consist of houses made by the Philippine government, which are made of wooden planks and iron roofs (Figure 2.5). These houses remain unaltered but individuals living in them may change.

Figure 2.5: Permanent Agta camp with a wooden house.

During Minter's fieldwork in 2002-2005 only one of the camps in Palanan was heavily settled, now this trend has extended and at least four of 20 camps in our sample have churches, permanent housing and water pumps. Therefore, the average camp movements may have reduced in recent time (but without solid data this is difficult to establish) and more camps are becoming more permanent. Nonetheless, we find that 26.8% of Agta households were in mobile camps, comprised of temporary housing (lean-tos) without the presence of infrastructure such as toilets or water pumps, or the presence of a church. As we conducted our research collection over two years we were able to get a sense of the changing nature of camps, demonstrated in Figure 2.6. There is significant variability in the degree of mobility between camps, as some camps such as Djago, in the top of Figure 2.6, had 83% the same individuals living in the camp between two visits, while another camp had only 24%. This figure ranged from 0% (when the camp was completely abandoned) to a maximum of 86% similarity. The mean figure was 0.59 ± 0.23.

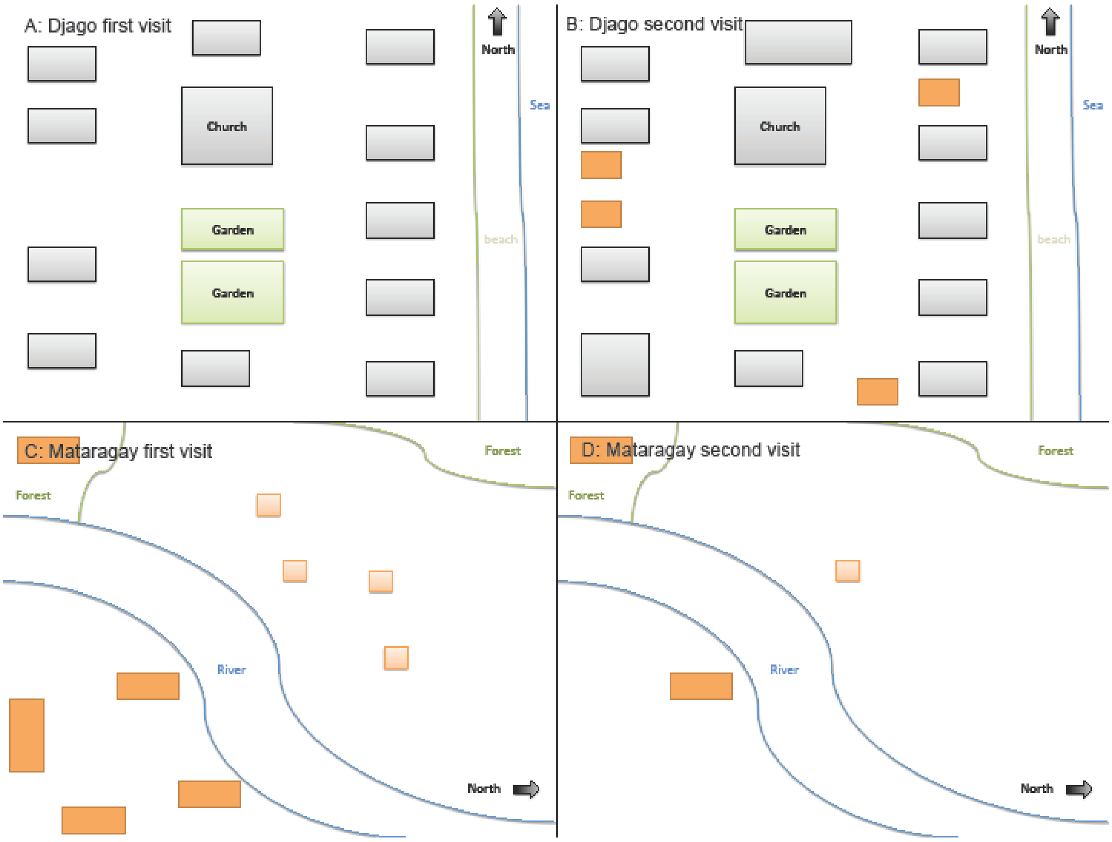

Figure 2.6: Two camps (A-B) Djago and (C-D) Mataragay between two visits (*left* first visit and *right* second). Black icons are wooden houses, dark orange are semi-permanent Agta huts and pale orange are lean-tos. Any other key camp features are labelled on the maps.

2.4 Subsistence and Diet

The Agta are predominantly marine and river fisher-gatherers, as out of 2,168 work activities 53.6% were spent fishing, 2.9% hunting, and 20% gathering. Non-foraging activities consist of cash labour (9.5% of activities), cultivation (12%) and trade (2.1%). Thus, the Agta continue to rely heavily on foraging modes of subsistence (76.5%) versus non-foraging activities (23.5%). Nonetheless, this varies significantly according to gender, location (coastal or inland ecologies) and degree of sedentarisation.

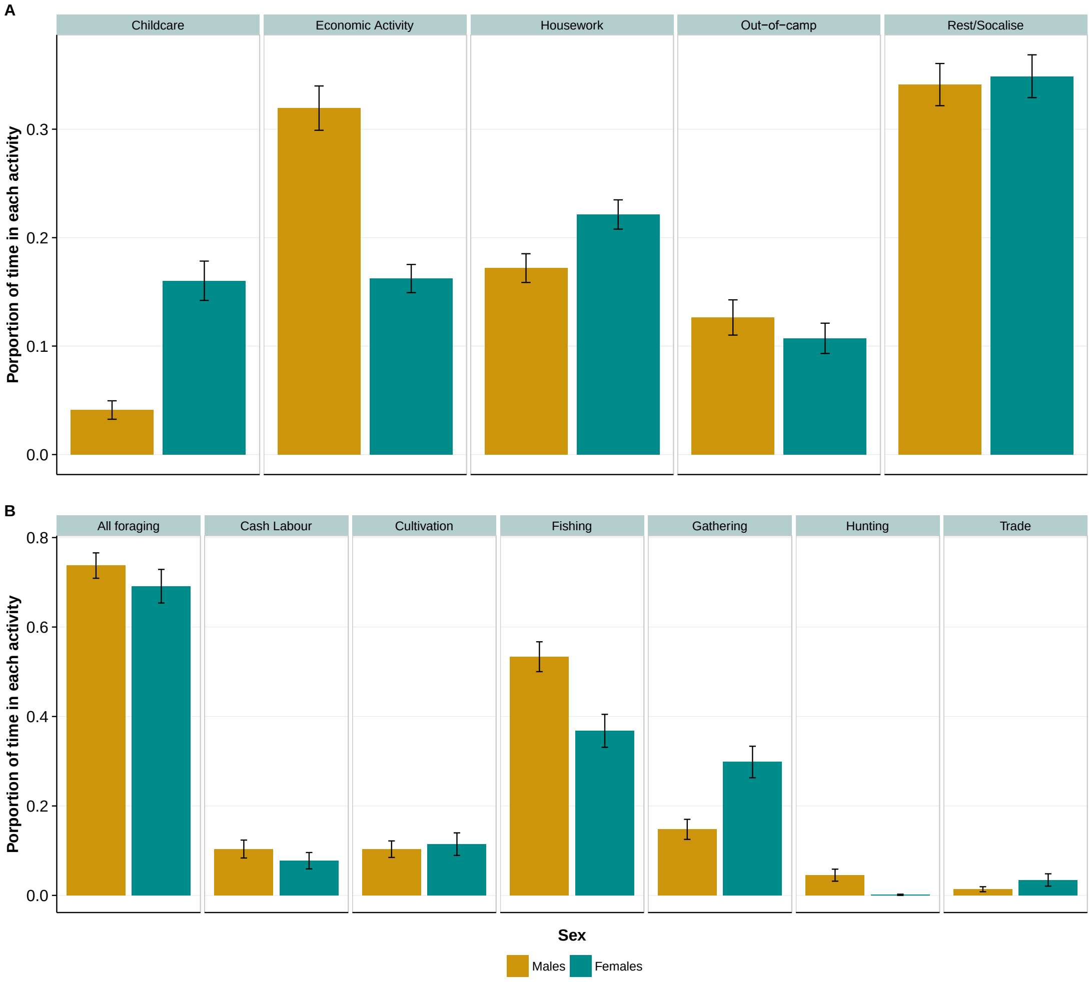

Figure 2.7: Summary data on (A) the proportion of time individuals spent in all activities and (B) proportion of time individuals spent in different types of economic activities, separated by sex. Here, and in the figures below, 'Economic activity' in plot A includes all activities broken down in plot B. 'All foraging' represents all fishing, gathering and hunting activities in opposition to all 'non-foraging' tasks which includes cash labour, cultivation and trade. In this case, this reveals that while males and females spent the same amount of economic activities foraging, males spend more time in fishing and foraging while women spend more time in gathering (*n* = 914). Error bars are standard errors of the mean.

2.4.1 Division of labour

The sexual division of labour among all human groups, including hunter-gatherers appears universal (Kelly 2013). Commonly cited reasons for this division include the incompatibility between hunting and childcare (Washburn & Lancaster 1968; Lee 1968). Gathering is seen as more conducive to reproduction as children can be placed into a 'crèche', gathering can be put-on-hold when required and tubers and fruits are not scared away by the sound of children. This has led to the paradigm of 'man the hunter' and 'women the gatherer' in anthropological studies of foragers (Estioko-Griffin & Griffin 1981b; Lee 1968). However, among the Agta of Cagayan, women have been historically known to hunt habitually, along with reports in the Mbuti, Tiwi and Ainu (Goodman *et al.* 1985; Estioko & Griffin 1981; Estioko-Griffin & Griffin 1985). Estioko-Griffin and Griffin (1985) report six women hunting on 16 days after 163 observation-days, and found no significant difference in fertility (or fertility measures such as age at menarche) between women who hunted or not. Thus, Estioko-Griffin and Griffin conclude that hunting is compatible with normal fertility patterns. Such extensive female hunting has not been reported since among the Agta.

In our own data, hunting is significantly less important, and many men were never witnessed to hunt. Out of 2,168 work activities only one woman was witness to go hunting once, producing an effective female hunting rate of 0.001 (Figure 2.7B). Nonetheless, women do spend a significant amount of time fishing (36.5%), catching octopus, crabs and other shellfish. Often these trips would consist of family day trip to a good fishing spot, where they would fish with their husband and older children. Women would also go fish alone or with other women, particularly younger, unmarried teenagers. There is still a gender bias in gathering however, as while males spend more of their work activities in fishing they spend less time gathering. Examining Figure 2.7A also reveals a significant difference between men and women. Women conduct far less subsistence related work activities in general, however maintain similar proportion of their time 'resting' (which includes socialising, sleeping and resting) as males. This is because women spend significantly higher proportion of their time involved in childcare activities (including carrying, playing or feeding as well as keeping an eye on children) and housework. Thus, the Agta match trends seen in many other populations in relation to the gendered division of labour (Kelly 2013).

2.4.2 Ecological variability in diet and activity

On average only 19.6% of food is produced from cultivation while the remaining 80.4% is produced by foraging activities (fishing, hunting and gathering), matching the activity data. However, this figure varies significantly according to the degree of settlement; settled camps produce less food by foraging (78.4% ± 5.7%) compared to mobile camps (90.4% ± 9.2%, Figure 2.8). Furthermore, there is significant ecological variability in these trends, depending on whether groups live at the coast or inland.

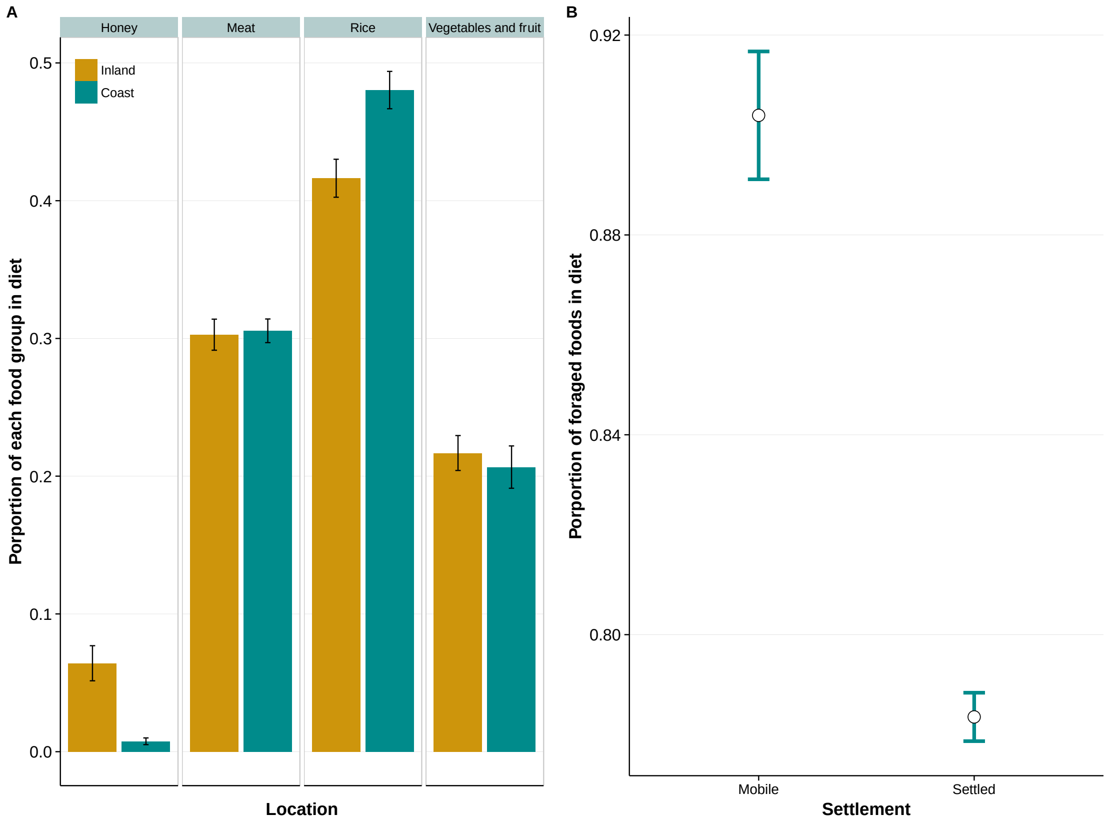

Figure 2.8: (A) proportion of each food group consumed depending on whether a household lived on location and (B) the proportion foods which were acquired via foraging (hunting, fishing or gathering) compared to cultivation or trade, depending on degree of settlement (n = 914). Error bars are standard errors of the mean.

2.4.2.1 Coastal Agta

The main task for males is spear fishing in the shallower coastal waters. Women also plant small swiddens in the treeline. Minter (2010) argues that the gathering of fruit or vegetable products does not seem a significant element in subsistence. Allen (1985) also noted the distinct lack of vegetables in the Agta diet. However, we see little variance in proportion of vegetables and fruit between inland and coastal Agta (Figure 2.8). What we do see is a significant increase in rice consumption in coastal groups. Since rice is often directly exchanged for fish and other marine resources, this increased rice consumption is likely reflective of a higher fishing return rate at the coast. Examining the breakdown of daily activities below by location (Figure 2.9A), it does appear that costal groups spend significantly longer resting, implying that the coast may be a more bountiful ecology. Figure 2.9B demonstrates that coastal groups spent more time fishing than cultivation, gathering and hunting suggesting they are focused on marine resources. These results are supported by foraging returns data (Table 2.4) as mean package size is 20.1% larger at the coast than inland, while fishing at the coast is significantly more effective as hourly returns are 62.2% higher. Thus, it is likely that at the coast foragers reach their daily needs faster, thus spend longer in other activities. Furthermore, it appears that coastal foraging trips were significantly less variable comparatively to inland trips; coefficient of variation at the coast represents only 49.5% and 62.3% of the inland variation in package size and the hourly calorie return rate, respectively. Thus, while the variability in foraging return rate is nonetheless high (the standard deviation is consistently larger than the mean), reflective of hunter-gatherer foraging niches in general (Kelly 2013), coastal environments appear relatively less variable.

Table 2.4: Foraging return rates separated by location. SD represents standard deviation, CV coefficient of variation. Data collected by Mark Dyble.

Location	Number of trips	Mean package size (kcals)	SD package size	CV package size	Mean kcal per hour	SD kcal per hour	CV kcal per hour
Costal Camp	193	2322.7	3024.2	1203.47	704.7	901.4	58.56
Inland camp	99	1855.3	4874.5	1874.04	266.7	522.8	14.23

2.4.2.1 Watershed Agta

The Agta living inland are more dependent on hunted resources. A good male hunter is highly valued as a husband and camp mate (Minter 2010: 112). Hunting has traditionally been with a bow and arrow but now also occurs with the more powerful homemade shotguns. However, shotguns are not always preferred due to their noise and the difficulty in reloading with speed compared to the silent and speedy bow and arrow. Hunted items include the long tailed macaque (*Macaca fascicularis*), Philippine warty pig (*Sus philippinensis*) and the Philippine brown deer (*Cervus mariannus*), as well as a number of bird and bat species that adults and children regularly shoot down as snacks.

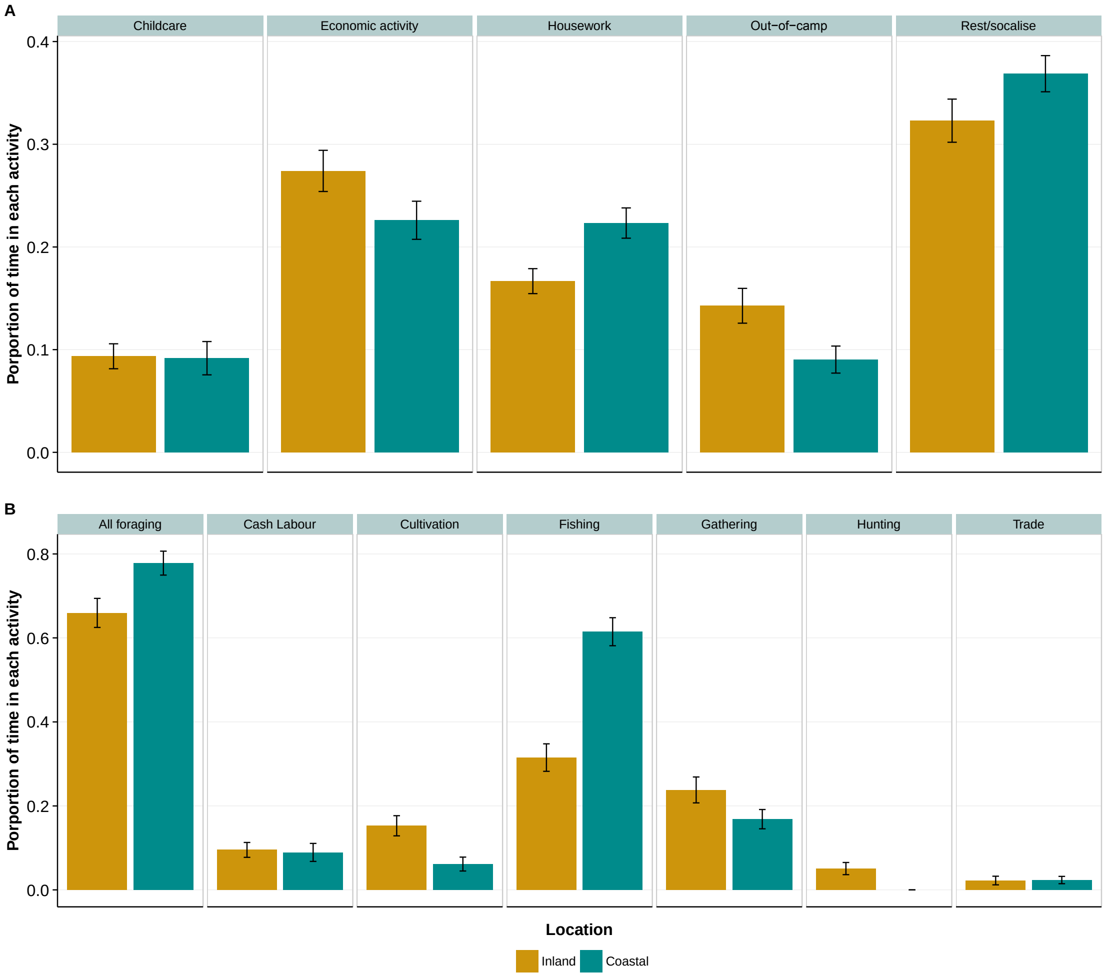

Figure 2.9: (A) the proportion of time individuals spent in different activities and (B) proportion of time individuals spent in different types of economic activities, separated by location ($n = 914$). Error bars are standard errors of the mean.

We witnessed no hunting in coastal groups while it consisted of 0.05 ± 0.2 of activities in inland groups. Thus, fishing is still a primary subsistence strategy (0.32 ± 0.4). Individuals living inland devote more time to gathering than their peers on the coast (0.24 ± 0.35 versus 0.17 ± 0.24). Commonly gathered foods include fern shoots (*pako*; *Deplazium esculentum*) and the hearts and shoots of various palms and forest fruits. Inland groups also spend significantly more time in cultivation (0.15 ± 0.27 versus 0.06 ± 0.18). Minter (2010) finds similar trends, with inland groups tending to their own land a higher percentage of their time than coastal groups (0.08 versus 0.05). This implies overall there is a significantly different subsistence strategy between these two groups, even when they are often as little as 10km apart.

Minter (2010: 282) also argues that the coastal-dwelling Agta's diet are much richer in animal protein compared to the river groups; one coastal group she studied from Dimasalansan consumed animal protein at 79% of their meals (*n* = 90), compared to a river group in Diangu at 41% (*n* = 102) and another watershed group in Disabungan who consumed animal products at 26% of meals (*n* = 51). We do not find this result in our data, however. It appears that coastal (0.31 ± 0.09) and inland Agta (0.30 ± 0.1) in Palanan consume remarkably similar proportions of animal protein in their diets.

2.4.3 Variability by sedentarisation

As argued by Minter (2010) the agricultural practices, and their economic importance, of the Agta has often been ignored. The literature portrays them as 'unsophisticated' or 'hobby' farmers as they gain few and irregular returns from their efforts (Estioko-Griffin & Griffin 1981a; Griffin 1985; Headland 1986; Rai 1982). However, in Minter's recent research she finds that both the domestication of animals and cultivation is becoming increasingly present, however, varies greatly by location. Time spend in cultivating their own land (clearing, planting, tending and harvesting) ranged between 4-11% for males and 3-13% for females in three different environments (coastal, interior and watershed). From this work the crops yielded an average of 283 kg of rice per household, enough for 113 days given an average daily rice consumption of 2.5kg. Accordingly, we find that 13.1% of all activities were spent in cultivation. However, this figure not only varies by ecology but also degree of sedentarisation (Figure 2.10B). Mobile groups spend only 3.5% of their work activities in cultivation and 0% of activities in cash labour and trade. Comparatively, settled groups spend 11.6%, 10% and 2.5% of their work activities in cultivation, cash labour and trade, respectively. As a result, while settled groups spent only 69.3% ± 36.1% of time in 'foraging' activities (the combination of gathering, fishing and hunting), mobile groups spent a mean of 96.2% ± 10.3%. Interestingly, while settled groups appear to spend significantly less time in work activities overall (0.24 ± 0.2 versus 0.33 ± 0.29) this is not translated into greater rest time on average. The major increase is in time spent out-of-camp for settled groups, which is often associated with going to the market to trade goods. Thus, while non-foraging activities may have higher returns (hence less time spent in food production itself), they do involve additional activities to exchange these items for foods or cash. As a result it seems that settled, mobile, inland and coastal Agta all follow different subsistence strategies.

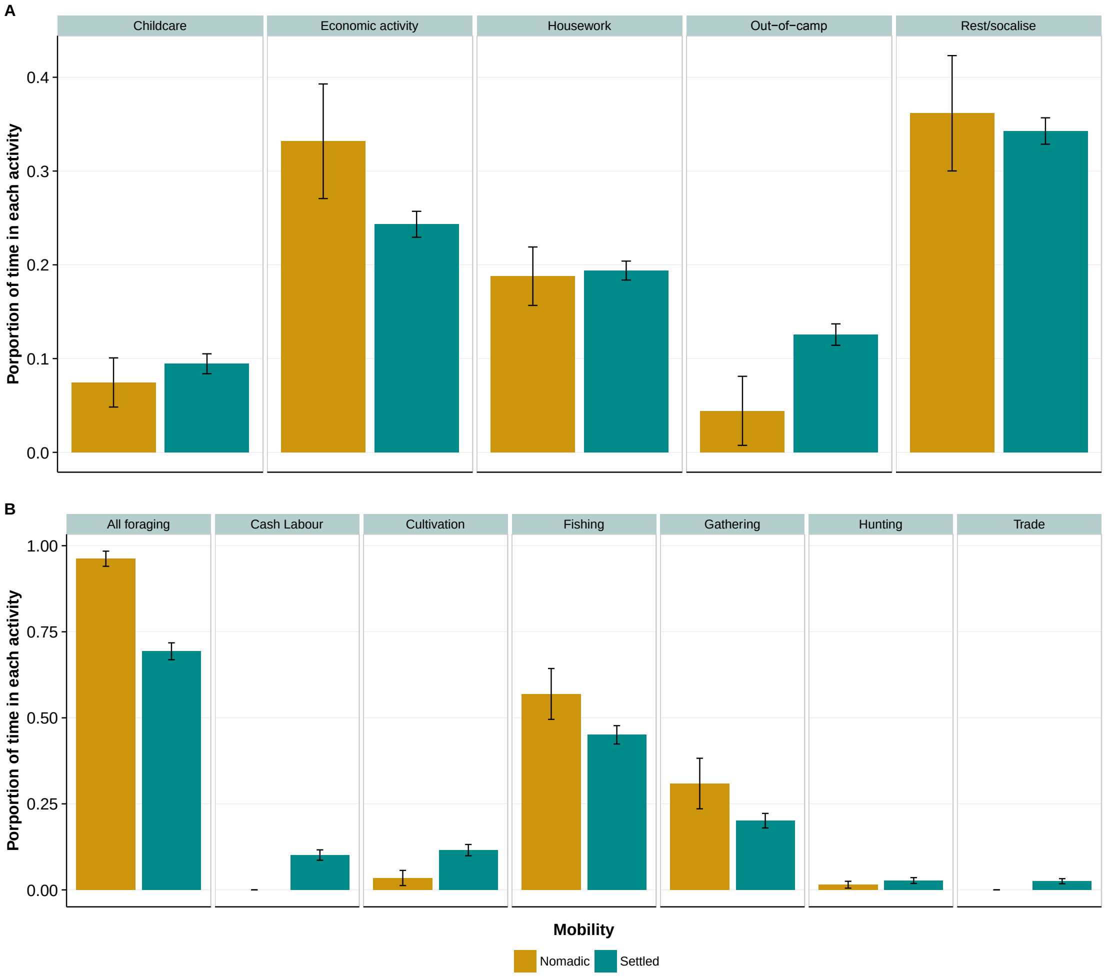

Figure 2.10: (A) the proportion of time individuals spent in different activities and (B) proportion of time individuals spent in different types of economic activities, separated by degree of mobility (*n* = 914). Mobility is denoted by whether they were witnessed to move camp or not at least once during the two-year field period. Error bars are standard errors of the mean.

2.5 Wealth, camp permanence, food storage and security

As previously discussed, immediate-return hunter-gatherers are often defined by a few highly connected traits, such as low levels of food storage and wealth, low camp permanence, and a high level of mobility. These features are all linked to the high mobility and fluidity of these groups as they extract what they require from the environment (Woodburn 1982; Smith *et al.* 2010). In particular, many of these features have been associated with the ways of mitigating risk in the foraging niche (see section 3.4 on risk management). For instance, high mobility is a form of risk reduction as individuals spread their exposure to risk spatially. Depending on the degree of mobility, this strategy significantly limits other forms of dealing with risk. Wealth and food storage are forms of risk retention and only possible in more sedentarised communities. Additionally, as forms of risk retention are not possible, hunter-gatherers have been argued to focus more on risk transfer, including risk pooling (i.e. reciprocity). Extensive norms of sharing are often associated with egalitarianism, demand sharing and 'levelling' behaviours to ensure individual accumulation does not occur (Wiessner 1996; Gurven 2006; Cashdan 1985). Consequentially, risk pooling and risk retention are two methods of mitigating risk as individuals who accumulate wealth and/or food storage are in less need of risk pooling and often extract themselves from sharing networks (Fafchamps 1992). As a result specific traits are often highly associated with one another.

This is not to imply that this is a matter of progression or that sedentarization only occurs in the context of cultivation; settlement should occur when there is local abundance and the costs are lower for settling than moving to patches of lower productivity or unknown/unpredictable returns. Thus, cultivation is only one possible example of this scenario (Kelly, 2013). Historically, delayed returned hunter-gatherers were able to settle due to significant resource abundance, defendable resources, food storage and seasonality, such as North Western Native American populations. However, if cultivation increases an individual's resource return rate, reduces variability in returns and produces enough food from a single location to ensure survival, then it can result in decreased mobility. Sedentism can be either in the form of more permanent villages or reductions in individual movement between locations as the need to care for and defend cultivated land increases (Kelly 2013). Furthermore, cultivation results in food storage making mobility increasingly difficult. Thus, it is possible to consider these traits as different strategies to deal with variability and risk; if extensive food sharing and mobility are one form of insurance against risk then subsistence diversification, wealth accumulation and food storage are another.

Figure 2.11 shows significant correlations between proportion of food produced from foraging (gathering, fishing and hunting) and key 'transition[4]' traits. The correlations indicate that while extensive foraging, low camp size, high mobility and few household belongings characterize some Agta camps; others exhibit more food production, larger camp size, little mobility, and a greater number of household belongings. Furthermore, Figure 2.12A reveals that settled groups have significantly higher food storage, house permanence and household wealth. As argued by Kelly (2013), these traits should not create a binary system, rather there

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[4] I use the word 'transition' to refer to the process of change in mobility, subsistence, sharing and egalitarian ethos. Transition needs not be unidirectional, permanent or inevitable but dependent on ecological conditions following the principles of HBE.

is extensive variance both between and within populations, which is demonstrated by the Agta in terms of significant variance of wealth, camp permanence and food storage depending on their ecology.

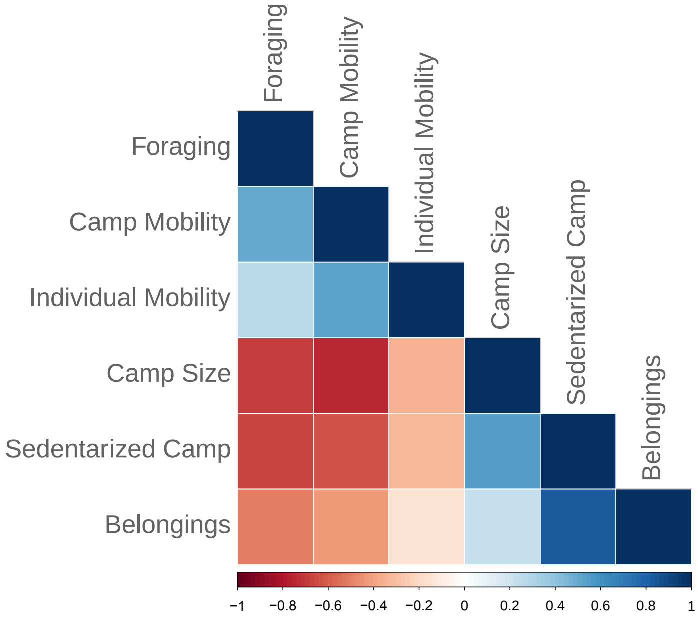

Figure 2.11: Correlation plot for six key 'transition' variables. Positive correlations are marked in blue shades, negative in red shades. The stronger the shade, the stronger the correlation, represented on the bar legend. All correlations are statistically significant at $p < 0.05$. Variables are: sedentarised camp (number of permanent structures within a camp); belongings (an index quantifying household wealth); individual mobility (whether an individual was ever witnessed to move camp over a two-year period, 0 = never moved); camp mobility (number of people leaving a camp); and foraging (proportion of food that individuals acquired from foraging activities versus food production and wage labour).

I have argued above that the coastal environment can be considered less risky given its higher return rate and more predictable resources given the lower coefficient of variation. As a result, we may expect individuals to report greater food insecurity inland. The fact that the levels on food insecurity are equal (Figure 2.12B) in both environments, indicates that individuals have successful buffers in place to mitigate shortfalls. For instance, above we saw that cultivation is greater inland than at the coast, as is food storage. Thus, perhaps inland groups are practicing risk reduction by subsistence diversification and storage. However, wealth is significantly higher at the coast, which is likely the reflection of increase trade at the coast; as marine returns are high (up to 7kg in one trip), individuals frequently trade additional fish for cash and rice.

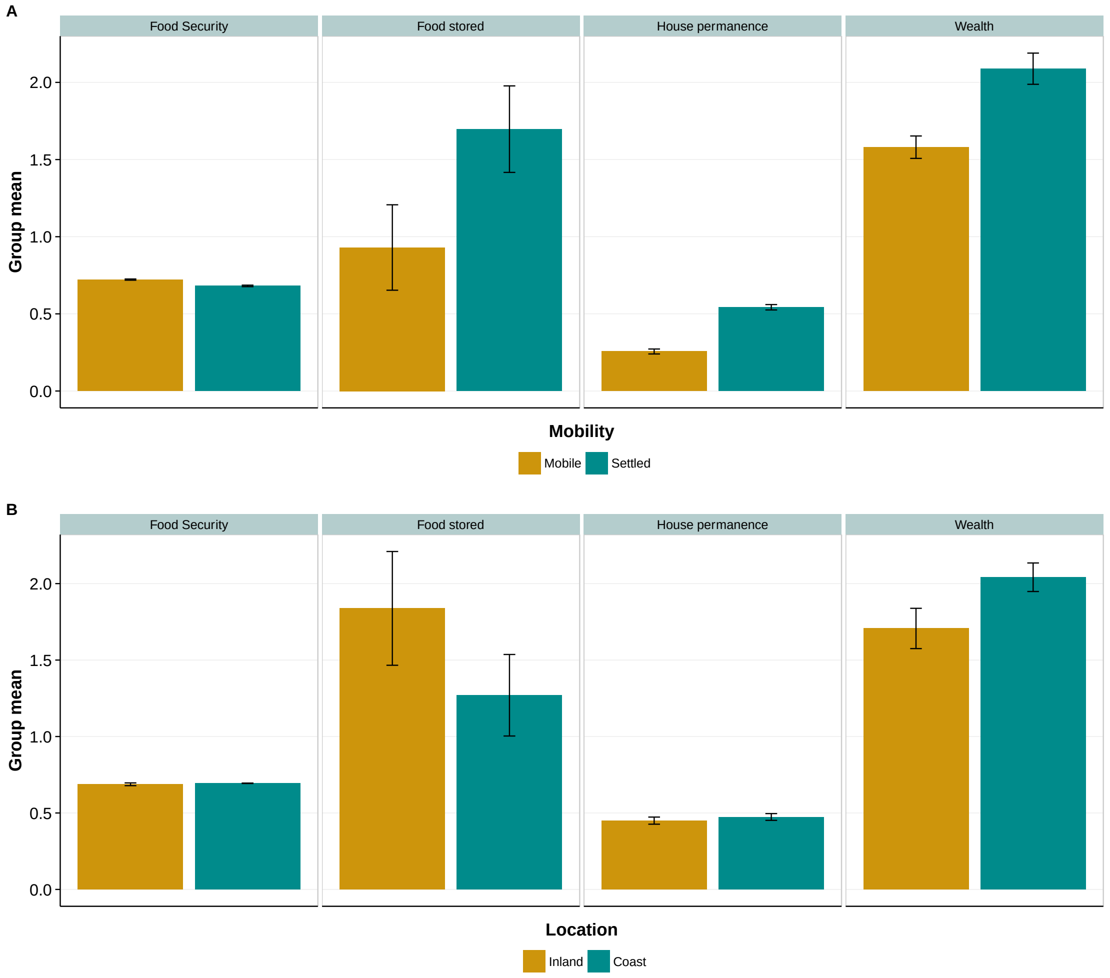

Figure 2.12: Group means for key traits associated with immediate return foragers separated by (A) mobility and (B) location. Error bars are standard errors of the mean (*n* = 914).

2.6 Transition versus resilience

The ethnographic literature on the Agta is some of the most pessimistic, focusing on their extinction due to high mortality, increasing social ills (such as violence and alcoholism), encroachment and exploitation from 'outsiders' and deforestation (Minter 2010). Certainly, the Agta are not an example of an isolated, untouched tribe (but then if anthropology was to rely on this definition of foragers the field of hunter-gatherer studies would all but disappear). The assimilation of the Austronesian language family long before linguistic records indicates a history of long contact once farmers arrived between 5,000 and 3,500 years ago (Bellwood 2010). The archaeological record worldwide suggests that continuous and significant interactions between indigenous populations and farming migrants (Piperno & Pearsall 1998; Bar-Yosef & Meadow 1995; Price & Gebauer 1995; Inomata *et al.* 2015). Thus, it is not necessarily the case that when foraging groups first come into contact with outsiders they are immediately replaced or wiped out. Nonetheless, in the rapidly developing, globalised world these pressures are significant and important to document to understand their consequences.

A high proportion of the ethnographic record on the Agta predicts their cultural loss and extinction. Rai's (1990, 1982) work focuses on the Agta's transition to a 'non-foraging way of life' and intensive dependence on non-traditional strategies of trade, cash labour and horticulture. Since this is argued to be in 'sharp contrast to their earlier stable system', it is portrayed as a progressive, linear move away from foraging subsistence. Rai (1990: 3) believes he is witnessing the last traditional activities as "time seems to be finally catching up with the Agta…" due to environmental degradation and socioeconomic subjugation. Similarly, Headland's (1986) research is focused on population decline, acculturation and loss of knowledge and group cohesion in the Casiguran Agta due to external forces, high mortality and the Agta's inability to defend their culture and acceptance of their subordination (Early & Headland 1998). In fact, Griffin and Headland (1994: 73) go so far as to predict that the "ancient Agta culture will be extinct as well [by the year 2005]". Wrapped up in these grandiose statements is the assumption of a once pristine, static and ancient Agta culture being rapidly lost in the second half of the 20th century. Such concepts of static culture are unsupported in anthropology, particularly human behavioural ecology, as individuals are understood to adapt to environmental (be in natural or social) change. Inflexible cultural systems are improbable, and there is no reason to suspect that once 'non-foraging' behaviours occur the pathway to farmers or landless labourers is inevitable, or irreversible (Oota *et al.* 2005). For instance, Griffin (1996, p. 15) later argued that one period of fieldwork can be deceptive as you accept all 'new' behaviour as cultural change, and ignore how cyclical it can be. This is precisely the perspective I take of Agta 'transition' and behaviour. Some individuals may be more settled than others, and as discussed above this leads to significant alterations to their subsistence strategies. However, by no means do I expect this to be a permanent change. Rather, I view these behaviours as adaptations to prevailing conditions.

Both Headland (1986) and Griffin and Griffin (2010) have argued that the Agta are failed farmers due to their subordination to non-Agta neighbours who seize or destroy their land. Thus, the Agta become marginalised, landless labourers rather than peasants (Early & Headland 1998). However, I have already discussed the significant amount of cultivation the Agta are involved in, remaining remarkably consistent between Minter's 2002-2005 fieldwork and our own. The Agta of Palanan appear able to consistently engage in farming to a degree which brings in a significant amount of calories. Furthermore, rather than being completely subjugated by non-Agta farmers, there appears to be an element of mutualism in their relationships (Peterson 1978; Minter 2010). The Agta themselves view recent changes in their way of life and interactions with non-Agta farmers and the state with mixed emotions. Older males appear to seek some form of unity in being 'Agta' and the ability to freely move throughout their lands. However, women and particularly mothers when asked are very positive about settling down to access education and health care. But, of course both of these viewpoints are influenced by me the interviewer. Women might say they want to live in a town because this has been governmental policy to development and 'civilise' (Minter 2010). Consequentially, as a white outsider this is what is repeated to me. Many Agta recognise the possible financial benefits of increased market integration and are actively engaged in selling off (illegally) rights received for 'Agta' by the National Commission for Indigenous Peoples. Nonetheless, others have been fighting for land rights not dependent on sedentised lifestyles at the national level. This is reflective of the diversity of possible futures and how individuals adapt to given circumstances.

The notion of a 'grim future' of the Agta in part stems from the particular social history of the Agta living in Casiguran studied by Headland, as it is this population that collapsed once a road was built from Dilasag to Casiguran in 1977. A sudden influx of migrants, logging and extractive industries brought with it increased violence, homicide and alcoholism as well as increased mortality rates. Thus, the Agta became synonymous with population decline, social problems and cultural loss. However, this is only one population and focusing on it ignores the resilience and adaptability of the Agta groups throughout the Philippines who have remained a cohesive population in the face of external pressures. In our own data, we have found a wide variety of foraging and non-foraging strategies. The Agta, 40 to 50 years after the original 'grim future' predictions were made are still a cohesive population involved in a significant amount of 'traditional' foraging modes of subsistence. Thus, Minter's (2010) argument for the resilience and adaptation of the Agta is far more convincing. Resilience is the concept of how systems can withstand an external and internal insult and adapt to meet its challenges to ensure its survival. This concept then, falls completely in line with key concepts of human behavioural ecology, and underscores this thesis. We should not expect the Agta to have maintained a 'traditional' culture up until 40-50 years ago, rather the degree they are involved in cultivation, hunting, fishing and the nature of their interaction with non-Agta would had varied throughout time according to their needs (Minter 2010).

2.7 Conclusions

The Agta have many features in common with other immediate return foragers worldwide. However, they do seem exceptional for their high fertility. It seems also that the Agta of Palanan suffer slightly lower infant and childhood mortality rates than reported for surrounding groups. There appears a significant sex bias in both births and deaths, suggesting that more males are born to counter the particularly high male death rate during the ages 1 – 5. While the Agta have had intensive interaction with farming populations for many generations, they have maintained some important components of the forager lifestyle such as mobility, flexible residence and bilateral descent systems, little material wealth and inequality and a significant proportion of time devoted to foraging. Nonetheless, these traits all significantly vary according to location and degree of sedentarisation. It is this variation and its consequences I seek to explore in the following analysis chapters.

Chapter Two

Risk and the Evolution of Cooperative Childcare

3.1 Cooperative breeding: its definitions and questions

Cooperative breeding occurs in 9% of bird species (Riehl 2013), compared to only 3% of mammals (Hrdy 2009). Yet, within the mammalian class cooperative breeding is widely distributed and has independently evolved in rodents, Herpestidae (monogooses), Canidae (dogs) and primates (Lukas & Clutton-Brock 2012). While cooperative breeding is absent from all non-human great apes (Hrdy 2009) it occurs extensively among humans (Ivey 2000; Hewlett 1991; Konner 2005) and the benefits of kin presence has been recorded in temporal and spatial cross-sections of the world's populations (Sear & Mace 2008).

Given cooperative breeding's wide phylogenetic dispersal, one clear direction of research is exploring why it evolved repeatedly and independently. As a 'cooperative' act, cooperative breeding denotes the evolution of a childcare behaviour because it is beneficial to other individuals, not simply the individual helping (West *et al.* 2011; West *et al.* 2007). Cooperative acts often appear costly as the energy invested into another individual's offspring cannot be re-invested elsewhere (Tardif 1997). Thus, it is puzzling why individuals behave 'altruistically'. Strictly speaking, altruism is any action which results in an ultimate fitness cost to the altruist but benefits others, thus is the true 'selfless' act (Foster *et al.* 2006). Such altruism appears contradictory to the selfish gene paradigm in which each gene strives to increase its frequency in future generations (Dawkins 1989), thus evolutionary biologists and anthropologists attempt to reconcile apparent altruism with evolutionary theory. This has resulted in confusion over the term altruism; research often describes behaviour as altruistic if it is costly in the short-term and ignores possible benefits, such as indirect (kin altruism) or direct but delayed (reciprocal altruism) benefits (West *et al.* 2007). As stated by West and colleagues (2007), this results in altruism becoming synonymous with cooperation. While this appears like simple semantics, they require different ultimate explanations; cooperation entails the quantification of fitness returns. Here, altruism will be used *only* in its strictest form as I seek to explore what benefits individuals receive from assisting other individual's offspring.

As Solomon & French (1997: 2) put it, there is a "dizzying array of labels in the literature" for cooperative breeding which are often used interchangeably, lacking any clear definition. In the strictest sense, cooperative breeding implies a monopolisation of breeding by a dominant female who is aided by non-breeding allomothers. This is also referred to as singular (or pair-nesting in birds (Riehl 2013)). This system is found in callitrichids (Bales *et al.* 2000) and meerkats (Clutton-Brock *et al.* 2001). Communal breeding (or plural breeding and cooperative polygamy) refers to systems in which multiple females reproduce, often pooling their resources and young (Lukas & Clutton-Brock 2012). Communal breeding does not preclude the presence of non-breeding helpers, only the absence of a breeding monopoly (Riehl 2013). Communal breeding is rarer in mammals, found in some nocturnal strepsirrhines, black-and-white ruffed lemurs (*Varecia variegata*) and humans in the order primate (Baden *et al.* 2013). In the human literature this distinction is unclear. The term cooperative breeding is used loosely to refer to when someone other than the mother assists in the rearing of offspring (Russell 2004; Jennions & Macdonald 1994), following the general definition of cooperation. Others argue that humans demonstrate elements of both communal and cooperative breeding as pre-reproductive and post-reproductive life-stages can be considered to be 'reproductive suppression' (Lukas & Clutton-Brock 2012; Hawkes & O'Connell 1998). However, it is unclear the degree to which these non-reproductive periods are the product of cooperative breeding (i.e. suppression) or are simply the consequence of slow life histories and prolonged periods of growth, development and skills learning (Kaplan et al. 2003). Therefore, to a degree there is an unwillingness to place humans into either category, hence the uncritical use of terminology.

However, the difference between these two systems is profound, as sacrificing reproduction entails a large cost. As reproduction is not delayed in communal breeders, individuals can gain direct and immediate benefits from breeding in a group (Lewis & Pusey 1997). The most important feature of communal systems is plurality in breeding; even if some helpers are non-reproductive it is unclear if such a trait arose specifically to facilitate cooperative breeding (Riehl 2013). Furthermore, cooperative breeding systems are defined by strict dominance-subordinate relationships where dominant mothers firmly and often violently suppress subordinates reproduction (Hrdy 2009). Yet immediate-return foraging groups are broadly egalitarian, as is common in other communal breeding species (Baden *et al.* 2013).

Hence, the motivations and structures surrounding these two systems are expected to differ significantly. Consequentially, here I define humans as communal breeders, with an awareness that this may be facilitated by extensive juvenile and post-reproductive periods. This bears little weight on the review of existing literature on human allocare, given that few researchers had these definitions in mind. However, the distinction increases in importance for inter-species comparisons and theoretical perspectives; the evolution of cooperative breeding has been mainly explained with indirect fitness benefits in constrained environments (Emlen 1982), however, if multiple individuals can breed simultaneously one ultimate explanation of communal breeding could lie in reciprocity. Thus, throughout this thesis I will refer to humans as communal or plural breeders, using cooperative breeding to refer to singular breeders and as a catch-all phrase when discussing the 'cooperative breeding literature' on all species.

The anthropological approach to communal breeding has focused on topics such as the evolution of pair-bonding, male provisioning and the post-menopausal lifespan (Bogin 1997). An assumption in early research was that the evolution of pair bonding guaranteed males provisioning of women and children, who would otherwise be unable to procure enough food for survival (Darwin 1871; Lovejoy 1981; Kaplan *et al.* 2003). However, Hawkes *et al.* (1997) argued that post-reproductive Hadza females devoted significant amounts of energy to grandchildren. Energy from gathered foods can easily overtake that of hunted foods due to high failure rates of hunts (Hawkes 2000; Blurton Jones *et al.* 2000). Thus, Hawkes and colleagues have argued that humans' post-menopausal lifespan evolved due to the fitness benefits conferred on grandchildren when grandmothers were present (Hawkes & Coxworth 2013). Problematically, however, data from South American foraging groups reveals that grandmothers are of little importance as males supply 97% of calories to their young (Kaplan *et al.* 2003). Even through females commonly contribute a higher proportion of items (Kelly 2013), the calorific value of hunted goods is often greater (Gurven & Kaplan 2006; Hill 1993).

Little consensus has been reached on this topic and the debate remains active today, however, Marlowe (2003) cautions about swinging between extremes of the spectrum. Both fathers and grandmothers have important roles in different contexts; among the Hadza, adult females brought more calories back to camp when they did not have infants, if they did, males' production was higher. Due to a particular focus on these two extremes, anthropological research has primarily sought to understand how care from one particular kin type could increase child quality or survival (Sear *et al.* 2000; Meehan *et al.* 2014; Sear & Mace 2008; Sear *et al.* 2002; Hawkes *et al.* 1997), maternal fertility (Sear *et al.* 2003; Crognier *et al.* 2001; Bereczkei 1998; Kramer *et al.* 2009; Tymicki 2004) or how allocarers reduce the maternal energetic burden (Meehan *et al.* 2013a). As a result the role of unrelated individuals and why they would provide care has been under-examined (Apicella *et al.* 2012). This is not, however, the case within the large food sharing literature in which reciprocity has been demonstrated to play an important role in who shares with whom (Gurven, 2006, 2004a; Jaeggi and Gurven, 2013; Kasper and Borgerhoff Mulder, 2015). Food provisioning is a major form of cooperation in humans (Hill & Hurtado 2009), as is common in other communally breeding species (Brown 2014; Caraco & Brown 1986). I take extensively from this literature to inform my analysis of childcare and I will now review the major theories explaining why individuals cooperate.

3.2 Why breed communally? Theoretical perspectives

3.2.1 Which level to start at?

One of the aims of this thesis is to understand why individuals may be cooperative from an inclusive fitness perspective, and as such it focuses on the individual as the level of selection for behavioural strategies. As a result, while it is not discussed at length in this thesis I will here summarise recent debates about individual versus group selection for completeness. The recent paradigm in evolutionary science has been one of the gene as the unit of selection (Dawkins 1989), in contrast to the group or species (Wynne-Edwards 1962). In the traditional understanding of group (genetic) selection individuals were considered to limit their reproduction for the sake of the group or species as this would limit population growth. However, as pointed out by Williams (1966) such cooperative groups would quickly fall prey to cheats who would out-reproduce the co-operators. Thus, for cooperation of be maintained due to the benefit of the group, these 'groups' would require low migration rates as well as intense selective pressure at the group level caused by high enough levels of group extinction (Smith 1976). However, since then the theory of group selection has been developed and altered causing controversy in the field. New group selection arguments can be separated into multilevel selection and strong reciprocity (otherwise known as cultural group selection). I will discuss each of these and suggest that, ultimately, it appears that the most parsimonious explanation remains that of individual selection (Wild et al. 2010).

3.2.1.1 Strong Reciprocity

The theory of strong reciprocity has been particularly developed to explain humans apparently 'extreme' cooperation, dependent on culture and social learning (Bowles et al. 2003; Fehr & Fischbacher 2004). Here, the argument is that individuals who are 'strong reciprocators' are those who reward co-operators and norm-abiding individuals and punish defectors or norm-violators (Boyd et al. 2003; Laland & Brown 2011). Thus, these individuals are argued to altruistically punish to maintain cooperation in the cultural group, for the good of the group. However, as excellently pointed out by West *et al.* (2007) this then assumes that the individual does not benefit from this group benefit. This is what is defined as 'weakly altruistic' in which the focal individuals suffer a fitness decrease compared to the rest of the group, however this behaviour could still be selected for as it increases an individual's direct fitness overall (i.e. at the population level, which is in evolutionary terms what matters). In short, such perspectives ignore the mutualistic benefits which are possible even when individuals do suffer a cost relative to the local group as natural selection selects genes in the population, not "some other arbitrarily defined scale such as social partners" (West et al. 2007: 422).

3.2.1.2 Multilevel selection

Other arguments stemming from group selection have reconceptualised the group as within populations (compared to between-populations), emphasising that (as the name suggests) there are multiple levels which selection can act on. As a result, here both individual level and group level selection can occur, sometimes opposing one another (Traulsen & Nowak 2006). For instance, in a modelled evolutionary game Traulsen and Nowak (2006) detail how in a mixed group of defectors and co-operators, defectors have a higher pay-off than co-operators as defectors receive the group benefit without paying the cost of cooperating. However, in a homogenous group of co-operators it is the co-operators who have the higher payoff due to mutualism (i.e. the whole group functions better increasing the returns for the individuals). In this context invading defectors are initially favoured by individual selection as the groups are mixed however later the 'emerging higher-level selection among homogenous groups' favours co-operators (Traulsen & Nowak 2006: 10952). Similar models have been developed to explain the evolution of reduced virulence in which the utility of the multilevel approach is demonstrated. However, in fact mathematically group-level and individual-level processes are identical, and are, in fact, different perspectives on the same mechanisms rather than being different mechanisms (Hamilton 1975). This leads some to conclude that multilevel selection should be given the same weight as individual fitness within evolutionary science (Wade et al. 2010). However, as pointed out by Wild et al. (2010) while there can be multiple levels of selection, there cannot be group adaptationism (as this falls into the original pitfalls of group selection), consequentially individual selection remains the parsimonious explanation, as while group selection and individual selection can work simultaneously, it is the individuals fitness which is maximised (Hamilton 1975; Wild et al. 2010). Consequentially, for the rest of the theoretical review I will explore explanations of cooperation focused on individual fitness.

3.2.2 The primacy of kin (selection)

Cooperative breeding theory was developed in birds with singular breeding systems. In avian species, allomothers are usually previous years clutches which remained philopatric due to resource competition hindering independent breeding (Emlen 1995). As a result, much cooperative breeding theory and research has centred on species which primarily nested with closely related individuals (Solomon & Hayes 2009; Hatchwell 2007). Therefore, indirect fitness stemming from kin selection (Hamilton 1964) was considered a sufficient explanation for allocare. Hamilton's theory states a costly strategy may be selected for, if it benefits individuals carrying the same genes (measured by coefficient of relatedness, r), depending on the degree of the costs to the helper (C) weighted by expected benefits (B), or otherwise put: $rB > C$ (Hamilton 1964). Thus, an individual would be expected to help a relative if the benefit to their indirect fitness outweighs the costs of the initial action, a benefit determined by the number of shared genes. Extensive evidence has been produced supporting the role of relatedness in a number of cooperative species including eusocial insects (Foster *et al.* 2006), birds (Koenig & Dickinson 2004) and mammals (Solomon & French 1997), including small and large scale human societies (Nolin 2010; Koster & Leckie 2014; Alvard 2009; Nowak 2006).

Whilst this is a pervasive explanation for cooperative behaviour, the explanatory power of this theory has been overstated (Clutton-Brock 2002). Firstly, many cooperative breeding groups are not as closely related as first thought. For instance, callitrichids originally assumed to be monogamous, now appear to live in polyandrous and polygynous groups (Tardif 1997). This fact alongside the frequent inter-group migration means that relatedness is significantly lower than originally assumed and males often provide care for non-related offspring (Clutton-Brock 2002)). Furthermore, approximately 44% of bird species nest in groups containing unrelated helpers who are engaged in cooperative breeding (Riehl 2013). The trend of living in family groups is much more common in singular rather than plural breeders. As such, kin selection may have less explanatory importance in communal breeding species. For instance, hunter-gatherers have been demonstrated to reside in camps which contain a significant number of non-kin (Dyble *et al.*, 2015; Hill *et al.*, 2011). Given that on average individuals reside with only 25% consanguineal kin (Dyble *et al.* 2015), in an average camp of 30 individuals, only seven individuals would be consanguineously related to ego, significantly limiting within kin allocare options. For this reason alone it is essential to examine the role of non-kin allocare.

Even if a group was comprised of closely related individuals, individuals may be cooperating for different reasons. Individuals may assist one another due to shared space rather than shared genes (Clutton-Brock 2002). For instance, neighbours cooperate due to lower transaction costs, greater knowledge of the cost-benefit ratio of any given action and an increased likely of future interactions (Nolin 2010). This fact of co-residence may lead to an overstatement of the role of kin selection if one simply examines who provides care, rather than why. This is what has been termed as an association index in the anthropological literature (Koster & Leckie 2014), a measure of the 'multi-faceted interdependences that characterise [households] relationships' (Koster & Leckie 2014: 101) as households cooperate in multiple arenas, often entailing physical proximity. The association index is a measure of this proximity, as a proxy for the longer-term dependent relationships. Thus, as kin in small-scale societies characterise these relationships, the role of association is overlooked while the importance of kinship is overstated. For instance, Alvard (2009) explored the composition of Lamalera (whale hunters from Indonesia) cooperative hunting crews. While finding they were significantly more related than expected by chance, the composition of hunting crews was better predicted by lineage membership than simple relatedness. Without the inclusion of lineage membership in the model, the importance of relatedness was significantly overestimated. While a number of studies have indicated the importance of the association index in food sharing (Nolin 2010; Gurven *et al.* 2000; Gurven 2004a; Allen-Arave *et al.* 2008; Koster & Leckie 2014), it is important to note that co-residence is not random, but is frequently structured around close kin (Gurven & Hill 2010; Nolin 2010). Consequentially, even if individuals cooperate due to shared space, if they preferentially share space with kin, then kin selection continues to occur. As a result, it is difficult to separate the influence of these two forces. Nonetheless, these complexities reveal that kin selection is not the 'magic bullet' of cooperation; it is part of a complex web of other explanatory variables that structure human interaction.

Hence, to investigate if indirect fitness explanations are valid, one must examine how the degree allomothering varies according to relatedness (Griffin and West 2003). More related individuals are expected to provide more care. However, single species studies paint an inconsistent picture on this front; when related and unrelated infants were presented to captive pygmy marmosets (*Cebuella pygmaea*) there was no difference in caregiving response (Wamboldt *et al.* 1988). Similarly, Eberle and Kappeler (2006) find that, while grey mouse lemurs (*Microcebus murinus*) have the ability to discriminate kin, they do not offer discriminatory care. However, these distinctions were made by male meerkats (*Suricata suricatta*) when feeding related young (Clutton-Brock *et al.* 2004) and male golden lion tamarins (*Leontopithecus rosalia*) who both preferentially carried more related offspring (Baker 1991). Griffin and West (2003) examined this question across 18 cooperatively breeding vertebrates (15 birds and three mammals), finding that relatedness significantly predicted allomothering and accounted for 10% of its variance. However, this effect was dependent on the fitness cost (i.e. less resources to reproduce) and fitness benefits (i.e. increased survivorship of related broods) of helping; when the benefits were low the motivation was removed and care reduced (Griffin and West 2003). This is a vital and frequently overlooked point: any test of kin selection must examine how cooperation varies according to the cost and benefit. For instance, Clutton-Brock *et al.* (2001a, 2000) found that while allocaring meerkats (*Suricata suricatta*) were related to offspring, the allocarers physical condition (indicating the cost of the care) predicted the amount of care provided significantly better than variance in relatedness (Griffin & West 2002). As a result, kin selection predicts that related individuals should preferentially assist those in greater need of their help, particularly if costs are low and benefits are high (Allen-Arave *et al.* 2008).

Few empirical studies have explored this relationship between costs, benefits and relatedness. For instance, Kasper and Borgerhoff Mulder (2015) found that the best predictor of cooperation was having needy relatives to help. As need is high, this implies that the fitness benefits are also high. Thus, following predictions of kin selection, aid was given to relatives in need (i.e. Hamilton's B) dependent on degree of relatedness. This finding is reflected in Hooper *et al.* (2015) examination of food sharing according to cost and need (number of producers versus dependents in the receivers and givers household). Hooper and colleagues (2015) found that among the Tsimane, individuals with high production transferred more resources to households with high consumption, low production and high relatedness. Thus, this matches the clear predictions set out by kin selection.

Few studies of direct childcare rarely test kin selection in such a manner. For instance, as evidenced below, the majority of studies limit their perspective to comparing different kin types (i.e. fathers versus grandmothers) rather than comparing non-kin versus kin or a continuous variance in the coefficient of relatedness (Sear & Mace 2008; Snopkowski & Sear 2013; Sear & Coall 2011a; Apicella & Crittenden 2013). The food sharing literature is based on advanced multivariate analysis controlling for association index, reciprocity, cost-benefit ratios, dyadic relationships, clustering and non-independence. In contrast, childcare analysis is often simplified into linear regressions examining whether care increases with relatedness (Crittenden & Marlowe 2008; Ivey 2000).

3.2.2.1 Paternity certainty

When paternity is unknown significant differences in magnitude of care are predicted between matrilineal and patrilineal kin. A mother is always sure of her 50% contribution to her offspring, however due to internal gestation, a father can never have the same level of confidence of his 50% share. This insecurity can affect a male's desire to invest in a child as he may be misdirecting his care (Kleiman & Malcolm 1981). This same uncertainty influences matrilineal and patrilineal kin. Grandparents should be 25% related to their grandchild, however their confidence will change according to their lineage and sex: a maternal grandmother is 100% sure of her 25% stake in a grandchild, followed by maternal grandfather who has to consider the uncertainty in his relationship with his daughter and the paternal grandmother who has to consider the likelihood of her son's cuckoldry. Finally, the paternal grandfather is the most uncertain as he must consider the likelihood of his son's cuckoldry as well as his own. Thus, if investment is based on degrees of kinship, we should find this pattern in the amount of allocare offered, assuming paternity certainty is of a significant level. Consequently, the benefit received by the offspring and/or mother should be proportional to the degree of relatedness and paternity uncertainty (Danielsbacka *et al.* 2011).

3.2.3 Reciprocal altruism (cooperation[5])

Among the Agta "the return may be made at a later date but it will be expected" (Peterson 1978: 40)

Trivers (1971) developed the theory of reciprocal altruism to explain how a costly behaviour can be selected for when the recipient is distantly or completely unrelated to the giver. Here, cooperation can evolve if the cost of helping in the present is outweighed by the benefits the giver receives at some point in the future, lessened by the probability that this benefit may or may not occur. As a result, due to long-term interactions cooperation can evolve without relatedness. This was formalised into the Tit-For-Tat (TFT) model of cooperation by Axelrod and Hamilton (1981). In its strictest form TFT requires significant score-keeping and extremely discriminative players: as a result unlikely to occur in nature (Gurven 2004b; Gurven 2006). In reality, reciprocal exchanges are frequently unequal because the marginal value of a resource varies between the giver and receiver. For instance, the marginal value of an additional kilo of meat produced by the skilled hunter is significantly lower than for an inefficient juvenile (Hooper *et al.* 2015), thus it costs little to give and benefits a lot. However, in future this situation will reverse as the juvenile develops and the skilled hunter has a run of bad luck. Even if the skilled hunter never receives the exact same number of kilos in return, as long as the transaction meant both parties benefited more than if they had not participated in the exchange, reciprocal altruism can be favoured (Gurven 2006). This reveals that the cost benefit ratio is as important in reciprocal altruism as it is in kin selection, and thus cannot be used to distinguish between the models (Franzen 2004). What does firmly separates the models, however, is contingency, defined as the relationship between what A gives B and what B gives A (Gurven 2004b). Contingency does not predict kin selection as the benefits are indirect and do not require future reciprocity.

Reciprocal altruism theory is clear: help an individual if the cost of helping now is lower than the expected future returns. However, demonstrating contingent cooperation 'on the ground' is more difficult, particularly if it is not perfectly balanced (Allen-Arave *et al.* 2008; Gurven 2004a). Two major difficulties in quantifying reciprocal altruism include the appropriate time frame for examining contingency and which 'currency' this contingency is in. Jaeggi and Gurven (2013) argue that helping is best predicted by long-term contingency, however, as many studies are conducted over several weeks or months they do not capture exchange which occurs over a generation or lifetime (Gurven 2004b). Thus, a lack of an

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[5] If the altruist receives long-term benefits for their costly activity this act is no long strictly altruistic but cooperative (Foster et al. 2006).

association may be due to study duration. Furthermore, reciprocity may be present but in multiple currencies, leaving studies focusing only on food sharing or childcare unable to capture the explanatory power of reciprocity (Allen-Arave *et al.* 2008). Here the association index is of importance, given that long-term, more generalised contingency is more likely in individuals who frequently associate (Gurven 2006), however, this is rarely explicitly examined. Finally, individuals may suffer an significantly unbalanced relationship if it functions to signal their generosity or 'sharing intent', permitting enlarged networks to fall-back on in times of need (Allen-Arave *et al.* 2008; Gurven *et al.* 2000; Wiessner 2002; Patton 2005). For instance, Nolin, (2012) found that among the Lamelera, men holding leadership roles gave more than expected based on their household productivity, while among the Ache, sharing was predicted by relative generosity (i.e. total given divided by total produced (Gurven *et al.* 2000)). Quantifying all these dimensions in actual populations is difficult and never (understandably) conducted in its totality.

While these limitations of the examination of reciprocal altruism must be kept in mind, researchers have nonetheless found a significant role for reciprocal altruism in many populations including the Dolgan and Nganasan (Ziker & Schnegg 2005), Ache and Hiwi (Gurven 2004a; Gurven *et al.* 2000; Allen-Arave *et al.* 2008), Lamelera (Nolin 2010) and among the Mpimbwe (Kasper and Borgerhoff Mulder 2015). In fact, in a recent meta-analysis of food sharing in human and non-human primates, Jaeggi and Gurven (2013b) find that contingency accounted for 20% of the variance in food sharing among 32 primate species, more (but not significantly so) than relatedness. However, it is an error to suggest reciprocal altruism and kin selection are mutually exclusive; many of their predictions overlap and both processes can be acting simultaneously (Jaeggi and Gurven, 2013; Nolin, 2010). For instance, among the Ache, Allen-Arave et al. (2008) find that nepotistic reciprocal altruism best describes food sharing; individuals are more likely to participate in long-term exchange partnerships with close kin who they trusted and have a high likelihood of continued interaction with. Furthermore, kin were not significantly more likely to give food if they had not received food from the household previously, thus it appeared kin selection had little role in maintaining nepotistic food transfers. Similar results have been found in the Lamalera (Nolin 2010) and Dolgan (however, kinship still independently predicted sharing here (Ziker & Schnegg 2005)) indicating that kinship may be important in partner selection, but contingency is what maintains it (Nolin 2015). This is perhaps not surprising given that reciprocity will overtake kin selection whenever the probability of future interaction is higher than the dyadic coefficient of relatedness, a common situation in small-scale societies (Axelrod & Hamilton 1981; Gurven *et al.* 2001; Allen-Arave *et al.* 2008).

3.2.4 Loss and unpredictability

Regardless of whether ego is closely related or not, what motivates individuals to cooperate and take a risk on whether their cooperation will be returned (Hames 2004)? Given that much of the cooperative literature has stemmed from food sharing among hunter-gatherers, a primary explanation of function arose from the inherent daily variance in food returns in a stochastic environment (Winterhalder 1986). Strictly speaking, risk refers to the probability of loss given the distribution of outcomes, while variance refers to stochastic or unpredictable outcomes (Winterhalder 1986; Winterhalder *et al.* 1999). Food sharing is seen as a form of risk-pooling to reduce the variance across individuals; individuals share today since they may not be successful hunting for a week, thus will later be dependent on their sharing partners, be that kin or unrelated individuals (Gurven 2004b; Gurven 2006; Nolin 2010).

Hunting success rates are surprisingly low in many foraging groups: only 23% and 27% of hunts were successful among the savannah !Kung and Hadza, respectively (Lee 1979; Hawkes 1991). These figures are increased among South Asian tropical forest foragers: 59% and 63% of hunts were success among the Batek and Palanan Agta, respectively (Endicott & Endicott 2008; Griffin & Griffin 2000). However, from our own data it is apparent that fishing success rate (89%) is significantly higher than hunting (65%, Dyble n.d.). Winterhalder (1996) established that given small degrees of asynchrony (i.e. success rates) between foragers, sharing as a form of risk pooling mitigated the likelihood of shortfalls even among groups of only six to eight foragers. As a result, sharing has been demonstrated to lead to significant nutritional improvements among the Ache (Kaplan & Hill 1985) and significantly lowers mortality (Jaeggi and Gurven, 2013). Unsurprising then, egalitarianism and sharing norms are often strongly enforced in foraging societies, and 'levelling' tactics commonly used to keep the best hunters arrogance in check (Wiessner 1996; Lee 1979; Woodburn 1982).

Individual variance is also influenced by sickness and disability; among South American forager-horticulturalists, Ache adults were found to be sick on 6.5% of all days, the Yora 8% and 90% of Shiwiar were reported to have suffered a disability for 14 days or longer (Gurven *et al.* 2000; Sugiyama 2004; Sugiyama & Chacon 2000). As a result, Sugiyama (2004) reports that 60% of the Shiwiar in his sample would have been unlikely to survive in the absence of food sharing. Thus, individuals survival also depends on medium term 'health insurance', by perhaps signalling generosity in periods of good health to ensure provisioning is received during periods of ill health when returns cannot be immediate (Sugiyama & Chacon 2000; Gurven *et al.* 2000).

These theories have been specifically developed with economic transfers, such as food sharing, in mind. Thus, their applicability to childcare appears, at a glance, obscure. However, given individuals energy budgets must encompass food production, household tasks and childcare there is plenty of room for stochasticity in childcare. For instance, if a husband is unsuccessful hunting then the mother's foraging efforts require increasing, significantly reducing the amount of time she is available for direct childcare. Or, if a child falls ill they require significant increases in high intensity care, which a mother can provide but then her foraging efforts and direct care to other offspring must decrease (Sugiyama & Chacon 2000). Simply put, a deficit in one area due to unpredictability results in a deficit of childcare which can be met with allocare. Within the human communal breeding literature, reciprocity is rarely (if ever) examined, however, environmental uncertainty has been theoretically linked to the evolution of cooperative breeding in birds and mammals.

Emlen (1982) modelled the evolution of allocare by unrelated individuals, finding that fitness payoffs were higher for helping if the environment was marginal, unpredictable and restrictive for reproduction. This model has been supported by Rubenstein and Lovette (2007) who conducted a phylogenetically controlled comparative analysis of 45 species of African starlings, finding that cooperative breeding was more prevalent in areas of high temporal variability. Furthermore, Jetz and Rubenstein (2011) found, among 9,310 non-marine avian species, that temperature and rainfall variability were strong predictors of cooperative breeding. Cooperative breeding has also been associated with unpredictable habitats in naked mole rats (*Heterocephalus glaber*, (Faulkes *et al.* 1997)) and black-and-white ruffed lemurs (*Varecia variegata*, (Baden *et al.*, (2013)), while environmental uncertainty has been forwarded as an explanation for allomaternal care in Malagasy strepsirrhines in general (Tecot *et al.* 2012).

Human mothers do not only face short-term unpredictability but also face what Hill and Hurtado (2009) label as 'predictable life-history shortfalls'. Given humans' production of multiple, highly dependent offspring, there are specific times during a mothers reproductive life course that she cannot provide all the specific care an infant, toddler or dependent child require (Kramer 2010). However, as parents age, previously dependent children function as allocarers (Kramer 2011), until they cease reproduction and ultimately have more household provisioners than dependents. As a result, there are predictable times in a household's life course in which it will be in need of care and others when it can provide care. While this is not related to environmental stochasticity it is a risk which requires buffering: either by siblings once available or, if not, then by distant or non-kin. Hunter-gatherer mothers face a particularly difficult predicament in which they must deal with a baseline childcare deficit, and *then* meet any further care deficits arising from illness, disability and foraging failure. Perhaps then, the phrase "it takes a village to raise a child" is not so surprising (Apicella & Crittenden 2013).

In summary, there seems a significant amount of evidence that humans require assistance in childcare, which is likely structured by kin selection and reciprocal altruism. Yet, the role of reciprocal altruism has been comparatively ignored in the cooperative breeding literature outside of food sharing. This is a product of a poor conception of what is reciprocal altruism and how it can maintain cooperation. For instance, Clutton-Brock (2009) argued that delayed returns from reciprocity are not likely to be a driving force behind allomothering, due to a problem of free-riders over a long time period. This point holds true in singular breeding species in which allocare entails a significant fitness cost (i.e. the cessation of the allomothers own reproduction) and unpredictability of when/if the current allomothers will become the dominant reproducing female. However, plural breeding species hold no such cost, nor necessitate extended periods between reciprocity. Multiple females (and their non-dependent offspring) can aid each other in breeding, creating a crèche style of caretaking. Moreover, even dependent children produce a significant amount of resources which are transferred to older generations, thus as Kramer (2010) points out, resource transfers are often bidirectional. As pointed out by Ivey (2000) and Kramer (2010) the costs of allocare for juveniles may be relatively low, given their lack of economic productivity and the fact that they are provided for by adults in terms of food, shelter and other resources. Young females may also gain direct benefits from allocaring; Lancaster (1971) posited that they learn and develop mothering skills, especially given the higher infant mortality rate experienced by nulliparous mothers (Baker & Wood 1992).

3.3 Anthropological Literature

There is a large array of anthropological literature on which type of kin provides the most care and what benefit this bestows on both mothers and their offspring. Research spans from small-scale societies in which data collection consists of intensive observation or large-scale correlational studies (in modern and historical populations) examining the benefits associated by kin presence or absence. Rarely are these approaches combined (for an exception, see Gibson and Mace (2005)). It is important to note that much of the observational research is based on childcare received by a small number (10 – 30, on average) of infants (2.5 years or under); little is known about who cares for toddlers and dependent children and data may be easily skewed by small sample sizes. The larger scale studies are based on much bigger sample sizes, however run into a problem of a lack of data depth. Often analyses are conducted on whether or not a grandparent or father was 'present' in a village or residing nearby and the effect this has on child and maternal outcomes. This makes causation more difficult to trace. Nonetheless, a combination of both types of studies in the following review produces a meaningful view of communal breeding in humans.

3.3.1 The essentiality of mothers

Mothers are the main caretaker of infants: in Kramer's (2010) review on the topic, mothers were found to, on average, provide 48.8% of direct care (nursing, feeding, carrying, holding and grooming) to younger children (mainly infants, but ranges to 0-4 years; Table 3.1) in small-scale societies. Overall, when examining the different subsistence types in Table 3.1 there is remarkable consistency of maternal care regardless of whether the population are hunter-gatherers (Aka, Efe, Agta, Alywara and Hadza) or horticulturalists (Ye'Kwana, Maya, rural Trinidad and Toba). Thus, mothers are consistently important caretakers of infants. Similarly, Sear and Mace's (2008) meta-analysis of 45 studies on 'who keeps children alive' (ranging from historical Japan to small scale pastoral villages in the Gambia) found that maternal death has a highly detrimental effect on infant survival. However, this effect is strongly dependent on child age; after weaning the effect on child mortality almost disappears. Thus, while few observational studies examine who provides care to children post-weaning, it appears likely that the maternal effect lessens as additional allocarers take over (Sear & Mace 2008). Crittenden and Marlowe (2008) explore which camp mates carried Hadza children under the age of four (*n* = 56) and found that age negatively predicts the amount of time a child is held, while Meehan *et al.* (2014) found that among the Aka maternal care declines rapidly from late infancy into the second and third years of life.

Table 3.1: Cross-cultural proportions of direct childcare from different caretakers

Group	Moth	Fath	Bro	Sis	Sib	GM	Other	Ref
Ye'kwana[a]	49.0%	2.7%	1.9%	16.7%	-	11.2%	20.6%	Hames (1988)
Aka[b]	42.7%	15.8%	-	-	-	-	13.2%	Hewlett (1988)*
Efe	50%	6.0%	14.0%	13.0%	-	9.0%	9.0%	Ivey (ND)*
Agta	51.7%	4.4%	1.1%	10.2%	-	7.6%	-	Goodman *et al.* (1985)*
Maya	46.1%	1.6%	4.6%	31.6%	-	1.2%	OTH: 11.2% NON: 2.8%	Kramer (2005)
Alyawara[c]	53%	<1%	-	-	31.0%	-	16.0%	Denham (1974)*
Trinidad[d]	44.2%	10.3%	-	-	16.3%	-	29.3%	Flinn (1992)
Mardu[e]	32.3%	2.7%	-	-	5.0%	14.3%	29.8%	Scelza (2009)
Toba	50%	-	4.0%	33.0%	-	13.0%	-	Valeggia (2009)
Hadza[cf]	68.7%	7.1%	-	1.2%	-	MGM: 3.7%, PGM: 1.2%	OTH: 3.6% NON: 12.4	Crittenden and Marlowe, (2008)*
Averages	48.8%	6.3%	5.1%	17.6%	17.4%	7.7%	14.8%	

Notes: Direct childcare includes nursing, feeding, carrying, holding and grooming. [a] includes children 0-40 months. [b] values for mothers and fathers include children aged 1-18 month(s). Other may include siblings and grandmothers. [c] values reported for carrying children only. [d] includes children 0-4 years old. [e] includes children 0-3 years old. [f] includes children 0-4 years, includes carrying children only, sister is older sisters only. GM stands for grandmother. References followed by a * are those conducted with immediate-return foragers most similar to the Agta. The other groups (Ye'Kwana, Maya, rural Trinidad and Toba) are small-scale horticulturalists and agriculturalists. The Mardu aboriginals were once mobile hunter-gatherers but have since experienced extensive settlement and acculturation. Adapted from Kramer (2010: 421).

3.3.2 Is father care obligate?

While previous work has focused on paternal support as key for maternal and child survival (Kaplan *et al.* 2000b), sole dependence on male childcare appears a risky strategy (Hrdy 2008) and in only 47% of studies (n = 15) did fathers have an effect on child survival (Sear & Mace 2008). Nonetheless, while overall fathers provide a fraction of the care of mothers (averaging

6.3%), among the Aka, fathers interact significantly more (15.8% (Hewlett 1988)). Fathers may offer lower investment care (such as proximity, watching or touching) rather than high investment care (carrying, grooming or feeding), thus are relatively ignored in child observational studies which focus on high investment care (frequently carrying). Furthermore, a father's importance may increase in later life as he plays a greater role in arranging marriages, teaching or playing with older children (Scelza 2009; Sear & Mace 2008; Sear 2011). Consequentially, the consistent sampling of infants or children under the age of four years may systematically underestimate the role of fathers. Furthermore, paternal care may be dependent on the presence of other caregivers. Meehan (2005) recorded how, when an Aka family resided matrilocally, infants received 2.5 times more physical contact from allomothers. However, in a patrilocal camp where the number of allomothers was significantly reduced, males increased their interactions by 20%. Therefore, a lack or presence of allomothers and their effect, may depend on who else is investing in a child. Overall while paternal care appears variable across populations this does not demonstrate any consistent pattern according to subsistence.

3.3.3 Helpful grandmothers and child survival

Grandmothers, as originally argued by Hawkes *et al.* (1997), are expected to be major allocarers of children. As they are post-reproductive their costs are low and inclusive fitness benefits high (i.e. $r = 0.25$, assuming no paternity uncertainty). Thus, their care and presence are expected to have positive effects on child survival and/or maternal fertility. Sear and Mace (2008) found maternal grandmothers have the most consistent positive effect, correlating with child survival in 69% of studies ($n = 46$). Paternal grandmothers were positively associated with child survival in 53% of statistically valid studies ($n = 17$). Furthermore, Sear *et al.*, (2002, 2000) found that maternal grandmother presence increased child height, weight and survival from the age of 18 months in rural Gambia. This is likely related to the importance of assistance during weaning, a period of significantly higher mortality (Cassidy 1980). In rural Ethiopia it appeared that maternal grandmothers had beneficial effects on child survival and height due to increased engagement in heavy domestic tasks (Gibson & Mace 2005). Similarly, in Meehan's (2013) study Aka grandmothers were found to significantly decrease maternal energy expenditure by 150 kcal.

Observationally grandmothers appear to be of importance, often providing more care than fathers (Hames 1988; Ivey 2000; Goodman *et al.* 1985; Scelza 2009). Furthermore, grandmothers appear to be more likely to provide more demanding childcare tasks (Scelza 2009). However, several studies show that grandparents have little involvement with their grandchildren (Crittenden & Marlowe 2008; Kramer 2005), particularly among more immediate-return hunter-gatherers (Table 3.1). For instance, among the Hadza, Efe and Agta the average amount of direct care is 5.4%, compared to horticultural populations with an average of 9.9%. However, many hunter-gatherer studies are limited by their small sample sizes. Due to the labour intensive nature of observational studies, samples frequently contain around 10 – 15 infants. Only a few studies include more than 20 infants (Crittenden & Marlowe 2008; Meehan *et al.* 2013a). As a result, it is difficult to examine variability within the sample. For instance, in a large-scale Indonesian study (*n* = 16,250), grandmothers assistance was mediated by the needs of her dependents; grandmothers provided more financial help to poorer couples or conducted more household tasks for working mothers (Snopkowski & Sear 2015). This suggests that grandmaternal care may be contextual according to need, prevailing conditions and what other types are carers are available. For instance, among 127 Aka children aged 0 to 10 years, Meehan *et al.* (2014) found that grandmothers had a positive influence on child developmental and nutritional outcomes (weight-for-age, height-for-age and weight-for-height) during the 9 – 36 month period. However, children in matrilocal camps did not suffer when maternal grandmothers were not present, while children in patrilocal camps did. Thus, it appears that the importance of grandmothers may lie with access to other allocarers, potentially distorting overall results.

The fact that sample sizes are small is indicative of another practical limitation on the scale of grandmothers' assistance. For instance, in Ivey's (2000) study, the sample size consisted of 20 infants with four grandmothers, i.e. a significant number of infants did not have a grandmother around to provide allocare and those that did would have to share. Considering the likelihood of grandmothers death and co-residence, Hill and Hurtado (2009) established that only around 10% of middle aged (defined as late 30's) Ache women co-resided with their mothers. Thus, similar to fathers it seems a risky strategy to rely on the presence of a grandmother. Furthermore, even once a grandmother is present she is likely to also invest in other offspring and grandchildren, particularly if some are in greater need than others. This indicates the possible negative side of kin; bigger kin networks can lead to competition among close relatives for resources in constrained environments (Borgerhoff Mulder 2007).

3.3.4 Not so helpful grandmothers and grandfathers?

Sear (2008) found in a matrilineal Mali society that maternal grandmothers and aunts were associated with an increase in child mortality. This is the result of excessive competition for resources at the household level, as older individuals drain limited household resources (Strassmann & Garrard 2011; Strassmann 2011). Furthermore, given earlier ages at first birth, grandmothers are often still reproducing when their first child reproduces, suggesting that they may wish to devote little energy outside of their own direct reproductive interests (Tymicki 2004). Furthermore, in a historical German population it appeared that while maternal grandmothers increased the odds of 5-year survival for children by 23%, paternal grandmothers *decreased* it by 19% (Beise & Voland 2002). The relative impact of both matrilineal and patrilineal kin does appear dependent on context. Among the Pimbwe, a horticultural population from Tanzania, women with larger kin networks suffered if they had greater wealth due to excessive demands on their resources. As a result, a child's nutritional status was dependent on wealth and its interaction with the number of kin, revealing significant breeding competition rather than cooperation (Hadley 2004). Similar results have also be found among the Kipsigi, in which paternal kin are of greater importance in richer patrilineages while maternal kin buffer offspring from the negative influences of poorer patrilineages (Borgerhoff Mulder 2007).

The negative influence of paternal grandparents on child outcomes may equally be the product of increased investment in fertility rather than child quality. For instance, in the same 18th century German population as above, a household containing a paternal grandmother was associated with higher overall fertility alongside reduced child survival as the father's kin appeared to increase fertility, not survival (Beise 2005). Sear and Coall's (2011b) review of kin effects on fertility established that paternal grandmothers and grandfathers were significantly more likely to affect a daughter-in-law's fertility rate, an effect replicated in rural Gambia (Sear *et al.* 2003) and Thailand (Snopkowski & Sear 2013). The proximate mechanisms are unclear, but it may be related to kin influence on the age at first reproduction (Snopkowski & Sear 2013) or kin priming of information which encourages higher fertility (Mathews & Sear 2013). This emphasis on fertility is a possible cause of the negative association between paternal grandfather presence and child survival in 25% of studies in Sear and Mace's (2008) meta-analysis, while maternal grandfathers had positive influences on child survival in 17% of studies. No negative associations were found for maternal grandfathers; however, they are rarely associated with providing much care or had much positive influence on child outcomes (Sear *et al.* 2000; Kramer 2010). Consequently, maternal grandfathers appear to have a greater positive impact than paternal grandfathers while overall grandfathers seem to matter little. This pattern is demonstrated in the absence of grandfather interactions or allocare in observational studies (Meehan 2005; Meehan *et al.* 2013a; Ivey 2000; Crittenden & Marlowe 2008).

3.3.5 Siblings

Siblings are 50% related, the same amount they would be to any future offspring. Thus, they can be predicted to invest heavily in one another (Hamilton 1964). Furthermore, children do not suffer from opportunity costs due to helping as they are not yet reproductively active (Tucker & Young 2005). As a result, during the juvenile years a child's best fitness strategy may be to invest in embodied capital and their younger siblings (Kramer 2011). This appears the case in the observational data as siblings provide, on average, 17.4% of direct childcare across nine populations. There is a trend towards siblings providing more childcare in foraging populations (16.7% versus 14.5%), however the results are patchy, as studies do not consistently separate brothers from sisters or report care from siblings at all (Table 3.1). Thus the pattern is unclear, particularly since children can also be considered to be competitors for parental investment and household resources (Jones 1986; Bohler & Bergstrom 1995; Alam 1995). As such, having a large number of siblings has often been associated with poorer child outcomes, given the relationship between household size and child survival (Lawson *et al.* 2012). Therefore, siblings are predicted to have a mixed effect on child and maternal outcomes, mediated by birth order and household resources (Kramer 2010).

Turke's (1988) seminal piece in Ifaluk found that having a first-born girl increased a woman's fertility by acting as 'helpers-at-the-nest' and reducing the woman's labour and childcare demands. This is hypothesised to occur in the 'ecological constraints' model (Emlen 1982) when offspring are not yet able to establish territory or gain enough resources for independent breeding. Rather than invest everything into growth, juveniles invest some energy into indirect fitness via sibling care, particularly if in high mortality environments, their long-term survival is unknown (thus making excess investment in embodied capital a poor evolutionary strategy (Hagen & Barrett 2009)). For instance, Hadza children (aged 3-17) while not net producers, collected a substantial proportion of daily nutritional requirements, and thus made significant contributions to the family pot (Crittenden *et al.* 2013). This opens the door to bidirectional transfers and the pooling of resources. Kramer *et al.* (2009) argues that children contribute to the 'energy budgets' (created with provisioning, domestic, economic or childcare labour) of their siblings and mothers. For instance, without child production Maya parents (small-scale farming society from Mexico), would have to increase their workload by 2.5 fold (Lee & Kramer 2002) while Venezuelan Pumé forgers would not be able to enter reproductive maturity at 15.5 years (Kramer *et al.* 2009). Thus, juvenile production should not be ignored (Kramer & Boone 2002; Kramer 2011; Kramer 2005; Kramer 2010; Lee & Kramer 2002).

These predictions are broadly found in the literature. Bereczkei and Dunbar (2002) found that in a Hungarian Gypsy population, mothers whose firstborn was a girl had a higher completed fertility compared to mothers with firstborn boys. While similar results have been found in the Aymara, the gender of the helper child is not always important (Crognier *et al.* 2002). However, in 89 !Kung women who had completed their fertility, Hames and Draper (2004) found no effect of having a first born girl on mothers fertility or survivorship. This they argue may be due to the dangerous nature of the Kalahari bush; mothers would often have to supervise the childcare by older siblings. Therefore, the role of siblings might be dependent on the ecology; in dangerous or difficult environments children may need increased time to learn the skills to be a competent caretaker and provisioner (Kramer 2005).

Other studies have demonstrated that sibling presence is correlated with negative fertility influences. For instance, in the Gambia while older sisters had no fertility effect, older brothers decreased the probability of giving birth. In this patrilineal society it may be that after giving birth to a girl, women slow down reproduction to avoid having another girl (Sear *et al.* 2003). Similar results are apparent in a historical Polish dataset where it appeared that the *absence* of maternal siblings increased the risk of transition to the next birth, as much as by 40% (Tymicki 2004). The influence of siblings may also be gender dependent; in the Kipsigis the greater number of brothers limited parental investment in sons, resulting in marriage delays. However, more sisters or brothers had no influence on female fertility while more sisters increased parental investment in sons (Borgerhoff Mulder 1998). This is the result of sex biases in parental investment resulting in son competition for limited resources only. Thus, siblings cannot be assumed to act as helpers-at-the-nest.

The evidence of the influence of siblings on child survival and nutritional status is similarly mixed. Overall, five of six studies examining the influence of siblings found positive effects, however the topic is less commonly investigated and comparisons are few (Sear & Mace 2008). The research conducted by Sear and colleagues (2002) in the Gambia also found that that older sisters increased the survival of younger siblings. However, one study among Shuar hunter-horticulturalists found that number of sisters negatively correlated with BMI while brothers had a quadratic relationship with BMI; the optimal number of brothers was two (Hagen & Barrett 2009). Hagen and Barrett (2009) suggest that girls receive preferential feeding to improve fecundity and marriage prospects leaving less food for young children, hence the negative effect of female sibs. Similarly, among the Tsimane, girls with older brothers and younger sisters had a lower nutritional quality regardless of household wealth (Magvanjav *et al.* 2012). Thus the role of siblings appears mediated by ecological context, household resources and biases in parental investment (Sear & Mace 2008; Sear *et al.* 2003).

3.3.6 Distant kin and unrelated individuals

The literature is extremely limited on the influence of allocare from more distantly related kin and unrelated individuals on child survival and maternal fertility. However, humans live in societies, whether they are small-scale villages or large urban centres, which contain a high proportion of unrelated individuals. Extensive cooperation is still common without the necessity of relatedness, indicating the importance of wider social networks in human social evolution (Apicella & Crittenden 2013). Furthermore, a brief review of the literature above reveals the importance of flexible caregiving, particularly in highly mobile societies like foragers. Given the high mortality rate and likelihood of being resident with any given kin type, sex or age, it would be a highly risky strategy to place all your eggs into one allocare basket (Hrdy 2005). Thus, throughout the life course, women may have to rely on alternative sources of help dependent on conditions (Kramer 2010). As a result these networks are likely to encompass not only distant kin (aunts and uncles, cousins (of all types) and affines) but also individuals who are not related consanguineously. Given that this consists of around 75% of hunter-gatherer camps (Dyble *et al.* 2015; Hill *et al.* 2011), focusing cooperative networks on only kin significantly reduces who can actually provide for children.

There is more outcome data for the presence of aunts and uncles. As they share 25% of genetic material with their nieces and nephews, exactly the same as grandparents, they could be expected to provide a significant proportion of care. However, unlike grandparents, aunts and uncles are reproductively active during a similar time period as the focal mother, and therefore have their own children to invest time and energy into. Consequently, their impact on child outcomes is dependent on the cost of their actions (i.e. less resources to invest into their own reproduction) and the overall benefit; the benefit of investing into a niece or nephew would need to be twice that of investing into one's own reproduction. Sear and

Mace (2008) cite only six studies which have examined the topic, each of which produced opposing results. For instance, Hill and Hurtado (1996) without distinguishing between matrilineal and patrilineal kin, found no effect of aunts and uncles on Ache child survival. However, Ache women suffered lower fertility when they co-resided with adult brothers, whose fertility benefited from adult sisters' presence. Thus, sisters supplemented male fertility, perhaps by increased caretaking. Similarly, among the historic Polish sample, female siblings significantly reduced their sisters fertility and total survivorship to age 16, indicating clear competitive relationships of maternal kin, particularly while they are reproductively active (Tymicki 2004). While negative effects of maternal and paternal aunts have been found on child survivorship in both Malawi and historical China (Sear 2008; Campbell & Lee 2002), among Hungarian Gypsies the number of adult siblings significantly increased maternal fertility (Bereczkei & Dunbar 2002). Following kin competition hypothesis, however, these relationships may be dependent on local resource availability (Griffin *et al.* 2004). For instance, among the Pimbwe, the number of maternal aunts and uncles increased child relative weight, however this was contingent on household socioeconomic status. Richer households suffered from many requests on their resources, while poorer households could rely on these richer households to provide these resources due to kin ties (Hadley 2004). However, only a few studies have examined the influence of kin competition by resource availability (Borgerhoff Mulder 1998; Borgerhoff Mulder 2007; Mace 1996) limiting any firm conclusions.

There are two non-mutually exclusive possibilities for why distant kin may be greater competitors than non-kin. Firstly when considering costs of caring, the reproductive scheduling of *some* distant kin will match the focal mother's scheduling. For instance, siblings (and thus the child's aunts and uncles) are commonly reproducing at the same time as the mother, thus childcare from them is particularly costly. This can also be true of younger grandparents under the age of approximately 50 years. Likewise, older children within the aunt's household (cousins of the focal child) may be involved in caretaking of their siblings. Thus, families of the same generation, as is common with distant kin, can compete for allocare resources. Of course, this is not the case for all distant kin. Similarly, non-kin may equally be at their peak reproductive stage; however, a difference is that they will be dependent on a different pool of resources. This is the second possibility of why distant kin maybe more competitive than close kin. Among the Agta we have found that households tend to cluster into groups with two or three other households between which the majority of food sharing occurs. These cluster households contained significantly more grandparents, uncles and aunts than expected by chance. As a result, distant kin are dependent on the same pool of energy and labour resources and increasing numbers of dependents will act as competitors for their food pot (Dyble et al. 2016). In contrast, non-kin reside outside of the 'resource clusters' and are not in competition for resources.

In the few observational studies which have reported on the investment from aunts and uncles they seem to provide exceedingly little care; among the Hadza, maternal aunts provided only 1.9% of direct care (carrying in this instance (Crittenden & Marlowe 2008)), while among the Agta maternal aunts averaged around 0.9% of direct care, paternal aunts only 0.5% (Goodman *et al.* 1985). However, in comparison among the Hadza, non-kin frequently carry children (12.4%) particularly female juveniles (aged 8-12 years), a pattern also noted in the Aka (Meehan 2005), Ache and Hiwi (Hill & Hurtado 2009). Furthermore, Ivey (2000) reported that when parents lacked support, unrelated allocarers were recruited. As a result, it appears that while distant kin are competitive, non-kin have an important role in the hunter-gatherer contexts of ensuring children receive the support they require by providing flexible childcare. However, only one study I am aware of examines the influence of non-kin on child outcomes. Borgerhoff Mulder *et al.* (2011) finds among the horticultural Pimbwe that a mother's relational wealth, (her social support network) is the largest predictor of child survival. However, because kin had a negative effect on child survival, the most important components of a mother's social network are unrelated. This role for non-kin may be theoretically more important in foraging populations given the stochastic nature of not only the resource ecology but also demography (Kramer 2010).

3.4 Flexibility, variability and risk avoidance

Human allomothering systems are highly flexible and context dependent. Who exactly increases the survival or fertility of a mother and her children varies according to the demographics, residence patterns, levels of resource competition, mortality risks and type of subsistence. However, these trends within a single population have only been explored by one study. Valeggia (2009) examined how allomothering varied among two Tabo groups from the South American Gran Chaco and found that in the 'traditional' community mothers provided 50% of care to infants under 24 months, young unrelated girls provided 33%, and grandmothers 13%. Fathers provided only 2% of care. However, in the urbanised community, mothers provided 77%, fathers 7%, sisters 4% and grandmothers 3% of care. While this study does not explicitly test what features of these communities specifically correlated with allocarer change, the differences are extreme enough to indicate an effect of urbanisation. If, as supposed throughout the cooperative breeding literature, cooperative breeding evolved in response to environmental hardship and uncertainty (Emlen 1982; Jetz & Rubenstein 2011) then the influence of cultural and/or subsistence change on the structure of allocare may be significantly related to risk avoidance.

Above, I discussed communal breeding as a buffer from predictable and unpredictable shortfalls in the environment. However, there are multiple ways to buffer an individual from risk (i.e. probability of loss), which depends on the resources available and subsistence patterns. Aktipis *et al.* (2011) discusses four ways of dealing with risk. Firstly, *risk reduction* includes any action that lowers the probability of loss, such as moving to a resource-rich and predictable environment. A second form is *risk avoidance*, which occurs when individuals diversify subsistence by participating in different economic activities or reducing exposure to risk across space with mobility (Winterhalder *et al.* 1999). This tactic is common in east African pastoralists attempting to mitigate the influence of cattle disease or climatic fluctuations (Little *et al.* 2001) as well as in foragers. The third type is *risk transfer* which is any action which exchanges risk between individuals or groups (Fafchamps 1992) and defines informal insurance networks worldwide, particularly in developing nations (Caudell *et al.* 2015). Risk pooling is an example of this where individuals/groups face an immediate small loss but decrease the severity of larger, unpredictable losses in the future. As a result, it can be best described as a needs-based transfer (Hao *et al.* 2015; Aktipis *et al.* 2011), thus matching reciprocity exactly. In particular, for reciprocity to be effective individuals within the pooling network must be independent and the number of units exposed to the risk large (Cashdan 1985). As a result, risk pooling is a useful method of reducing risk exposure when individuals face shortfalls independently. This remains true of foragers in terms of variability production, sickness and lifetime childcare deficits; the mixed age demographic of hunter-gather groups means that there is always a significant number of non-reproductive individuals present.

The fourth and final way of dealing with risk is *risk retention*, which involves accepting risk by being able to absorb losses. This includes increases in wealth and food storage, two forms of risk buffer often placed in contrast to reciprocity in hunter-gatherer studies (Winterhalder *et al.* 1999; Cashdan 1985). When individuals have increased wealth their need for pooling-networks are reduced as they are independently able to protect themselves from shortfalls. Furthermore, individuals with increased wealth may, given the need-cost dynamics of reciprocity, be obligated in sharing networks to provide a significant amount of support for individuals in need (Hadley 2004). Thus, ultimately risk-pooling becomes less viable than wealth accumulation and wealthier individuals attempt to remove themselves from such wide sharing networks (Fafchamps 1992). Furthermore, reciprocity often hinders wealth accumulation and shortage, given its association with widespread sharing and egalitarian social norms (Wiessner 1996). As a result, in foraging populations involvement in cultivation and/or wage labour is associated with increased sedentarisation (thus swapping one risk avoidance strategy for another). However, without mobility the limitations of wealth accumulation and food shortage are removed, reducing their dependence on risk pooling (Cashdan 1985).

There is sufficient theoretical work to suppose that subsistence and/or lifestyle change in small-scale foraging communities will result in significant changes to sharing networks. Certainly, among the Mpimbwe it appeared that wealthier individuals engaged less in reciprocal exchange, and rather engaged in the cash economy (Kasper & Borgerhoff Mulder 2015). Similar results have been found in the Dobe !Kung (Yellen 1990), Machiguenga forager-horticulturalists from Peru (Henrich 1997) and in rural Tanzania (La Ferrara 2002). However, among the Tsimane Gurven *et al.* (2015) recently found that market integration was not a like-for-like substitute of traditional resource pooling, and individuals with more wealth gave a higher percentage of food to others. Why these differences in patterns occur is unclear, and warrants significant further investigation. Nonetheless, it appears that we may expect childcare behaviour to vary significantly according to factors such as wealth accumulation, food storage and involvement in diverse forms of subsistence.

3.5 Summary

Overall, it appears that human allomothering is defined by its flexible nature and context dependency (Sear & Mace 2008). In exploring 'who cares' and what are the consequences of this allocare it appears there is no human universal allocarer, or singular 'ace-in-the-hole' (Hrdy 2005). Particularly, in foraging societies defined by fluctuating group membership, short life spans and limited resources, it appears that maintaining a wide, flexible childcare networks may be a less risky strategy than focusing on one single allocarer. Following this, of particular interest is the significant variability in allocarer providers within populations. Given the hypothesis that allocare acts as a buffer to risk, it is theoretically interesting to explore how then allocare changes with different ways of dealing with risk.

It is explicitly evident that direct childcare studies rarely test how cooperative breeding can be maintained among populations of selfish individuals. I am aware of two observational studies which approach this problem (Ivey 2000; Crittenden & Marlowe 2008), finding that the amount of care given is significantly related to kinship. However, without exploring need, costs, association, among other influences, it seems to be premature to come to the conclusion that "…nepotistic investment appears to be the primary motive for allomothering among the Hadza" (Crittenden 2009: 109). At the same time, the literature contains many examples of a significant proportion of care being offered by non-kin, a topic currently unexplored due to the focus on infants in observational studies. Furthermore, given that mother's successful recruitment of allocarers appears imperative for her children's survival, we know very little about how mothers ensure they have access to the allocarers they need.

As a result, my work on cooperative breeding (chapters 5 to 8) will focus on *(i)* robustly testing the predictive power of different cooperative hypotheses, specifically kin selection, reciprocal altruism, helpers-at-the-nest and grandmothering; *(ii)* examine the influence of risk, subsistence (i.e. increased cultivation), ecology and wealth on childcare; *(iii)* explore how mothers may manipulate their social networks to facilitate childcare; *(iv)* examine the consequences of allocare on child outcomes and/or maternal fertility; *(v)* focus not only on infants, but also on all dependent children under the age of 12 years, using a significantly larger sample size; *(vi)* and explicitly examine the role of non-kin and their importance in flexible caregiving.

Chapter Three
Methodological Approach and Data Collection

Here I summarise all data collection and statistical analysis used throughout this research. Any methodological approach or statistical analysis applied in only one chapter are discussed in depth in their relevant chapters. This thesis is a product of one year's worth of data collection, spanning two field seasons (April-June 2013 and February-October 2014). During this time the Hunter-Gatherer team collected a range of genealogical, anthropometric, behavioural and aging data. We also piloted an innovative data collection procedure to examine proximity networks and childcare with the application of motes, wireless proximity loggers (section 4.3). Using the latest in technological advances it was possible to collect a depth of data on contact networks which has not been possible in hunter-gatherers previously.

4.1 Hunter-Gatherer Project

The data collection which underpins this thesis was collected as part of the hunter-gatherer research project at UCL. This five year project was funded by the Leverhulme Trust to explore hunter-gatherer resilience using interdisciplinary methods spanning anthropology and genetics. The project was headed by Andrea Migliano and co-investigators three Mark Thomas (UCL Genetics, Evolution and Environment), Ruth Mace (UCL Biological Anthropology) and Jerome Lewis (UCL Social Anthropology). As part of the biological anthropology research six PhD were engaged in the grant to: develop new research methods; set up two new field sites in the Philippines (Agta) and Congo Brazzaville (BaYaka foragers); and explore questions in human behavioural ecology and human evolution. These PhD students include Deniz Gul Salali, Nikhil Chaudhary and James Thompson who worked with the BaYaka foragers and Mark Dyble, Daniel Smith and myself who worked with the Agta. Sylvain Viguier was also hired as a consultant to implement the motes as an embedded software engineer but also conducted a significant amount of data collection in the Philippines.

At the start of the project one major aim was to conduct data collection in two foraging populations following the same protocols. This is particularly the case for the census period of data collection. Our first aim was to collect full genealogies, age estimates, reproductive histories and anthropometric data on all the individuals we met during our pilot period from April to June 2013. Consequentially, in the first quarter of 2013 we worked as a team to create these data collection protocols, which are explained in depth below. During this time I also spent a significant amount of time conducting logistics for fieldwork. Data collection in the field (both in 2013 and 2014) was also a shared exercise in terms of data which was useful for all members of the team. This includes the genealogies, aging procedures, reproductive histories, interviews and camp scans. By working as a team we were able to collect a large amount of information about each individual which spans all aspects of their lives. This data is freely shared among the group as it is the product of everyone's work. However, at the same time we each had particular areas of data collection relevant to our PhDs. For instance, Mark Dyble collected data on food production and food sharing, Daniel Smith conducted interviews about norms and economic games while Sylvain Viguier and I implemented the motes experiments, conducted focal follows of infants and children and I conducted the anthropometrics and medical survey. Each of these specific data sets are shared within the project, however the use of them is, of course, dependent on the agreement of the main researcher and collaboration.

Section 4.5 deals with how the team created a method for reliable aging; while data collection and protocols were developed collaboratively with the Hunter-Gatherer team, the subsequential analysis was developed by Yoan Diekmann, Pascale Gerbault and Mark Thomas and remains wholeheartedly their work. Full data collection protocols and forms can be found in appendix A while more technical details about the motes and the statistical method used in the aging process can be found in appendix B.

4.2 Data collection

We collected observational, interview, anthropometric and health data over two field seasons from April to June 2013 and February to October 2014. During this time we met 914 Agta from a population of around 1000 residing in the Northern Sierra Madre Natural Park

(NSMNP). Permits for all fieldwork were awarded by the Department of Environment and Natural Resources based in the NSMNP as well as the local government in Palanan. We also sought permissions to work with the Agta from several 'chiefs' prior to the start of data collection. In the first fieldtrip we (MD, DS and I) conducted a census, genealogical interviews and anthropometrics. Our major aim here was to meet a large number of Agta across a number of different camps. As a result, this data collection was primarily conducted over two to three days in each camp, depending on its size. We were based in the barangay (district) centre and would travel out to the camps by boat or foot depending on the location. Travel time was a short as a one-hour walk or as long as a six-hour boat ride. On this occasion we worked with two field assistants who would translate and assist in data collection. When we first arrived in a camp we would introduce ourselves and arrange a community meeting in which we would show posters and act out/explain what it was we were doing and why. During this time we would collect informed consents from each of the adults who would sign on behalf of their children. After this we would conduct a camp map and find out about everyone living in the camp and broadly who was related to whom. After all of this we would conduct the genealogical interviews as well as collect anthropometric data (described fully below).

In the second period of fieldwork, the aim was the return to the camps in which we had originally conducted the census to collect more detailed information. On this occasion we (MD, DS, SV and I) were primarily based in Palanan town where we would get supplies. From here we would travel out to the surrounding Agta camps in all directions for 10 – 14 days at a time (depending on the size of the camp and if the weather permitted leaving). Between February and July 2014 (the dry season) we revisited 13 camps throughout Palanan. We each conducted shared data collection (genealogies, interviews and camp scans) as well as our own focused data collection (specified below). After July we (SV and I) returned to all the camps once more to conduct shorter data collection focused on the medical aspects of this thesis. We collected anthropometrics for all children and adults, as well as blood samples and conducted the medical questionnaire. Therefore, we had visited the majority of camps three times over the two-year fieldwork period, noting births, deaths, individual movements as well as camp changes. I will now detail the exact protocols we followed, separated into observational data collection, interviews, reproductive histories, medical survey and the application of the motes.

4.2.1 Camp Scans

In each camp we conducted four daily camp scans to record activity patterns. These scans were based on spot observation techniques (Gibson & Mace 2005; Borgerhoff Mulder & Caro 1985). We categorized each individual's activity at the allocated time, and if they were out of camp their reported location and activity was recorded. We found out about their location from enquiry with family members who were in camp during the scan time. To produce an unbiased time sample the first scan was rotated daily (start times from 6:30 to 9:30 at 30 minute intervals and then three more scans were conducted every four hours from this starting point). We also recorded with whom individuals were with while conducting this activity. We recorded individuals as a 'group' if they were within three meters of one another (i.e. relaxing in a lean-to). The activity groups included childcare, foraging, cash labour, agriculture, household tasks, relaxing, being out-of-camp, playing and socialising. Therefore, we had four points during each day we knew the exact composition and activities of each member of the camp. From these data it is possible to extract the variables such as how long individuals spent foraging compared to hunting, fishing, cash labour and food production.

4.2.2 Food Diaries

Dietary data were collected at the household level at the end of each day. Our data collection for diet was primarily based around activities, rather than an in-depth dietary recall. We asked the mother and the father at the end of the day (between 17:00 – 18:00) what foods they had eaten that day. To create variables from these data we counted up the total amount of meals we had recorded for a household and established what proportion of these consisted of meat, vegetables, fruits, honey and rice. These data was primarily collected by Mark Dyble and Andrea Migliano.

4.2.3 Interviews

We conducted household interviews to quantify demographics, household wealth and food security and storage. For consistency, we conducted the questionnaire with the mother of the household.

4.2.3.1 Reproductive histories and genealogies

During both our fieldwork periods we collected full genealogies and reproductive histories from each mother. We recorded not only living children, but also miscarriages, stillbirths and infant and child mortality. To help establish ages (see aging methodology in section 4.5 below) we would ask roughly how old was the first child when the second was born (i.e. had he/she stopped breastfeeding, or started walking etc.). We would always specifically enquire whether a mother had experienced any miscarriages or stillbirths, as these would often go unreported. If there was a large interbirth interval between any two children we would enquire if there was a specific reason, which may prompt a mother to report a deceased child. If a child had died, we would enquire about the causes, roughly how old the child was and when it happened. Often mothers did not know 'when' or 'how old' but it was always possible to associate an individual's age and year of death with another event that we did know. For instance, we would ask, "who were you breastfeeding when child X died?" or "which of your children is the most similar in age to child X when he/she died?" Since we robustly aged all living children, with this information it is much easier to triangulate ages and date of death for deceased children; however, for older individuals this becomes increasingly more difficult since life-stages become a lot larger. Often individuals were said just to be 'older than me' or 'older than my parents' at death. Therefore, our ages for childhood mortality (under 16 years old) are more precise than our ages for adult mortality.

We then went up the genealogy and enquired about ego's parents, siblings, and grandparents. For many, it was quite rare that they would know who their grandparents were, what area they had lived in or what they had died of. Similarly, people seemed to know family members who lived nearby very well, but families of any brothers or sisters who had moved to a more distant area were often unknown. We would ask about individuals' sibling's husbands or wives and their offspring if they were not co-resident in camp. As we often collected the same family tree from several individuals, we did find inconsistencies in the data, such as an additional child or a very different birth order. To produce the most accurate genealogy we took either the genealogy from the most knowledgeable individual (i.e. the mother over the aunt) or the genealogy that reduced other inconsistencies (i.e. avoiding impossibilities such as six month interbirth intervals).

Overall the genealogies we collected contained 2,953 living and dead Agta from Palanan and neighbouring municipalities of Maconacon, Divilican and San Mario. From this data it was possible to establish the consanguineous relatedness (*r*) of each individual we met and calculate maternal fertility and childhood mortality rates. There are inherit limitations with self-reported reproductive histories, however. For instance, mothers commonly do not report miscarriages, stillbirths or early life mortality (Ellison et al. 2000), a common finding in our own data. Furthermore, as the Agta do not like to say the name of the dead (for fear of invoking a spirit) they are unwilling to name individuals who have died. Therefore it is possible that we are underestimating the number of ever-born offspring, and as a consequence neonatal and infant mortality. This is likely the case in Headland's dataset of the Agta communities from Casiguran (Headland, Headland and Uehara 2011), which reports very few infant deaths. Given that we find a mortality rate of 36.9 prior to the age of 1 (including all conceptions reported, all live births is 19%), which falls into line with previous research findings among immediate-return foragers and other Agta populations, we do not believe this is grossly underestimating early childhood mortality. Nonetheless, this is still likely to be an underestimate.

4.2.3.2 Food security

To establish how secure or insecure individuals felt in terms of food supply we asked a series of food security questions adapted from the 2014 survey for US households (Coleman-Jensen *et al.* 2014, appendix A Table 1). By removing questions related to grocery shopping, access to resources and money we were left with 10 questions. Each individual answer was scored 1 to 3 marks according to their answer. The most insecure answer was scored with 1 while the most secure answer was scored with 3 marks. We then totalled these marks up for each mother. To control for the fact that some individuals did not have children, the answers were weighted according to how many questions they answered. For instance, if a mother answered all questions she would have had a maximum score of 30. For a wife without children questions 5, 6, 8 and 10 were not relevant. As a result, her maximum score was 18. Therefore, if the mother with children had a score of 15 her adjusted score was 0.5 (15/30) while the wife without children with the same score would have an adjusted score of 0.83 (15/18). At the same time, we inquired about how much rice (kg) each family had in their household at time of interview as a measure of food storage. We did not weigh this rice directly, thus measurement may be unreliable according to interviewees skill at estimation.

4.2.3.3 Household belongings

Our interview also included a quantification of the numbers of belongings owned or '*material wealth'*. To create an 'emic' based list, we first sought to establish the most important items from a sub-sample (*n* = 16) of households. We asked each household to name 10 of the most important belongings an Agta could own. Based on this we created a list of 14 household items that were mentioned the most frequently. This list was then shown to each household, asking whether they had these items and if they did, how many did they have. As some items were more important than others we weighted each item according to the number of times it appeared in the list. For instance, as most households owned cooking pots, a family without one would be considered quite 'poor' since these are an essential daily item. Thus, these items were weighted the highest. This system assumes that the 'most common' are the most valued, since it would be erroneous to compare cooking pots to spoons 1-to-1. However, it does undervalue rare, luxury items (such as radios or guns). The object, count and proportion can be found in Table 4.1. Overall, this method was thought to be more nuanced than taking the monetary value of items since this is unlikely to be directly reflective of the value the Agta place in the items.

Table 4.1: List of household objects and their weighting used in creation of household belonging variable.

Item	*n*	Proportion	Weight
Goggles	31	0.053	5
Blanket	37	0.063	6
Hunting bow	7	0.012	1
Cups	65	0.111	11
Air gun	5	0.009	1
Kettle	45	0.077	8
Knife	65	0.111	11
Mat	15	0.026	3
Net	12	0.020	2
Plates	93	0.158	16
Cooking pot	123	0.210	21
Radio	4	0.007	1
Spear gun	35	0.060	6
Spoon	50	0.085	9
Total	587	1.000	

4.2.4 Camp descriptions and mobility

During the two years of fieldwork we visited each camp multiple times (at least twice, sometimes three times depending on whether it was abandoned or not), therefore we were able to create mobility variables. This was broken down to *individual level mobility* and *out-of-camp mobility*. For camp-level mobility we conducted a camp survival analysis that quantifies the proportion of individuals leaving camps. If all individuals who had been present on our first visit remained so during later visits, the camp had a survival rating of 1. If, however, camp composition completely changed the camp had a survival rating of 0. Therefore, this measure quantifies out-of-camp mobility. Leaving was defined as any departure from camp which was longer than overnight. At the individual-level people were either allocated as mobile or settled depending on whether or not we had ever witnessed them to move (again for longer than one night) at least once during our fieldwork.

While these mobility variables capture peoples' movement, the degree of camp sedentarisation was also coded according to housing type. The *housing* variable is on a three-point scale, 0 being the most temporary and includes camps with lean-to shelters, which frequently change in either location or position. Camps allocated to 2 on the scale were fully settled camps in which the houses were permanent (wooden huts with metal roofs) and unable to move. Camps with a mixture of both of these features had a temporary measure of 1. Finally, for a binary analysis the camps were simply separated into a category of settled or not, based on the presence of permanent housing, churches and infrastructure such as water pumps. Therefore, with these measures we have both a sense of the permanence of camps as well as individuals' mobility in and out of them.

4.3 Motes

Sylvain Viguier and I designed the motes as a new methodology of increasing the resolution of studies of hunter-gatherer social networks. In particular, they have been designed to capture proximity interactions which mimic traditional childcare observations. The coding and testing was conducted by Sylvain Viguier and further details of which can be found in appendix B.

Motes are low-powered and compact wireless sensing devices. Multiple devices communicate and store these communications without the need for infrastructure (such as WiFi or local hubs (Cattuto *et al.* 2010)) and create *ad hoc* wireless sensing networks (Panisson *et al.* 2012). The device we utilised was the UCMote Mini (with a TinyOS operating system) with some custom modifications. It comprises a main processor, a wireless communication module, a memory storage unit and a battery which allows the devices to run for up to four weeks with one charge. Motes allow us to produce high-resolution proximity networks for a larger sample than previously possible. Each device sends a message that contains its unique

ID, a time stamp and the signal strength at a programmed interval. This message is picked up and stored by any other mote within a specified diameter around the emitting mote (Figure 4.1). At the end of the experiment these data are downloaded for analysis.

The major innovative aspect of using motes or other similar proximity loggers is the increased time sample. Previous research in small-scale populations examining childcare has relied on focal follows which commonly due to high intensity consist of following and observing what a single child does over 9 hours across three separate days. Given the small time period this data can easily be skewed by particular events. Therefore, while the motes capture much coarser grain data (i.e. only proximity) we able to collect data for a full one week period on multiple children, reflecting a much larger sample period than previously possible in human populations. However, one-week data collection period remains short, and will only capture interactions during this one snapshot in time. Therefore, the results within this thesis should but be considered as static or defining of the population. Particularly in terms of the social networks discussed in chapter 7, it is much more reasonable to consider that the social networks and the individuals within them will change overtime.

4.3.1 Previous applications of ad hoc networks

The growing interest in emerging dynamics of social networks in both humans and non-human animals has led to the development of a variety of technological advances to ‘data mine real-world interactions’ (Isella, Stehlé, et al. 2011). For instance, mobile phones signals have been utilised to track and map mobility patterns of 100,000 individuals (González *et al.* 2008). Others have focused on examining the structural elements of social interactions using WiFi and Bluetooth networks created by mobile phones (O’Neill *et al.* 2006; Eagle & Pentland 2006). In a developed, industrial world where individuals are rarely separated from their mobile phones and other essential electronics, the electronic signals they emit are valid proxies for social interactions (Cattuto *et al.* 2010). However, these have little application in traditional anthropological fieldsites without electricity, infrastructure, telecommunication systems or portable electronics.

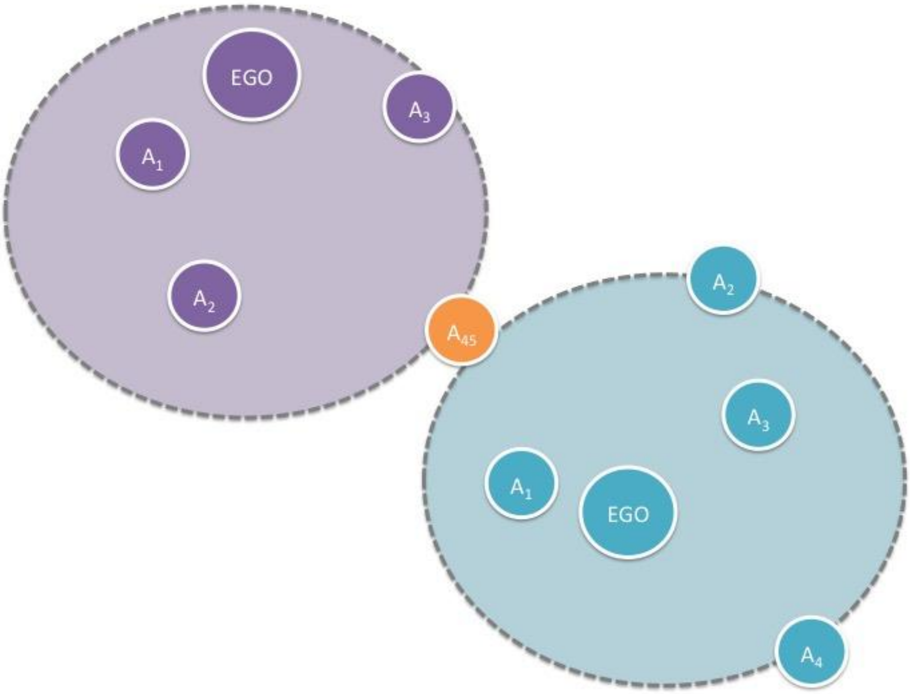

Figure 4.1: Motes proximity networks. Visualising the functionality of the motes. Each individual wears a mote, which transmits and receives messages every two minutes from other motes within approximately 3-metres. Messages beyond this threshold are disregarded and not stored. For instance, here all the blue nodes are within 3-metres of the blue Ego, and these interactions are stored. However, the purples nodes are beyond the threshold and these packets are disregarded. The singular orange node straddles both proximity networks and is stored by both Egos.

The Sociopatterns project have pioneered and developed small, inexpensive and unobtrusive active RFID (Radio Frequency Identification Devices) which sense face-to-face interactions up to one meter proximity (Cattuto et al. 2010; Isella, Stehlé, et al. 2011; Barrat & Cattuto n.d.). Passive RFID technologies include contactless payment systems and urban travel cards (such as the Oyster card used by Transport for London). However, these are read-only devices that means a unidirectional communication with a reader. Cattuto *et al.* (2010) altered these standard RFID tags so they were able to engage in bi-directional communications among themselves, in a peer-to-peer fashion, thus, forming an *ad hoc* network. Each tag has a 'transmit phase' in which packets are sent out on a radio channel. While the other tags are in a 'receiver phase' they listen to the same channel to pick up a packet sent within the programmed signal strength (i.e. distance). However, this technology was designed to function in modern contexts (Stehlé *et al.* 2011). This means they are dependent on a data collection infrastructure, comprised of fixed radio receivers connected to a computer via the Local Area Network (LAN). Furthermore, data collection is limited then to the zone covered by the RFID readers; if individuals leave this area their data are not collected. Consequentially, we required autonomous devices, which also contained a memory and battery for prolonged, independent functioning.

These conditions are met by motes, and to our knowledge have only been used once before by Kazandjieva and colleagues (2010) in exploring social contact networks and infectious disease spread in a US high school. They conducted their study over one day, which involved 792 motes sending broadcast messages to approximately 9-meter diameter every 20 seconds. This meant at the end of the 9-hour experiment they collected and downloaded 3 million records of contacts between participants. This study revealed that since each of these 7-byte interactions needed to fit into the 1MB flash memory, there is a significant trade-off on the duration, frequency and thresholds (i.e. two metres versus 15) applied in any study. This research also highlighted the importance of the 'human factor' since their motes experienced significant reboots (1500 over 500 devices) due to sudden shocks and loose batteries (i.e. banging motes against hard surfaces).

4.3.2 Range and calibration

The radio links were adjusted to allow a mote to record all other radio signals within a radius of approximately three metres. Three metres was utilised as not too include too many individuals in the camp who may not be necessary interacting with ego. Since camps are small and open-plan, some individuals with huts around 10 metres away may have no meaningful interaction but continually stored as proximate by the motes (Figure 4.2). The second factor was that three meters is a common threshold used in child observation studies (Meehan 2009; Meehan *et al.* 2013b; Crittenden 2009) to denote when a carer may be providing low-effort investment (such as watching or 'proximity' babysitting) as well as more high-investment activities such as teaching, playing or talking. Therefore, we felt this was a suitable threshold that captures close proximity which is necessarily for important interactions, such as childcare, playing, hunting, foraging, cultural exchange (i.e. showing, learning and sharing) as well as disease transmission (Kazandjieva *et al.* 2010; Stehlé *et al.* 2011). Thus, 3-meter spatial networks are a proxy for meaningful behavioural interactions (Barrat & Cattuto n.d.). Three-metres equates to a programmed power level of 5 within the embedded software; therefore, if signal strength is lower than 5 the packet is discarded. If it falls within this threshold the entry is stored in a buffer in the volatile memory, which once it is full it is written to the flash memory.

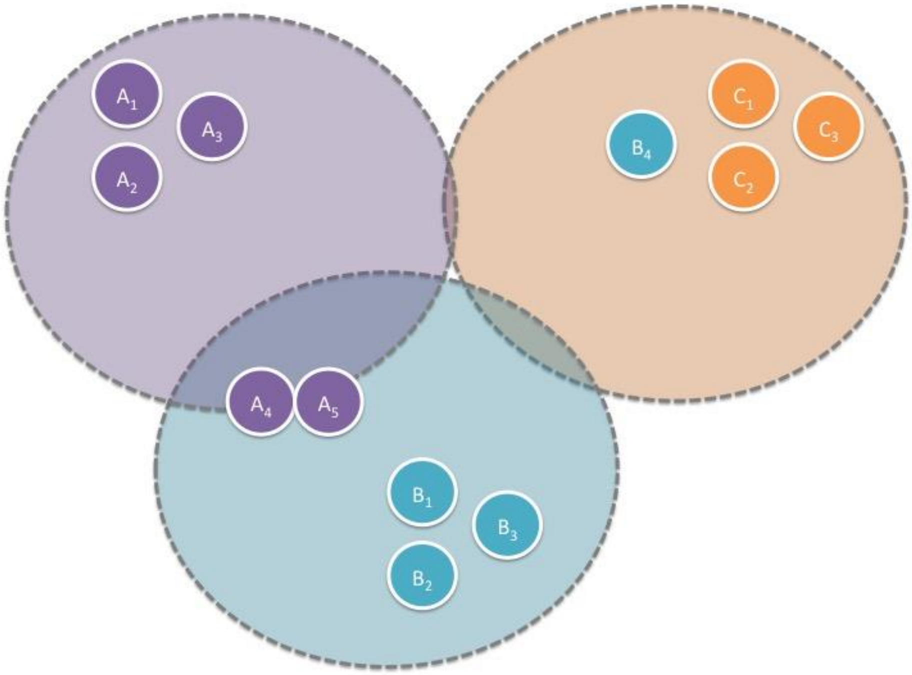

Figure 4.2: Agta camp layouts and motes thresholds. Here, when some members of household A come closer to household B their mote messages will be stored; however the reminder of household A and household C remain outside the signal range and will be discarded.

4.3.3 Mote utilisation in the field

Once the motes were protected from water damage, they were sealed into wristbands, armbands or belts (depending on the size of the individual, Figure 4.3). Out of the total 13 camps we visited we conducted the motes experiment in six camps containing 200 individuals. The study was undertaken in one camp at a time. After explanation of methods and discussion of data anonymity, participants signed informed consent forms and were given a mote. Many of the Agta are not literate so we underwent a three stage process to make sure they understood what we wanted to do and why. Firstly, with the whole community we presented what we wanted to do (motes, anthropometrics and genealogies) using posters and images which we handed out. These were described in the Agta's own language. After this we would go around each household and discuss with them in more details about the motes in particular to makes sure they were happy with the process and understood what was happening. We then asked them to put an ‘x’ in the signature box of the consent form to comply with UCL ethnics regulations. A limitation here is that I do not believe the Agta are truly ‘informed’ about the end consequences of the data collection and research as it has little bearing on their daily lives. However, we (Andrea and I) hope that by working on the empowerment of the Agta alongside NGO like Minority Groups International in future research that we can engage in community led research which has the ability to be purely ‘informed’.

Each mote was labelled with a unique number and identified with coloured string to ensure swaps did not occur. All individuals within a camp (from newborns to elderly individuals) wore the motes from a period ranging from five to seven days depending on the camp. A few individuals per camp decided they did not want to partake in the experiment; however, this was rare as once a few people took part everyone would. If a mother or father did not wear a mote, their whole family was removed from the experiment in the data processing. This was so we did not bias the data used in the childcare analysis with apparently ‘absent’ parents.

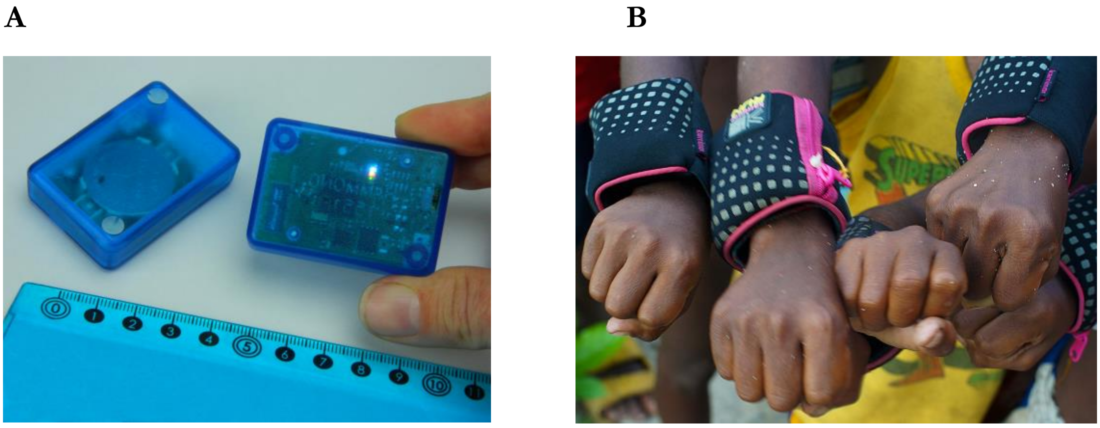

Figure 4.3: Mote utilisation in the field. (A) Motes switched on before packaging and (B) Agta children wearing their motes in armbands. Credit: Rodolph Schlaepfer and Sylvain Viguier

While the motes were worn throughout the night, data were only selected from between 5:00 and 20:00. This was to avoid long hours of simply recording who slept in the same lean-to. If individuals arrived at a camp during the experiment they were promptly given a mote, and entry time was recorded. Similarly, if an individual left a camp at any time before the end of the experiment, the time they returned the mote was recorded. A small compensation (usually a thermal bottle or cooking utensils) was given to each participant when the mote was returned at the end of the experiment. To ensure swaps did not occur individuals were regularly (twice daily) asked to check they were wearing the correct armband. Swaps most usually occurred among siblings or young playmates as they would take off the armbands and play with them. As a result they would not always know whose-was-whose when putting them back on. This is why the string was important so everyone knew their own colours and put the correct armband back on. All mote numbers were also checked when they were being handed back to ensure we always knew who had worn each mote. Any swaps were recorded during the experiment and adjusted in the final data processing.

4.3.4 Data processing

Data recovery from the motes produced a two-by-two matrix containing the frequency of interactions between each dyad that partook in the experiment. These raw frequency matrixes were then adjusted according to the length of the experiment; the raw number of interactions was divided by the number of hours the experiment was conducted for. Thus, the resultant dependent variable reflects the hourly average number of interactions between an allocarer and a child. I refer to this variable throughout the analysis as *'number' or 'frequency' of interactions*. To bring my results into line with the cooperative breeding literature in hunter-gatherers in general, I have also presented the descriptive statistics as proportion of interactions. These were produced by establishing the total number of hours an allocarer was present in camp (representing possible interactions), then dividing this by the number of actual interactions between an allocarer and child. Consequentially, this figure represents how long an allocarer spent with a child as a proportion of *the allocarers* total time while in camp. This result is referred to as '*proportion of interactions'*.

4.4 Focal follows and childcare

A large aspect of my fieldwork was focal follows of 80 infants and children aged 0 to 6 years, conducted by myself and Sylvain Viguier. This is, to my knowledge, the largest sample of focal follows among hunter-gatherer children. This work is extremely time intensive, in terms of data collection, data entry and data processing. As a result, I have only been able to enter and process 40 children (20 infants and 20 children) from six camps (which are the same as the camps the motes experiment was conducted in), which are discussed in chapter 5. Nonetheless, these data will form the basis of future work on this topic.

The focal follows were conducted using focal sampling techniques (Meehan 2005; Meehan *et al.* 2013b; Fouts *et al.* 2005; Hewlett *et al.* 2000). In this technique a focal child is observed for 12 hours over several days to ensure a range of activities are captured. This 12-hour period is broken into three 4-hour intervals (6:00 – 10:00, 10:00 – 14:00 and 14:00 – 18:00) during which, the researcher records who is interacting with a child and what type of interaction this is every 20 seconds (observe for 20 seconds, record for 10 seconds) within a three-meter radius. These 4-hour intervals were conducted on non-consecutive days to reduce any sampling bias (i.e. the father was out of camp for those two days). Due to the intensive nature of the data collection, 15-minute breaks are essential every hour, thus in total each child was observed for 9 hours. This produces 1,080 observational points per child over three days, compared to an average of 3,150 mote points over one week. During the focal follow the following pieces of information are recorded for up to six individuals within three meter proximity to a child: distance (touching, arms reach, three meter proximity); high investment activity (carry, feed, groom, medical attention, teach and play); low investment activity (talking to, watching and being just in proximity); whether individuals are part of a playgroup; the child's state (crying or sleeping); and maternal activity (collecting water, firewood, cooking, childcare, repair, foraging, sleeping and relaxing etc.).

4.5 Aging

The aging protocols were developed and conducted by the whole Hunter-Gatherer team. The subsequential analysis method was developed and conducted by Yoan Diekmann, Pascale Gerbault and Mark Thomas and remains wholeheartedy their work. Further details of the Gibbs sampling Markov chain Monte Carlo (MCMC) analysis can be found in appendix B.

Many studies of hunter-gatherers struggle to accurately age their population, particularly if this is the first quantitative data collection with the group. Foragers do not have the same concepts of dates, years or time as their researchers, thus little idea about how old they are. When asked they will often suggest any reasonable (or unreasonable) figure, or simply state 'old' or 'young'. However, aging is essential for the exploration of life history events (age at first menarche, age at first and last birth, age at menopause and age at death) as well as accurate anthropometrics and growth projections for children and age-controlled fertility for women. Thus, it was essential that we were able to accurately age all individuals in the population.

Surprisingly, as a fundamental and underlying problem in much of the hunter-gatherer research, there has been limited innovation in developing robust methodologies for aging previously unstudied populations. Some researchers often make use of what Hill and Hurtado (1996: 112) refer to as “guesstimates”, based on how old you personally consider an individual to look, to establish the ages of their sample (Chagnon 1974). However, this is problematic as we expect the physical appearance trajectories of hunter-gatherers to be significantly different. Babies are often born smaller and remain so, thus the age of children is frequently underestimated. On the flipside, due to harsh environmental conditions, adults frequently appear older to western researchers resulting in an overestimation of their ages. Other researchers, as reviewed by Hill and Hurtado (1996, chap. four), use: dental examinations based on teeth eruptions (however, the extreme range in when teeth erupt results in a large age bracket); relative age lists and clustering into age cohorts; and statistical techniques (Blurton Jones *et al.* 1992; Wood *et al.* 1985; Borgerhoff Mulder 1989). Early and Headland (1998) used an ‘age calendar’ to establish unknown ages, which entailed a calendar of dated local events (the arrival of a mine at one location, when anthropologists came or when particularly big typhoons made landfall) which Agta mothers were asked to relate the birth of their children to.

Two studies - Hill and Hurtado (1996) and Howell (1979) - have attempted to use robust methodologies to overcome this key limitation in forager research. Howell’s (1979) demography of the Dobe !Kung contained an extensive aging procedure referred to as a ‘steady-state model’. Based on a relative age list of all individuals (i.e. A is older than B and E, but younger than C and D, while D is older than C) this method assumes a static population structure based on fertility and mortality trends. By comparing the !Kung demography to an appropriate stable population model, Howell was able to age individuals by taking the life-table which most overlapped with her own data. Thus, individuals are assigned ages due to the expected proportion of the population who should fall into each age group (i.e. 79% of infants surviving to their first birthday, 64% to their 15 and 10% to their 50th birthday). Hill and Hurtado (1996), however, extensively critique this method on a number of points. Firstly, stable population models are unfeasible as populations are not stable due to epidemics, drought and famine as well as periods of population growth and expansion. Secondly, these population models are based on western population schedules, and they should not be considered to be universal. There is no reason to assume that mortality rates are proportional between different age brackets, as these models do. For instance, Migliano *et al.* (2007) suggest that pygmies suffer from high mortality rates, leading to reduce growth and faster life-histories. Thus, attempting to force foragers' unique demography and life history schedules into these models risks obscuring actual patterns.

Consequently, Hill and Hurtado's (1996) demography of the Ache is based on a robust aging method which did not rely on static population models. The method follows a number of processes to arrive at more accurate ages. Firstly, the population was broken into age cohorts, in which individuals we asked to age-rank all others in their own cohort, as well as cohorts above and below them. Age-ranking was ego based, thus each individual was asked if alter was older or younger than them. A final relative age list was produced by using the ranking that minimised the number of contradictions, and the age cohorts were joined together to create a master list. To move from relative ages to absolute ones, Hill and Hurtado utilised dated events (similar to Early and Headland (1998)), photos of children at first contact, estimates of age differences between children to create an 'age chain' of birthdays and birth certificates as an anchor. The age chain method consisted of establishing which child A of known age now is of a similar age to ego when a child B (also of known age) was born. Thus ego's age is age of A plus the age of person B. By the end of this process the ages of 97 individuals out of 443 were either known or estimated. With these 97 individuals as anchors, the ages of the ranked individuals were established by mapping them on a fifth-order polynomial regression, using relative age as the independent variable and age of the known individuals as the dependent variable.

While this is certainly an elaborate and more robust method compared to previous methodologies there remain significant limitations. For instance, the use of the age chain is problematic due to the uncertainty associated with an individual's age at the time of another person's birth (Diekmann et al. n.d.). Each of these small errors accumulate and amplify along the age chain. Hill and Hurtado (1996: 127) find a mismatch between actual and estimated ages to be +0.52 ± 1.2 years. Thus in the age chain method ages may have been overestimated by a half a year each 12.5 years (the average age of person A in the age chain). As a result, the oldest individuals may be around two years older than estimated. This results in a deviation between +6.8 and -2.8 once the level of error is factored into the analysis.

However, Hill and Hurtado (1996) only used point estimates that do not account for this uncertainty in age estimates.

We used a new statistical methodology, developed and conducted by Yoan Diekmann, Pascale Gerbault and Mark Thomas (paper in preparation) and data collection methodology (developed by the hunter-gatherer team), employing a Gibbs sampling Markov chain Monte Carlo (MCMC) algorithm that avoids these shortcomings. Unlike Hill and Hurtado's (1996) method, this approach takes the inherent uncertainty of age estimates into account, as well as age-rank structures among individuals and produces a distribution of possible ages as an output for each individual. This approach produces a more accurate age point estimate than regression-based approaches. The initial age range or distribution can be chosen to reflect the level of confidence in the *a priori* estimate. For example, if an individual's birthday is known with certainty (e.g. when a birth certificate is available[6]) one can assume a point mass as the initial distribution, while wider *a priori* distributions may be chosen for age estimates solely based on physical appearance. Additionally, this method does not require age 'anchors' of known or estimated ages to produce age estimates for all individuals in a population. This is particularly useful in populations where absolute ages for all or most individuals are not known, as an age distribution will still be produced for each individual, and can be sampled in a Monte Carlo fashion for downstream analyses.

4.5.1 Methodology of aging

In the field, for infants and younger children we established birth years and seasons as much as possible. When collecting reproductive histories, we noted birth order of all children and asked mothers to approximate the gap between these children. Thus, at the family level we knew the exact age of the youngest child, particularly if it had been born during our fieldwork, and then the order of the remaining children. Furthermore, during anthropometric data collection we took the teeth age of children under 13 years of age. This meant that we would have an age bracket to place each child in. We then placed all individuals into age groups (0-2 years; 2-5 years; 5-10 years; 10-15 years; 15-25 years; 25-45 years and 45 + years) based on the above information sources. As we had photos of each of the individuals in each age group, we printed these out to conduct a pile sort. Each individual

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[6] Some birth certificates, particular of older individuals were issued many years after birth. Therefore, we have distinguished between 'known' dates of birth and approximated ones. This is possible using the MCMC method.

was asked to sort out their own age group according to age, starting with themselves. Therefore, they were first presented with their own picture. Next they were shown a picture of individual A, and asked are they older or younger than you? Or do you not know them well to know their relative age? This process continued until all individuals had been allocated a relative rank. Then the individual would be asked to do this for the age group one older and one younger themselves. For the young age groups (0-2 and 2-5 years) mothers and teenagers were asked to conduct the aging, since younger children were not capable of relatively aging individuals. Thus, at the end of this process, we had multiple relative age lists for each age category.

After we had the age ranks, each individual was given an age bracket based on the additional information we collected in the field (such as teeth or estimated ages). This bracket was smaller for children, or larger for older adults as there is little by which to anchor their age (i.e. the difference between 70 and 80 is difficult to ascertain). A screening procedure was then developed to check the accuracy for each of the age ranks. Firstly, given the age brackets developed, were any individuals placed in the wrong order (i.e. if person A has an age 3-5 years, yet has been placed as older than person B who is between 6-9 years). Secondly, using known birth orders, checking whether siblings are placed in the wrong order in their age ranks. Any inconsistencies were then removed from the age rank. After this first trimming stage, each individual's age ranks were collated. For instance, if one individual had ranked their group as ABC, and another had ranked the group as BCD, this would be merged into ABCD. At this point, the MCMC algorithm was used to allocate ages, based on a probabilistic framework. The Gibbs sampler approach significantly reduces the difference between the known and estimated ages compared to the regression methods (0.94), compared to third-order polynomial regression (2.37) used by Blurton Jones *et al.* (1992), or the fifth-order polynomial regression (2.33) used by Hill and Hurtado (1996). Therefore the MCMC method is a significant and large improvement on all previous methods of aging in hunter-gatherer populations.

4.6 Health survey

As part of my research, I conducted a health survey with 420 individuals in our sample. This entailed more traditional assessment of nutritional condition using anthropometrics, as well as recent medical history, faecal analysis for intestinal helminths and blood tests for iron-deficient anaemia and white blood cell composition to examine the types of pathogens the

Agta face. To organise this data collection, I worked in close collaboration with the Palanan field hospital and Rural Health Unit. I would each week go to one of the Agta camps with two field assistants and one trained health care assistant from the Rural Health Unit to collect the health data and conduct medical tests. I would then return to Palanan town with the samples and test results for diagnosis by the doctor and to collect all relevant medicines (primarily for helminth infections and iron deficiency) and get these to the relevant participants. Individuals with suspected TB or medical conditions which required antibiotics or further treatment (primarily respiratory conditions or gastro-intestinal disorders) were taken to the hospital and made sure they received all medical treatment. Treatment was given as we (Andrea and I) felt it was one of the immediate impacts that our research could have on the Agta which they would be able to witness. I fully acknowledge that it is highly likely that, without removing the underlying causes of high helminth load, for instance, it is extremely likely that all the children treated become re-infected. Therefore, any benefits are short lived. However, regardless I do believe it is important for the Agta to understand that research should be done with their interests at heart, rather than extractive. Consequentially, our future research proposal approach important applied questions in the Agta's lives, primarily focused on empowerment and access to medical services. To initiate this process, at the end of the fieldwork, I was awarded funds from the UCL Beacon Bursary to conduct a health and medical care awareness workshop with the Agta and medical providers.

4.6.1 Anthropometrics

The anthropometric measurements were conducted according to standards developed by Food and Nutrition Technical Assistance (FANTA, Cogill 2003) using a Harpenden anthropometer. Height was measured to the nearest 0.1mm. Ensuring the subject was standing upright, with a straight back without shoes. Weight was taken to the nearest 0.1 kg on bathroom scales, used on a hard, flat surface with subjects wearing light clothing. Since anthropometrics have wide inter-observer reliability all anthropometrics used in this research (conducted during 2014) were done by one researcher (myself).

4.6.2 Medical Questionnaire

I conducted a medical questionnaire to quantify symptom history over the past two weeks as well as any longer illness such as TB. These questions were developed with the assistance of medical doctors at the Palanan Station Hospital, with reference to the World Health Organisation and Médecins Sans Frontières book, *Clinical Guidelines: Diagnosis and Treatment Manual* (Broek *et al.* 2013). The questionnaire was broken down into a few sections: gastro-intestinal disease, influenza and fevers, respiratory tract infections, intestinal parasite symptoms, skin conditions, malnutrition and physical status, and finally, questions relating to medical care, frequency of access and cost. The questions for each of these conditions specifically focused on key diagnostic symptoms, such as a long-term wet cough (TB), cyclical fevers (malaria) or an itchy anus (helminths). I would also enquire how severe or common the symptoms were, and whether the individual had sought any medical attention for them. The questionnaire was conducted with a qualified health care assistant (Ata Rosie, Figure 4.4). The completed questionnaire was then handed back to the doctor along with the blood test results for diagnosis.

Figure 4.4: Conducting medical questionnaires.

4.6.3 Blood composition analysis

Blood composition analysis was conducted as a proxy for examining the different types of disease pressures the Agta face. I looked at haemoglobin concentrations to examine both nutritional condition. The methodology and rationale behind this approach is discussed below.

Figure 4.5: Collection of blood samples for haemoglobin count.

4.6.4 Blood Collection Protocol

The standard protocol for blood collection is as follows. A blood sample, obtained by a Haemolance Normal Flow lancet, of approximately 10 µL was drawn into the cavity of the specially designed microcuvette by capillary action. Following best procedure, blood was always taken from the end of the middle or ring finger on the right hand (Morris *et al.* 1999, Figure 3.6). The first two or three drops were wiped away. Clotted samples were discarded, and the sample was always taken within one minute prior to analysis. If multiple samples were required (due to a lost sample, clotting or lack of flow) a different finger was used each time. If blood flow clotted before this was possible, a second prick was made on a different finger. The blood flow was never encouraged by squeezing due to the altering effect this has on the blood sample (Morris *et al.* 1999). The microcuvette was then placed into each analyzer. The Hb 301 (device name for analysis) displays its results within 10 - 20 seconds by measuring the absorbance of the whole blood at an Hb/Hb02 isobestic point. All filled microcurvettes were collected alongside any other medical waste and returned with sample samples for further testing to the hospital for disposal.

4.6.4.1 Haemoglobin

Haemoglobin is an iron-based component of red blood cells, which binds oxygen, helping the red blood cells to transport oxygen from the lungs to the rest of the body (Mitaishvili 2010). There is a wide normal range of haemoglobin levels for men, women and children, which are subject to daily variation. However, haemoglobin values below 130 g/L for males, 120 g/L for females and ≤ 110 g/L children aged are considered anaemic. Haemoglobin analysis was conducted on HemoCue® Hb 301 for 345 individuals older than three months. The Hb 301 system is calibrated against the hemiglobincyanide (HiCN) method, the international reference method for the determination of the haemoglobin concentration in blood. The measuring range of the Hb 301 is 0-25.6 g/dl.

While comparative studies have found the Hb 301 system to have remarkably accuracy and precision (HemoCue 2014) Morris and colleagues (1999) discuss the problems of reliability in association with samples taken from the left or right hand (correlation of variation of 6.3%) and measurements taken on four consecutive days (7% correlation of variation). There is significant indication that this within-subject variability arises from *(i)* not consistently using the same finger, *(ii)* incorrect handling of the finger, i.e. 'milking' leading to contamination with extracellular fluid (Morris *et al.* 1999), *(iii)* incorrect filling of microuvettes and *(iv)* the presence of air bubbles (Tatsumi *et al.* 2002; Muñoz *et al.* 2005). These factors result in significant alterations to the reliability of correlation coefficients between researchers (Neville 1987), and inconsistent results (Rippmann *et al.* 1997; Agarwal & Heinz 1992). However, the reliability can be greatly reduced by reducing operator error with proper training, standardized procedures and consistency (Morris *et al.* 1999; Neville 1987; Agarwal & Heinz 1992; Rippmann *et al.* 1997; Tatsumi *et al.* 2002; Briggs *et al.* 2012; Srivastava *et al.* 2014).

As a portable, battery operated machine, which is easy to use, the HemoCue system remains optimal particularly for fieldwork over large, remote areas without adequate laboratory facilities (Srivastava *et al.* 2014; Sari *et al.* 2001; Akhtar *et al.* 2008). Furthermore, the majority of studies have found the HemoCue system to have remarkable precision, accuracy and sensitivity in both adults and children (Sari *et al.* 2001; Akhtar *et al.* 2008; Srivastava *et al.* 2014; von Schenck *et al.* 1986; Rechner *et al.* 2002; Medina Lara 2005; Rosenblit *et al.* 1999; Hudson-Thomas *et al.* 1994; Teli *et al.* 2002; Kim *et al.* 2013; Morris *et al.* 1999; Gwetu *et al.*

2014; Hinds *et al.* 2007; Spielmann *et al.* 2012; Neufeld *et al.* 2002; Sanchis-Gomar *et al.* 2013). While studies with less supportive results do exist (Bhaskaram *et al.* 2003; Saxena & Malik 2003; Neufeld *et al.* 2002; Neville 1987; Seguin *et al.* 2011), such as differences between capillary and venous samples (capillary samples generally being less accurate than venous ones (Shahshahani *et al.* 2013; Mills & Meadows 1989; Srivastava *et al.* 2014)), it is argued that these differences are not clinically relevant if correct, standardized procedures are used (Schalk *et al.* 2007; Radtke *et al.* 2005; Tatsumi *et al.* 2002; Muñoz *et al.* 2005). Furthermore, the majority of recent systematic reviews on the reliability, accuracy and precision of the HemoCue Hb technique find the majority of work to be in support of this method of assessment of anaemia, particular in rural resource poor settings in the developing world (Gwetu *et al.* 2014; Sanchis-Gomar *et al.* 2013; Srivastava *et al.* 2014; Akhtar *et al.* 2008).

4.7 Statistical Analysis

All chapter-specific forms of analysis are discussed in-depth within the relevant chapter. However, since I use reproductive residuals, multilevel models and the same modelling procedure throughout this thesis these are discussed below.

4.7.1 Fertility, mortality and reproductive success residuals

To examine fertility and survivorship to age 16 the non-linear effect of age needed to be eliminated. To create age-specific fertility and survivorship to age 16 I used the residuals from a polynomial regression between fertility (all live births), survivorship to age 16 (my proxy for reproductive success) and child mortality. All models were run with a Poisson distribution due to the discrete nature of the data. The polynomial regressions for reproductive success and fertility were fitted with three degrees while mortality has fitted to two degrees to compromise increasing complexity, and thus better accuracy, of the fitted model with the significance of the coefficients (residual models results shown in Table 4.2).

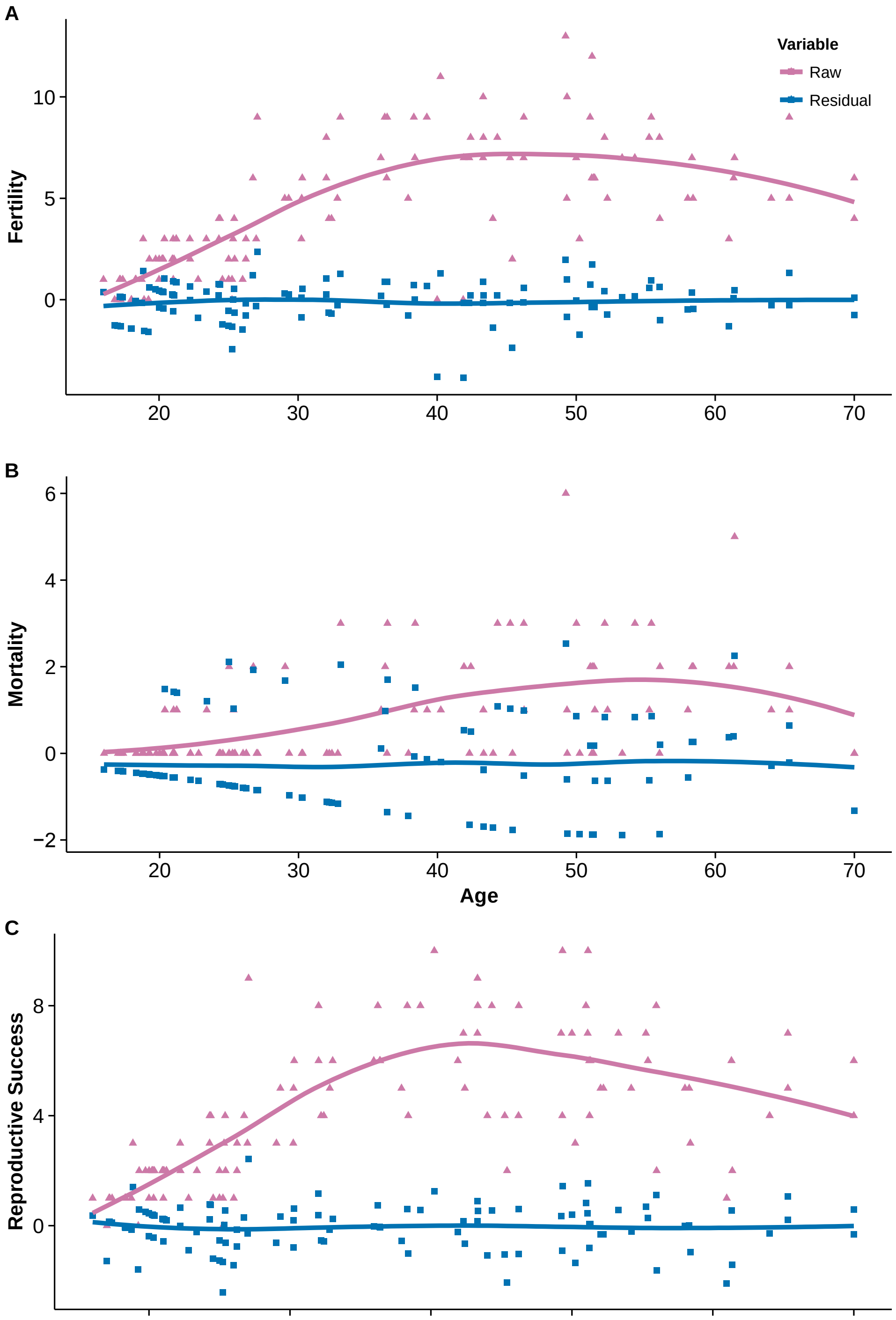

Figure 4.6: Relationship between age and A) fertility, B) maternal child mortality and C) reproductive success. The pink line represents the raw data and its relationship with age. The blue line is the age-specific residual age controlling for age using a polynomial regression with a Poisson distribution.

By using each mother's residuals from this analysis I can examine how high or low their fertility is, given their age. Thus, an age-specific fertility residual of 0 represents the average fertility of the sample of that given age, negative values are below average fertility while positive residuals are above average. These residuals had no significant relationship with age and its quadratic term ($p = 1$ in all cases) after this transformation. Thus, these residuals are used in all final analysis and no longer present a significant relationship with age (Figure 4.6).

Table 4.2: Results from polynomial regression (with Poisson distribution) between age and fertility, $n = 117$.

Model	**Degree**	**Coefficient**	***p***
Fertility	1	0.4370	0.0000
	2	-0.0083	0.0001
	3	0.0000	0.0025
Mortality	1	0.2537	0.0000
	2	-0.0024	0.0001
RS	1	0.4471	0.0000
	2	-0.0087	0.0002
	3	0.0001	0.0031

While a common method, the use of residuals to control the effect of a known relationship has been critiqued within ecology as it can result in parameter bias (Freckleton 2002; Darlington & Smulders 2001). When two independent variables are correlated multicollinearity can occur, which is usually picked up with variance inflation factor (VIF) during model checking. However, once the effect of the confounding variable (here age) has been removed from the dependent variable (measure of fertility) if there is a relationship between age and the predictor variable then the collinearity may occur which is ignored by VIF and thus inflated variance may lead to biased slope estimates. Nonetheless, when hypothesis testing the bias is normally conservative when independent variables are correlated. Thus, significant results are commonly unaltered, however false negatives are a particular concern (Darlington & Smulders 2001). Given these avenues to error, running a multivariate regression would be a simpler approach. However, in the relevant chapter I have used residuals due to the small sample size ($n = 38$). To control for the effect of age completely on measures of fertility a third order polynomial is required, therefore, if this is to be included within any analysis directly it significantly reduces the power, increasing the likelihood of a type II error. As a result, within the relevant chapter (8) I will detail how the residual model is a better fit in multiple domains and how this critique of residual analysis does not undermine the key research findings.

4.7.2 Kin categories

Throughout this thesis I use three different kin categories: close kin, distant kin and non-kin. Close kin refers to all individuals who are related $r > 0.25$, thus includes parents and siblings. Distant kin ($0.125 \leq r \leq 0.25$) includes grandparents, half siblings, aunts and uncles and first cousins. Non-kin ($r < 0.125$) subsumes both distantly related individuals (first cousins once removed and double second, second, third and fourth cousins) as well as individuals completely unrelated. Distant cousins accounted for 29.6% of the non-kin sample (50% of which share coefficients of $r < 0.031$). This division has been made since in family histories individuals could rarely trace genealogical relationships beyond grandparents and their immediate siblings and cousins.

4.7.3 Definition of children, adults, carers and dependents

I have consistently established the cut-off between dependent children who require the receipt of some allocare after 11 years. While children are nowhere near net producers at this age, they no longer are fully dependent on adult care. From our own observations, from the age of 12 juveniles are free to travel between camps and do not receive any particular 'caring' attention from adults. Such patterns are common among hunter-gatherers in which older children experience significant freedoms (Konner 2005; Kramer 2005; Kramer 2002; Peterson 1978). Furthermore, I draw a line between younger and older children within the under 12 category. Before the age of 6 children are fully dependent on other individuals, be that mothers, siblings or older children in playgroups. They are not capable of providing care to younger children. However, between the ages of 6 – 12 years' children can be defined as both dependents and carers. It is not uncommon for a six or seven-year-old child to carry a younger sibling around in a playgroup, which is often overseen by one to two teenagers. As a result, while younger children's childcare requires additional supervision, it should not be ignored. Thus, when exploring cooperative breeding I consider all proximity care received by children aged under 12 years. These children can be cared for by a child over the age of 6 if they are younger than that child: i.e. a six-year-old can provide care for a three-year-old while a six year old cannot provide allocare to a nine year old.

4.7.4 Multilevel models

As the Agta are hierarchically nested (individuals within households residing in camps) logistic and linear multi-level models (MLM) were used to avoid problems of non-independence. MLM distributes the response variance into each of the levels. These levels are the 'random-effects' entered into each model (Koster *et al.*, 2015; LEMMA, 2015). All models were originally run with level 1 as the individual, level 2 as the household and level 3 as the camp. Levels that failed to improve the model were removed to produce the most parsimonious model.

Due to the levels in MLM, an additional concern is sample size at each cluster of the analysis; while one may have many level 1 observations (for instance, here in one analysis I have 2,045 observations), levels 2 and 3 are necessarily significantly reduced in a hierarchical structure (here reducing to six camps in analysis based on the motes data). Some have argued for setting a role of thumb of a minimum of ten observations at each level of the analysis (Maas & Hox 2005). However, such specifications are difficult to adhere to, particularly in hunter-gatherer studies where population sizes are often small. Nonetheless, how problematic small sample sizes are depends on the research objective of the analysis and the parameter being tested (Snijders 2005; Bell *et al.* 2010). Here, I am primarily interested in the predictive value of fixed effects and regression coefficients which are distributed across multiple levels to account of the non-independence of observations rather than the variance distribution of the random effects *per se.* A small sample size (as small as two level-2 units) in one of the levels can result in biased random effect variance estimates (Clarke & Wheaton 2007; Bell *et al.* 2010). However, studies have consistently showed little or no bias to the estimates of fixed effects, which is of interest here (Clarke & Wheaton 2007; Maas & Hox 2005; Bell *et al.* 2010; Gelman 2006). In chapter 8 it is level one which is primarily of interest (i.e. maternal centrality) while in chapter 5 it is level one, two and three which is of interest (i.e. the dyad, the giver and the receiver), all of which have larger sample sizes (ranging from $n = 39$ to $n = 2{,}045$). Thus, it is these sample sizes which are of main importance; the other cluster sizes (i.e. $n = 6$ in level 2, 3 or 4 depending on the analysis) are not as important for the power of such tests (Snijders 2005). Smaller sample sizes at higher levels may result in the computed variance of 0, however given that regressions without levels are simply models without a group-level variance (i.e. variance pre-set at 0) then having the ability to attribute some variance due to non-independent clustering is preferable (LEMMA 2015). As a result, I retained the camp as a level in the multilevel models to capture the nested nature of the sample.

The relative explanatory value of random effects is established using variance partition coefficients (VPC); a VPC is calculated by dividing the variance of one level by the sum of all other variance components. 'Fixed-effects' are then entered into this base model (referred to as intercept-only), which includes all predictive variables of interest. To produce an estimation of variance reduction with the inclusion of fixed-effects (i.e. the predictors) I followed the procedure cited by (Koster *et al.*, 2015; LEMMA, 2015). This procedure allows for an estimation of the percentage reduction in the unexplained variance at each level by the inclusion of a predictor variable. To establish this figure an intercept-only model is produced which contains only random-effects (i.e. the levels). The residual variance in this model is used as the baseline to examine how much residual is reduced once fixed-effects are included by removing the new residual figure from the intercept-only figure and dividing this by the original figure (see Koster *et al.*, (2015) for a fuller discussion). This figure can then be compared to the variance explained by the control only model to compute how much of the variance the measure independently accounts for. As a result, VPC provide insight into the influence of fixed-effects has on the overall variance in the dependent variable (Koster *et al.* 2015). Variance explained figures are reported in the main results tables (labelled as VAR or variance reduction).

4.7.5 AIC

Only theoretically interesting variables are included in each set of models as well as controls known and/or suspected to confound relationships. As a result, no variables are systematically removed from the model (i.e. stepwise model fitting) to increase model precision. Rather an information theoretical (IT) approach is relied on to establish the 'best fit' model. IT approaches favour models that have the most explanatory value without being overly complex (i.e. containing many parameters (Burnham & Anderson 2004)). One measure of this is Akaike's Information Criterion (AIC), which estimates the distance of the model from the data weighted according to the complexity of the model. Models with too many parameters which do not significantly reduce the distance between the model and data are penalised with a higher AIC score (Burnham & Anderson 2004). The AIC value in and of itself means very little; howeve it is useful for model selection as it allows for relative comparison between models to see which fall closest to the data. Burnham and Anderson (2004) state the common threshold that models with AIC scores 2.0 lower that others are considered the 'best-fit', a threshold I follow here. While I do not conduct any systematic model selection, I do present a 'best-fit' model to justify additional complexity with the inclusion of interactions as well as when comparing different sets of predictors.

4.7.6 Software

All statistical analysis was conducted on R version 3.1.2 (R Core Team, 2014) using the following packages:

- Multilevel modelling in lme4 (Bates *et al*. 2013)
- Social network analysis in igraph (Csardi 2015) and CePa (Gu 2012)
- Genealogical analysis and coefficient of relatedness in pedigree (Coster 2012) and kinship2 (Therneau *et al*. 2015).
- Data manipulation in plyr (Wickham 2011)
- Variance inflation factor in car (Fox and Weisberg 2011)
- Plotting in ggplot2 (Wickham 2009) and cowplot (Wilke & Wickham 2015)

Chapter five

Proximity as a measure of allocare?

5.1 What is allocare and why is proximity important?

In the introduction to this thesis I defined allocare as childcare from any individual other than the mother. Previous studies, particularly in small-scale societies have focused of 'high-quality' forms of childcare such as carrying (Crittenden & Marlowe 2008; Kramer 2010), grooming and medical treatment (Scelza 2009). These are active tasks directly focused on a singular child. However, as the ultimate function of allocare is to reduce maternal workload, allowing her to reinvest energy into other children, herself (and as a consequence her fertility) or provide higher quality childcare, then the definition of allocare cannot be limited to high-quality investment. Meehan and colleagues (Meehan et al. 2013a; Meehan 2005) discuss this topic at length, arguing that sole focus on high-investing caretakers (juveniles carrying siblings, for instance) effectively ignores allocarers who engage in passive childcare (proximity, touching and watching). While these activities do not take a significant among of effort or attention, individuals who are watching or proximate to younger children are those who intervene and respond to a child when specific situations arise (Meehan 2005; Ivey 2000). Therefore, the presence of such low-investing allocarers still means that mothers are able to re-focus time and energy into other activities, such as domestic tasks, looking after another child or increasing somatic maintenance, promoting increased fertility. As a result, it is important to capture 'proximity' or the ability to invest within the measure of allocare.

Certainly measures of proximity have been used to denote important social interactions in both humans and non-human primates (Flack *et al.* 2006; Brent *et al.* 2011; Isella *et al.* 2011; Powell *et al.* 2009). However, it remains important to quantify what proximity is in the Agta childcare context as the results in the following chapters are based solely on the mote data, which represents interactions at approximately three meters. As this is an innovative application of remote sensing technologies in human populations it requires validation and ground-proofing. Furthermore, understanding what types of interactions are captured within three-meter proximity has important implications for interpreting the results described in chapters 6, 7 and 8.

Consequentially, this chapter has two aims: firstly, to directly validate the motes results I will compare the proportion of interactions with different kin over the same time period with the motes and the childcare observations (as described in the methodological chapter 4). Secondly, this chapter seeks to describe what proximity means for different kin types (separated into close, distant and non-kin in keeping with the following results chapters) and by life stage (juvenile, adult and post-reproductive adult) using observational data from 20 infants (aged less than two years) and 20 toddlers (aged two to five years). These descriptive analyses will demonstrate that: *(i)* data from the motes and observations of proximity at three-meters closely map on to each other, validating the motes as a method of capturing close proximity interactions; *(ii)* allocarers are *only* in proximity at three meters and not engaging with any other caring activities for 15.6% of interactions with children and 15.9% of interactions with infants, but this is dependent on the age of relatedness of the allocarer; *(iii)* juvenile allocarers are most frequently playing or in playgroups with dependent children, and as a result least often *only* proximate at three meters; and *(iv)* overall 'active' norms of childcare are not common beyond infancy, passive forms of childcare which can be directed at multiple children (play, talk, sit next to, touch) dominate. As result of these findings this chapter concludes that motes capture a meaningful measures of proximity, which commonly denotes a low-cost form of childcare, including only being in proximity which is an important form of allocare that is commonly ignored.

5.2 Are the motes capturing proximity at three meters?

To establish whether or not the motes were, in fact, recording proximity at approximately three meters I compared the motes data for five toddlers I had simultaneously conducted focal follows on. While children were not always wearing the motes when we conducted focal follows there was a significant amount of overlap. However, the motes collected data other more days (five to seven) compared to the observations which were over three days (of which only three hours were sampled). As a result, there is a slight difference in sampling, however the time period is the same and as a consequence, if the motes are to accurate reflect behaviours then the general trends should remain similar. Therefore, we can examine if the observers recorded interactions with different individuals at three meters' overlaps which the messages stored in the motes. To compare the results both sets of data were transformed into the proportion of the child's interactions (i.e. a child spent 50% of time with their mother, 25% of time with their father and so forth). However, these proportions do not sum up to one since children can be with more than one individual at any one observation point.

Means were produced for the proportion of time five children spent with specific kin categories based on the motes and observational data. The differences between the two datasets are minimal, and the distribution of observations with specific kin types is not significantly altered between the two methods (Table 5.1). For instance, the motes recorded that children spent on average 34 ± 26% of time with mothers, 11 ± 5% of time with fathers, 24 ± 13% of time with siblings and 6 ± 6%, 7 ± 7% and 23 ± 13% for grandparents, distant kin ($r \leq 0.25$ and ≥ 0.125) and non-kin ($r < 0.125$), respectively. These same toddlers were observed to spend 37 ± 26% of time within three-meters of their mothers, 19 ± 19% with fathers, 24 ± 19 % with siblings and 2 ± 1%, 7 ± 8% and 24 ± 20% of their time with grandparents, other kin and non-kin, respectively (Figure 5.1). Therefore, the two types of data collection produce remarkably consistent and similar pictures of proximity at three meters. The main differences are between fathers and grandparents between the two methods of data collection, however this is likely the product of the difference in time sample. Both fathers and grandparents are not consistently around camp to interact with children. For instance, fathers leave camp regularly for a two or three-day fishing trip, while grandparents go visiting other places they live or visit other camps. Therefore, the slight differences in means may be a product of the shorter sampling period (only nine hours, a major limitation of observational data) of the focal follows. Overall, the consistency between the observational and motes data leads me to conclude motes have a high reliability and represent proximity at approximately three meters.

Table 5.1: Proportion of time toddlers spent with any given kin category for motes and focal observations. GP refers to grandparents. Non-kin are all individuals related less than $r = 0.125$, and distant kin between 0.25 and 0.125. Categories that include multiple individuals (such as GP, siblings, other and non-kin) are summed across category, thus toddlers spend 23% of time with all non-kin, and however, on average they spend only 2% of their time with any given non-kin individual.

	Motes	**Focals**
Mother	0.34	0.37
Father	0.11	0.19
GP	0.06	0.02
Siblings	0.24	0.24
Distant kin	0.07	0.08
Non-kin	0.23	0.24

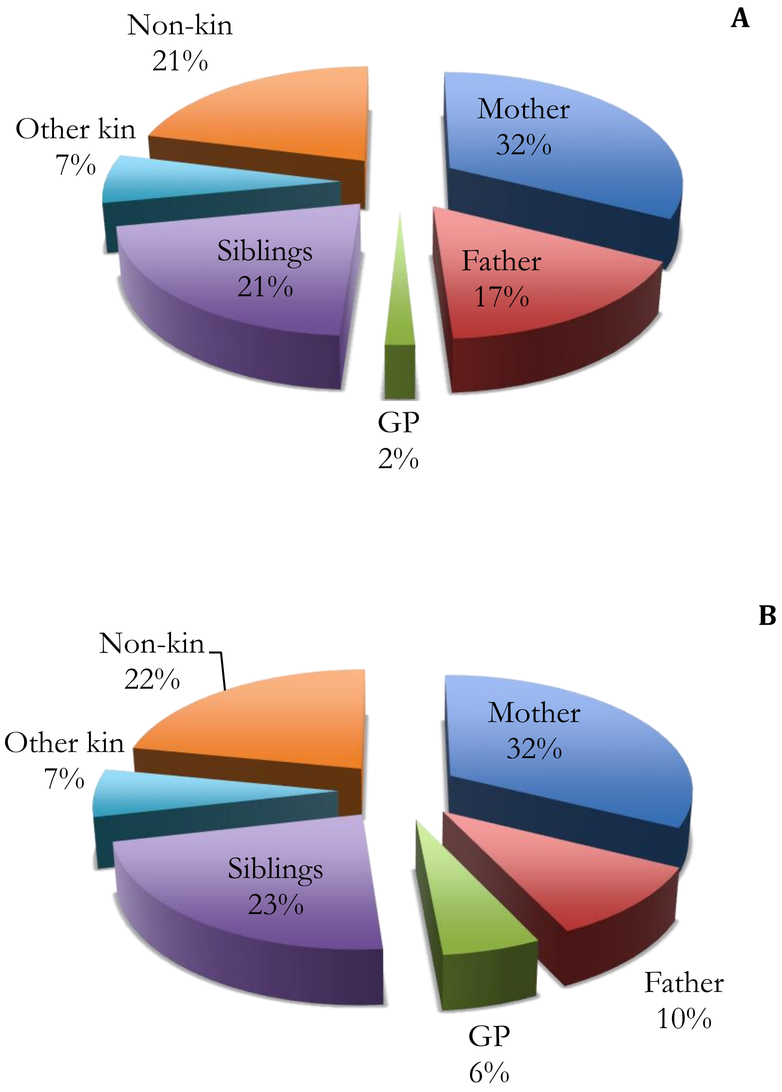

Figure 5.1: Proportion of time toddlers spent with different kin categories for data collected by (A) focal observations and (B) motes. GP represents grandparents.

5.3 What happens at three meters' proximity?

To explore what types of behaviours are captured ay three meters' proximity for close kin, distant kin and non-kin at different life stages I took a sub-sample of the focal follows for each of the six camps the motes experiment was conducted in. This sub-sample included 20 infants aged under two years and 20 toddlers aged two to five years, and represents halve of the total sample of focal follows we conducted. The original observations were coded according to whether the allocarer was close, distant or non-kin as well as whether they were juvenile (aged 15 or under), adult (aged 16 to 50) or post-reproductive adult (aged 50 and above). For each of these groups I established the total number of interactions ever recorded at three meters (ranging between 45,659 interactions between 20 infants and close kin to 10,078 interactions between 20 children and distant kin), and from this worked out the proportion of which interactions fell under the following categories: high-investment, directed childcare separated into carry, hold and care ('care' comprises of feed, groom, provide medical attention and teach); less intensive investment separated in play, touch, talk, watch and playgroup (the separation of play and playgroup lies in the number of individuals involved, play captures a dyadic interaction focused on the child while playgroups capture the child's participation in a group where many individuals interact to a lesser degree); and passive, undirected activities including *only* (i.e. not being involved in any other activity while being proximate) being next to a child (conceptualised as being within touching distance but not touching) and proximity at three meters. Therefore, for each kin type and age group I have the proportion of interactions which were high-investment, low-investment and passive childcare, separated into infancy and toddlers as they represent significantly different periods in terms of who a child interacts with and the type of childcare they require. The results of this descriptive analysis are shown in Table 5.2, Figure 5.2 for infants and Table 5.3, Figure 5.3 for toddlers.

Table 5.2: Break down of activities occurring at three meters for 20 infants cared less than two years. 'Post' refers to post-reproductive adults.

	Allocarers separated by age group and kin type							
	Close kin		**Distant Kin**			**Non-kin**		
	Juvenile	Adult	Juvenile	Adult	Post	Juvenile	Adult	Post
Carry	0.057	0.199	0.015	0.010	0.044	0.014	0.057	0.054
Care	0.017	0.118	0.010	0.004	0.014	0.001	0.020	0.038
Play	0.059	0.028	0.050	0.017	0.020	0.038	0.016	0.036
Touch	0.103	0.308	0.069	0.031	0.091	0.033	0.076	0.131
Talk	0.227	0.062	0.197	0.122	0.215	0.369	0.301	0.172
Playgroup	0.124	0.000	0.073	0.000	0.000	0.099	0.004	0.000
Watch	0.003	0.006	0.003	0.004	0.020	0.002	0.000	0.018
Next to	0.292	0.181	0.390	0.458	0.463	0.314	0.340	0.311
3 meters	0.118	0.097	0.193	0.354	0.133	0.131	0.186	0.240

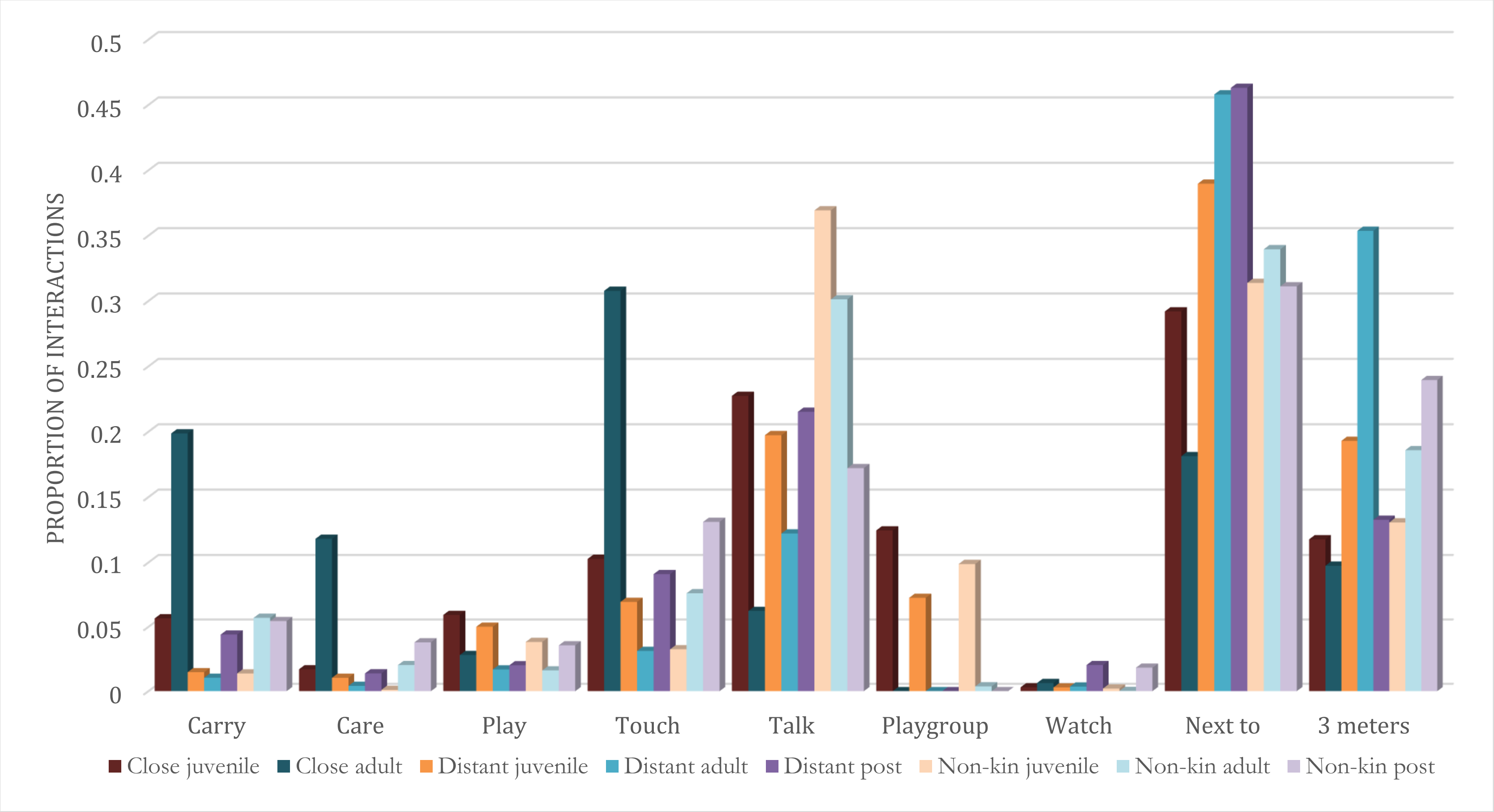

Figure 5.2: Proportion of interactions allocarers spent in different childcare activities with infants separated by juveniles (orange shades), adults (blue shades) and post-reproductive adults (purple shades) as well as close kin (darkest shades), distant kin (middle shades) and non-kin (lightest shades). Visualisation of data shown in Table 5.2.

Reviewing Table 5.2 and Figure 5.2 reveals several trends. Firstly, it appears that parents (close adult kin) provided the majority of high-investment forms of childcare, reaching 20% for carrying and 11.8% for caring activities. Nonetheless, parents appeared to spend the most amount of time simply touching an infant, suggesting active but low investment care. Juveniles of all kin types appeared to spend the most of their activities playing or in playgroups. Interestingly, there is little variability (expect parents) in the proportion of activities spent simply sitting next to an infant, and in fact it is most common among distantly related adults, a trend repeated in the proximity at three meters as distant kin adults spent 35.4% of interactions only in proximity to infants. However, the median percentage of only proximate interactions is 15.9% (mean = 18.1%, SD = 7.9%), the lowest amount found for parents (9.7%), which is comparable to proportion of activities spent talking to (6.2%) and caring for (11.8%) children. Overall then, while parents provided more active care, the majority of interactions with infants appears defined by lower-investment, passive activities.

Table 5.3: Break down of activities occurring at three meters for 20 toddlers age two to five years. 'Post' refers to post-reproductive adults.

	Allocarers separated by age group and kin type							
	Close kin		**Distant Kin**			**Non-kin**		
	Juvenile	Adult	Juvenile	Adult	Post	Juvenile	Adult	Post
Carry	0.001	0.018	0.004	0.001	0.021	0.008	0.000	0.002
Care	0.006	0.024	0.005	0.001	0.041	0.002	0.003	0.010
Play	0.135	0.024	0.123	0.021	0.013	0.173	0.016	0.004
Touch	0.026	0.124	0.035	0.009	0.181	0.060	0.010	0.015
Talk	0.195	0.175	0.169	0.146	0.097	0.184	0.337	0.203
Playgroup	0.250	0.010	0.309	0.040	0.000	0.326	0.016	0.000
Watch	0.000	0.013	0.000	0.001	0.009	0.005	0.014	0.028
Next to	0.274	0.457	0.260	0.624	0.393	0.147	0.321	0.244
3 meters	0.112	0.154	0.095	0.158	0.231	0.096	0.283	0.481

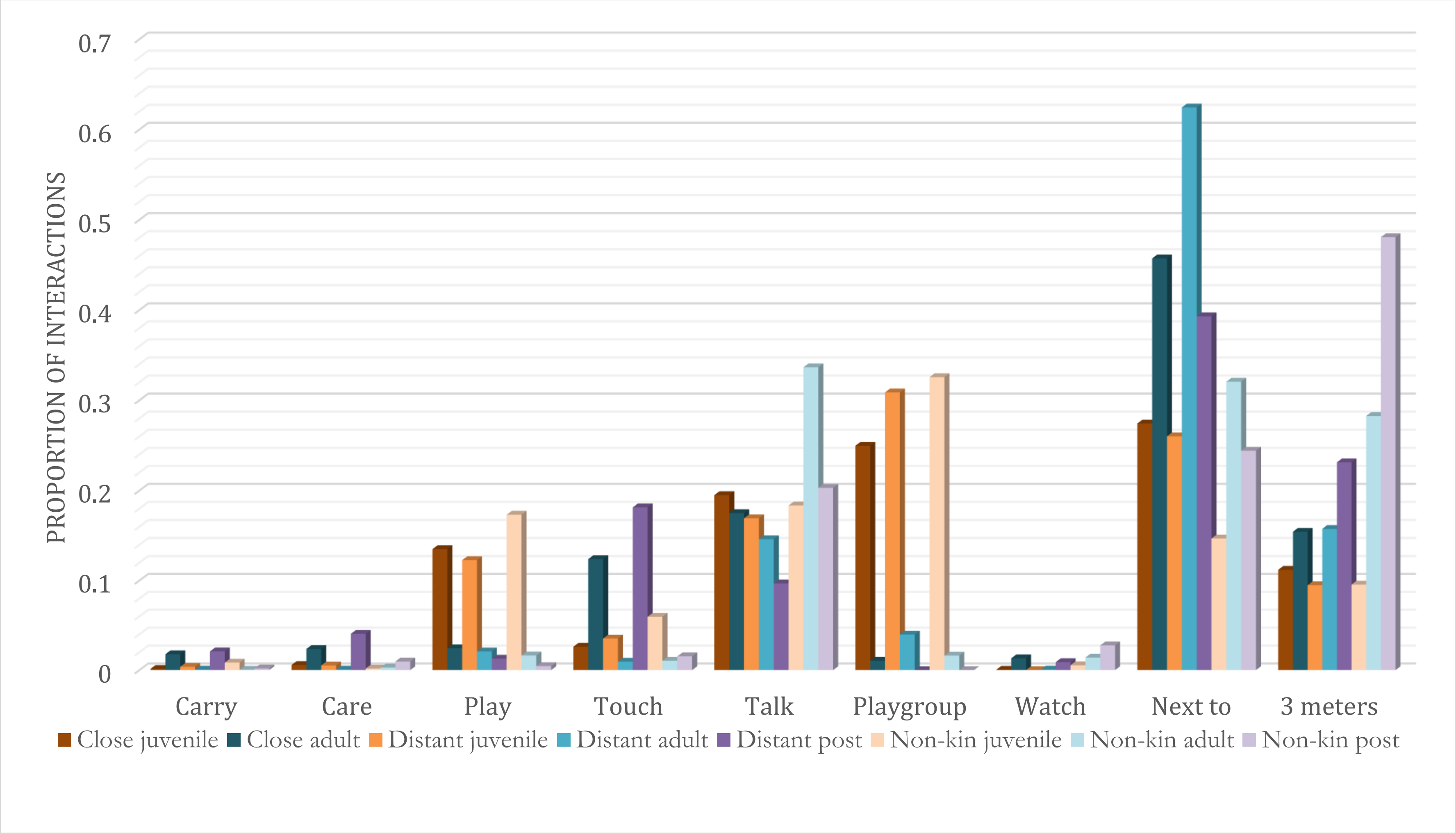

Figure 5.3: Proportion of interactions allocarers spent in different childcare activities with toddlers separated by juveniles (orange shades), adults (blue shades) and post-reproductive adults (purple shades) as well as close kin (darkest shades), distant kin (middle shades) and non-kin (lightest shades). Visualisation of data shown in Table 5.3

Examining Table 5.3 and Figure 5.3 revels several important tends about the nature of childcare in children aged two to five years. Firstly, in contrast to the results for infants, child carers only spend on average 0.9% (SD = 1%) of their activities in high-investment behaviours such as carrying, feeding or grooming. Consequently, the majority of childcare activities are lower investment activities which can be directed at multiple individuals. Similar to the trends in infants, juvenile allocarers provide the most play related care, peeking in playgroups at 32.6% of activities. Consequentially, being in a playgroup with a non-related child is the most common form of activity for non-kin juveniles when they are within three meters' proximity to that child. The second most common activity is talking to (18.4%) followed by playing (17.3% of activities). A similar pattern across all three domains (play, playgroup and talk) is repeated for close and distant kin juveniles. In terms of being next to a child this again seems most common for distant kin adults (62.4% of activities) followed by parents. In fact, the most common activity for parents within three meters is simply being within arms-reach of their child (45.7% of activities), suggesting that childcare after the age of two becomes very low-investment and passive even for the closest relatives. Post-reproductive non-kin adults spend the most of their activities only within three meters of children, capturing almost 50% of their activities (48.1%). This falls in line with my observations with the oldest individuals often remain in huts due to illness or disability while children (often in playgroups) play nearby. Juveniles of all kin types spend the least amount of activities only in proximity, being lowest for non-kin and distant kin (10% of activities). Overall, the median amount of activities for only proximity is 15.6% (mean = 20.1%. SD = 12.3%), therefore on average child takers are more frequently engaged in some 'intentional' childcare activities.

5.4 Discussion and Conclusions

These descriptive analyses have demonstrated that proximity at three meters captures a range of childcare behaviours which are commonly intentional while often being low-investment. As a result, being only in three-meter proximity with a child is not defining of Agta childcare. Nonetheless, we see that childcare among the Agta is defined by low-investment, less active childcare which care be provided to multiple children at the same time. Simply being next to a child captures a significant number of interactions, as does talking, touching and being in a playgroup. In contrast, beyond infant-parent interactions carrying and high-intensity caring activities are uncommon. As a result, capturing interactions such as touch, playgroup, talk or simply proximity is important as it makes up the majority of childcare in the Agta. Ignoring these aspects would remove a large number of a child's interactions with child takers. Unlike more westernised childhoods, it appears that the Agta mode of childcare cannot be defined by high-investment, high-quality childcare. Accordingly, while proximity at three meters is not excessively important, it is among some individuals such as post-reproductive non-kin in children or distant kin adults in infants, and this should not be ignored as a form of allocare regardless of the passiveness of the activity. Being only within proximity means that an individual is able to intervene and provide care when needed, which has been found to be the case among the Aka where individuals nearby children were the most responsive to their needs (Meehan 2005). Interactions with children are frequently sporadic while they are conducting other tasks or interacting with other children. As a result, individuals frequently move between proximity at three meters and play, and thus, proximity as measured by the motes is a robust proxy for capturing these types of interactions.

Importantly for the findings discussed in chapters 6 and 7 it seems that juvenile allocarers, particularly non-kin, are least frequently only in proximity of infants and children. They spent many more interactions in activities such as playgroups, playing and talking. This suggests that proximity for juveniles captures many meaningful interactions which constitute allocare. If, as I define here, allocare is any behaviour which has the ability to reduce maternal energetic burden then such activities as playgroups or simply being within arms-reach of a child are important means of doing so. Given the nature of childcare among the Agta in general, allocare cannot be assumed to be active, high-investment, high-quality activities such as feeding, grooming or teaching as these were relatively uncommon occurrence, especially outside of infancy.

If proximity, as measured by the motes, is an important form of allocare while also being a useful proxy for a range of low-investment activities, this means that the implementation of motes can be a useful methodological tool in research on childcare. Given that the majority of datasets on childcare constitute very small sample sizes collected over only 9 hours, the motes while only capturing proximity mean that the sample period of one week for more than 200 individuals is an important step for improving our understanding about the nature of childcare in hunter-gatherer societies.

Chapter six

The Behavioural Ecology of Communal Breeding: Who Cares for Agta Children?

The review in chapter 3 revealed different types of kin have been demonstrated to play important roles in childcare. Primarily focus has been placed on both grandmothers and juveniles as 'low-cost' helpers, while fathers have primarily been highlighted as food providers rather than allomothers. Hunter-gatherer studies however, reveal that grandmothers do not always interact a significant amount with their grandchildren and the results are mixed in relation to the role of siblings, fathers and more distantly related individuals. A limiting factor in observational studies in the past has been their sample size, making it difficult to examine trends. Here I explore the composition of childcare among the Agta using three-meter proximity data from the motes as a proxy for low investment childcare. With this innovative technology I have captured allocare relationships between 200 individuals during a full week at two-minute intervals. I examine not only infants, but also allocare received by all dependent children under the age of 12. In particular, I focus on the roles of grandmothers, juveniles and unrelated individuals to explore the composition of communal breeding among the Agta. I find that grandmothers were rarely co-resident and shared few interactions with their grandchildren. Revealing the importance of kin selection dependent on costs, however, was the fact that siblings offer significantly more care than grandmothers, as did fathers. Nonetheless, non-kin can also be considered significant allocarers as it is *only* proximity from non-kin that decreased maternal care, suggestive of a reduction in workload. This suggests that communal breeding cannot be explained by kin selection alone, opening the path to explore why individuals breed communally in chapter 7. These results have significant implications for our understanding of the role of grandmothering and the juvenile period, particularly in reference to human life history evolution.

6.1 Agta childcare

As with most hunter-gatherer populations the Agta style of childcare has been argued to be indulgent, affectionate and intensive; infants and toddlers are permanently held, cuddled or played with (Minter 2010: 67). The majority of childcare among the Palanan Agta is high intensity, which includes breastfeeding, carrying, playing, feeding and providing medical care. Younger Agta children are frequently looked after by various member of their families as well as spending a significant amount of time in mixed-aged play groups which form a type of *ad hoc* crèche (Konner 2005) in which care was provided by unrelated children. Griffin and Griffin (1992) sum up the situation perfectly:

> "*The baby remains against the body of the mother nearly constantly in its first weeks, but it is also in contact with the father, siblings if any, and other kin that may drop in to visit, nap or play…Grandparents may take in toddlers and older children on a "drop-in" basis or in the case of the parents overnight departure for hunting and fishing. During the first 12 months an infant is usually carried in a sling at the mother's back, side, or front…Nursed on demand, it is returned to the back for sleeping after suckling… An infant under 1 year may be passed among several adults and youths being returned to its mother if it becomes fussy*" (Griffin & Griffin 1992: 301).

Chapter 3 discussed the importance of communal breeding; without able helpers providing direct childcare and provisioning, foraging mothers would have to extend their economic and childcare activities to such a point that they could not sustain multiple dependent offspring at one time. Thus, we return to Lack's (1954) principle that the number of offspring is a product of both the mother's fertility and her ability to ensure dependents reach reproductive maturity. Ultimately then, it is of theoretical interest whether direct allocare significantly increases maternal reproductive success and how this occurs, a topic not yet explored among the Agta. Here my aim is to detail the nature of Agta childcare - focusing on the importance of grandmothers, juveniles and non-kin. Reviewing the current evidence stemming from observational studies in small-scale societies reveals some inconsistencies, arguably due, in part, to small-sample sizes and short observational times.

Observational studies are extremely labour intensive, and require one researcher to follow a focal child for a number of hours, recording observations at a set time interval. One extremely in-depth method of focal follows used by Meehan *et al.* (2013a) among the Aka foragers from central Africa, involves the researcher observing one child for nine hours over three days in four hour periods making observations each 20 seconds. The amount of detail captured by such a method is impressive, and it is possible to observe the complex dynamics of childcare as well as maternal activities and household tasks. However, it reduces the sample size as it takes a long time to observe a significant number of children (for instance, it took eight months to observe 80 Agta children with two researchers observing children six to nine hours a day). Sample sizes are often in the range of 10 – 20 in studies among the Efe, Aka and Martu (Ivey 2000; Meehan *et al.* 2013b; Scelza 2009), making variability (such as by age or sex) difficult to explore. Several studies with larger sample sizes rely on hourly instantaneous camp scans to observe a particular activity (Crittenden & Marlowe (2008) observed 68 Hadza children 13 times a day to quantify infant carrying) or self-reported childcare (Valeggia (2009) collected information of childcare behaviour from 200 Tabo adults), thus lack the same breadth and detail as the observational studies. Furthermore, given that older children are hard to follow or find, observational studies are often limited to infants and younger toddlers (approximately at 2.5 years), while Crittenden and Marlowe's (2008) focus on child carrying meant their sample contained children aged less than four years. As a result, the majority of what we know about allocare from small-scale societies is about who cares for infants, rather than the wider system of allocare for dependent children.

Overall, research of direct allocare is much more patchy than the investigation of indirect childcare (i.e. food provisioning), thus summaries are far from definitive. Nonetheless, bearing in mind the small sample sizes and focus on infants, it seems that grandmothers do not appear as important in hunter-gatherer societies compared to other small-scale societies, while care from fathers, siblings, extended family members and non-kin seems variable and understudied (Table 3.1 and references therein). As a result, this chapter has three interconnected aims: *(i)* to use high-resolution data for a larger sample of individuals than previously possible in observational studies in exploring *(ii)* who cares for Agta infants, toddlers *and* children aged less than 12 years and *(iii)* how this allocare substitutes maternal care, theoretically allowing her to invest additional energy into increases in child quality and/or quantity.

This chapter will proceed as follows: I will summarise the major predictions based on the review of the literature in chapter 3 and detail the specific methods used in this analysis. This will be followed by descriptive and inferential statistics about who looks after Agta children and how this care substitutes maternal and paternal care. The results will be summarised in a discussion of the relevance of this work to the existing literature, focusing on the role of grandmothers, juveniles and non-kin. Why individuals' provide allocare and the fitness consequences of this allocare is explored in chapters 7 and 8.

6.2 Hypothesis and Predictions

I hypothesised, following the extensive literature review in chapter 3, that allocare is an important means of childcare in the Agta, which will be explored by examining the nature of childcare (who interacts with children) and how this influences the number of maternal interactions with dependent offspring.

Kin selection predicts that individuals should provide allocare dependent on indirect fitness benefits weighted by degree of relatedness (rB) and the direct fitness cost of the cooperative action (C, Hamilton (1964)). As a result, closely related family members, such as juvenile siblings, are expected to provide a high proportion of care given that their relatedness is high and their costs are lower as they are currently not reproductively active (Kramer 2005). Thus, I predict that juvenile siblings will spend a significant proportion of time interacting with dependent children.

Grandparents are predicted to provide a significant proportion of childcare to their grandchildren given their 25% genetic similarity and completion of their reproductive lifespans. Following the grandmothering hypothesis, I expect being a grandmother significantly increases the number of interactions with a dependent child (Hawkes *et al.* 1997). This is predicted to be meditated by paternity certainty; maternal grandmothers are completely sure of their 25% genetic share in a grandchild, while this confidence decreases for both maternal grandfathers and paternal grandmothers, being lowest for paternal grandfathers (Danielsbacka *et al.* 2011). Thus, maternal grandmothers are expected to provide the most contact interactions with grandchildren, followed by maternal grandfathers, paternal grandmothers and finally paternal grandfathers. I expect extended family members (referred to throughout this thesis as distant kin when $r \leq 0.25$, thus including grandparents, aunts and uncles and cousins) to offer significantly less care than closer kin. However, childcare may also be motivated by reciprocity, particularly from less related individuals as indirect benefits are easily overtaken by direct returns when r is reduced (Axelrod & Hamilton 1981). Thus, non-kin are also expected to provide allocare.

Overall, if care of any type is to be beneficial to mothers it must reduce their workload. As a result, I predict that a child's contact with close kin, distant kin and non-kin to substitute maternal care, allowing the mother to re-invest energy into fertility and/or child survival resulting in increased fitness for the mother and indirect fitness for the allocarer.

6.3 Methods

The level of the analysis was the child (*n* = 81) and the dependent variable was the proportion of interactions different types of caregivers shared with a child. Children were defined as all dependents under the age of 12. Caregivers were separated into close family (mother, father, brothers and sisters), grandparents (separated by lineage), distant kin (cousins, uncles and aunts; $0.125 \leq r \leq 0.25$) and non-kin ($r < 0.125$). I conducted a two-sample Wilcoxon signed-rank test to compare if the proportion of interactions were significantly different between types of kin (i.e. grandmothers versus sisters). The non-parametric version of the t-test was used due to the data's non-normal distribution (established by Shapiro-Wilk tests, $p < 0.05$) and the non-independent nature of the data as mothers, siblings and grandparents are shared between some children. This analysis is followed by a multilevel model (MLM) which explored the relationship between care from allocarers (siblings, distant kin, grandparents and non-kin) on the number of interactions parents had with their children.

To bring my results into line with the cooperative breeding literature in hunter-gatherers in general I have presented the descriptive statistics as proportion of interactions. This variable was produced by establishing the total number of hours an allocarer was present in camp and dividing this by the number of actual interactions recorded between an allocarer and child. Consequentially, this figure represents how long an allocarer spent with a child as a proportion of *the allocarers* total time while in camp. This result is referred to as '*proportion of interactions'*. To keep data manipulation to the minimal for the inferential analysis (substitutive care) I used the number of interactions two individuals shared on average per hour of the motes experiment (to control for differences in experiment time in different camps) as the dependent variable. I refer to this variable throughout the analysis as *'number' or 'frequency' of interactions*. I use this latter variable for all future analysis.

Over six Agta camps (three being coastal camps, three inland) I conducted the motes experiment with 200 individuals (107 males). Of this sample, 81 were children under the age of 12 (49 males). The average age of the child sample was 5.2 ± 3.3 years (ranging from 0.2 – 11.5 years) while the average giver age was 25.6 ± 3.2 years. Children under 12 received on average 4,287 ± 1,687 mote messages over the course of the experiment from 148 allocarers, representing close proximity interactions (at three metres). However, this varied widely according to camp size, duration of the experiment and child age; range 448-8,128 messages. Children were almost always in the presence of several individuals and rarely left unattended while young or without friends and siblings when older. In total, I recorded 2,195 dyadic interactions, of which parents represented 6.8%, siblings 6.3%, grandparents 2.3%, distant kin 19.8% and non-kin 64.6% of said dyads. The average number of interactions between a dyad per hour was 1.2 ± 2.2 but ranged between 0 to 20.3 recorded messages. On average, carers spent 4.5% ± 8% of possible interactions with a dependent child, peaking at 52.0% for mothers with young infants.

6.4 Results: who cares and how much?

Figure 6.1 and Table 6.1 reveal that mothers were the single most important caregivers as they spent 30.9% of all possible interactions with their offspring. This significantly increased to 51.9% for infants less than 2.5 years old. Mothers were in close interaction with toddlers between 2.5 to 5 years and children over 5 years for 32.8% and 19% of the time, respectively. Paternal interactions with infants, toddlers and children were roughly half that of mothers, but nevertheless, paternal care diminished as offspring aged. Comparatively, sibling care remained more consistent throughout childhood and brothers spent 34.7% more time than sisters interacting with siblings (Wilcoxon test; V = 868, $p = 0.04$).

Table 6.1: Proportion of all possible interactions kin spent with children under 12 years. PGF refers to paternal grandfather; PGM: paternal grandmother; MGF: maternal grandfather; and MGM: maternal grandmother. Non-kin are all individuals related $r < 0.125$ (excluding any paternity uncertainty). Infants are aged under two years, toddlers from two to five years while children are aged 6 to 11 years inclusively.

	Kin type									
Age group	**Mother**	**Father**	**Sis**	**Bro**	**PGF**	**PGM**	**MGM**	**MGF**	**Other kin**	**Non-kin**
All	0.309	0.167	0.15	0.202	0.01	0.006	0.022	0.009	0.053	0.048
Infants	0.520	0.255	0.11	0.263	0.02	0.008	0.037	0.016	0.056	0.039
Toddler	0.328	0.157	0.16	0.210	0.01	0.001	0.032	0.007	0.042	0.040
Child	0.190	0.107	0.16	0.165	0.01	0.007	0.008	0.007	0.058	0.057

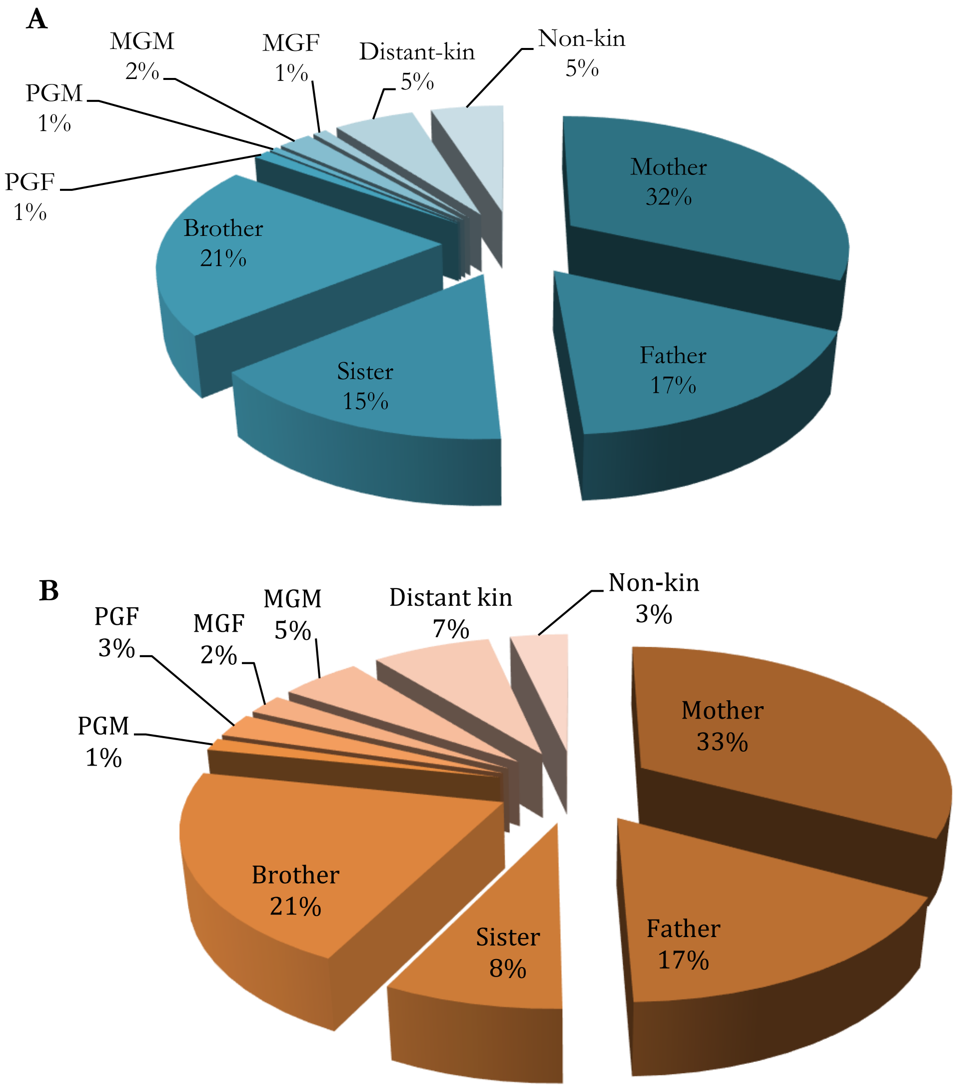

Figure 6.1: Pie chart of the mean proportion of interactions with different kin. A) Full sample ($n = 81$). Each of these proportions are significantly different from each other category at $p < 0.05$, except between fathers and sisters (Wilcoxon signed rank tests, V = 1339, $p = 0.6$), fathers and brothers (V = 1137, $p = 0.2$), MGM and PGM (V=128, $p = 0.2$) and PGF versus MGF (V = 181, $p = 0.9$). B) Reduced sample ($n = 34$) adjusting for grandparental presence. Includes children with grandparents present.

It is surprising that, on average, brothers interacted with siblings more than sisters, given that female juveniles are frequently expected to provide more allocare. However, this average is significantly influenced by an absence of sisters, particularly in households with infants and toddlers. This appears to be a product of the skewed sex ratio in the sample, therefore is reflective of which type of sibling is present rather than how much care is performed when they are present. In fact, being a female juvenile compared to a male juvenile positively predicted the number of interactions with a dependent child, indicating that, when available, females do provide more allocare ($B = 0.6, p < 0.001$, 95% CI [0.3, 1]). Once sibling presence is controlled for in Table 6.3 there is no significance difference between the average number of interactions sisters and brothers have with younger siblings.

Neither paternal nor maternal grandparents spent much time in close proximity with their grandchildren. Co-residence with any grandparent was not the norm as only 41.5% of children resided with at least one type of grandparent (Table 6.2). There is a slight (marginally significant in a two-way proportion test, $p = 0.09$) matrilineal bias as 21% of children reside with a maternal grandmother, compared to 15% residing with paternal grandfathers. Overall, however, 72% of Agta children did not reside with either grandmother, while only 8% resided with two grandparents (which is either patrilineal or matrilineal, never combined). Thus, grandmothers are not a common resource among the Agta. Switching to the grandparental perspective ($n = 27$), 48.2% did not live with any grandchildren. Examining just grandmothers ($n = 14$) reveals that 50% live with at least one grandchild, while on average grandmothers co-resided with 48.9% $\pm$ 0.36% of their living grandchildren. Proximity with a grandparent was dependent on a combination of grandparental survival and co-residence: of the 103 surviving grandparents-child dyads only 49 co-resided (47.6%).

Table 6.2: Proportion of children under 12 years with different types of grandparents present in camp at time of data collection ($n = 81$).

Number of children	MGM	MGF	PGM	PGF	Grandmothers	Grandparents
0	0.79	0.81	0.94	0.85	0.72	0.76
1	0.21	0.19	0.06	0.15	0.28	0.16
2	-	-	-	-	0	0.08

Only one child resided with their grandparents in the absence of both parents. Examining the reduced data set of 34 children living with either maternal or paternal grandparents we can explore the amount of care grandparents offer when they are present. When present all types of grandparents interact with dependent children (PGF = 0.06, PGM = 0.09, MGM = 0.13 and MGF = 0.02), they still interact significantly less than other kin types (Figure 6.1B, Table 6.3). Re-running the Wilcoxon signed rank tests revealed that while most other kin categories continue to have significantly more interactions than each type of grandparent even when that grandparent is present, the difference no longer reaches statistical significance for sisters for all grandparents expect MGM (MGF, p = 0.3; MGM, p = 0.9; PGF, p = 0.1; MGM, p = 0.04). While there is no statistical difference in the amount of interactions between grandfathers (V = 181, p = 0.9), MGM have 44.3% more interactions than PGM (V =174.5, p = 0.04) while PGM offer significantly more interactions than PGF (V = 67, p = 0.03).

Table 6.3: Proportion of all possible interactions kin spent with children under 12 years adjusted for kin presence.

	Present Kin type							
Age group	**Mother**	**Father**	**Sis**	**Bro**	**PGF**	**PGM**	**MGM**	**MGF**
All	0.324	0.201	0.221	0.238	0.062	0.088	0.127	0.016
Infants	0.657	0.385	0.246	0.285	0.074	0.041	0.104	0.026
Toddler	0.379	0.192	0.235	0.182	0.073	0.060	0.078	0.050
Child	0.214	0.164	0.213	0.236	0.070	0.138	0.101	0.045

6.4.1 Kin versus non-kin

In the following analysis I wanted to explore the role of non-kin in a more in-depth fashion than the existing literature. However, 'non-kin' is a broad category encompassing many individuals. As a result, it is important to define who are non-kin in terms of age and sex.

6.4.1.1 Who are non-kin

In terms of the age of non-kin - child dyads (n = 1426), the non-kin 'allocarers' appear to be predominantly children aged 6 to 15 years (33.5%) and reproductive adults aged 16 to 50 years (51.7%) while post-reproductive adults represent only 14.8% of interactions. The sex of these individuals is divided equally as 51% are males (and this division remains equal throughout the age groups). However, an important consideration is that these dyadic interactions may capture individuals who are only interacting once or twice, and thus the occurrence of a dyad does not necessarily imply a meaningful interaction. To this end I explored the impact of age and sex on the number of interactions between a dyad. I ran a multilevel model (level 1 the child, level 2 the allocarer) containing terms for age (juvenile, adult and post-reproductive adult) and sex (Table 6.4). This reveals that being a juvenile compared to an adult is significantly associated with an increase in the number of dyadic interactions, as is being a female. Thus, while a range of non-kin come into contact with a dependent child, it is juveniles and female non-kin who interact significantly more.

Table 6.4: Result from MLM exploring predictors of interactions between non-kin and dependent children dyads. The reference for the age groups 'juvenile' and 'post-reproductive' is adult. VPC stands for variance partition coefficient and details how much of the variance the levels account for.

Fixed effects				
	B	**SE**	**z-score**	**p-value**
(Intercept)	0.504	0.135	3.718	0.000
Juvenile	0.410	0.151	2.716	0.007
Post-reproductive adult	0.159	0.217	0.730	0.465
Giver sex female	0.377	0.139	2.706	0.007

Random effects			
	Variance	**SD**	**VPC**
Child	0.519	0.720	0.232
Allocarer	0.231	0.481	0.104
Residual	1.483	1.218	0.664

The average distant kin and non-kin individuals spent 5% of their time with all dependent children, increasing to 6% for children over 5 years of age. However, the importance of kin is influenced by the method of quantification of proximity across the sample. Here, proportion of interactions with non-kin represents the average over multiple non-kin. Averages are significantly impacted by extremes, particularly since the frequency distribution of ties among unrelated individuals demonstrates a right skew (Figure 6.2). As a rule, children exhibit a pattern of intense interactions with one or two individuals and weaker connections with a large number of other non-kin. This trend does not only occur among children (here 2 to 11 years), but peaks in teenagers (12 to 17 years, Figure 6.2). Children have between 1-2 individuals they interact with as much as close kin. This does not occur in infants who interact mainly with close kin. Thus, this pattern is reflective of children having one or two close non-kin allocarers (who are predominately other juveniles and female according to the analysis above) who interact with them just as much as their mother, father and siblings.

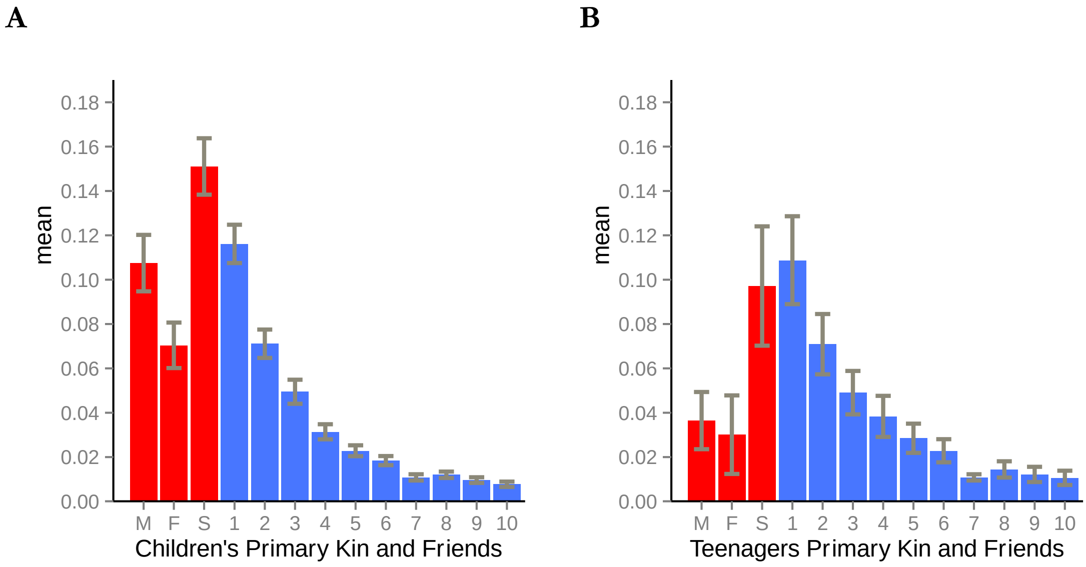

Figure 6.2: Proportion of a child's close-range interactions with close kin and unrelated individuals. (A) children (2-11 years) and (B) teenagers (12-17). Red bars: from left to right, proportion of interactions with mother, father and siblings. Blue bars: proportion of interactions with unrelated individuals ranked from left to right by frequency of interactions, up to the 10th strongest relationship. Shaded area represents the range of frequency of interactions with close kin. Error bars represent SEM (*n* = 81).

The effect this relationship has on the distribution of the data is portrayed in Figure 6.3. Figure 6.3A represents the proportion of interactions a child has with the average individual from each kin category, and is reflective of the pie chart in Figure 6.1. Here we see that mothers are the most important caregiver until age 9, when sisters, distant and non-kin have more interactions. Figure 6.3B is based on the proportion of *a child's time* they spent with different kin types. Now that distant kin and non-kin are no longer averaged over many individuals we see that children spend a higher proportion of their own time with distant relatives and unrelated individuals. Thus, examining the interactions as a proportion of the child's time by kin group, I find that children spend on average 34 ± 26% of their time with mothers, 11 ± 5% of time with fathers, 24 ± 13% of time with siblings and 6 ± 6%, 7 ± 7%

and 23 ± 13% for grandparents, other kin and non-kin, respectively (Figure 5.1). Both of these perspectives are important as, on the one hand they reveal the cost of childcare to mothers and how this cost diminishes with age, while on the other hand showing that children interact with a significant number of less related individuals, which increases with age.

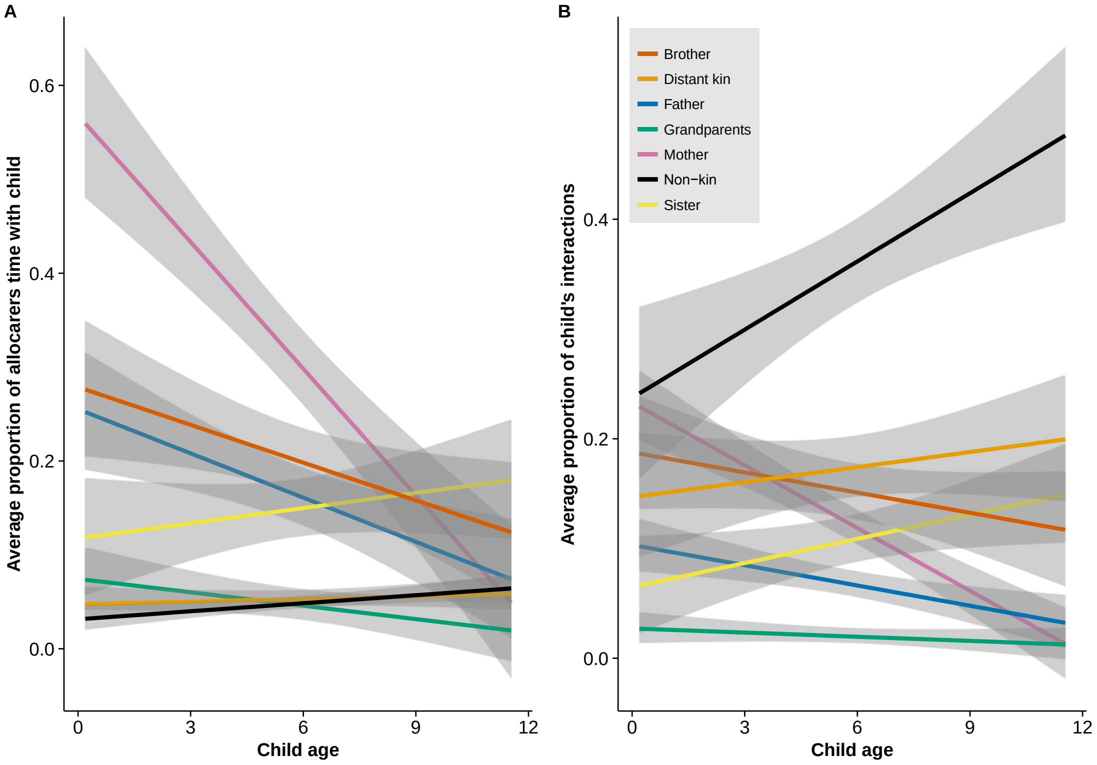

Figure 6.3: The relationship between number of interactions and age separated by whether the dependent variable is A) the average proportion of allocarers' time spent in childcare or B) the average proportion of care a child received from different types of allocarers (*n* = 81).

To conclude this section, it is evident that I did not confirm my original predictions. Grandparents are not significant allocare providers. However, following the expectations of paternity certainty, maternal grandmothers did provide the most care amongst grandparents. Nevertheless, there is no significant difference between maternal grandfathers, paternal grandmothers and paternal grandfathers in the amount of interactions. Furthermore, paternal grandfathers' interactions with grandchildren are the second highest after maternal grandmothers, in opposition to the paternity certainty hypothesis, painting an inconsistent picture. While close kin evidently provide the most amount of care, non-kin seem more important than expected based on kin selection theory alone, while siblings do appear to be frequently proximate to their dependent siblings, more so than fathers at later ages. Thus, by examining the composition of Agta childcare it appears that, after mothers, it is siblings who provide a significant amount of care while the role of non-kin should not be underestimated.

6.5 Results: substitutive care

I explored the relationship interactions from different individuals had with the amount of interactions a child had with their mother and father. For instance, are maternal interactions low when grandmaternal interactions are high? The aim was the capture whether care from parents was reactive to care from allocarers or vice versa (as causality cannot be distinguished). Fathers consistently interacted significantly more (blue line in Figure 6.3) than grandmothers. However, several grandparents did interact more (maximum proportion of interactions: MGM = 0.34; MGF = 0.18) when fathers were absent or provided little direct care. This suggests that grandparental care may be of greater importance when parents were unavailable. Thus, I predicted that grandparental allocare would increase when paternal care is low. It is expected that for mothers to receive fitness benefits from allocare that this allocare is significantly associated with reductions in maternal workload, allowing her to reinvest the freed up time and/or energy into current or future reproduction. Consequently, I predicted that care from different caregivers would decrease maternal childcare.

MLMs were run with level 1 as the child, level 2 the household and level 3 the camp. Child age and sex were controlled for in each analysis. Five separate models were run containing one grandparent each to avoid overfitting the model with an excess number of predictors with diminishing sample size (for instance, only 6 children resided with a sister and maternal grandparents, none resided with all four grandparents). These models (Table 6.5) revealed that increased contacts from fathers ($B = 0.35$), siblings ($B = 0.4$) and PGM ($B = 1.1$), had a positive effect on the number of maternal interactions. Furthermore, distant kin demonstrate a similar trend ($B = 0.36$), however the relationship is not significant ($p = 0.09$). MGM demonstrated no significant influence on maternal childcare. Thus, increased contact with close and distant kin did not reduce the amount of interactions a mother had with a child.

Interactions with non-kin were significantly associated with a reduction in maternal ($B = -1.5$) and paternal childcare ($B = -1.6$). In terms of paternal care, it is interesting to note (bearing in mind the extremely small sample sizes at this point, $n = 6$) that while PGM appeared to increase paternal interactions (i.e. fathers' mothers are more likely to be present at the same time as fathers themselves), maternal grandparents demonstrated the opposite relationship. Contact from both MGF (*B* = -2.0) and MGM (*B* = -0.6) reduces the amount of time fathers are in contact with their offspring (albeit insignificantly in the case of MGMs, *p* = 0.1) suggesting that maternal grandparents offer more care when fathers are otherwise engaged or vice versa.

Table 6.5: MLM results on the effect of interactions with different kin types on parental-offspring interactions.

	Covariates parameters							
	Model	**Covariate**	**B**	***p***	***n***	**Family**	**Camp**	**Residual**
Maternal	1	Age	-0.71	< 0.0001	81	1.281	0.548	16.986
		Sex	0.162	0.86				
		Father	0.346	0.002				
		Siblings	0.402	< 0.0001				
		Distant Kin	0.361	0.09				
		Non-kin	-1.452	0.04				
	2	MGM	0.697	0.227	20	0.000	0.000	22.150
	3	MGF	-0.211	0.85	18	12.418	0.000	9.548
	4	PGM	1.052	< 0.0001	6	0.000	0.000	1.165
	5	PGF	-1.094	0.25	14	19.524	12.792	1.737
Paternal	1	Age	-0.255	0.01	81	12.985	1.365	4.458
		Sex	0.327	0.575				
		Mother	0.157	0.01				
		Siblings	-0.07	0.19				
		Distant Kin	0.526	0.003				
		Non-kin	-1.376	0.012				
	2	MGM	-0.555	0.13	20	22.640	0.000	2.760
	3	MGF	-2.013	0.02	18	11.307	0.000	3.721
	4	PGM	0.8	< 0.0001	6	0.000	0.000	0.418
	5	PGF	-0.206	0.77	14	11.000	19.860	2.470

Note: Due to diminishing sample size five separate models were run: one containing the nuclear family, distant kin (excluding grandparents) and non-kin and the reminding four separating the different types of grandparents. The table shows the results for five independent models which are numbered and separated by shades of grey. Sample sizes vary according to the model and are reported separately for each model in the table. Dependent variable is the number of interactions reported with parents averaged across the length of the experiment.

Consequentially, while it appears that paternal and maternal grandparental interactions are reactive to one another, suggestive of substitutive relationships, it is only proximity from non-kin which significantly reduces maternal contact with her offspring. However, the small numbers of grandparents removes the power from this analysis and my ability to speak about their relationship with parental care with any certainty.

6.6 Discussion

The picture of Agta childcare cannot be simply explained by 'kin selection', nor is it particularly defined by grandmothering. It is evident that non-kin do have a not insignificant role in childcare, consisting of around 23% of children's interactions. Furthermore, all children interact with one or two unrelated individuals as much (if not more) than close kin. However, these dynamics are frequently overlooked due to a focus on distant kin (i.e. grandmothers). Overall, I find little evidence in support of grandmothering, while juveniles and fathers appeared to be more important allomothers. Supportive of previous findings (Sear & Mace 2008) I find that maternal care decreases with age, however by exploring allocare with a larger age range of children reveals that grandparental and paternal care all also decrease with increasing age. On the other hand, siblings and non-kin become increasingly important, particularly after ages five to six. Therefore, the importance of allocarers is dependent on the age of the child as well as relatedness and the ability of the individual to provide allocare, revealing the advantages of larger sample sizes spanning different age groups.

6.6.1 Absent grandmothers

The extensive human post-reproductive lifespan has remained an open evolutionary question: given that natural selection selects for traits that increase reproductive success, not being able to reproduce for 10, 15 or 20 years seems like a significant limitation on this (Williams 1957; Hawkes *et al.* 2003; O'Connell *et al.* 1999). It is not reproductive senescence which is particularly 'unique' (Whitehead 2015; Foote 2008; Hawkes & Coxworth 2013; Brent *et al.* 2015), nor is its timing, but the fact that humans' have an extended post-reproductive lifespan (Hawkes *et al.* 2003). While foragers, on average, survive for up to 20-22 years (based on post-menopausal life expectancy from the !Kung, Hadza and Ache), less than 6% of chimpanzees are alive past the age of last birth (Kaplan *et al.* 2000; Hawkes *et al.*

1997; Hill & Hurtado 1996; Howell 1979; Hill *et al.* 2001). As a result, Hawkes and colleagues (Hawkes *et al.* 1997; Hawkes *et al.* 2003; Hawkes & Coxworth 2013) put forward the grandmothering hypothesis for post-menopausal longevity in humans. Mothers whose own mothers assist in childcare increase fertility without deteriorating reproductive success as grandmaternal presence allows for shortened birth intervals without increasing childhood mortality (Hawkes *et al.* 1997). As a result, long living post-menopausal grandmothers will increase their fitness relative to shorter-lived grandmothers due to indirect fitness gains (Hawkes *et al.* 2003), propagating the post-menopause longevity trait.

Hawkes and colleagues argued that grandmothering is part of a cluster of life history traits in humans that create our 'unique' fast and slow strategy, given that extended longevity drives delayed maturity (Charnov & Berrigan 1993), resulting in the excessive dependency of offspring. It is the care and provisioning from grandmothers which allows us to have multiple dependent offspring as their allocare permits for earlier weaning and shortened IBI (Hawkes *et al.* 2003). As a result, a major quest in the anthropology of cooperative breeding has remained the quantification of the role of grandmothers and their influence on child survival and maternal fertility. As reviewed in chapter 3, in a range of small-scale and historical populations, maternal grandmothers play a significant role in improving child quality and maternal fertility (Sear & Mace 2008; Sear *et al.* 2002; Snopkowski & Sear 2015; Sear *et al.* 2003). Consequentially, many have come to see grandmaternal care as a defining feature of human life history (Hill & Kaplan 1999).

The picture is not, however, so clear in foraging societies, particularly among the Agta. For instance, referring back to Table 3.1, it is apparent among the more immediate-return hunter-gatherer groups (Agta, Aka, Efe and Hazda) the proportion of high-investment care received from grandmothers is low, averaging at 5.4%. Similarly, in this study, grandmothers were only proximate to children for 1.6% of the time they were in camp, peaking at 3.7% for maternal grandmothers. Simply put, all other kin and non-kin provided more care than grandparents. As suggested by Hill & Hurtado (2009), this is in part influenced by the shorter life expectancy in hunter-gatherers matched with fluid camp composition, meaning that many children do not reside with any grandparent, maternal or otherwise. For instance, Migliano *et al.* (2007) demonstrated that among many pygmy populations residing in high mortality environments, post-15 life expectancy spans between 20 to 23.5 years. As a result, only 13-31% of pygmy mothers survived to past last reproduction. In contrast, the Turkana (pastoralists) survive for 46.6 years after age 15 and 63% survive past last reproduction.

Consequentially, high mortality environments, such as those common in many foraging populations (Hill & Hurtado 1996; Hill *et al.* 2007; Kramer & Greaves 2007; Hill *et al.* 2001; Gurven *et al.* 2007; Stock & Migliano 2009; Early & Headland 1998), are not conducive to the presence of grandmothers. This suggests that the role of grandmothers may lie in lower mortality environments where they can be relied on as more predictable sources of allocare (Kaplan *et al.* 2000).

Furthermore, the high mortality of foraging populations like the Agta poses another problem for the role of grandmothers. Given that age at maturity is governed, in part, by expected age at death (why risk waiting to reproduce when the life expectancy at adulthood is as low as 20-33 years (Charnov & Berrigan 1993; Promislow & Harvey 1990; Migliano et al. 2007)) populations residing in higher mortality environments tend to reach reproductive maturation earlier. For instance, Turkana women start reproducing four years later than the Aeta (Migliano *et al.* 2007), a trend apparent in developed nations (Nettle 2010; Nettle 2011) and throughout the Primate order (Walker *et al.* 2006). Despite the harsh environmental conditions which could result in disrupted reproductive functioning, such as poor nutrition and high pathogen load, it appears that the Agta maintain early first births and relatively high reproductive rates (with the youngest birth occurring at age 15 and average interbirth intervals of two and a half years). Consequentially the generational time is shortened and when grandmothers are present they often still have dependent offspring. This is certainly the case among the Agta: only 4.1% of the 148 allocarers could be defined as completely post-reproductive (i.e. grandmothers without dependent children aged under 12 years). However, their average age was 69.5 years and only one of the three grandmothers was physically able to provide care and/or food. All other grandparents still had dependent (i.e. under the age of 12) offspring, and thus perhaps unable to offer much assistance. The results detailed above are suggestive of this pattern, for both grandmothers and distant kin in general.

Nonetheless, we also see that grandparents are reactive to paternal care (or paternal care is reactive to grandparental care); increases in the number of interactions with maternal grandfathers and grandmothers correlated with reductions in paternal contacts (albeit only of marginal statistical significance for grandmothers). The causality is, of course, unclear here as fathers may do less when grandparents do more, or vice versa. However, these result follow those of Meehan *et al.* (2014) who found that maternal grandmothers presence only influenced child nutritional outcomes in patrilocal camps where fewer allocarers were present. Thus, the importance of grandmothers may lie in substituting paternal care, as unlike in other studies the Agta fathers provided consistently more allocare than grandmothers (Scelza 2009; Ivey 2000). Similar to the Aka (where fathers provide 15.8% of care (Hewlett 1988)) then, Agta fathers are important caregivers as they spend 16.7% of their time with their offspring. An important distinction here is the difference in measurement; I have recorded proximity only, thus many fathers may spend their time 'caring' by simply being present and conducting other tasks. In many other studies investigating high quality care, the father's role may have been overlooked if they commonly provided lower investment care. Being within three meters of a child can be considered an important form of childcare in terms of watching over them and being able to intervene when required. It does not seem that fathers actively increase their proximity care as children grew, as this drops down to 10% after the age of 5 years. Thus, studies focusing on younger children may not necessarily underestimate the father's role, yet studies focusing just on tasks like carrying, feeding or grooming may do just that. It is only possible to conclude that fathers are less important than mothers in direct childcare, however their importance likely stems also from family provisioning. Combining both direct and indirect childcare is a clear avenue of future research, allowing for greater insight into the evolution of cooperative breeding and pair bonding in humans (Kaplan *et al.* 2000; Washburn & Lancaster 1968; Kaplan *et al.* 2003).

6.6.2 Helpers-in-the-lean-to

Agta siblings appear to be major providers of allocare, however, compared to grandmothers, care from juveniles has received little attention for their role in cooperative breeding (Kramer 2011). Theoretically sibling care should be significant: they are 50% related thus suffer no fitness costs relative to care they could provide to future offspring (assuming paternity certainty here); as juveniles are in a pre-reproductive period they do not suffer a reproductive opportunity cost in caring; and they can develop skills required to be a successful parent later in life (Lancaster 1971). Consequentially, juveniles can be considered both dependents *and* carers. However, this is frequently overlooked as siblings are expected to be competitors for parental resources and large sib sets are associated with decreases in survival and poorer outcomes (Lawson *et al.* 2012). A lot of early work focused on the optimality of human reproduction, based on Lack's (1954) original observation that fitness is maximised by ensuring offspring survival, extended by Triver's (1972) theory that parental investment will be biased to offspring who can maximise reproductive success. While the evidence for a quantity-quality trade-off optimising human reproduction is mixed (Strassmann & Gillespie 2002; Hill & Hurtado 1996; Blurton Jones 1987; Pennington & Harpending 1988; Borgerhoff Mulder 2000), there is substantial support for the presence of older siblings having a negative influence on maternal fertility (Sear *et al.* 2003; Tymicki 2004; Borgerhoff Mulder 1998) and child nutritional condition (Hagen & Barrett 2009; Magvanjav *et al.* 2012). Significant sex and wealth effects mediate many of these relationships as siblings often compete more for resources which are limited and/or with siblings of the same sex (Borgerhoff Mulder 1998). As a result, juveniles have more often than not been considered competitors rather than co-operators. However, as stated by Kramer (2011: 533), there is a significant difference between raising a brood of offspring simultaneously and raising a newborn into a household with existing offspring.

Evidence from the Agta clearly supports this hypothesis, as does the majority of observational studies in small-scale societies; of the six studies which document the amount of care received from both grandmothers and siblings in Table 3.1, 66.7% report that sibling care as higher than grandmaternal care. The exception being the Mardu, where siblings carried children only 5% of the time compared to grandmothers who carried them for 14.3% and the Hadza where siblings carried children for 1.2% of observations. However, Crittenden *et al.* (2013) argue that children's role in the Hadza is focused on food production rather than direct childcare (Crittenden *et al.* 2013; Crittenden & Zes 2015). Siblings, on average, are reported to engage in direct childcare 17.4% of the time across the ten studies reported in Table 3.1, firmly in line with 15% and 20.2% number of interactions reported here for sisters and brothers, respectively. This care, alongside other subsistence activities (such as foraging, tending animals, cultivation, food processing, firewood and water collection) enables mothers to re-invest freed-up energy and time into other activities (Kramer 2011). In short, if children were unable to provide this assistance (i.e. be completely dependent) parents would be unable to increase their workload to sufficiently subsidise all their offspring and ensure their survival (Kramer 2005; Lee & Kramer 2002). As a result, Kramer (2011) argues that humans are able to maintain their fast/slow life history traits because juveniles provide allocare (direct or indirect) which allowed mothers to start reproducing earlier (Kramer 2008) and shortening birth intervals without significant increases in mortality.

Focusing on juvenile help may shed more light on the hypothesis of the evolution of the highly dependent juvenile period due to the embodied capital requirements in skilled foraging niches and increased cognitive development (Kaplan *et al.* 2000; Kaplan 1994; Walker *et al.* 2006). Lancaster and Kaplan (2009) posited that the extended juvenile period evolved as a result of humans' intensive extraction of high quality foods using advanced techniques. Human's foraging return rates and brain sizes are significantly higher than chimpanzees, and following Kaplan and colleagues' (2003) argument, this results in a 1.4-fold longer juvenile stage devoted to skills and intellectual development. Thus, the juvenile period is selected for as it ensures the investment in embodied capital (i.e. growth, soma, immune function as well as skills and knowledge) which allows for a higher reproductive rate once maturity is reached which maximises reproductive success (Kaplan *et al.* 2000; Pagel & Harvey 2002). Delayed maturation is only possible in environments of reduced mortality; compared to chimpanzees, hunter-gatherers today experience double the life expectancy at birth and adulthood (Hill *et al.* 2001). In Kaplan and colleagues' (2000) model of human life history evolution they find that if, unlike Charnov's (1993) model, actors can influence their mortality rates (i.e. they are not completely exogenously determined) by investing in embodied capital then energy is diverted to mortality reduction by extending the juvenile period.

However, across the Primate order, more complex foraging skills (denoted by diet) are not consistently associated with prolonged juvenile periods, particularly in New World monkeys, while diet has no influence on relative brain size (Walker *et al.* 2006). Consequentially the link between foraging niche, cognition and prolonged development is not clear-cut, and other social factors may have an important role alongside skill development (Pagel & Harvey 2002; Dunbar 2003). A supplementary and comparatively unexplored hypothesis is that juvenile periods may also be selected for due to the social role of juveniles. This is not to suggest that the main cause of the extended pre-reproductive period is allocare (akin to reproductive suppression in cooperative breeders). However, if due to the humans' intense investment in embodied capital allocare carries a low opportunity cost for siblings then, given their 50% relatedness to siblings, a prolonged period of skills development is not costly in terms of immediate indirect fitness as they are able to assist younger sibs. If this is the case, then the inclusion of the impact of low-cost allocare on lifetime fitness would be an important factor to explore in life history models.

The under-exploration of this question results from a systematic neglect of children's contributions due to a focus on 'net' production (i.e. the age at which an individual can sustain themselves) rather than production, which is not insignificant, albeit not selfsustaining (Kaplan 1994; Lee & Kramer 2002; Cain 1977). Few hunter-gatherer studies examine the food production of children, even though it appears to be substantial (Crittenden & Zes 2015; Crittenden *et al.* 2013), while children's heavy involvement in domestic tasks are equally ignored (Kramer 2011; Meehan *et al.* 2013a). If juveniles play an important role in ensuring maternal reproductive success, and vis-à-vis, their own indirect fitness, delayed maturation would also be selected for if this combination of investment into current indirect fitness (allocare) and delayed reproduction (via embodied capital) maximised genetic contributions to future generations. Including indirect fitness returns into life history models would greatly benefit understanding when it pays to cease growing and providing allocare given environmental mortality rates. This would be an intriguing avenue of future research, given the current limiting dichotomy between pair bonding and grandmothering in attempting to explain human longevity, allocare and juvenile periods.

Nonetheless, there is a snag in this argument: increased contact with siblings did not significantly reduce the amount of time a mother spent with that child, and in fact increases it. This pattern is also true for paternal and grandmaternal interactions, thus these allocarers do not replace maternal care, and without significant reduction of the maternal energy burden it is unclear how allocare would be associated with improvements to child condition, survival and/or maternal fertility. Certainly this study is limited to direct childcare only and does not explore maternal activities and domestic tasks. Furthermore, due to the coarse nature of the data (i.e. only proximity), the quality of the level of care is hidden. For instance, Scelza (2009) suggests that older siblings conduct more demanding, high quality childcare tasks which significantly reduce the maternal energy burden. Thus, while mothers are still present (here within three meters), the simultaneous presence of older siblings to groom, feed, play with and hold children means that the mother can relax, can conduct other activities or conduct higher investment activities in another child. Anecdotally, the occurrence of playgroups with one or two mothers or adults watching from a distance was not uncommon, suggestive of this pattern. However, a quantitative examination is critical to further explore the role of juveniles as allocarers.

Nonetheless, proximity care from non-kin did significantly decrease the number of interactions mothers had with their children, indicating that there is a direct substitutive effect. This reveals that non-kin may have significance in hunter-gatherer systems; given the stochastic variation (mortality, mobility, sickness and variability in food production) in who is actually available to provide allocare, reliance on any one particular carer, such as an older sister, grandmother or father would be a risky strategy (Kramer 2010). As a result, one possible way of mitigating losses is ensuring very distantly or unrelated individuals are able to provide care.

6.6.3 Kin selection and non-kin allocarers

The data support the hypothesis that children spend the most time in proximity with close kin, providing them with the large opportunity to provide allocare. This is in keeping with Crittenden & Marlowe's (2008) finding that among the Hadza, more closely related individuals held a child for longer, as well as Ivey's (2000) work with the Efe showing that relatedness consistently predicted care from adult males, juveniles, reproductively and post-reproductively aged women. Furthermore, referring back to the detailed results in chapter 5, we see that it is closer kin than contact more of the high investment tasks such as carrying, feeding and grooming (Figure 5.2 & Figure 5.3). Therefore, the immediate family members are key providers of childcare. However, here I have demonstrated that non-kin also interacted with dependent children to a significant degree (23%), and while the majority of non-kin interact infrequently, a few provide a level of contact comparable to close kin. Thus, similar to the results among the Hazda (Crittenden & Marlowe 2008) and Efe (Ivey 2000), non-kin are interacting with dependent children, indicating their importance. This raises the question: why do unrelated Agta allocarers provide care? I suggest that reciprocal altruism is a potential solution to shortfalls in household energy budgets as allocare consists of a form of risk pooling. This hypothesis is tested in the next chapter (7, "Why breed Communally"). Furthermore, as argued in section 3.2.1, kin selection cannot be tested by simply demonstrating that specific kin types provide more allocare than less related individuals, as this may well be equally influenced by reciprocity, association or spatial distance. To explore the ultimate 'why' behind communal breeding the confounding effects of relatedness, reciprocity, costs, benefits and association must be separated in multivariate analysis. This analysis is conducted in chapter 7.

One evident reason for previous results emphasising the importance of grandparents and deemphasising the importance of siblings and non-kin is the problem of small-sample sizes and a focus on infants. While Agta grandparents never offer a large amount of care, it is most certainly increased during infancy where maternal grandmothers spend 3.7% of their time proximate to an infant. By age six onwards this decreases to 0.8%. Therefore, arguably the importance of grandmothers lies in earlier years. These results are mimicked in Meehan *et al.*

(2014) study of the influence of presence of different kin on weight-for-age, height-for-age and weight-for-height z-scores among 127 Aka children aged less than 10 years. Here grandmothers were associated with higher z-scores (for weight-for-age, height-for-age, and weight-for-height) during the 9 to 36 month period, with diminishing effect sizes over time. Similar results are apparent in a large cross-section of studies on grandmaternal effects on child outcomes (Sear & Mace 2008).

The role of siblings and non-kin has not been explored with the same level of detail of grandparents, thus there is little to compare these results to. However, it follows that as children age and parental care decreases, it is likely that these interactions are taken up by other types of individuals. This trend is demonstrated by Figure 6.2, which reveals that children spend more time with siblings than parents, and share intensive relationships with one or two non-kin individuals. Given the findings in chapter 5 and the exploration here it appears that these are likely to be non-kin juveniles engaged in low-investment activities such as playing or being within a larger playgroup. While this trend increases further into teenage years, it is not present in infants aged less than two years who do not interact with non-kin as much as they do with primary kin. Therefore, by exploring allocare across a large sample containing a range of ages, it is possible to see the importance of non-kin and siblings.

Finally, the larger sample size also produces more confidence in our results, as they are less likely to be biased by a few individuals who happen to provide significantly more care. Nonetheless, even here there are simply not enough grandparents to explore these relationships in-depth with any confidence, further indicating the problem of relying on grandparents for allocare.

6.7 Conclusions

Here I have explored allocare through close proximity interactions and thanks to the application of the motes, the larger sample size of 200 individuals sampled over a week greatly increases the statistical power of this analysis. These data should go hand-in-hand with more time-consuming but finer grained observational data to aid better interpretation of the results, setting a direction for future research. Nonetheless, being able to examine allocare across a larger age range of children has revealed some interesting trends. *Contra* to my original predictions Agta childcare is defined by a lack of grandmothers and the importance of juveniles and non-kin. This undermines the grandmothering hypothesis and indicates more research should be focused on a comparable ‘juvenile hypothesis’ as well exploring non-kin allocare. Overall I do still find, as predicted, that close kin including mothers and fathers are key providers of childcare. The question of why individuals provide costly allocare has yet gone unanswered and I turn to this question in the next chapter.

Chapter Six
Why breed communally

The review in chapter 3 revealed that the literature is awash with examples of indirect and direct benefits which occur from cooperation, yet this paradigm is rarely (if ever) applied with the same robusticity to allocare. Therefore, here I examine the role of both kin selection and reciprocity in understanding why individuals breed communally. As in chapter 6, I use high-resolution proximity data from 200 individuals, including 81 dependent children to explore the ultimate reasons behind allocare, in particular exploring the influence of costs, benefits and reciprocity as well as relatedness. Interactions with dependent children (here 'allocare') appear driven by kin selection; however, this is primarily limited to related juveniles. Grandmothers provide little care and are unreactive to household childcare needs, as are distant kin in general. These relationships may be defined more by competition for resources than cooperation. Reciprocity does not predict allocare in the full sample; however, reciprocity is important for more distantly and unrelated individuals, suggesting their care is provisional on short-term returns. These results support the hypothesis that allocare is a form of risk mitigation, as does the finding that degree of cultivation and material wealth influences the nature of allocare, shifting the perspective from wider, unrelated networks to the nuclear family. This chapter demonstrates the importance of hypothesis testing, revealing that communal breeding is much more complex than kin care and can be considered an important behavioural strategy when facing risky environments with many dependent offspring without material wealth.

7.1 Introduction

Given that the successful reproduction of offspring who survive to maturity is a key component of an individual's lifetime fitness, getting additional childcare from allocarers surely would result in a fitness payoff (assuming the childcare standards were high enough of course). Thus, why mothers allow other individuals to provide allocare for their children is not such an evolutionary puzzle. However, the same cannot be said for understanding why the allocarers provide costly childcare, particularly when they are distantly related or unrelated. The majority of research on communal breeding in humans has indicated that allocarers care due to indirect fitness benefits (Crittenden & Marlowe 2008; Mace & Sear 2005; Sear & Mace 2008; Meehan *et al.* 2014; Kramer 2010). However, as revealed in the literature review contained in chapter 3, previous studies have rarely separated the effects of relatedness from reciprocity, shared proximity as well as the confounding effects of costs and benefits. The majority of studies that explore these questions do reveal that more related individuals provide more allocare (Ivey 2000; Crittenden & Marlowe 2008) or that more closely related individuals have a positive influence on child outcomes (Sear & Mace 2008). However, they cannot reveal that this trend occurs due to kin selection or explain why non-kin provide costly allocare. As a result, here I intend to explore why allocarers provide care by further extending the results established in chapter 6. This requires reconciling the apparently costly behaviour (allocare) with inclusive fitness theory, in which individuals should be optimising behavioural strategies to ensure increased genetic representation in future generations. This question will be separated into two interconnected parts in this chapter. First, I will explore what benefits givers of allocare receive from interacting with dependent children. This can be broadly separated into indirect fitness (kin selection) and direct benefits (reciprocity). Secondly, I further explore the role of cooperative breeding as a form of risk reduction by examining how it varies according to ecology and foraging returns as well as subsistence diversification and wealth accumulation.

7.2 Why do selfish organisms cooperate?

Exploring why individuals cooperate from an evolutionary perspective has led to the development of a series of models, some specific to cooperative breeding, others more general. Following evolutionary logic they attempt to explain human behaviour from the perspective of individualistic gains as true altruism is not an evolutionary stable strategy (Foster *et al.* 2006; Rand & Nowak 2013). While these theories have been discussed in depth in chapter 3, they are now recapped below and their main predictions are summarised in Table 7.1. It is important to note that these are not mutually exclusive hypotheses and are all expected to be in operation to some degree. For instance, an extended family member may be more likely to receive help because they share, on average, 25% of their genes with the recipient. However, given that they do not share 75% of their genes, cooperation may be dependent on reciprocation, which is not predicted by kin selection. Thus, their behaviour is predicted by both reciprocal altruism *and* kin selection. Furthermore, grandmothering and helpers-in-the-nest are sub-predictions within kin selection that consider differences in reproductive stages and the influence this has on the cost benefit ratio in kin selection.

7.2.1 Kin selection

Kin selection predicts that individuals should provide allocare dependent on indirect fitness benefits weighted by degree of relatedness (rB) and the direct fitness cost of the cooperative action (C, Hamilton (1964)). As a result, care should diminish with increasing cost and decreasing relatedness, but increase the greater the benefit of the recipient. Care driven by kin selection is not expected to be influenced by reciprocity (Gurven 2006). As in chapter 5, I predict that juveniles or 'helpers-at-the-nest' will provide a significant proportion of care given that their relatedness is high and cost is low. However, following the lack of importance of grandmothers in chapter 6, I predict that being a grandmother will not significantly predict the number of interactions with a child. Nonetheless, I expect juveniles and grandmothers will offer more care when the need of the recipient is high enough, as the benefits would then outweigh the costs.

Overall, given that kin can afford, in fitness terms, to invest a significant amount in their relatives' offspring, they can be considered to be reliable caretakers, particularly due to their likely co-residence. This would result in tightly clustered childcare networks around the nuclear family.

7.2.2 Reciprocity

Childcare motivated by reciprocity should be dependent on the needs of the recipient household and the cost of the action to the giver (Gurven 2004b). However, unlike kin selection, reciprocity is defined by contingency (i.e. cooperation which is dependent on expectations of future cooperation based on prior sharing patterns (Allen-Arave *et al.* 2008)). Reciprocity does not need to be evenly balanced, but the giver should expect that the long-term benefits of giving outweigh the immediate cost of giving (Gurven 2006). Contingency should become an increasing important predictor of cooperation as r diminishes as direct benefits soon outstripped indirect ones (Allen-Arave *et al.* 2008). Thus, I predict that distantly related kin (referred to throughout this chapter as distant kin when $r \leq 0.25$, thus including grandparents, aunts and uncles and cousins) and unrelated individuals' allocare will depend on contingency, the need of the receipt household and giver cost.

Table 7.1: Evolutionary models explaining cooperation and allocare. None of these models are mutually exclusive.

	Indicators				
Theory	r	**Contingency**	**Benefit**	**Cost**	**Clustering**
Kin selection: care pooling (Hamilton 1964)	Increases care	Not present; needs based imbalance	Essential: to the offspring and/or mother (indirect fitness).	Dependent on relatedness and benefit	Cooperative networks clustered around kin
Reciprocal altruism: risk pooling (Trivers 1971; Aktipis *et al.* 2001; Gurven 2006; Cashdan 1985)	-	Essential but may be delayed and unbalanced	Essential: to the offspring and/or mother	Proportional to expected returns	Dispersed networks ensuring wide risk transfer
Helpers-at-the-nest (Lancaster 1971; Lee & Kramer 2002)	Siblings provide care due to indirect fitness	Not present	Essential: to the offspring and/or mother (indirect fitness).	Low: juveniles are not yet reproductively active	Cooperative networks clustered around household
Grandmothering (Hawkes *et al.* 1997; Sear & Mace 2008; Strassmann & Garrard 2011)	Increased care from MGM due to paternity certainty	Not present	Essential: to the offspring and/or mother (indirect fitness).	Low: care from post-reproductive females	Cooperative networks clustered around the distant kin

Note: throughout this thesis I separate close kin (primary family including parents and siblings) from distant kin (grandparents, aunts and uncles etc. at $r \geq 0.125$) and non-kin ($r < 0.125$). These divisions are consistent. Throughout this analysis I do not focus on the role of the father, thus I am examining alloparenting rather than allomothering (i.e. exploring what predicts childcare from all individuals who are not parents).

7.2.2.1 Risk-pooling

Communal breeding is arguably a form of risk-pooling to mitigate the losses occurring from either short-term variance (i.e. foraging failure) or long-term need given mothers' life history schedules (referred to as predictable life history shortfalls (Hill & Hurtado 2009)). I divide these two types of risk pooling into *variance pooling* and *care pooling*, respectively.

Variance pooling ensures that individuals can face short-term shocks without suffering larger losses as they pay an immediate smaller cost by cooperating now (Aktipis *et al.* 2011).

Foraging failure or periods of sickness will influence direct childcare as individuals' energy budgets encompass food production, household tasks and childcare. Therefore, a shortage in one area such as food production can result in a deficit in childcare, which can be met by allocare. For instance, household A provides childcare to household B because household B is experiencing a bad run of luck in food production, thus spends more time foraging. Household A will expect to be helped by household B at some point in the near future when the scenario is reversed. Variance pooling is expected to occur between distantly or unrelated individuals as the household has 'maxed-out' its energy budget: networks are expected to be wide given the necessity for exposure units to be independent (Cashdan 1985) to deal with variance and demographic variability in mobile camps. Variance pooling is thus expected to occur with distant kin and non-kin; however, distant kin should be less sensitive to the costs of providing allocare due to shared reproductive interests mitigating some imbalances in cooperation.

Care pooling occurs when a mother is chronically unable to provide care for her offspring due to a high number of dependents. Given the long-term nature of the exchange mothers are not readily able to reciprocate care, thus, siblings and extended family members are likely to provide care given their higher likelihood of future interactions, increased trust and degree of relatedness compensating for any allocare unreturned (Allen-Arave *et al.* 2008). Thus, I expect extended family to offer significantly less care than closer kin, and this care may be motivated by reciprocity as well as kin altruism as relatedness is low and indirect benefits are easily overtaken by direct returns (Axelrod & Hamilton 1981). Care from distant kin is expected to be more sensitive than close kin to the immediate fitness costs associated with cooperation, as r is significantly lower. Likewise, distant kin should provide care to the households in the most critical of needs since B has to be significant enough to adjust for the lower level of r. Thus, I predict that distant kin will provide more care the 'needier' a household is without immediate reciprocation. Non-kin on the other hand will be more determined by variance pooling which is dependent on short-term exchanges.

A second set of predictions centres on the effects of different types of risks and strategies to mitigate these risks. There are significant differences in variance of food production between coastal and inland groups (section 2.4.2); individuals relying on marine resources experience significantly larger package sizes, higher mean calorific return per hour and face lower levels of variance (Table 2.4). As a result, I predict that childcare networks at the coast will be more focused around the household than the extended family and unrelated individuals, as there is less need for wide childcare networks. Furthermore, markers of transition to more settled, cultivating and/or wage labour forms of subsistence are expected to alter the means by which individuals buffer risks. I predict that households involved in more foraging activities will have children who are cared for more by distant and unrelated individuals as it is difficult to conduct many foraging tasks in the presence of children (after weaning). Furthermore, individuals who spend more time engaged in cultivation and wage labour tend to be more settled and accumulate more material wealth accumulation (section 2.5). As a result, risks may be buffered by risk retention (i.e. storage of food and wealth) and wealthier households will extract themselves from wider networks to avoid demands on their wealth (Fafchamps 1992). Consequently, I expect that households with greater wealth will rely less on childcare from wider cooperative networks (such as the extended family and non-kin) and focus more on the nuclear household.

7.3 Methods

7.3.1 Dependent variables

The dependent variable for the statistical analysis is the number of interactions two individuals shared on average per hour of the motes experiment. I refer to this variable throughout the analysis as *'number' or 'frequency' of interactions.* The first analysis 'why allocare' is conducted on the dyadic relationships between each child and allocarer. The second analysis 'variability in allocare' is conducted at the child level, and the number of interactions with each kin type (mother, father, siblings, grandparents, distant kin and non-kin) have been summed into one outcome variable.

7.3.2 Independent variables

Measures of transition have been described at length in the methodological section 4.2, these are used in the second analysis examining the influence of subsistence change, mobility, wealth and food storage on the amount of allocare different individuals provide. The binary variables of grandmothers and juveniles were created to test both the helpers-at-the-nest and grandmothering hypotheses. If an allocarer was pre-reproductive (aged 15 or under) they were coded as 1, all other individuals were coded as 0. All maternal and paternal grandmothers were coded as 1. Descriptive statistics for all dependent and independent variables are presented in Table 7.2 and Table 7.3.

7.3.2.1 Reciprocity

To test the influence of reciprocity, a contingency variable was created for each dyad (Nolin 2010). As dependent children cannot reciprocate care for many years I developed a measure of reciprocity based on allocare between households. This measure is dyadic between two households, and for each household which now 'gives' (household *i*) care (i.e. interactions between a 'carer' and a dependent child) a composite value is created which captures all interactions dependent children in the now 'giving' household had received from the 'receiving household' (household *j*). In Figure 7.1, the now receiving household *(j)* is on the left, and have previously interacted with the dependent child in the now giving household *(i)* 25 times (an older child 10 times, the mother 10 times and the father 5 times). This figure (the interactions between allocarers of *j* to the dependent children of *i*) becomes the independent variable to explore its predictive value in understand the interactions between allocarers of *i* to dependent children of *j*. A limitation in this estimation is that it is restricted to the one week period of observation, therefore, similar to much of the literature on food sharing (Jaeggi & Gurven 2013b), this figure is likely underestimating long-term reciprocity.

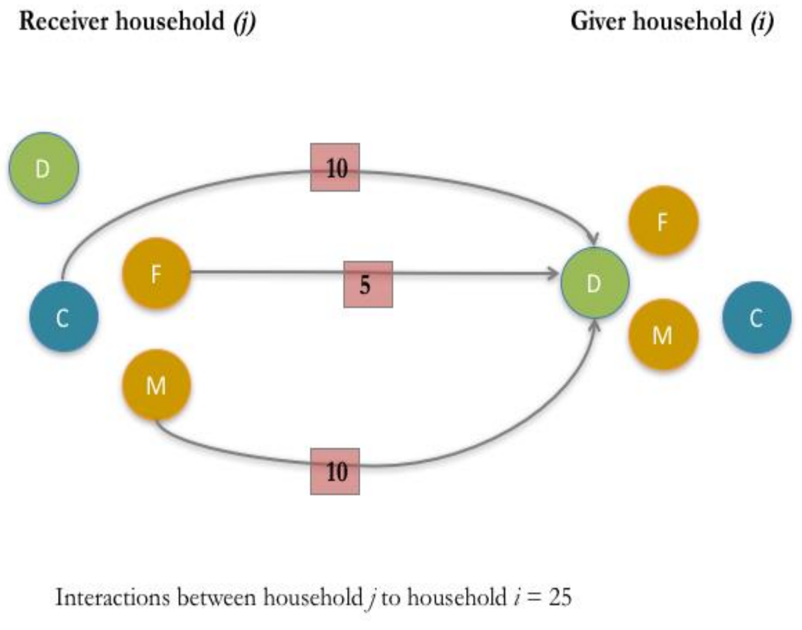

Figure 7.1: Visualisation of the contingency variable. D represents dependent child (green circle), C carer (blue circle), and M and F mother and father (orange circles), respectively. Red boxes represent the number of interactions between each individual in household *j* and to all dependent children in household *I,* which sum to 25.

7.3.2.2 Giver cost and receiver household need

Variables for giver cost and household care need were computed from the data. The cost (c) of offering proximity care is computed based on the number of dependents (d) and allocarers (a) in the giver household and ego's importance as a carer in their own household (defined below)(e), included to gauge opportunity costs of helping (Winterhalder 1996). This is weighted according to whether an infant was present in the household (infant present = 2, no infant = 1, infant defined as children aged under two years) (i) as allocare from households with infants are present is expected to be costlier. Children can be allocarers when they were aged 6 or older (as children aged 6 or older commonly provide care to younger siblings based on observations, such as carrying, playing and watching over). Thus, c is a product of:

$$c = (\left(\frac{\mathrm{d}}{\mathrm{a}}\right) * \mathrm{e}) * i$$

Ego's importance is based the distribution of care evident in the descriptive data (see section 6.4 above). As mothers provide the most care they were weighted as 0.5; fathers and siblings provide a significant amount of care but approximately half that of the mother, thus are weighted at 0.25. Thus, for a mother (Mc) from a household with four non-infant children and two allocarers the equation is:

$$Mc = ((4/2) * 0.5) * 1 = 4$$

Ego's importance is based the distribution of care evident in the descriptive data. As mothers provide the most care they were weighted as 0.5; fathers and siblings provide a significant amount of care but approximately half that of the mother, thus are weighted at 0.25. Siblings residing in the same household as the focal child were removed from the estimation of giver cost. Receiver household care need (D) is the product of the number of dependent children divided by the number of carers in a household multiplied by 2 if one dependent was an infant. Thus, the equation is:

$$D = \left(\frac{d}{a}\right) * i$$

7.3.2.3 Community detection

To attempt to understand association effects (Koster & Leckie 2014) a parental cluster variable was created. Here if the child's parents and allocarer belonged to the same proximity cluster they were coded as 1, otherwise 0. These clusters were created based on proximity in camps; lean-tos and shelters are commonly clustered together in twos and threes, and these reflect structures within the camps interactions. For instance, food sharing commonly occurs with these two or three nearby households (Dyble et al. 2016). Therefore, as a measure of repeated interactions due to shared space these clusters were used to capture association effects.

If a carer and a child were in the same cluster they were recorded as 1. As a result, the cluster variable represents the predictive value of the interactions between a child and their parents ‘associates’ or ‘neighbours’. Due to the fact that individuals were frequently clustered with close and distant kin the model may have suffered from collinearity when both the clustering variable and coefficient of relatedness were included. Consequentially, I checked the variance inflation factor (VIF) in full models and confirmed that VIFs did not raise above 2.5 and clustering and relatedness both had VIFs of 1.04, far below acceptable limits (Zuur *et al.* 2010).

Table 7.2: Descriptive statistics for binary variables at the dyadic level (*n* = 2,195)

Variable	Type	*n*	%
Giver sex	Male	1006	49.2
	Female	1039	50.8
Child sex	Male	1172	57.3
	Female	873	42.7
Pre-reproductive Juveniles	False	1259	61.6
	True	786	38.4
Grandmother interactions	False	2020	98.8
	True	25	1.2
Mobility	Mobile	886	43.8
	Settled	1136	56.2

7.3.3 Statistical analysis: why allocare

I ran multilevel models to explore the effects of coefficient of relatedness, giver cost, household need and reciprocity on the number of interactions a carer had with a child. In each analysis I controlled for location, child age and child sex. In contrast to the ‘who cares’ analysis in chapter 5, here interactions between parents and children were removed from the dataset, thus all remaining interactions reflect alloparents. The unit of analysis in the MLM was the dyadic relationship (level 1, *n* = 2,195) between a child and the giver (i.e. any individual interacting with them over the age of 6 years). As dependent children are all those under the age of 12 years there is overlap between the child and giver categories. To avoid this circularity children could only be 'cared' for by individuals who were older then themselves. For instance, a child of five years could be 'cared' for by an individual aged 8 years, a situation not uncommon from our observations and within the childcare literature in hunter-gatherers (Kramer 2010; Konner 2005). However, a child of 10 years could not be 'cared' for by the same 8 year old. These thresholds were felt to capture the crossover of juveniles as both dependents and carers (Kramer *et al.* 2009).

Table 7.3: Descriptive statistics for continuous variables (*n* = 200)

Variable	Minimum	Mean	Maximum	SD
Dyadic relatedness *(r)*	0	0.086	0.500	0.137
Giver cost	0	0.458	2.500	0.458
Receiver need	0.5	2.228	5	1.200
Reciprocity	0	5.239	53.4	9.481
Food storage (kg of rice)	0	1.527	14	3.407
Proportion of maternal activities foraging*	0	0.601	1	0.342

* Proportion of activities mother spent foraging compared to cash labour and cultivation

Working with dyadic data results in the pseudoreplication as each child and giver appears in the dataset multiple times. As a result, they are not independent data points and violate the basic assumptions in ordinary least squares regressions. However, the use of MLM overcomes this issue as it allows for clustering within the data (for full discussion see (Pollet *et al.* 2015)). The models in this analysis consider the fact that both the giver (level 2) and the child (level 3) are not unique entries, as well as the fact they are hierarchically clustered into camps (level 4). These models seek to test the competing hypothesis for why individuals perform costly care (kin selection, reciprocal altruism, grandmothering and helpers-at-the-nest). Thus I explore the relationships between coefficient of relatedness, household need, giver cost, reciprocity, association and reproductive stage on the number of interactions between each dyad.

7.4 Results

7.4.1 Do Agta mothers require allocare?

In short, yes. By examining the distribution of the household need index by maternal age (Figure 7.2) it is evident that swiftly after commencement of reproduction mothers have more dependents than carers. This peaks between the ages of 25 to 30 when mothers have several young offspring. For instance, it was not uncommon to witness young mothers with a newborn infant, a young toddler *and* an older child around five years. This childcare deficit does not start to significantly drop-off until between the ages of 35-40 years, when mothers have several older children to provide childcare. As a result, Agta mothers face up to 15 years of their reproductive lifespan with a shortage of care, indicating the importance of allocare from not only siblings (when available), but also from individuals outside the nuclear family. As a result, it is expected that distant kin may provide more care the more in childcare 'need' a household is in when mother's do not have older siblings available to provide allocare.

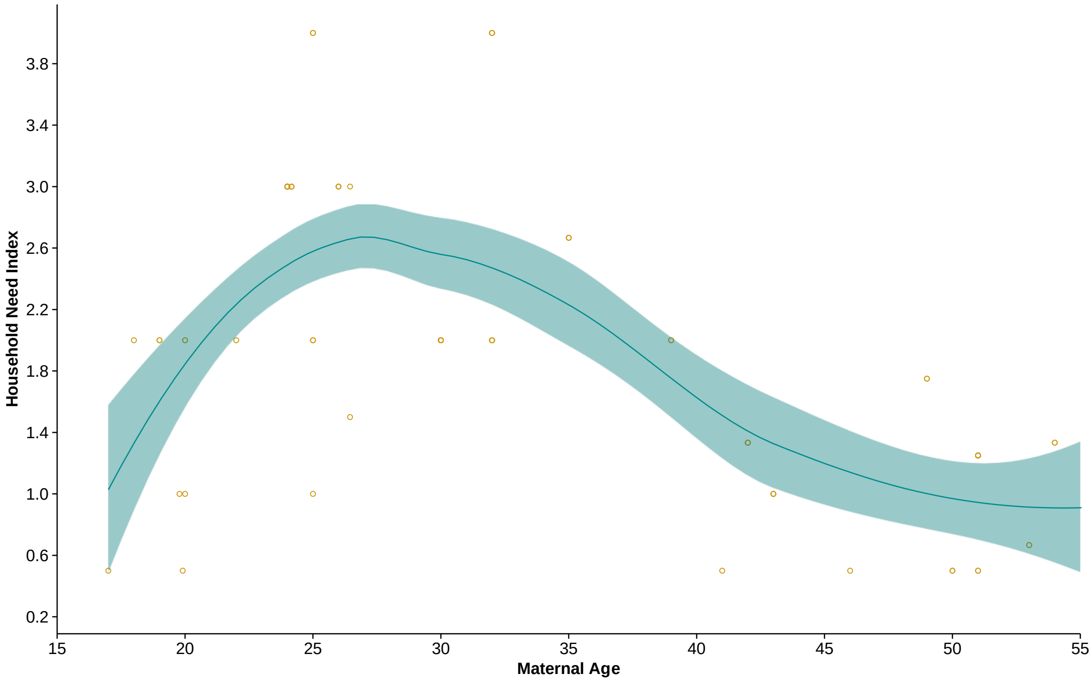

Figure 7.2: Relationship between maternal age and household care need. One outlier (need = 5) has been removed here to allow an improved view of the majority of the data. Shaded area represents 95% confidence interval of the smoothed regression between the household need index and age (with loess smoothed fit curve), *n* = 39.

7.4.2 Why allocare?

All models are presented in Table 7.4, the first panel being the intercept-only model which contains only random effects (i.e. the levels) with additional covariates being included in each following model (Koster *et al.* 2015). The VPCs (variance partition coefficients, see methods section 0) in the intercept-only model reveal that 12.9%, 7.6% and 7.5% of the variance in proximity interaction was attributed to the giver, receiver and camp factors. The remaining 72% of variance is attributed to unique dyadic factors. Giver cost ($B_4 = -2.5$), relatedness ($B_5 = 6.2$) and clustering ($B_6 = 2$), all predict the number of interactions between an allocarer and child. While related individuals or those who associated frequently with a child's parents are in contact with a child significantly more often, individuals whose proximity care comes at a higher cost (measured by the cost index noted above) are in contact significantly less. Giver cost, relatedness and clustering reduce the unique dyadic variance by 16.6%, 5.4% and 12.1%, respectively. Consequently, co-residence and cost seem to explain more variance than relatedness by itself.

Contra predictions, reciprocity did not significantly predict the amount of dyadic contacts; its inclusion in the model increased the AIC (from 7987.9 to 7989.9) indicating its lack of predictive power. Furthermore, household need held a negative relationship with the number of dyadic interactions ($B_8 = -0.2$, $p = 0.03$, 95% CI [-0.3, -0.01]). However, the inclusion of interactions demonstrates that more care is offered to the recipient household the higher the household need *if* the giver is related. The inclusion of interactions results in a reduction of the dyadic variance by 1.3% from the previous model. However, relatedness no longer independently predicts the number of dyadic contacts ($p = 0.3$), implying that the care offered by kin is contingent on recipient need. Furthermore, the interaction also revealed that allocarers less closely related to a child provide significantly less care when that child is from a needy household ($B_8 = -0.2$).

Table 7.4: Results from multilevel models examining different predictors for the amount of dyadic interactions. Table continues below.

	intercept-model		Giver cost		Relatedness		Cluster	
Parameter	**β**	**CI**	**β**	**CI**	**β**	**CI**	**β**	**CI**
Intercept	1.45**	0.82, 2.1	2.29**	1.52, 3.05	1.09**	0.27, 1.89	0.733	-0.24, 1.70
Child age	-	-	0.016	-0.04, 0.06	0.014	-0.04, 0.07	0.006	-0.04, 0.06
female child	-	-	-0.110	-0.44, 0.23	-0.105	-0.43, 0.23	-0.110	-0.43, 0.21
Costal			-0.048	-1.02, 0.98	-0.142	-1.18, 0.96	0.121	-1.18, 1.45
Giver cost	-	-	-2.48***	-2.83, -2.14	-0.52**	-0.83, -0.21	-0.476**	-0.78, -0.18
Relatedness	-	-	-	-	6.17***	5.41, 6.92	3.45***	2.69, 4.22
Cluster membership	-	-	-	-	-	-	1.97***	1.76, 2.18
Giver variance	0.653 (12.9%)		1.53 (29.5%)		0.65 (15.6%)		0.667 (17.2%)	
Receiver variance	0.385 (7.6%)		0.42 (8.2%)		0.412 (10%)		0.403 (10.4%)	
Camp variance	0.383 (7.5%)		0.17 (3.3%)		0.245 (5.9%)		0.409 (10.5%)	
Dyadic variance	3.656 (72%)		3.05 (59%)		2.849 (68.6%)		2.405 (61.9%)	
Model AIC	8755.700		8520.800		8298.800		7987.900	

Model betas are reported alongside 95% confidence intervals. Significant p-values at $p = 0.05$ are represented with '*', $p = 0.01$ with '**' and $p < 0.001$ with '***'. Giver, receiver, camp and dyadic variances are presented alongside VPC in brackets and represent the importance of each of these levels as sources of variation in interactions.

Table 7.4 continued

	Reciprocity		Household need		Reproductive stage		Full model	
Parameter	**β**	**CI**	**β**	**CI**	**β**	**CI**	**β**	**CI**
Intercept	0.74	-0.25, 1.76	1.2**	0.20, 2.27	1.09*	0.02, 2.15	1.15*	0.02, 2.28
Child age	0.01	-0.04, 0.06	0.00	-0.05, 0.05	0.00	-0.05, 0.05	0.00	-0.05, 0.06
female child	-0.11	-0.43, 0.21	-0.15	-0.48, 0.17	-0.14	-0.46, 0.18	-0.16	-0.49, 0.18
Costal	0.13	-1.20, 1.53	0.14	-1.16, 1.50	0.14	-1.21, 1.54	0.17	-1.27, 1.67
Giver cost	-0.5**	-0.78, -0.17	-0.6***	-0.88, -0.27	-0.49**	-0.81, -0.19	-0.34**	-0.65, -0.03
Relatedness	3.5***	2.69, 4.24	0.59	-0.63, 1.82	0.65	-0.58, 1.88	-0.48	-1.74, 0.77
Cluster membership	2***	1.78, 2.18	2***	1.79, 2.20	2.0***	1.79, 2.2	2***	1.79, 2.20
Household reciprocity	0.00	-0.02, 0.02	0.00	-0.02, 0.02	-0.01	-0.02, 0.02	-0.01	-0.03, 0.01
Household need	-	-	-0.20*	-0.35, -0.05	-0.2**	-0.35, -0.05	-0.19*	-0.35, -0.04
Relatedness*need	-	-	1.4***	0.91, 1.82	1.3***	0.87, 1.78	1.3***	0.84, 1.74
Grandmother	-	-	-	-	0.59	-0.12, 1.30	2.3**	0.60, 4.04
Juvenile	-	-	-	-	0.3***	0.12, 0.80	0.24	-0.24, 0.47
Grandmother*need	-	-	-	-	-	-	-0.77*	-1.44, -0.09
juvenile*r	-	-	-	-	-	-	1.6***	2.80, 5.02
Giver variance	0.665 (17%)		0.669 (17.5%)		0.637 (16.5%)		0.63 (16.1%)	
Receiver variance	0.403 (10.3%)		0.402 (10.5%)		0.401 (10.4%)		0.42 (10.6%)	
Camp variance	0.43 (11%)		0.405 (10.6%)		0.465 (12%)		0.51 (13.2%)	
Dyadic variance	2.41 (61.6%)		2.36 (61.5%)		2.36 (61.1%)		2.34 (60.1%)	
Model AIC	*7989.80*		7958.40		7955.10		7947.30	

Being a grandmother ($B_9 = 0.6$) did not significantly predict dyadic proximity. However, juveniles were in proximity to dependent children significantly more, dependent on relatedness (final panel, 'full model' in Table 7.4). The juvenile covariate had a significant positive interaction with relatedness, demonstrating that related juveniles interacted more with children. This effect is large and very significant ($B = 1.6$, $p < 0.0001$). As a result, unrelated juveniles did not offer significantly more care in the full sample ($B_{10} = 0.2$, $p = 0.2$). Thus, this indicates that a significant proportion of the relationship between kinship and proximity is driven by juvenile allocare. It is worthwhile noting that in the early model, kinship had a large effect on the amount of care offered to children ($B_5 = 6.2$), however the inclusion of the measures clustering ($B_3 = 3.5$), household need ($B_3 = 2.7$) and juveniles ($B_3 = -0.5$) resulted in a large reduction in effect and significance. Finally, grandmothers appeared, *contra* predictions, to provide significantly less care when the household was in need ($B = -0.8$) compared to when they were not in need ($B_9 = 2.3$). This reveals that grandmaternal care is not reactive to long-term care deficits of their offspring (as measured by household need).

Once all fixed-effects are entered into the final model, the resultant dyadic variance is 2.3, representing an overall decrease of 36%, mainly produced by relatedness and parental clusters, with a positive interaction between receiving household's childcare need and the relationship between pre-reproductive females and relatedness. The camp and receiver variances were otherwise unchanged, while giver variance decreased by 4.1% in the final model. Overall, it seems that lower costs and higher benefits of caring outweighed relatedness, particularly given the dependency of relatedness on reproductive stage (i.e. being a juvenile) and household need. Reciprocity appears to offer little explanatory power (however as noted it may not be capturing true reciprocity, just repeated interactions between households) in the full sample, thus it is unclear why less related or unrelated individuals provided proximity care. However, I hypothesised that this was due to different types of kin having different motivations. Thus, I made the following predictions: *(i)* care from close kin will be better predicted by kin selection, weighted by costs and benefits; *(ii)* distant kin and non-kin provide more care according to reciprocity, weighted by costs and benefits, however *(iii)* distant kin will offer costlier care than non-kin given that they can also receive indirect benefits if care is never returned.

7.4.3 Analysis by kin group

To explore how the predictive power of household care need, giver cost and dyadic reciprocity vary according to kin type the dataset was analysed with interactions with each of the three kin categories: close kin (*n* = 136), distant kin (*n* = 485) and non-kin (*n* = 1,424). Given that parents have been removed from this analysis, close kin includes *only* full siblings. These siblings range from age 6.2 to 27, with a mean age of 12.8 ± 4.8 years. Thus, the majority (73.5%) are juveniles while the rest are young adults. As a result, their giver cost measures are consistently lower. Distant kin includes grandparents, aunts and uncles and first cousins. Non-kin subsumes both distantly related individuals (first cousins once removed, second, third and fourth cousins) as well as individuals completely unrelated. All multilevel models control for age, sex, camp and household, retained the dyad at level one, giver at level two and child at level three. Full results are presented in Table 7.5**.**

Figure 7.3 reveals, as above, that close kin had significantly more interactions with children than distant kin and non-kin, however the slope of these relationships was dependent on the giver cost and household need. There was a significant interaction between household need and kin type; care from distantly and unrelated individuals decreased with recipient need, while care from close kin increased (Table 7.5).

Model one examining the influence of the cost of care demonstrates that while proximity with close kin, distant kin and non-kin decreases the more care was costly to the giver, the effect is not significant in the reference category of close kin (B = -0.19, p =0.7). As predicted cost was associated with decreased interactions with distant kin and non-kin (as compared to close kin), however contra predictions the effect was much stronger for distant kin than non-kin. In fact, the relationship between non-kin and cost is not significantly different to that of close kin and cost. As a result, as evident by Figure 7.3, at cost 1.5 non-kin are predicted to offer more care than distant kin.

In model two (receiving household need) we see that following predictions close kin interact more with dependent offspring the higher the household need. However, contra predictions both distant kin and non-kin interact less with children from needy households. Again we see the slope is much steeper for distant kin (B = -1.23) as compared to non-kin (B = -0.94), suggesting the negative effect of need is much stronger in distant kin. Rather than interacting significantly more when recipient need is high, suggestive of high benefits of care, at the highest need (4-5) distant kin care falls to the same level of non-kin care.

Table 7.5: Predictors of allocare separated by kin type. Multilevel model with dyadic relationship at level 1 (*n* = 2045), giver at level 2 (*n* = 148) and child at level 3 (*n* = 85). In these models the reference group is close kin. The predictor is relevant to the model (i.e. cost, need or reciprocity). The correct interpretation of these results are as follows: distant kin and non-kin are compared to close kin, the 'predictor' beta is that of close kin given it is the reference category and the interaction terms ('predictor*distant') refer to the effect of, for instance, high cost care on interactions with distant kin compared to close kin.

	Cost			**Need**			**Reciprocity**		
Parameter	**B**	***p***	**CI**	**B**	***p***	**CI**	**B**	***p***	**CI**
Intercept	1.762	<0.001	0.96, 5.57	0.938	0.035	0.06, 1.81	2.203	<0.001	1.48, 2.93
Location	-0.260	0.241	-0.70, 0.18	-0.241	0.277	-0.68, 0.20	-0.299	0.174	-0.73, 0.14
Child Age	0.009	0.733	-0.04, 0.06	0.003	0.919	-0.05, 0.06	-0.002	0.953	-0.06, 0.05
Female child	-0.117	0.505	-0.46, 0.23	-0.175	0.317	-0.52, 0.17	-0.095	0.570	-0.43, 0.24
Female carer	0.543	0.001	0.23, 0.87	0.352	0.024	0.04, 0.66	0.367	0.022	0.05, 0.68
Household	2.957	<0.001	2.36, 3.55	2.548	<0.001	2.03, 3.06	3.162	<0.001	2.64, 3.68
Distant Kin	0.565	0.103	-0.12, 1.25	1.911	<0.001	1.20, 2.62	-0.683	0.019	-1.25, -0.11
Non-Kin	-0.816	0.017	-1.46, -0.14	0.231	0.501	-0.44, 0.90	-1.432	<0.001	-1.99, -0.87
Predictor	-0.192	0.710	-1.2, 0.82	0.767	<0.001	0.48, 1.05	-0.036	0.004	-0.06, -0.01
Predictor*distant	-1.399	0.008	-0.12, -0.36	-1.229	<0.001	-1.51, -0.95	0.080	<0.001	0.05, 0.11
Predictor*non-kin	-0.423	0.411	-1.43, 0.59	-0.938	<0.001	-1.20, -0.67	0.042	<0.001	0.02, 0.07
Giver Variance	0.667			0.686			0.720		
Child Variance	0.485			0.470			0.435		
Residual	2.653			2.594			2.652		

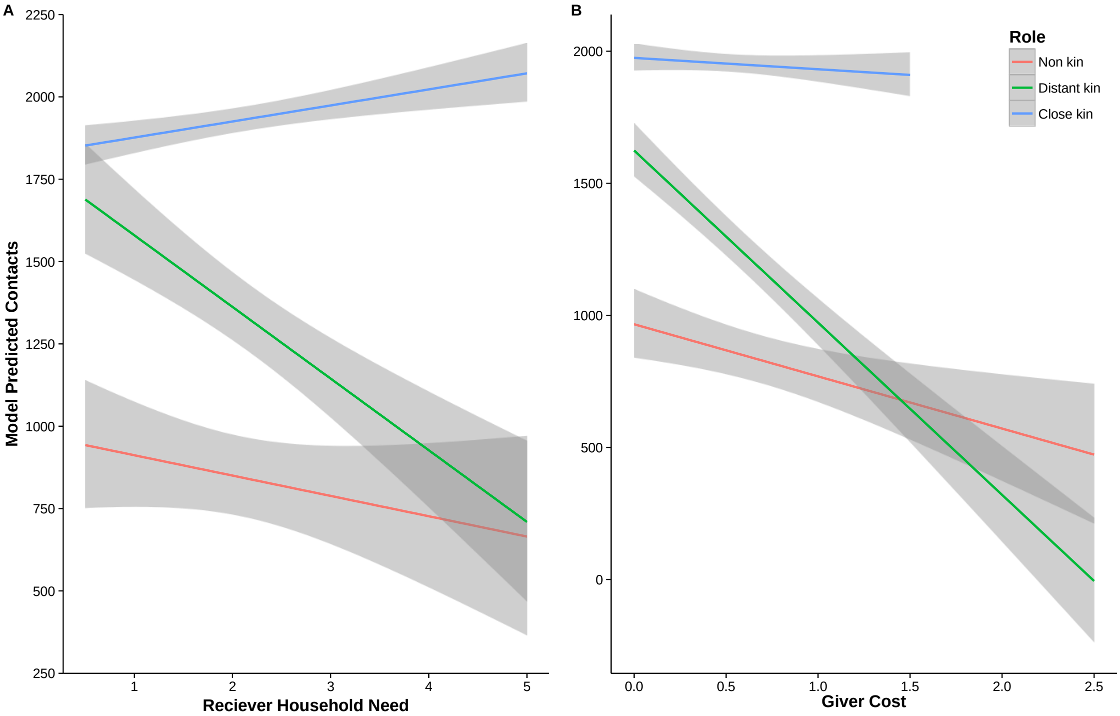

Figure 7.3: Model predicted number of contacts based on interactions between kin type and A) household need and B) giver cost. Siblings in plot B have a lower range in cost because their care is not as 'costly' as they are providing care within the household. Siblings outside the household are relatively young and have a lower giver cost as only just starting reproduction.

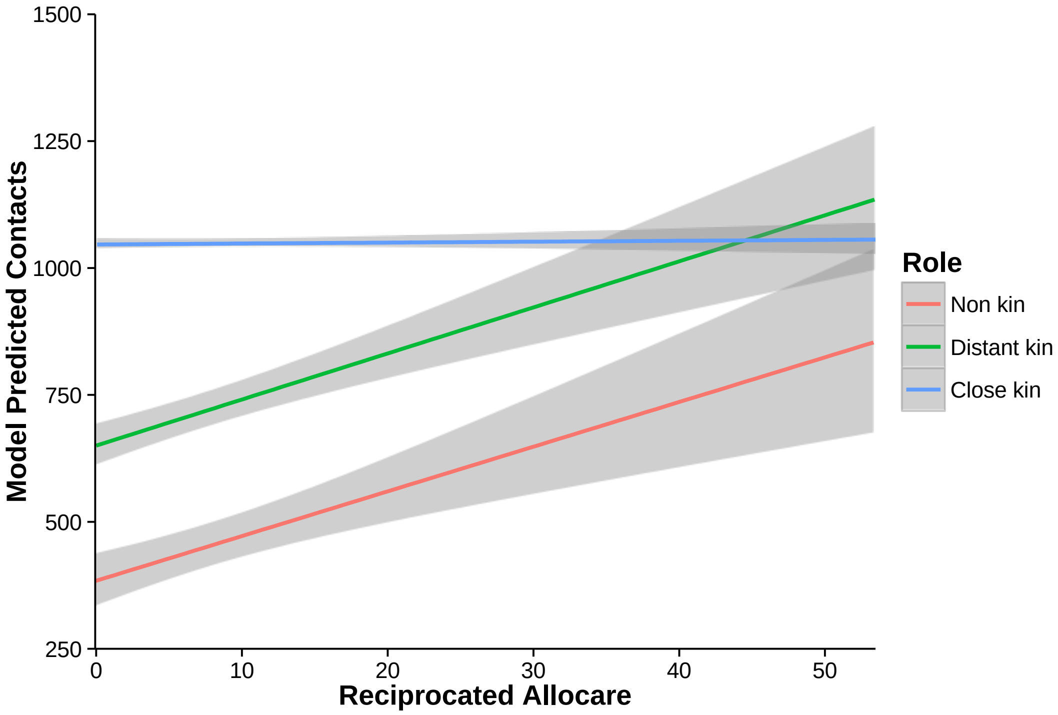

Figure 7.4: Model interaction plot separated by kin type for reciprocated allocare.

Consequently, close kin interactions appear to meet the predictions of kin selection exactly, as they offer the most care particularly at increasing household need, and are less reactive to the costs of the interaction. However, distant kin are not following the same pattern.

Proximity with non-kin (B = 0.04, $p < 0.001$) and distant kin (B = 0.08, $p < 0.001$) increases the more this proximity is reciprocated compared to close kin (i.e. children from household A whose allocarers are regularly in contact with dependent children from household B interact significantly more with the allocarers from household B, Figure 7.4); however, care from close kin significantly decreases (B = -0.04, $p = 0.004$) the less care is reciprocated between the households. This follows, given that close kin assist households more in 'need' of allocare, thus these are the households least able to reciprocate care, given their high numbers of dependents compared to carers.

Overall I find support for the predictions that interactions with close kin (here restricted to siblings as parents have been removed from the analysis) was best predicted by kin selection while distant kin and non-kin allocare was better predicted by reciprocity (Table 7.6). Again siblings' importance is reinforced as they interacted the most with dependent children, and were particularly reactive for long-term need. However, neither distant kin nor non-kin were reactive to long-term needs of the household, which makes the benefit of cooperation unclear. This may be because I have not captured the dynamics of short-term need, which they may be more reactive to (i.e. daily variability in childcare). Nonetheless, it appears that non-kin may be more reliable allocarers at high cost than distant kin. This begs the question of what benefits do non-kin gain from interacting with dependent children particularly at these high costs and how this is different from distant kin.

One likely factor is that the role of unrelated juveniles in providing childcare in the form of playgroups (or crèches, commonly without the presence of a mother). Observationally mixed-age and mixed-sex playgroups were common and included children aged from 2.5 to late teens (13 – 15 years). Often a few older children would watch over many of the younger children. While siblings would be present in this group, many of the interactions were with unrelated children. Thus, childcare is likely low cost for these children as they are providing care for multiple individuals simultaneously: some who are related, some who are not. An important point here, as discussed previously is the consideration of play to be a form of 'allocare' as it has the ability to reduce maternal energetic burden and is an important aspect of hunter-gatherer childhood as more 'active' forms of childcare are rare beyond infancy, such as teaching and grooming. This was demonstrated in chapter 5, revealing that childcare in the Agta is dominated by lower investment activities.

Suggestive of the trend of playgroups is the finding that in the non-kin dataset (n = 1,424) being a juvenile aged less than 16 significantly increased the number of interactions with a non-kin child compared to individuals of reproductively active age group (aged 16 to 50 years, B = 0.4, p = 0.006, 95% CI [0.1, 0.7]). However, no such trend was apparent in the distant kin data set (n = 485) as juveniles did not provide significantly more care than reproductively active individuals (B = 0.5, p = 0.3, 95% CI [-2, 1.2]). Thus, while non-kin care is defined by low-cost, juvenile allocare, distant kin care is not, and if many distant kin (i.e. aunts, uncles and grandparents) are reproductive active adults then their allocare would be highly influenced by their heavy cost of allocare due to reproductive stage. This is reinforced by chapter five which demonstrated that when proximate to dependent children non-kin are frequently involved in playing activities and are rarely simply proximate to that child.

Table 7.6: Results from interaction analysis with kin types. Minus symbols represent when the amount of interactions decreases with a predictor while plus signs are present when proximity care increases. Thus, in reading the second row "household need" this reveals that contacts from close kin increase with household need but decrease with household need from distant kin and non-kin.

	Kin types		
Predictor	**Close kin**	**Distant Kin**	**Non-kin**
Contact	High	Medium	Low
Household Need	+	-	-
Giver Cost	NE	-	-
Reciprocity	-	+	+
Supportive of…	*Kin selection*	*Reciprocity*	*Reciprocity*
Allocarers are…	*Siblings*	*All ages*	*Juveniles*

7.4.4 Variability in allocare: influence of ecology and 'transition'

Here, I explored the relationship between subsistence change and ecology on the proportion of interactions with different kin type. The total sample was reduced to 66 children due to missing wealth data. Separate models were run for each of the different dependent variables (interactions with mother, father, siblings, grandparents, distant kin and non-kin). All models initially included all four ‘transition’ predictor variables (settlement, household foraging, belongings, food storage); however, the maximal model containing all predictors suffered from multicollinearity (variance inflation factors above 2.5 (Zuur *et al.* 2010)). As a result, following AIC ‘best fit’ procedures (Burnham & Anderson 2004), food storage and mobility were removed from the models (in all cases except the grandparental care model, in which mobility was retained as it produced the model with the lowest AIC score). The relationship between foraging and childcare appeared mediated by location, thus all models were run with an interaction between foraging and location. If this interaction was non-significant it was removed to produce the most parsimonious model. Details and AIC values of the different models are shown in (Table 7.7). Due to the focus on the mother throughout this thesis I have chosen to use maternal proportion of work activities spent foraging as the household measure. However, in the case of examining what predicts paternal care it was appropriate to use paternal time spent in foraging, thus paternal foraging is used in the paternal care analysis *only*. The key predictions in this section are: *(i)* children at the coast receive care from a smaller network of individuals focused on the nuclear family due to relative bounty and a reduction of variance in foraging returns; and *(ii)* children from wealthier households with increased involvement in wage labour and cultivation will receive care from a smaller network of individuals focused on the nuclear family as risk-pooling is replaced by risk retention.

Final model results are detailed in Table 7.8 and demonstrate three trends. Firstly, as predicted, the proportion of time spent in foraging is associated with a reduction in interactions within the nuclear family (mother, father and siblings). However, there was no significant positive relationship between foraging and distant kin or foraging and non-kin. Nonetheless, it appears that more household belongings are associated with decreases in interactions from extra-familial sources, including grandparents, distant kin and non-kin (Figure 7.5). Furthermore, if we simply take all close kin ($r = 0.5$) we find that household wealth is significantly associated with more interactions with close kin ($B = 11.2$, $p < 0.001$, 95% CI [3.9, 18.2]). Thus it appears, that household wealth results in a more nuclear family focused network while increased foraging decreases it.

Table 7.7: Model selection details for each of the six analyses separated by kin type. Lowest AIC represent the best fit model and were used in the final analysis. Each maximal model consisted of all four 'transition' variables (food storage, mobility, household belongings and proportion of time spent foraging) as well as child age, sex and location (coastal or inland). Interactions were run with measures of transition of location in the first instance, all insignificant interactions were removed in final models. Z-scores greater than 1.96 are statistically significant (*n* = 66).

Dependent variable	Model	DF	AIC	Removed variables
Maternal care	Maximal model	12	-17.276	Food storage and mobility
	Best fit model	10	-20.516	
	Non-interaction	9	-14.197	
Paternal care	Maximal model	12	-64.886	Food storage and mobility
	Best fit model	10	-67.610	
	Non-interaction	9	-63.583	
Sibling care	Maximal model	12	7.831	Food storage and mobility
	Best fit model	10	4.033	
	Non-interaction	9	9.847	
Grandparental care	Maximal model	11	-154.850	Food storage
	Best fit model	10	-156.400	
	Interaction non-significant (z = -1.100)			
Other kin care	Maximal model	11	-239.302	Food storage and mobility
	Best fit model	9	-241.053	
	Interaction non-significant (z = -1.070)			
Non-kin care	Maximal model	11	-258.948	Food storage and mobility
	Best fit model	9	-259.583	
	Interaction non-significant (z = 0.112)			

The relationship between foraging and contact care from the nuclear family was dependent on location; children at the coast whose households partook in more foraging interacted more with their mothers, siblings and fathers. Such divergent results were unexpected; however, this result may be influenced by the relative bounty at the coast compared to inland.

Food production data comparing four inland and four coastal camps demonstrates the higher efficiency of marine fishing (Table 2.4). Consequently, individuals at the coast spent significantly less time in food production and more time socialising, resting and playing (Figure 2.7). Primary kin may then, have more time to spend with offspring if they spent a higher proportion of activities fishing. Anecdotally the nature of fishing trips was different depending on whether they occurred in the intertidal zone or in a river. River fishing was primarily conducted by males and unmarried or post-reproductive females; it was rare for younger children to be taken along. However, fishing on the reef allows a range of activities for older males (spearfishing) and women and children (octopus, shrimp and shellfish catching as well as collecting many other types of mollusc). As a result, fishing trips were often family affairs conducted over the course of a day as the family created a temporary shelter by the fishing spot. Thus, increased marine fishing need not necessitate a reduction in family care, as does hunting, gathering or river fishing.

Table 7.8: MLM results for predictors of care (age, location, subsistence and wealth) from different kin types. All covariates entered into the models are reported. Model betas are presented alongside 95% confidence intervals. Variables significant at $p < 0.05$ are highlighted in bold, $n = 66$. Child sex is controlled for in this analysis. GP stands for grandparents.

	Predictive variables				
Kin type	**Child age**	**Coastal**	**Foraging**	**Coast* Foraging**	**Household belongings**
Mother	**-0.05 [-0.1, -0.03]**	0.05 [-0.1, 0.2]	**-1.1 [-1.8, -0.4]**	**1.1 [0.5, 1.8]**	-0.07 [-0.2, 0.0]
Father	**-0.01 [-0.02, -0.0]**	-0.02 [-0.5, 0.01]	**-0.4 [-0.7, -0.1]**	**0.4 [0.1, 0.7]**	-0.03 [-0.1, 0.1]
Sibling	0.01 [-0.03, 0.01]	0.2 [-0.6, 0.1]	**-1.5 [-2.8, -0.4]**	**1.8 [0.7, 3.1]**	-0.1 [-0.2, 0.1]
GP	-0.004 [-0.01, 0.0]	**0.01 [0.01, 0.2]**	0.1 [-0.00, 0.14]	-	**-0.04 [-0.1, -0.00]**
Distant kin	0.002 [-0.00, 0.0]	**0.06 [0.03, 0.1]**	0.02 [-0.01, 0.05]	-	**-0.02 [-0.04, -0.01]**
Non-kin	**0.002 [0.0, 0.01]**	0.02 [-0.02, 0.1]	-0.02 [-0.1, 0.01]	-	**-0.02 [-0.04, -0.01]**

Child age and location have an effect on interactions from some kin types. Matching the results from chapter 6 (Table 6.1), it is evident that mothers and fathers provided statistically more care the younger the child was; however, with increasing child age non-kin became more important (Figure 6.3). Residing at the coast was independently associated with increases in care from grandparents and distant kin, however this did not reach statistical significance for non-kin ($p = 0.2$). Thus, there appears to be a trend of wider childcare networks at the coast (Figure 7.5, plots B and C) *contra* predictions. A possible explanation is that given the 25.2% larger packet sizes at the coast (mean size in kcal 2322.7 versus 1855.3) compared to inland, resources appear less constrained implying that the presence of greater numbers of distant kin may be sustainable at the coast (i.e. less competitive and demanding relationships), thus allowing for the aggregation of larger extended families.

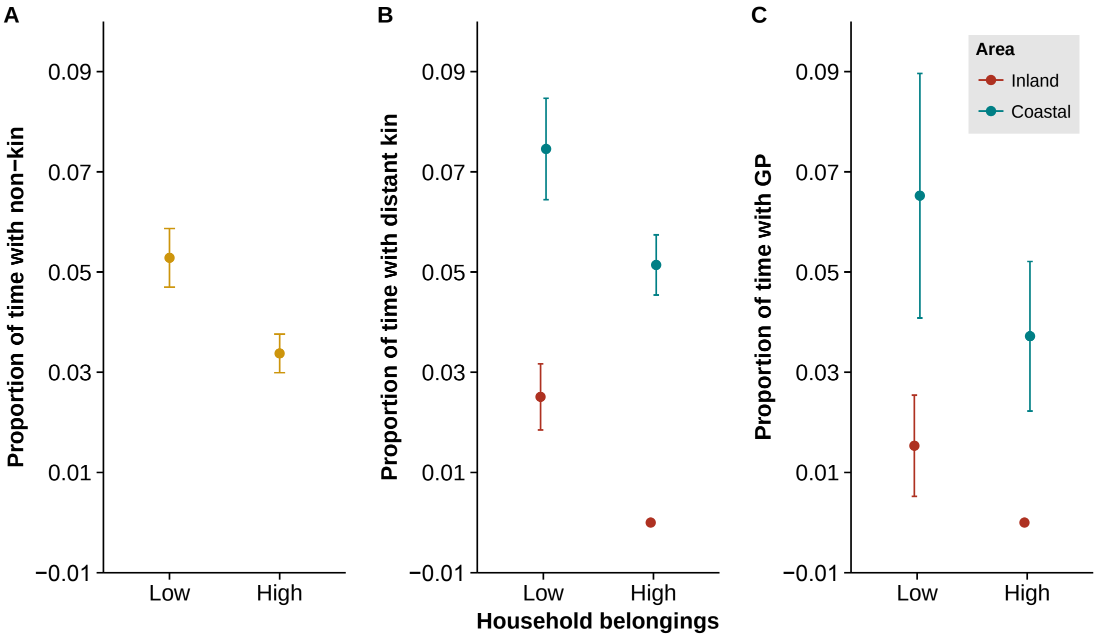

Figure 7.5: The relationship between household belongings and proportion of time spent with non-kin (A), other kin (B) and grandparents (C). Proportion of time spent with distant kin and grandparents is significantly affected by location; coastal children spent more time with individuals distantly related to them ($0.125 \leq r \leq 0.25$). High household belongings are those above the mean (1.7), and those with low household belongings are at or below the mean. Plot A only has one set of data points as there is no significant interaction between non-kin interactions and location ($n = 66$).

To summarise this section, the evidence is supportive of prediction *(ii)* that wider cooperative networks become replaced by increasing wealth and alterations in subsistence. However, the evidence does not support the prediction *(i)* that coastal groups will have smaller cooperative networks.

7.5 Discussion

7.5.1 Kin selection, reciprocity and the role of the unrelated allocarer

The data clearly support the hypothesis that close kin interactions are related to inclusive fitness benefits. Interactions increase with the coefficient of relatedness; close kin offer more care when the recipient household is in need; allocare by close kin is uninfluenced by contingency. Thus, this fills each expectation stemming from Hamilton's (1964) equation $rB > C$, and it can be deduced that siblings interact with the dependent children primarily for inclusive fitness gains (as compared to direct benefits, for instance). However here, it is helpers-at-the-nest or siblings who provide the majority of allocare, not grandmothers (Table 7.9).

Table 7.9: Summary of the main results from the 'why care' analysis. If the prediction was met the indictor is marked with a ✓, otherwise with a ✗. If the indicator was not explored, it is marked with a question mark.

	Indicators				
Theory	**R**	**Contingency**	**Benefit**	**Cost**	**Clustering**
Kin selection: care pooling	Closer kin offer more care	Not present among close kin; care given according to need	Increases care from close kin	Decreases care	Close kin offer the most care
	✓	✓	✓	✓	✓
Reciprocal altruism: variance pooling	-	Distant kin and non-kin care increases with reciprocation	Stochastic need not measured	Care decreases with increasing cost; non-kin less reactive than distant kin	Individuals outside the nuclear family participate in variance pooling
	-	✓	?	✓/✗	✓
Helpers-at-the-nest	Related juveniles interact more	Sibling care was not predicted by contingency	Increases care from siblings	Low cost significantly predicts care as siblings interact heavily	Care from within the household
	✓	✓	✓	✓	✓
Grandmother	MGM offer more care (chapter 5)	Distant kin offer more reciprocal care	Grandmothers offer less care when the benefits are high	Grandparents offer little care comparative to other kin types regardless of the low cost	Extended kin do not offer significant amounts of care (chapter 5)
	✓	✗	✗	✗	✗

Human mothers, due to their high reproductive rate, have multiple dependent offspring. Here, I have revealed that mothers face a major proportion of their lifespan with more offspring than they could arguably care for alone. This is what Hill & Hurtado (2009) refer to as predictable life history shortfalls as each mother will face the deficit of care arising from the relatively rapid production of offspring. This is a long-term shortfall, thus reciprocity should not be foreseeable in the near future, and consequentially kin are expected to provide more allocare given indirect fitness gains from cooperation (Allen-Arave *et al.* 2008; Hooper 2015). Accordingly, I have demonstrated here that siblings' allocare meets the expectations of 'care-pooling': that they offer more care the higher the need of the household (i.e. the more dependents versus carers) resulting in an imbalance, as care is unidirectional. Thus, I argue that without this, mothers would not be able to maintain such a reproductive rate, suggesting the adaptive value of helpers-at-the-nest. These results further support the results and conclusions of chapter 6.

However, *contra* predictions we do not see the same pattern among distant kin, given that distant kin, and grandmothers in particular, appeared to reduce interactions with increasing household need. This may occur because grandmothers increase food production to cater for more dependent grandchildren, thus combining food provisioning with direct childcare is an essential next step to explore these questions further. Nonetheless, here it appears that direct childcare is not unbalanced according to need (as predicted by kin selection) and distant kin cannot be argued to be care pooling due to long-term life history shortfalls, driven by indirect fitness gains. Similar results have been found elsewhere, as the effects of kinship quickly evaporate as r decreases (Koster & Leckie 2014). This dynamic is not unexpected as more distantly related individuals receive a higher fitness return from following a tit-for-tat strategy rather than kin selection (Axelrod & Hamilton 1981). Tit-for-tat is expected when $Bp > C$ (p = the probability of future interactions). Whenever the value of p exceeds the dyadic coefficient of relatedness, cooperation should be governed by reciprocal altruism, not kin selection (Allen-Arave *et al.* 2008; Gurven *et al.* 2001). This appears to be the case among the Agta; while in the full sample reciprocity was not a significant predictor of allocare, it is among distantly and unrelated individuals. Therefore, among distant kin, as has been found in food sharing among the Ache (Allen-Arave *et al.* 2008), it seems that even if cooperative dyads are related, their sharing is motivated by reciprocal altruism rather than kin selection. Thus, it is foolhardy to argue that nepotistic mechanisms drive cooperative breeding without exploring costs, benefits and conducting multivariate analyses to weigh up different hypotheses (Barclay & Reeve 2012). While this strategy does not reveal causality, it does effectively discriminate between causal hypotheses and allows for the controlling of confounders, such as association (Shenk & Mattison 2011).

Apicella & Crittenden (2013) lament the lack of data about childcare from unrelated individuals. Given that all societies maintain significant social ties with unrelated individuals, it seems a large oversight to ignore their role in communal breeding. In chapter 6, I demonstrated that non-kin comprised of a significant proportion of interactions with a child, and while the majority of non-kin interact infrequently, a few provide a level of contact comparable to close kin. Thus, similar to the results among the Hazda (Crittenden & Marlowe 2008) and Efe (Ivey 2000), non-kin are providing a significant amount of care, indicating their importance. This is not to undermine the role of close kin, indeed non-kin interact the least with children as compared to close kin and distant kin. However, a few non-kin do interact a significant amount which requires explanation. Given that, as revealed by Figure 7.2, even considering the role of older 'caring' siblings, mothers face periods of care shortage which can be amplified due to further unpredictable shortfalls in care, having additional allocarers fully outside the household can be considered to be important strategy of mitigating risk. This raises the question: why do unrelated Agta allocarers provide care? I suggest that reciprocal altruism is a potential solution for unpredictable shortfalls as a form of risk pooling.

Risk transfer is any action which distributes risks between different 'exposure units', in this case individuals and households. Units all accept immediate, but small losses (i.e. cooperation) when they can afford to do so and thus, mitigate the severity of future unpredictable and larger losses (Aktipis *et al.* 2011). As argued in section 3.2.4, this is another expression of reciprocal altruism in which actors suffer short-term costs for higher total returns at some point in the future. Cashdan (1985) argued that for risk transfer to be an effective method of buffering unpredictable shortfalls, the network of reciprocators must be large and the exposure units independent. Thus, it follows that here I find that contingency best predicts the amount of care received from distant kin and non-kin only. These individuals outside of the immediate household, thus experiencing different patterns in foraging returns influenced by sickness and disability as well as hunting success. Furthermore, reciprocity in childcare appears dependent on costs as both distant kin and unrelated individuals offer significantly less care when they themselves experience a high cost in childcare, supporting the variance-pooling hypothesis. However, I have not measured stochastic need in this study; thus it is not possible to conclude that short-term reciprocity is dependent on short-term childcare needs. A complete quantification of this question requires collection of data on fluctuations in foraging success and sickness for each household simultaneously as data is collected on childcare. Nonetheless the current evidence is supportive of the predictors for variance pooling laid out in Table 7.9.

Arguably, then reciprocal cooperation in terms of communal breeding is an important behavioural strategy to ensure that children receive an adequate amount of childcare regardless of household shortfalls in childcare labour or food production. Similar to the original argument by Emlen (1982) then, I argue that communal breeding may result in increased fitness returns for the giver when they are unrelated or more distantly related due to unpredictable environments. There is supportive evidence of the role of environmental unpredictability in the evolution of cooperative breeding in birds (Rubenstein & Lovette 2007; Jetz & Rubenstein 2011) as well as naked mole rats (Faulkes *et al.* 1997) and Malagasy strepsirrhines (Tecot *et al.* 2012). Therefore, an individual provides costly care now while they can afford the labour costs to ensure that at some point in the future they will receive allocare when they require it more. If by receiving allocare mothers and the household can spend more time in food production, somatic maintenance and/or child quality ultimately reciprocal allocare will increase child survival and/or maternal fertility. It is these questions I investigate further in chapter 8.

7.5.2 Less than cooperative distant kin and more cooperative non-kin?

By-and-large the aforementioned results matched predictions laid out in Table 7.1; however, several results did not follow expectations. As argued above, reciprocity is not possible in the short-term for life history shortfalls, thus kin are likely to bear the highest immediate cost in cooperating (Alvard 2009). As a result, distant kin are expected to be reactive to long-term household needs. This was not the case, and in fact grandmothers only interacted more than non-grandmothers when their offspring have 'low' need scores, or very few dependent offspring compared to number of carers. The second finding is that at high cost when distant kin are predicted to offer more allocare than non-kin due to the increased likelihood of future relationships *and* possible indirect benefits, it is non-kin who interact more with dependent offspring. Therefore, why do distant kin not provide allocare according to indirect fitness gains? Furthermore, why do non-kin react less to high cost allocare and ultimately provide more interactions than distant kin at high cost? One explanation is that distant kin energetically focus on their own families facing equally high care shortages and that non-kin allocarers are juveniles who crèche children, resulting in low cost care.

Mothers have a high need index when they have more dependent children compared to the numbers of carers available in the household. This peaks at the age of 25-30 years when mothers can have a newborn, toddler and a child less than five years. However, if we take the average age of first birth of 19.7 years among our sample, then a young mother aged 26 (who on average had 2.8 offspring at this age) has a mother who is 45.7 years old and still has, on average, 2.8 dependent children under the age of 12. Thus, even for later born children, a grandmother may not be fully available to provide care until later in life, when the hazards in the environment start to take their toll on older individuals. Therefore, at exactly the time when a mother is in need of allocare, co-residing grandmothers are unable to provide costly allocare without short-term reciprocation. Similarly, a mother likely has some co-residing siblings or siblings-in-law who are undergoing a similar reproductive stage, thus have high cost in providing allocare. Therefore, distant kin may be unreactive to needs due to simultaneously high childcare needs. Of course, non-kin also will be reproductively active and not all distant kin are reproductively active, however a key difference is that kin co-reside and may compete over limited resources.

Mathematically and experimentally increasing local competition due to limited dispersal of relatives significantly diminishes the predictive value of r in $rB > C$ as the cost benefit ratio is altered (West *et al.* 2001; Griffin *et al.* 2004). Given that resources are always finite, and kin prefer to co-reside (Dyble *et al.* 2015), an individual's main competitors are kin who come with a spouse and, in all likelihood, dependent offspring. As argued above, food sharing occurs primarily among 3 – 4 households which are significantly more related to one another than expected by chance, and in particular, contained significantly more grandparents, uncles and aunts (Dyble *et al.* 2016). In contrast, non-kin reside outside of the 'resource clusters' and thus, are not in competition. Therefore, increasing the fitness of a siblings' offspring may expand the number of competitors. While this may increase an individual's indirect fitness gains it would decrease their direct fitness: at low levels of $r,$ the fitness returns required to compensate for the fitness cost are significantly high (Hamilton 1964) and investing in direct fitness and providing allocare in a tit-for-tat manner may result in the highest fitness returns. Thus, distant kin are still cooperative, only they gain inclusive fitness gains vis-à-vis direct benefits of reciprocal cooperation rather than the indirect benefits associated with kin selection.

In Strassmann and Garrard's (2011) meta-analysis of 17 studies examining the effects of grandparents in patrilocal societies the data supported a local resource competition hypothesis. Given that children in patrilineal societies are in competition with paternal relatives - whose fitness interests are never fully in line with each child's fitness interests - maternal grandparents have a positive influence, as they are non-resident and thus, non-competitors. This is why, Strassmann and Garrad (2011) argue, maternal grandmothers and grandfathers consistently have a more positive effect on child survival than paternal grandparents. Similar results have been reported among the Kipsigi (Borgerhoff Mulder 2007) and Pimbwe (Hadley 2004). Specifically, among the Ache females during the forest period experienced a 10% reduction in age-specific fertility for each additional co-residing adult sibling, thus Hill and Hurtado (1996) interpret these results in terms of kin competition for group resources. Therefore, when kin co-reside cooperation may be reduced when the benefits and/or relatedness is not sufficient to counteract the high cost of allocare and increases in resource competition. These factors will significantly reduce the predictive power of kin selection (Hamilton 1967). A limitation here is that I have grouped together all distant kin regardless of lineage, reproductive stage and age. All these factors are likely to have a different influence of the degree of competitive or cooperative nature of the relationship. Further examinations should explore amount of care offered according to resource competition, particularly focusing on food sharing clusters, reproductive stages and cooperation between different kin types.

Turning to the second question above - why do non-kin appear relatively uninfluenced by the cost of allocare? Certainly the cost does reduce the number of dyadic interactions, however the slope is not dramatic and as a result they provide more allocare than distant kin. This, I argue, is the result of juvenile allocarers 'crèching' multiple children into playgroups, thus the addition of unrelated children costs the providers very little.

The ethnographic observation of mixed-age, mixed-sex playgroups in hunter-gatherer societies is significant (Konner 2005). Among the Agta, children from the age of two years have been reported to spend a significant amount of their time in playgroups (Peterson 1978), which is in agreement with my own observations. Often within these playgroups, children are involved in observational and experimental learning, particularly under the guidance of older siblings (Griffin & Griffin 2010; Kelly 2013; Peterson 1978). The playgroups consist of unrelated children who are watched over by a couple of older children who have one or two siblings in the group. My point is one of diminishing costs: if an older child must provide care for a sibling, the increase in cost of also providing proximity care to other children may be small or even insignificant. Perhaps the care will be of lower quality (see chapter 8), but it would certainly allow a mother to conduct other activities (as seen in chapter 6 where non-kin care significantly reduced maternal childcare). Supporting this hypothesis is that fact that relationships with non-kin are significantly assorted by age. We have shown here and previously that children aged between 2 and 12 years spend more time interacting with non-kin of their own age group (i.e. 2 – 12 years) than older individuals (Migliano *et al.* 2016). Furthermore, here I demonstrated that this is not the case for distant kin, indicating why these two types of allocarers interact differently with increasing cost. Chapter 5 also revealed that juveniles, particularly non-kin juveniles are primarily in playgroups with dependent children, thus further exploration to quantify observations of playgroups, understanding their structure and costs compared to the benefits received from participating mothers (i.e. those mothers who leave offspring in playgroups) is essential to explore these questions further.

7.5.3 Subsistence change, risk and how to mitigate it

The finding that, as predicted, subsistence change and wealth accumulation influence who provides allocare is supportive of cooperation driven by reciprocal altruism and risk pooling. Time spend foraging is associated with decreases in the amount of time spent with the nuclear family while increases in household belongings decrease contact with more distant kin and increase care from close kin (mothers, fathers and siblings). Due to the strong relationship between the amount of time spent in either cultivation and/or trade (i.e. non-foraging activities) activities and the amount of household wealth (section 2.5), these traits are considered significantly interrelated. Thus, more acculturated, settled Agta camps focus increasingly on the nuclear family compared to wider networks based on reciprocal altruism and risk pooling. However, this relationship is influenced by an interaction with location: while the proportion of time spent foraging has a negative influence on the amount of time spent with nuclear families inland, the opposite occurs at the coast. This result may be the outcome of both the higher returns per hour from marine sources, resulting in adults spending more time in camp resting, socialising or conducting domestic tasks (Figure 2.10).

This would increase the likelihood that members of the nuclear family are proximate to a child.

Nonetheless, the fact that changes in subsistence and wealth accumulation are associated with altered caregiving dynamics meets expectations based on risk mitigation. Risk can be dealt with either by risk transfer (i.e. cooperative breeding), risk reduction (residing in a resource-abundant environment), risk avoidance (subsistence diversification and mobility) and risk retention (using wealth and/or food storage to directly absorb and buffer losses (Aktipis *et al.* 2011; Hao *et al.* 2015). Individuals may mitigate risks in multiple ways, however some strategies close the door to others (Cashdan 1985; Winterhalder *et al.* 1999; Fafchamps 1992). For instance, mobility becomes increasingly difficult with increasing food storage and wealth, and individuals with a lot of wealth may want to extract themselves from sharing networks (Hadley 2004; Fafchamps 1992). This trend was found among the Mpimbwe of Tanzania, where individuals more engaged in the cash economy could afford to avoid risk pooling and removed themselves from sharing networks (Kasper & Borgerhoff Mulder 2015). In his review of the research on food storage, foraging, mobility and environment variability, Kelly (2013) considers mobility as essential for gathering social ties to ensure an insurance network is in place to help buffer from environment shortfalls without food shortage. Consequently, I would argue that rather than one single method of reducing risk, individuals have multiple options which function in different contexts. Movements towards cultivation and/or wage labour can result in the accumulation of household wealth and resources which reduce the need and ability to be mobile, while making other households dependent on wealthier households. Thus, wealthier households withdraw from insurance networks, resulting in more closed networks, as risks no longer require wide distribution but can be retained and absorbed within the household (Fafchamps 1992). A similar trend was found among two Tabo groups from the South American Gran Chaco in which more 'traditional' communities were defined by care from grandmothers and non-related juveniles, while increasing acculturation resulted in increasing amounts of childcare from mothers and fathers (Valeggia 2009).

This reveals that focusing on variance within populations and not seeking a singular description of childcare is key to understanding the selective pressures on the evolution of cooperative breeding. These results further support the hypothesis that communal breeding is related to unpredictable environments: if we, as I do here, assume that foraging modes of subsistence produce increased variability in food returns compared to mixed-modes of production then more extended networks of allocare dependent on reciprocity or variance pooling should be expected in foraging contexts, as we see here. Examining variability further within a population is an exciting avenue of future research that should, rather than assume that subsistence diversification reduces resource stochasticity, measure this directly and quantify the influence on behavioural strategies, particularly cooperation.

The results from the effect of ecology on childcare did not, however, meet predictions, as it appeared that coastal households relied more on care from grandmothers and distant kin. However, this trend was non-significant for non-kin painting a less consistent picture. The hypothesis that best explains these results is that residing in a resource-abundant environment (denoted by the larger package sizes at the coast) results in more cooperative, larger aggregations of extended families. Above I argued that in locally resource-poor areas, kin often become competitors due to limited dispersal (Griffin *et al.* 2004). However, if resource competition is limited and consistent in neighbouring areas then any competition between relatives is negligible and the importance of indirect fitness gains increases (West *et al.* 2001). Thus, in a resource-abundant area, as coastal regions often are (Kelly 2013), distant kin may cooperate more as the indirect fitness gains are higher without competition for resources. While this requires a significant amount of exploration, it does reveal interesting avenues of future research focused on how behaviour is affected by ecological variability.

7.6 Conclusions

This chapter set out to explore why individuals provided costly allocare, focusing on indirect fitness and the role of reciprocity in risk reduction. Overall, the predictions from kin selection are overwhelmingly met for close kin allocare. Thus, siblings gain direct inclusive fitness benefits from providing allocare, and thus provide the highest number of interactions compared to distant kin and non-kin. However, kin selection does not predict allocare from distant kin, which appears reactive to reciprocity rather than long-term childcare needs. Thus, I have argued that due to co-residence, lower levels of relatedness may result in a reduction in cooperation, particularly at higher costs, thus confounding the relationship between allocare and relatedness. Kin competition should be an equally important consideration in future research. Nonetheless, these results reveal that just because a dyad is related does not mean that allocare stems from nepotism; competing effects of reciprocity, costs and benefits must be separated for a more accurate portrayal of cooperation. Both distant kin and non-kin allocare are reactive to reciprocity suggesting that short-term returns are important. This follows the predictions of variance pooling which suggests that communal breeding is adaptive when individuals require buffering from unpredictability. In particular, I found that increasing wealth and subsistence diversification reduces wider allocare networks, which are dependent on reciprocity. This indicates the adaptive value of non-kin allocare may lie in buffering unpredictable risks. As non-kin allocare is rarely explored, these results are novel and offer important insights into communal breeding.

Chapter Seven

Betwixt and Between: Social Networks Effect on Allocare and Reproductive Success

There is significant evidence from non-human primates suggesting the adaptive nature of social ties, as they are associated with both increased longevity and fertility. However, the literature in humans, and in particular hunter-gatherers, has focused primarily on males' social status, hunting skills and fitness. Thus, while we know that indirect social ties (i.e. friends-of-friends) have implications for disease and information transmission, we know little about their role in female reproductive success. Here, I examine the adaptive function of direct (dyadic) and indirect social ties by exploring the role of social network position in soliciting allocare. I explored these questions by collecting reproductive histories, proximity networks, anthropometrics and disease data for 38 Agta mothers and 91 offspring living in six camps. I find that mothers aged over 25 with greater betweenness centrality (an individual with high betweenness links otherwise disparate parts of the network) had higher fertility and overall reproductive success at the cost of increasing poor health for both mothers and their offspring. The relationships appeared to be influenced by non-kin allocare: maternal betweenness is associated with increases in non-kin allocare, which is independently positively correlated with reproductive success while being negatively correlated with child quality. Therefore, Agta mothers appeared to focus on child quantity rather than quality in a high-risk environment vis-à-vis allocare. Furthermore, degree centrality (the number of dyadic ties an individual has) was negatively associated with reproductive success. I argue that simply having many direct ties equates to more competitors for resources, however being able to access disparate groups increases maternal ability to solicit allocare when facing childcare shortages, which increase with age. By expanding the cooperative breeding perspective to explore social networks I demonstrate that maternal centrality can be considered adaptive and a key component in ensuring successful reproduction of multiple offspring.

8.1 Introduction

Sociality arises when it benefits individuals' fitness above and beyond the costs of living in a group (Silk 2007b). Thus, social status and bonds have long been associated with positive fitness outcomes including increased longevity, offspring survival and fertility (Brent 2015; Silk *et al.* 2006; Seeman 1996; Cameron *et al.* 2009). For instance, as explored in chapter 6 it is evident that childcare by non-kin significantly reduces the number of interactions a mother has with a child. This theoretically allows her to invest more energy into either child quality or her own fertility, increasing her overall reproductive success. As a result, individuals are expected to be able to manipulate their social worlds to maximise their fitness (Barrett *et al.* 2012). However, individuals' social networks are more complex than simple dyadic (direct) ties; social structure arises from the indirect ties between whole groups of individuals (Brent, Lehmann, et al. 2011). For instance, your position in the network, who your friends are connected to (i.e. friends-of-friends) and the degree of network clustering are impossible to examine by only exploring dyadic relationships. These features play a central role in the transmission of information (Mann *et al.* 2012), disease (Weber *et al.* 2013; Keeling & Eames 2005) and even emotions (Fowler & Christakis 2008; Rosenquist *et al.* 2011). Thus, while we currently know much less about the influence of network position on an individual's fitness (Royle *et al.* 2012), the evidence suggests it could be under selective pressure and considered an extended phenotype requiring investigation (Formica *et al.* 2012).

Empirically, social ties appear to have a positive influence of fitness; however, the evidence suggests that social bonds can be beneficial when they are few and strong *as well as* when they are many and weak (conceptualised as strength and breadth). In both yellow (*Papio cynocephalus*) and chacma baboons (*Papio ursinus*) from Botswana it was strong, consistent social bonds, particularly with female kin, that predicted survivorship of both the mother and her offspring (Silk *et al.* 2009; Silk *et al.* 2010; Silk *et al.* 2006). Similarly, Schulke and colleagues (2010) find that in Assamese macaques (*Macaca assamensis*), strongly bonded males had significantly higher dominance positions promoting paternity success. However, the importance of a few strong social bonds is not consistently found. For instance, Cameron *et al.* (2009) showed that a composite measure of social integration in female feral horses (*Equus sp.*) was associated with increased fertility, while amount of grooming received from both male and female Amboseli baboons was associated with a significant increase in likelihood of females survival (Archie *et al.* 2014). Therefore, it may be the number of connections and degree of social integration which predicts fitness rather than strength of social ties, a finding also evident in Barbary macaques (*Macaca sylvanus*) and female vervet monkeys (*Chlorocebus* *pygerythrus* (Lehmann *et al.* 2015; McFarland & Majolo 2013; McFarland *et al.* 2015)). Thus, large extended networks consisting of many weak ties may be as important as a few strong ties.

Consequently, current research indicates that *some* type of social ties has fitness implications; however, which exact form seems highly variable. Murphy and colleagues (n.d.) specifically argue that weak and strong bonds may be more or less important given environmental hardship experienced in some baboon populations compared to others. Thus, in their sample, both strong and weak bonds are important as they allow mothers to maintain consistent support *and* flexible access to larger networks, which might be essential in less predictable environments. Examining the potential pathways by which sociality can promote fitness can shed more light on this issue. For instance, in chacma baboons, smaller, more focused grooming groups have been associated with lower glucocorticoid levels due to grooming's stress relieving effects (Wittig *et al.* 2008; Crockford *et al.* 2008; Silk *et al.* 2009). As glucocorticoids are well known reproductive suppressants (Cameron 1997) as well as an immunosuppressant (Cohen *et al.* 1997; Tamashiro *et al.* 2005), this indicates the protective role of close-knit and consistent networks among some baboons. However, in horses the fitness-promoting effect of social integration appears to stem from insulation from male harassment, which significantly reduced reproductive success. Thus, composition may matter less compared to how well connected individuals are (Cameron *et al.* 2009). Similarly, among barbary macaques more connections resulted in feeding tolerance and more coalition partners (Lehmann *et al.* 2015; McFarland & Majolo 2013) while in vervet monkeys more partners meant better thermoregulatory ability (McFarland *et al.* 2015). Thus, as with any trait, different forms of social networks appear adaptive under different ecologies, constraints and selective pressures.

In humans (*Homo sapiens sapiens)*, and in particular hunter-gatherers, the focus has remained on the direct benefits of cooperative action, rather than the influence of network structure and social position. For instance, there is extensive literature exploring why foragers engage in resource redistribution (Hooper *et al.* 2015; Jaeggi & Gurven 2013a; Kaplan & Gurven 2005; O'Connell *et al.* 1999) or who helps in childcare (Crittenden & Marlowe 2008; Hrdy 2011; Kramer 2011; Meehan 2005). These traits are argued to be flexible and context dependent (Sear & Mace 2008). However, it is unclear how individuals are able to manipulate this cooperation to optimise their fitness returns. Nonetheless, there is evidence that hunter-gatherer networks exhibit significant homophily (clustering according to similarity) allowing co-operators to preferentially connect to each other, thus facilitating redistribution (Apicella *et al.* 2012). At the same time, direct social ties are significantly correlated with human longevity (Holt-Lunstad *et al.* 2010; Giles 2005) while indirect ties predict the spread of obesity (Smith & Christakis 2008), happiness (Fowler & Christakis 2008) and depression (Rosenquist *et al.* 2011) throughout human social networks. Thus, network position has important implications for human wellbeing and survival; however, the implications for fertility are less clear. As a result, I bring these approaches together and examine the adaptive function of direct and indirect network ties on maternal fitness by exploring the possible role of network position in soliciting allocare.

8.2 Hypotheses and predictions

I have argued in section 3.4 and chapter 7 that hunter-gatherers, rather than rely on material resources such as property or wealth, buffer the risks of stochastic environments with relational wealth (Smith *et al.* 2010; Woodburn 1982; Chaudhary *et al.* 2015). As a result, I hypothesise that social networks function as a resource to facilitate cooperation. Thus, given humans' significant communal breeding and its implications in our evolution (Burkart *et al.* 2009; Sear & Mace 2008; Crittenden & Marlowe 2008; Hrdy 2011; Lancaster & Kaplan 2009; Hawkes & Coxworth 2013), maternal network position is expected to play an important role in the acquisition of allocare. I make the following two predictions: *(i)* measure/s of maternal network position will positively associate with child quality, maternal fertility and quality and *(ii)* more central mother's received more allocare from outside the household and/or the extended family.

Prediction *(i)* stems from the theoretical implications of cooperative breeding and life history theory. Allocare acts as a source of additional energy, lifting constraints off the mother. Thus, the mother is able to invest the additional energy into either current and/or future reproduction. Consequently, increased allocare should be associated with either increased fertility and/or maternal quality if investment is placed in reproduction. Or, allocare may equally well be associated with increased parental effort as mothers produce higher quality offspring. As discussed in section 1.2.3, these energy allocations are weighed against one another given extrinsic risks (Charnov 1993). Mothers may invest in multiple low quality offspring when they cannot mitigate environmental risks or receive diminishing returns for their efforts (Quinlan 2007). As a result, if prediction *(ii)* holds and maternal network position is associated with increases in allocare, I expect increases in either: maternal fertility; maternal quality (as a proxy for future reproductive effort); or child quality.

Here, I explored these hypotheses and predictions by examining the relationship between four measures of maternal network position or *centrality* (betweenness; eigenvector centrality; degree; and strength (Gilby *et al.* 2013)) and fertility, survivorship of offspring to age 16 (proxy for reproductive success), childhood mortality (all deaths under 16 years), child and maternal nutritional quality (BMI and haemoglobin levels) as well as self-reported sickness over the last two weeks. I further explored the degree to which the same measures of network centrality correlated with the amount of care a mother's offspring received from kin, non-kin and non-household members over the duration of one week using motes to capture three-meter proximity. From these analyses, I find two clear and consistent results: firstly, maternal betweenness is positively associated with allocare from non-kin, fertility and reproductive success while negatively correlating with maternal and child quality. Secondly, degree centrality negatively predicts fertility, reproductive success and maternal BMI. Furthermore, non-kin allocare positively predicts reproductive success while negatively associating with child nutritional condition. Thus, it appears allocare received from non-kin may mediate the association between fertility and maternal betweenness.

8.3 Methods

Full data collection methods for motes deployment, reproductive histories, medical exams, anthropometrics and household characteristics have been described in the methodological chapter 4.

8.3.1 Social Network Analysis

Social network analysis (SNA) is a useful tool for the exploration of the adaptive function of sociality as it quantifies the emergent properties of a social network (Barrett *et al.* 2012). Moving beyond dyadic or direct ties between individuals, SNA examines how the interaction between individuals creates a structure which impacts the behaviour and function of a system (Brent 2015; Newman 2010; Kurvers *et al.* 2014). Human social networks, similar to many other complex networks, are not homogeneous (i.e. each individual is connected to the same number of individuals). Rather some individuals have significantly more ties than others, resulting in a scale-free network (Keeling & Eames 2005). The existence of highly central, well-connected individuals results in differential access to the currency moved throughout the network, be it influence, information, resources or even disease (Kurvers *et al.* 2014; Newman 2010; Meyers *et al.* 2005). Thus, different measures of centrality are predicted to result in differential outcomes (Lehmann *et al.* 2015; McFarland & Majolo 2013; Murphy *et al.* n.d.). Here, I explore two different types of measures of centrality - direct and indirect - for 38 mothers. Each captures different pieces of information, which may be pertinent to an individual's fitness. As SNA entails its own new language please refer to box 1 for definitions of terms used throughout this chapter. The exact measures of centrality were chosen for two reasons: firstly their occurrence in the current literature on social bonds and centrality and secondly by presenting diverse measures of centrality, as they each capture very different forms of central network positions, as described below.

Box 1: Social network Analysis definitions

- **Node:** independent actors who structure networks. Here nodes are individuals.
- **Edges:** the links that connect different nodes.
- **Weighted network:** edges are not binary (unweighted network) but weighted according to the number of interactions between nodes.
- **Centrality:** how important edges are in a network. Multiple measures:
    - **Degree:** number of edges attached to a node
    - **Strength:** weighted version of degree, sum of the weights of all edges.
    - **Betweenness:** the number of geodesic (shortest) paths a node lies on between other nodes.
    - **Eigenvector centrality:** the sum of the degree and strength of the nodes connected to ego
- **Direct ties:** A is directly connected to B
- **Indirect ties:** A is indirectly connected to C via a direct tie with B

The two direct measures of centrality are *degree* and *strength*. *Degree* is the number of edges (ties or links) connected to a node (an individual) thus represents the number of an individual's social ties. This is one of the most common measures of an individual's network position as arguably an individual with more connections may have more prestige and influence. Degree is particularly useful when a network is binary or unweighted (Newman 2010). However, when a network is weighted (i.e. edges have different weights according to the frequency of interaction) then *strength* centrality captures more information. An individual's strength is the sum of all the weights on the edges connected to it, thus captures the differences between strong and weak ties by measuring an individual's gregariousness (Whitehead 2008).

Indirect ties capture not only dyadic interactions but also an individual's network position given the positions of all other nodes. Here I choose two diverse measures of indirect centrality: betweenness and EC. *Betweenness* quantifies the degree to which a node is 'between' two clusters of other nodes which do not share edges, as demonstrated in Figure 8.1 (Freeman 1977). Betweenness then, is a measure of the degree to which a node lies on the path between other nodes, and is proportional to the number of geodesic (shortest) paths it lies on between any given two nodes (Newman 2010). Thus, it acts as a 'broker' in the network as they have a large influence on the flow of resources throughout the network (Newman 2004; Brent 2015; Whitehead 2008). Interestingly, individuals with high betweenness may have low other centrality measures as they may be relatively peripheral to a couple of clusters. Betweenness, unlike other measures of centrality also exhibits a high range as it is significantly left-skewed (Newman 2010; Lusseau & Newman 2004).

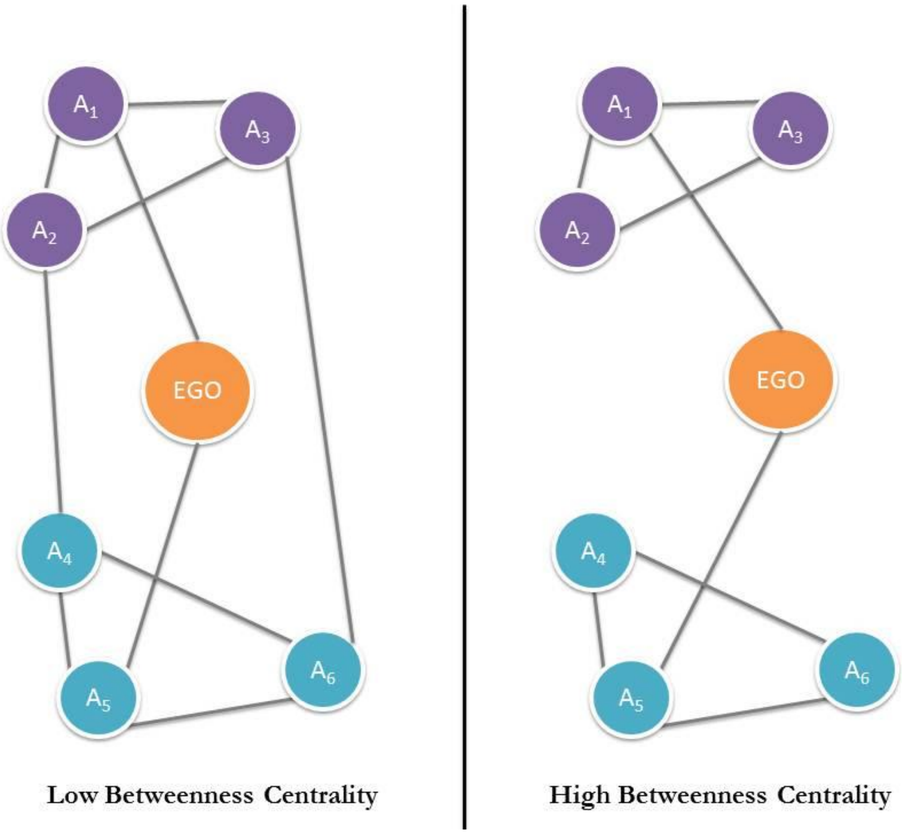

Figure 8.1: Example network demonstrating low and high betweenness centrality. On the right ego (the orange node) has significantly higher betweenness as they sit on the only edge between the blue and purple clusters. Adapted from Brent (2015)

The second measure of indirect centrality is *eigenvector centrality* (EC), which develops degree centrality in a weighted network as some edges are more important than others (Newman 2004). An ego's EC is proportional to the sum of the strength centralities of the nodes connected to ego; thus it takes into account both the number and centrality of a node's edges. Nodes connected to other well-connected nodes have a higher EC centrality, as do individuals with many neighbours (Figure 8.2 (Newman 2010; Brent 2015)). Similar to betweenness, EC is often high for a few nodes and low for the reminder of the network (Whitehead 2008).

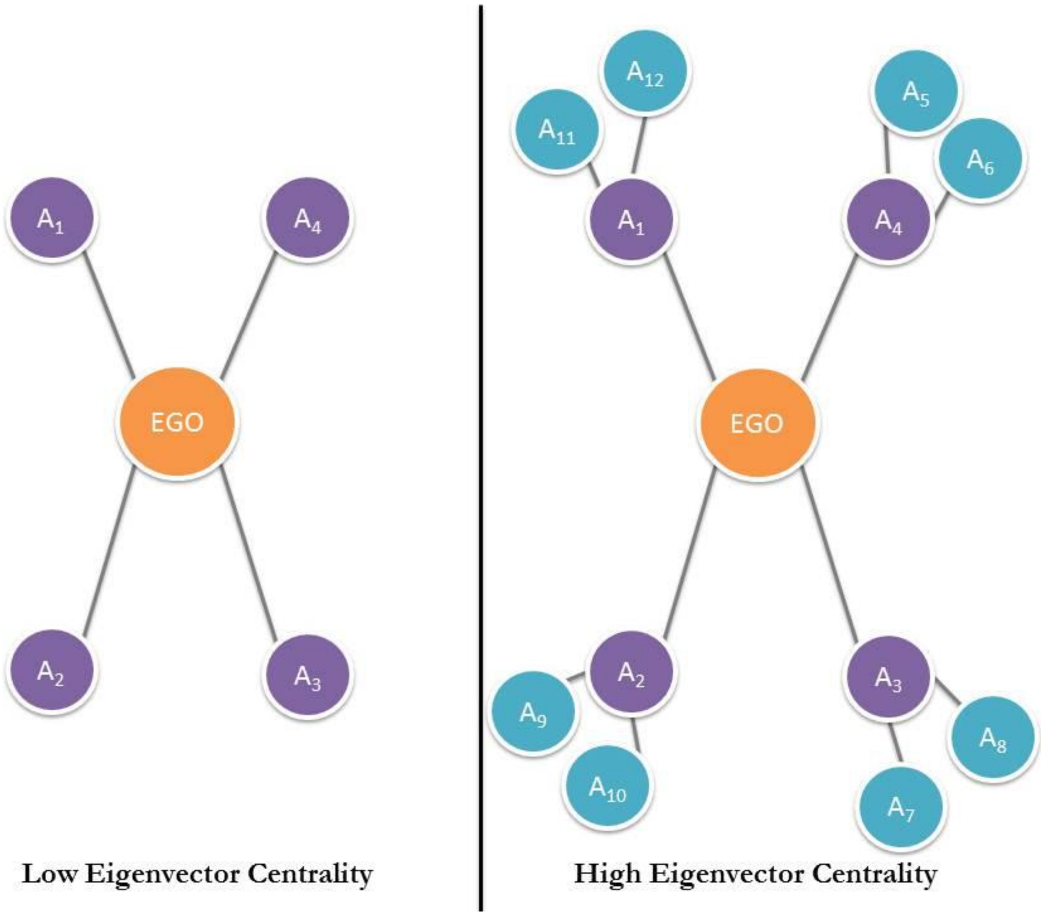

Figure 8.2: Example network demonstrating low and high eigenvector centrality (EC). On the right ego (the orange node) has significantly higher EC all their edges are shared with nodes who have many edges themselves. Adapted from Brent (2015).

The network is undirected and comprised of only ‘productive’ individuals aged 12 years or older, following the cut-offs applied in throughout this thesis (section 4.7.3). This threshold was applied as after the age of eleven, hunter-gatherer children conduct significantly more caring and economic activities. They also require less care and provisioning themselves (Konner 2005; Kramer 2005). Thus, they are deemed to be no longer fully dependent children and included in the adult network.

8.3.2 Proximity to kin, non-kin and non-household individuals

As the effect of maternal network on her reproductive success and health is at the maternal level (all females over the age of 15) I also established an ‘amount of care received’ variable at the mother’s level. For each child I summed the number of interactions they had with each individual who fell under the following categories: *kin* (coefficient of relatedness $\geq$ 0.125), *non-kin* (coefficient of relatedness < 0.125) and *non-household* individuals (all individuals excluding the nuclear household, i.e. parents and dependent siblings) based on genealogical relatedness. This figure was then summed for each mother, producing one allocare score that reflects all the interactions all her children had with different types of allocarers. This figure was significantly affected by the number of children a mother had; mothers with more children necessarily had higher interaction scores with non-kin, kin and non-household individuals, thus exploring whether allocare was associated with fertility would be self-fulfilling. Therefore, the results were standardised per family size; mothers were given an allocare score depending on how many interactions their children experienced compared to the sample norm for this family size. For instance, mothers who received significantly more allocare from non-kin compared to the mean of the sample with four dependent offspring were given a positive score, while 0 represents the average amount of allocare received given the family size. As a result of this standardisation procedure there is no significant relationship between household size and the sum of number interactions mothers offspring had with non-kin (p =0.92), kin (p = 0.94) and non-household individuals (p = 0.9). Thus, I can explore the relationship between maternal network centrality, number of interactions and reproductive outcomes without confounding the analysis.

8.3.3 BMI z-scores, haemoglobin levels and self-reported sickness.

I used three outcome variables to measure maternal and child 'quality'. BMI is a measure of children's energetic balance and a proxy of overall nutritional quality and more generalised calorie intake. Haemoglobin levels are a measure of micronutritional quality, capturing variability in the quality of food. Children of poorer nutritional quality, or those who experience less investment or poorer quality investment are expected to experience some form of immune depression, thus likely to report more cases of sickness over the last two weeks. Child age has a significant and non-linear relationship with BMI. As a result, BMI was standardised by the smallest possible age groups given our sample size. These groups were as follows: infants aged less than one year; toddlers between one and two years; young children aged two to six years; and older children aged six to eleven years. Once the BMI scores had been standardised within these age groups no significant relationship remained between BMI and age (p = 0.95).

8.3.4 Statistical analysis

The main multilevel model analysis was conducted at the maternal level (network effects of fertility and care received) and contained two levels: level 1 being the mother and level 2 the camp they resided in. The analysis conducted at the child level (haemoglobin levels, self-reported sickness and BMI scores) contained three levels: the child (level 1), the household (level 2) and the camp (level 3). As many of the network centrality statistics co-vary each of these terms were ran in separate analyses (Brent 2015; Wey & Blumstein 2012). Only theoretically informed variables were entered into the model and no terms were removed. All network measures were standardized by camp, thus represent whether or not a centrality score was high according to the camp average (Stanton & Mann 2012; Sueur *et al.* 2011).

Age-specific residuals (described in section 4.7.1) were used in all multilevel models with demographic outcomes. Therefore, the influence of age has been removed completely. As discussed in section 4.7.1 the use of residuals has been critiqued elsewhere as it can result in biased parameter estimates (Darlington & Smulders 2001; Freckleton 2002). The major limitation occurs when there is a correlation between the independent variables (here age and centrality) which is not picked up by variance inflation factor (VIF). As a result, I have explored the relationship between age and centrality. There is no linear relationship between age and centrality for each of the measures (Betweenness, p = 0.3; Degree, p = 0.6; Strength, *p* = 0.9; EC, *p* = 0.9). However, as is evident below, there does appear to be an important relationship between age and centrality resulting in the use of an interaction term centred at 25 years. As a result, if we remove all 'younger' women from our sample aged under 25 with smaller family sizes (i.e. all those with less than four children) we find that now betweenness is significantly *negatively* correlated with age (B = -0.03, *p* = 0.008, R^2 = 0.23), while this relationship does not exist for any other centrality measure (Degree, *p* = 0.9; Strength, *p* = 0.1; EC, *p* = 0.08). Therefore, older mothers after the age of 25 appear to have decreasing betweenness centrality. Why this occurs is unclear, however it may be a product of increasing family size altering their interactions with the wider camp. Nonetheless, this is in the opposite direction to the relationship between fertility and reproductive success and age, suggesting it will not confound the analysis with the use of the interaction term for age centred at 25 years.

Nevertheless, as a correlation between the independent variables is present I explored whether in a non-residual model the relationship between betweenness and polynomial age led to any collinearity. With VIF beneath 2.5 (Alin 2010) for both age (1.98) and betweenness (1.57) collinearly cannot result in biased parameter estimates. Given the small sample size the residual model has significant advances in terms of power, goodness-of-fit and information criteria. Accordingly, I examined two models over each of these domains. Each model contained betweenness and the non-residual model contained age with a third degree polynomial to match the residual results. As revealed in Table 8.1, the non-residual model has three more terms than the residual model significantly reducing its power. As a result, there is a 56.2% chance of making a type II error with a sample size of 38. In comparison the power of the residual model is significantly higher, resulting in a 35.8% chance which, while not ideal, is a significant improvement. Additionally, I find that there is significant evidence of a lack of fit in the non-residual model (Faraway 2002) and the AICc (AIC adjusted for small sample size) is significantly higher in the non-residual model (Table 8.1). As a result, while using residuals has inherit risks, in this case there is significant justification for using the model, especially without the occurrence of significant collinearity.

Table 8.1: Residual and non-residual model comparison

	Terms	**DF**	**Fit**	**Power**	**AICc**
Residual model	1	36	0.997	0.642	83.47
Non-residual model	4	33	0.0003	0.438	146.8

The fertility and allocare models contained no additional controls (given small sample sizes[7]); however, each model was examined with the inclusion of an interaction between age and centrality. If the interaction was non-significant at $p < 0.05$ then the interaction was removed from the model and the non-interaction model is reported. The dependent variable was the number of offspring reported to be born. For the power analysis alpha was set at 0.05 and the effect size was 0.15 (low to medium effect).

Age in this analysis has been centred to 25 years, as I wanted to explore the relationship between centrality, fertility and allocaring according to reproductive career stage. Under 25 years the majority of mothers have 1 to 2 offspring (average 1.5 ± 0.7), less or equal to the number of adult carers present within the household (average 2.1 ± 0.7, a relationship expressed in Figure 7.2). Therefore, they are not in high 'need' of allocare and were more able to provide for the offspring themselves. However, at around 25 years this relationship switches as mothers on average have 3.7 ± 0.98 dependents versus 2.9 ± 0.97 carers, thus were more in need of allocare. As a result, this interaction with maternal age has been included to explore these relationships. The health models controlled for child and maternal age, child sex, whether the camp was 'settled' (binary, 1 being settled representing a camp with permanent housing and a church and/or water pump) and 'household belongings' (a continuous measure quantifying wealth) as these have known relationships with health and wellbeing (Page *et al.* 2016). In the analysis on child outcomes I also controlled for number of siblings and maternal condition (i.e. maternal sickness, maternal haemoglobin concentration and maternal BMI in each of the relevant analyses).

Descriptive statistics for all variables can be found in Table 8.2 (residals) and (non-residuals). All null results not presented in the main text can be found in appendix C, alongside intercept-only models. All multilevel analysis was conducted with the variables as continuous outcomes, however descriptive results demonstrating increases in reproductive success are expressed using the binary measure for centrality (i.e. high or low according to sample thresholds). This is simply to express the fertility results in a more useful manner for interpretation.

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[7] Originally the models were run with controls for degree of sedentism and household wealth. Their inclusion made little impact to the results, thus given the small sample size were removed from future analysis to increase the power of the analysis.

Table 8.2: Descriptive statistics for the sample for mothers (*n* = 38) and their children (*n* = 91). All network centrality measures are z-scores to standardise the results per camp, as are amount of care received from in different categories of allocarers (controlling for household size), child BMI (controlling for the non-linear influence of age on BMI during childhood) and the reproductive measures.

	Maternal Descriptive Statistics			
Variable	**Min.**	**Mean**	**Max**	**SD**
Maternal Age	17	36.29	75	15.937
Betweenness	-1.131	-0.061	3.049	0.927
Degree	-1.591	0.113	1.439	0.67
Strength	-1.606	0.198	1.778	0.781
EC	-1.332	0.178	1.766	0.856
Mortality	-1.884	-0.355	2.255	1.023
Fertility	-1.292	0.159	1.734	0.676
RS	-1.418	0.097	1.547	0.749
Non-kin care	-1.689	0	2.169	0.939
Kin care	-1.409	0	2.745	0.939
Non-household care	-1.785	0	1.688	0.939
BMI	12.69	18.27	23.38	2.267
Haemoglobin	38	107.8	149	27.53
Cases of sickness	0	0.806	2	0.71
	Child Descriptive Statistics			
Child Age	0.006	5.369	11	3.366
BMI	-1.751	0	4.39	0.992
Haemoglobin	31	110.9	148	19.387
Cases of sickness	0	1.564	4	0.768
Sibling number	0	4.444	8	1.844

Table 8.3: Descriptive statistics for the sample for mothers (*n* = 38) based on raw data

	Non-residual Descriptive Statistics			
Variable	**Min.**	**Mean**	**Max**	**SD**
Betweenness	0.000	13.940	78.000	18.623
Degree	12.000	33.000	42.000	7.392
Strength	14.190	57.460	180.400	35.459
EC	0.083	0.574	1.000	0.283
Mortality	0.000	0.116	0.714	0.195
Fertility	1.000	4.947	12.000	2.986
RS	1.000	4.342	10.000	2.623

8.4 Results

8.4.1 Agta social networks

From the motes experiment among the six camps we created weighted high-resolution proximity networks over the one week period (Figure 8.3). These networks, similar to many westernised populations are examples of optimised or 'small-world' networks which maximise overall efficiency in connectivity, and thus in information and resource transmission (Latora & Marchiori 2001). In a separate analysis we explored the determinants of this global network efficiency in these six camps, finding that it was the ties between unrelated individuals (blue ties in Figure 8.3) which optimises global efficacy (Migliano et al. 2016).

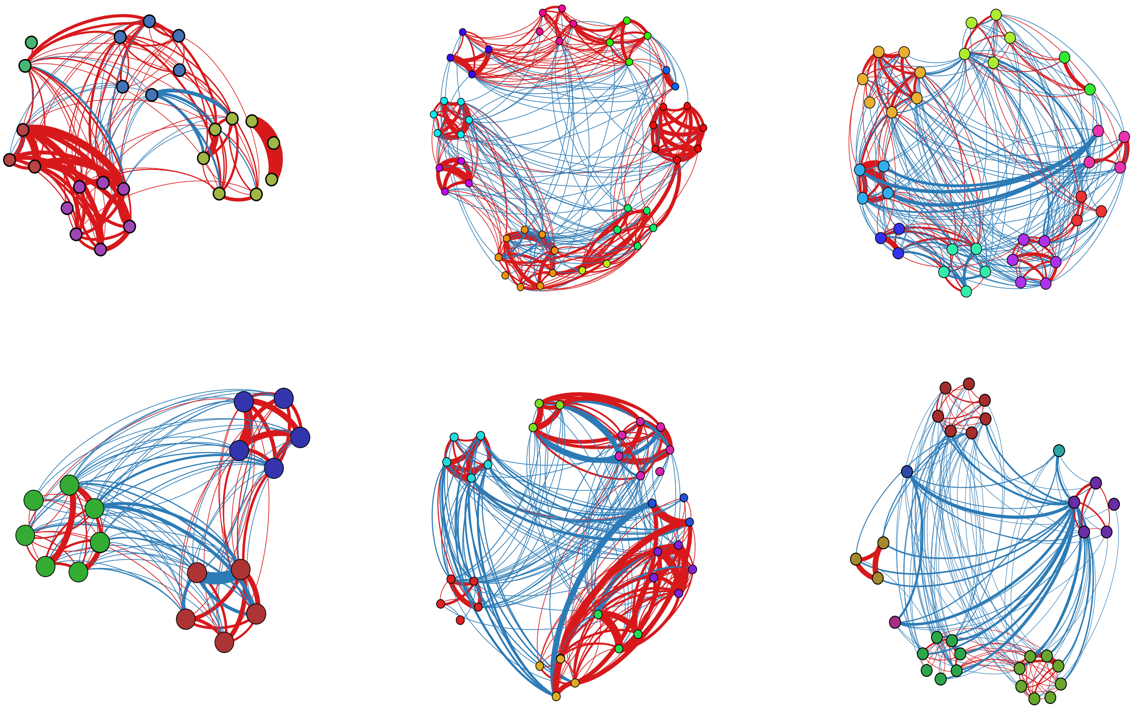

Figure 8.3. Diagrams of networks for the six camps in the Philippines. Nodes represent individuals, node colours represent households. Red ties represent close kin and distant kin, and blue ties connect unrelated individuals. Tie thickness represents intensity of relationship as measured by number of recorded close-range interactions over a week, revealing strong non-kin ties between individuals from different households. Graphs display approximately the 60% strongest links. Figures from (Migliano et al. 2016). Figures by Mark Dyble.

8.4.2 Centrality correlates with fertility and reproductive success

8.4.2.1 Mothers with higher betweenness demonstrated higher fertility and reproductive success

Overall the 38 mothers who took part in the motes experiment, distributed across six camps, had an average number of 5 ± 3 live births, ranging from 0 to 12. Of these, the mean survival rate to age 16 was 4 ± 2.6, ranging from 6 to 10 mature offspring. Mother's with the highest betweenness had greater reproductive success (i.e. number of children surviving to 16 (Figure 8.4)) however this relationship was dependent on maternal age, revealed by the significant interaction between age (centred at 25 years) and betweenness. Thus, betweenness only significantly predicted reproductive success once a mother was 25 years or older, accounting for a sizable 27% of the maternal level variance in reproductive success. While betweenness had no significant relationship with mortality, it did with fertility. Again this relationship is dependent on age as only mothers over age 25 demonstrated increasing fertility with higher betweenness (Table 8.4). This model accounted for 19% of the maternal level variance in all live births.

Table 8.4: Multilevel models of maternal network characteristics, fertility and reproductive success (survivorship to age 16). Due to significant similarities between predictors each of the different network characteristics were included in separate models. VAR represents the amount of the individual level variance each predictor accounted for compared to the intercept-only model. The variance at the individual level in the intercept-only model was 0.4 for fertility and 0.5 for reproductive success. Models only included the measure of centrality and age centred at 25 years (*n* = 38).

	Fertility					**Reproductive Success**				
Parameter	***B***	***p***	**2.5% CI**	**2.5% CI**	**VAR**	***B***	***p***	**2.5% CI**	**2.5% CI**	**VAR**
EC	-0.16	0.18	-0.37	0.09	0.12	-0.19	0.15	-0.47	0.08	0.04
Betweenness	0.10	0.34	-0.12	0.32	0.27	0.02	0.77	-0.23	0.28	0.19
Betweenness*age	0.02	0.04	0.00	0.03		0.03	0.01	0.01	0.04	
Degree	-0.48	<0.001	-0.88	-0.20	0.32	-0.43	0.01	-0.76	-0.10	0.16
Strength	-0.23	0.07	6.67	0.04	0.19	-0.24	0.10	-0.53	0.05	0.07

Age-controlled relationships are presented in Figure 8.4 as well as the raw survivorship (i.e. non-age controlled) results were used to describe the role of betweenness on demographic measures in more meaningful terms (i.e. not standardised residuals). By doing so, it is apparent that 'high' betweenness mothers (in or above the 3rd quartile; 0.98[8]) aged over 25 had 0.75 or 14.3% more offspring surviving to age 16 than mother's with 'low' betweenness (less than the 3rd quartile, Table 8.5). These women with higher betweenness came from a range of camps (in terms of ecology and degree of settlement) and tended to be in peak reproductive years; women in the top quartile of betweenness have an average age of 33 ± 10.8 years.

8.4.2.2 Maternal degree negatively associates with fertility and reproductive success

No other network variable had a significant, positive relationship with fertility, reproductive success or mortality. However, degree centrality is associated with a significant decrease in reproductive success via reductions in fertility (Table 8.4; Figure 8.4). As above, non-aged controlled reproductive success rates revealed that mothers with low degree (below the mean; 0.11) had 1.45 or 30.9% more offspring survive to age 16 than did their peers with high degree (above the mean, Table 8.5). As with betweenness age does not have a significant relationship with degree confounding these results ($B = -0.003$, $p = 0.6$). The interaction between age and degree was insignificant for both reproductive success ($p = 0.2$) and fertility ($p = 0.1$) and removed from the final models.

Table 8.5: Non-age controlled fertility and reproductive rates for women aged 25 years and over according to high and low betweenness and degree centrality. Age-controlled residuals are expressed visually in Figure 8.4. SD stands for standard deviation, SEM: standard error of the mean ($n = 38$).

Measure	Level	Mean	SD	SEM
Betweenness & fertility	Low	6.2	1.504	0.328
	High	6.571	2.122	0.802
Betweenness & RS	Low	5.250	1.826	0.399
	High	6.0	1.870	0.707
Degree & fertility	Low	6.786	1.981	0.511
	High	5.769	1.211	0.336
Degree & RS	Low	6.143	1.845	0.476
	High	4.692	1.716	0.476

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[8] Betweenness has been separated consistently at the third quartile rather than mean due to the significant left skew in the data. Most individuals demonstrated little variance in betweenness while a few demonstrated a lot. Degree on the other hand was more evenly distributed, and hence separated at the mean (Whitehead 2008).

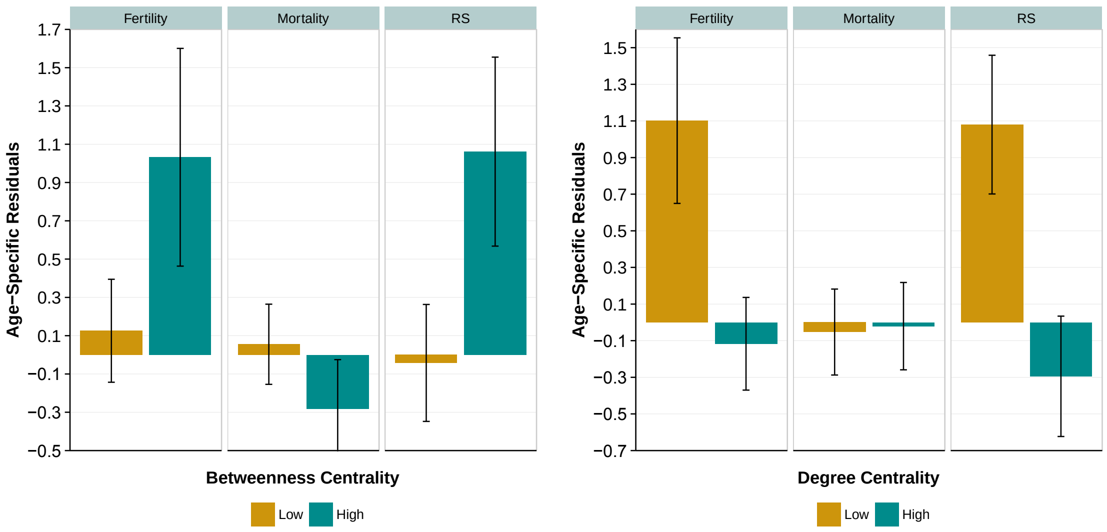

Figure 8.4: The relationship between betweenness, degree and age-specific residuals for fertility, mortality and reproductive success, $n = 39$. Maternal centrality has been transformed into a binary variable. Individuals with betweenness below the third quartile (0.98) were coded as having 'low' betweenness. Individuals with betweenness of 0.98 or more had 'high' betweenness. For degree the standardised mean is 0.11, above which is denoted as 'high' degree. Error bars represent standard errors of the mean. Fertility, mortality and reproductive success (survivorship to age 16) are all measured by age-specific residuals. RS stands for reproductive success.

Table 8.6: Multilevel models examining the relationship between the proportions of interactions between non-kin, non-household and kin proximity and maternal centrality. Significant variables ($p < 0.05$) are highlighted in bold, marginal predictors ($p < 1$) are in italics. The variance in the intercept-model was 0.94 for non-kin, 0.95 for non-household and 0.95 for kin. Interactions were only retained if significant at $p < 0.05$, models contain age and the measure of centrality only ($n = 29$).

	Kin proximity			**Non-household proximity**			**Non-kin proximity**		
Parameter	***B***	**95% CI**	**VAR**	***B***	**95% CI**	**VAR**	***B***	**95% CI**	**VAR**
EC	91.10	-0.5, 0.4	0.00	-0.305	-0.8, 0.2	0.05	-0.158	-0.7, 0.3	0.01
Betweenness	-0.092	-0.4, 0.3	0.01	0.102	-0.3, 0.5	0.01	**0.540**	**0.01, 1.1**	**0.14**
Betweenness*age	-	-	-	-	-	-	**0.043**	**0.01, 0.1**	
Degree	0.274	-0.2, 0.8	0.04	*-0.468*	*-1, 0.1*	*0.09*	-0.310	-0.9, 0.2	0.04
Strength	0.103	-0.4, 0.6	0.01	-0.102	-0.6, 0.4	0.01	0.016	-0.5, 0.5	0.00

8.4.3 Maternal betweenness predicts non-kin proximity

Of the 38 mothers in the sample, 29 had living children (n = 81) who took part in the motes experiment. Maternal betweenness positively correlated with the amount of time children were in proximity with non-kin. No other network characteristics were significantly correlated with non-kin allocare or kin and non-household proximity (Table 8.6). Thus, maternal betweenness is *only* associated with non-kin proximity to their children.

8.4.4 Households with more non-kin interactions demonstrate higher fertility and reproductive success.

Mothers whose children have more interactions with non-kin have significantly higher fertility and reproductive success: an effect that is again dependent on age (Table 8.7). The inclusion of non-kin proximity with the interaction with age decreased the maternal level variance by 38% for fertility and 33% for reproductive success. Overall then, it appears that among mothers older than 25 non-kin interactions is significantly correlated with increases in fertility and overall reproductive success. There is no significant relationship between the amount of contact received from non-kin and child mortality, and increases in non-household or kin proximity are not associated with any reproductive outcomes. Overall then mothers aged 25 and over with high non-kin z-scores (more than the mean; 0.1) experienced 1.1 more offspring surviving to age 16 than their peers in receipt of fewer contacts from non-kin (5.9 ± 0.5 versus 4.8 ± 0.5, respectively). This results in an increase in fitness, as measured by survival to maturity, of 21.9%.

Table 8.7: Multilevel models examining the relationship between the proportions of interactions between non-kin, female fertility, and reproductive success. The variance in the intercept-model was 0.5 for fertility and 0.4 for reproductive success. Models contained no other controls and only significant interactions between age and allocare were retained (n = 29).

	Fertility				**Reproductive Success**			
Parameter	***B***	***p***	**2.5% CI**	**2.5% CI**	***B***	***p***	**2.5% CI**	**2.5% CI**
Intercept	0.05	0.76	-0.28	0.39	0.09	0.56	-0.27	0.49
Non-Kin	-0.18	0.17	-0.47	0.10	-0.18	0.15	-0.45	0.08
Non-kin*age	0.03	0.00	0.01	0.05	0.03	0.01	0.01	0.05
Model Residual	0.38				0.33			
Variance explained from controls	0.23				0.20			

8.4.5 Centrality and allocare are associated with maternal and child quality

8.4.5.1 Betweenness positively correlates with maternal sickness, degree negatively correlates with maternal BMI

Of the original 38 mothers who took part in the motes experiment I conducted a medical questionnaire on 36 to quantify bouts of sickness over the last two weeks. Mothers with higher betweenness reported significantly more bouts of sickness (B = 0.3, p < 0.01, 95% CI [0.1, 0.5]). The inclusion of betweenness into the model reduced the unexplained variance at the individual level by 22.6% compared to the model with controls. There is a significant relationship between fertility and sickness for more than two instances of sickness (B = 0.2, p = 0.01, 95% CI [0.03, 0.3]), but not for fewer cases (B = -0.3, p = 0.39, 95% CI [-0.2, 0.1]). This suggests the association of betweenness with self-reported sickness is somewhat mediated by having more offspring. No other network measures were associated with increases in self-reported sickness or haemoglobin levels. However, maternal BMI is negatively associated with degree *only* (B = -1.2, p = 0.01, 95% CI [-2.1, -0.2]), accounting for 11.6% of the unexplained variance compared to the control-only model. Thus, while mothers with higher betweenness suffer more sickness, mothers with higher degree demonstrate poorer nutritional condition.

8.4.5.2 Maternal betweenness negatively correlates with child BMI and haemoglobin levels

The 39 mothers who took part in the motes experiment had 91 children from whom I had anthropometrics and 81 children I had collected blood samples from. Mother's betweenness is negatively and significantly associated with both her offspring's haemoglobin concentrations (B = -5.0, p = 0.04, 95% CI [-9.8, 0.3]) and BMI z-scores (B = -0.2, p = 0.03, 95% CI [-0.4, -0.02]). Thus, mothers with high betweenness had children who were in a worse nutritional condition and suffer from iron-deficient anaemia.

One hypothesis is that mothers with higher betweenness invested in fertility rather than child quality, increasing sibling competition and resulting in poorer outcomes for their children. Sibling number was of marginal significance as a predictor for child BMI (p = 0.09) but not for haemoglobin levels (p =0.5). As a result, I explored the influence of presence of younger and older siblings on BMI and haemoglobin levels with the full sample of under 12's (n = 181, Figure 8.5). This demonstrated that the association between BMI and maternal betweenness may be influenced by sibling competition effects, as the number of younger siblings is associated with a significant decrease in BMI z-score (B = -0.17, p = 0.01, 95% CI [-0.3, -0.04]), resulting in a 35.8% decrease in household level variance compared to control-only models. However, the inclusion of this did not reduce the significance of maternal betweenness in the full model, but the beta did drop slightly (from -0.2 to -0.18). Therefore, mothers with higher betweenness may increase sibling competition due to increased fertility (i.e. quantity over quality). However, betweenness maintains an independent relationship with BMI despite the inclusion of sibling effects, suggesting other pathways. There is no relationship between haemoglobin concentrations and younger (*B* = 0.5, p =0.7, 95% CI [-3, -2.3]), or older sibling (*B* = 1, p =0.2, 95% CI [-0.6, 2.7]) presence, suggesting then that the relationship between haemoglobin concentrations and betweenness was wholly unrelated to sibling competition.

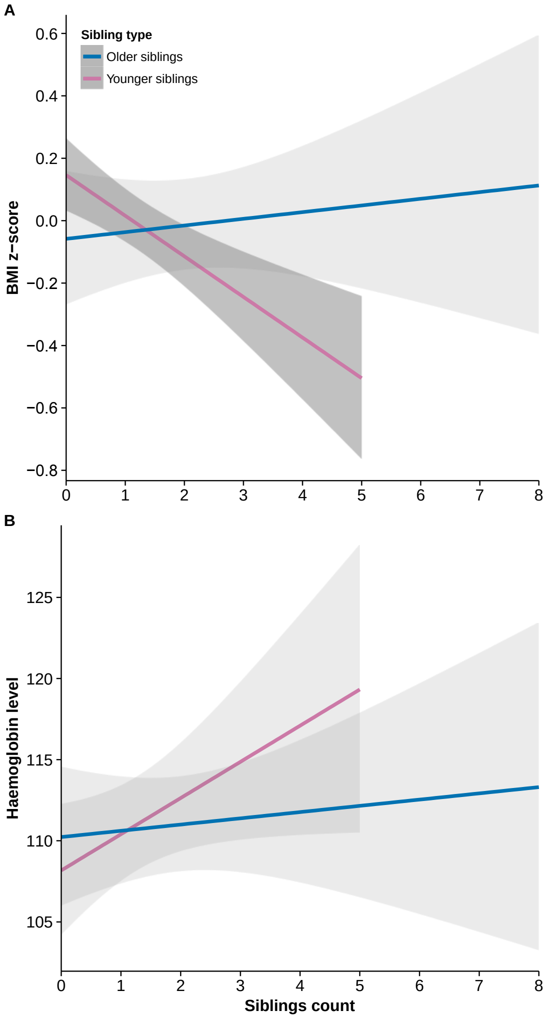

Figure 8.5: The relationship between number of younger and older siblings and (A) BMI z-scores and (B) haemoglobin levels. Non-significant results are faded (*n* = 181).

8.4.5.1 Maternal degree positively predicts child haemoglobin levels

While no measure of centrality significantly predicted child sickness, maternal degree was positively correlated with child haemoglobin levels (*B* = 10.2, p = 0.006, 95% CI [2.8, 17.5]) but not with child BMI scores (*B* = 0.04, p =0.8, 95% CI [-0.08, 0.4]), Figure 8.6).

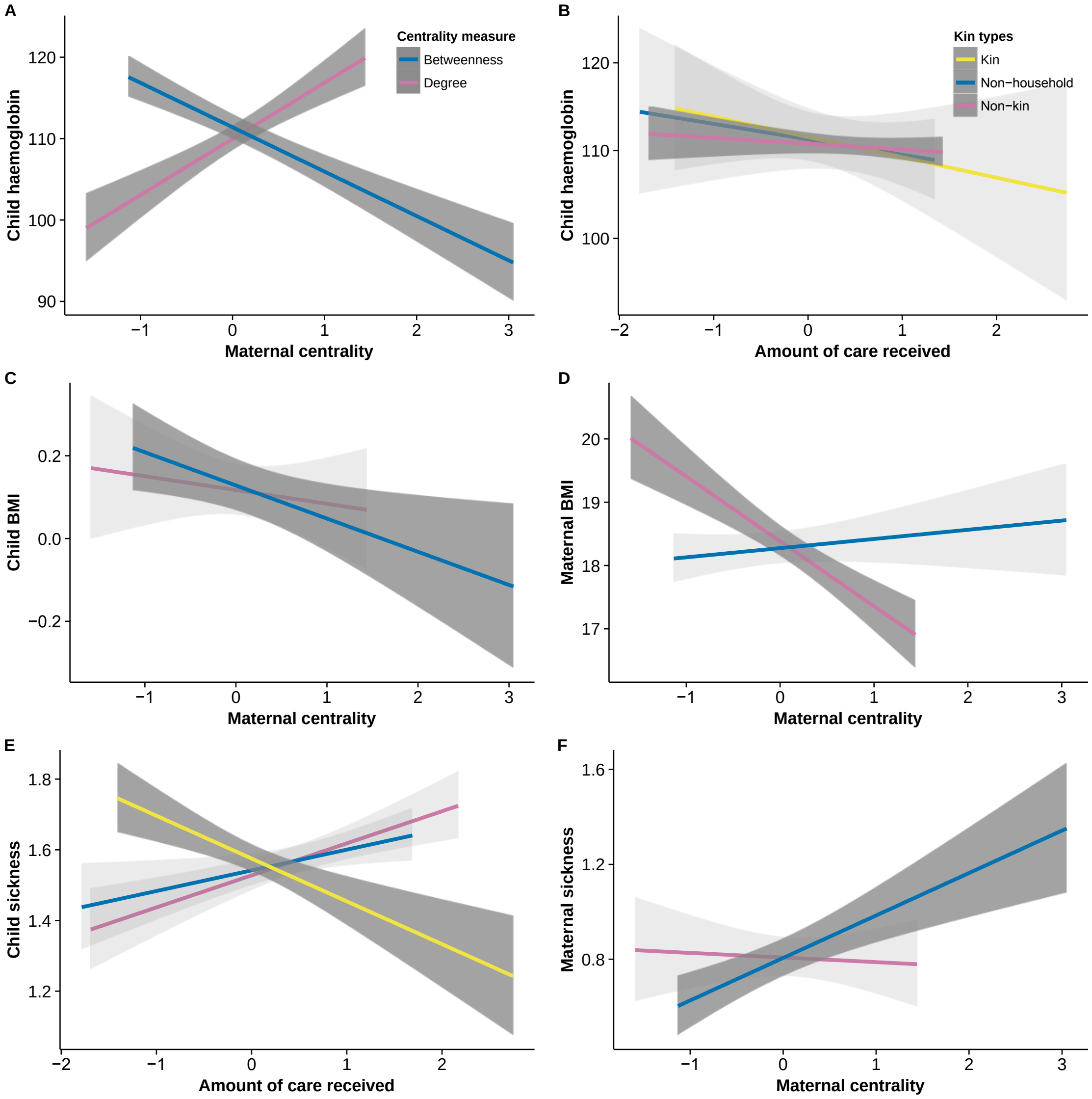

Figure 8.6: Maternal and child outcomes according to maternal centrality (degree and betweenness) and amount of care received from different categories (non-kin, kin and non-household). First row presents results for child haemoglobin levels by centrality (A) and amount of care (B). Second row presents results for child BMI (C) and maternal BMI (D) by centrality. Final rows presents results on child sickness by amount of care (E) and maternal sickness by centrality (F). Non-significant results have 95% confidence intervals faded.

8.4.5.1 Child outcomes by interactions with allocarers

Increased proximity with kin significantly decreased the instances of sickness over the last two weeks (B = -0.23, p = 0.02, 95% CI [-0.4, -0.04]). The inclusion of kin interactions decreased the individual level variance in sickness by 4.5% from the controlled model. The amount of interaction with non-kin is associated with a reduction in a child's circulating haemoglobins (B = -5.4, p = 0.05, 95% CI [-10.7, -0.02]) and BMI z-scores (B = -0.3, p =0.001, 95% CI [-0.5, -0.1]). As above, the separation of younger and older siblings did slightly reduce the size of the effect for non-kin proximity (from -0.3 to -0.25), however it remained a significant predictor of BMI z-score demonstrating the independence of the relationships between increased fertility, sibling competition and BMI.

8.5 Discussion

While research into the adaptive consequences of network centrality and indirect social ties has received little empirical attention in humans, I have demonstrated that they have clear fitness implications (Table 8.8). These results suggest that mothers with greater betweenness have higher fertility and reproductive success at the cost of increasing poor health, while mothers with higher degree centrality demonstrate lower fitness. I hypothesised that the positive relationship between reproductive success and betweenness is related to the solicitation of non-kin allocare, further suggested by the relationship between fitness, betweenness, allocare and age. By centring age at 25 it is possible to capture reproductive career effects; under the age of 25 mothers had a 43.8% surplus of carers within the household, but over the age of 25 they face an average 30% deficit in household childcare. As a result, non-kin childcare becomes increasingly important as mothers continue reproducing and the household is no longer a sufficient provider of childcare, particularly in the face of further unpredictable shortfalls. Thus, I hypothesised that mothers seek more non-kin allocare with increasing fertility, which reduces their workload and allows investment in fertility without diminishing overall reproductive success. However, the reverse causality is also possible, in which mothers with more children have higher centrality and non-kin interactions due to the higher fertility. However, the direction of the causality does not alter the importance of children's interactions with non-kin and maternal network centrality.

8.5.1 Betweenness, non-kin allocare and fertility

Individuals with high betweenness can be referred to as 'brokers' as they connect disparate parts of the network (Brent 2015). For instance, Lehmann and colleagues (2010) found that the simulated removal of high betweenness individuals in 11 Old World monkey species significantly reduced the connectivity of the networks (but did not destroy connectivity completely in bottlenose dolphins (Lusseau & Newman 2004)). This trend is associated with 'small-world' networks; networks are more 'efficient' transmitters of information, disease or resources not when each individual is connected to one another (i.e. high degree) but when clusters are linked by a few central nodes (i.e. brokers (Brent, Lehmann, et al. 2011)).

Table 8.8: Results summary. NE stands for no effect, / represents un-tested relationships, + a significant positive relationship, - a significant negative relationship. * represents a significant, positive interaction with age centred at 25 years.

	Measures of maternal centrality				Measures of allocare		
Dependent variable	**Degree**	**Strength**	**Betweenness**	**EC**	**Kin**	**Household**	**Non-kin**
Fertility	−	NE	+*	NE	NE	NE	+*
Mortality	NE	NE	NE	NE	NE	NE	NE
RS	−	NE	+*	NE	NE	NE	+*
Kin proximity	NE	NE	NE	NE		/	
Household proximity	NE	NE	NE	NE		/	
Non-kin proximity	NE	NE	+*	NE		/	
Maternal BMI	-	NE	NE	NE		/	
Maternal sickness	NE	NE	+	NE		/	
Maternal haemoglobin	NE	NE	NE	NE		/	
Child BMI	NE	NE	−	NE	NE	NE	−
Child sickness	NE	NE	NE	NE	-	NE	NE
Child haemoglobin	+	NE	−	NE	NE	NE	−

If foragers buffer risk and stochastity in unpredictable environments using extensive food sharing and cooperative breeding (Chaudhary *et al.*, 2015; Jaeggi and Gurven, 2013; Meehan *et al.*, 2014; Smith *et al.*, 2010, section 1.2.3), then the structure of cooperation or insurance networks may impact the effectiveness of this method. For instance, if you only cooperate with one other household, this household would soon become overburdened or unable to help when required. In contrast, having ties to disparate parts of the network increases the number of possibilities. Furthermore, for communal breeding to function as an efficient means of risk pooling, 'exposure' units must be independent and unconnected to one another (Cashdan 1985). For instance, closely related households participated in the majority of food sharing; 88.3% of Agta households shared food only with three other closely related households (mean coefficient of relatedness = 0.1 (Dyble *et al.* 2016)). Time spent foraging reduces the amount of time and/or quality of childcare, thus, if a mother relied on the same households to provide care and provisioning there would be a childcare deficit when the food-sharing cluster had a shortage of food. Exactly when a mother had to increase her foraging activities is when potential caretakers would also do the same, resulting in few available allocarers. Therefore, due to the lack of independence of potential caring units, mothers would not be able to receive all the care required to raise multiple costly offspring. Put simply, as suggested by Hrdy (2005), it is not wise to put all your eggs into one allocaring basket. This suggests why *only* non-kin allocare was significantly associated with both betweenness and fertility. This interpretation is further supported by the finding in section 7.4.4 that non-kin allocare is associated with reductions in household wealth, suggestive that it plays a role in risk mitigation.

Overall, mothers connected to more disparate parts of the network maximised reproductive success, which may be due to increased access to allocare. Chapter 6 already revealed how increased non-kin interactions with children significantly reduced the amount of time mothers were proximate to their children. This indicates that, unlike interactions with siblings or fathers, individuals independent from the household provided substitutive care, hence reducing maternal energy burden. As mothers who acted as brokers in the network had higher fertility, perhaps this allocare allowed them to increase investment in foraging, producing more calories resulting in a faster resumption of fertile cycles (Sear *et al.* 2003). Or perhaps they simply reduced energy expenditure overall, and thus spent more time relaxing. The combination of reduced workload and increased nutritional condition has long been known to positively influence fecundity. For instance, Au forager-horticulturalists resumed menses sooner after childbirth if they were better nourished (due to wage labour) independently of duration of breastfeeding (Tracer 1996). Similarly, in rural Ethiopia the addition of water pumps into the village significantly reduced women's workload (given they no longer had to walk long distances with heavy burdens). As a result there was an immediate reduction in interbirth interval as mothers were able to conceive again sooner (Gibson & Mace 2002). This influence of decreased energy expenditure can function independently of nutritional intake; even if rural Polish women had a positive energy balance (the relationship between energy expenditure and intake), periods of intense labour were associated were ovarian suppression (Jasieńska & Ellison 1998). Consequently, care from non-kin may have resulted in a significant fertility increases due to reductions in maternal workload. Further investigation on this topic should use time allocation data to explore mothers exact activity budgets given the amount of allocare received and from whom. This method was successful in the Aka foragers, where it was evident that caregivers significantly reduced mothers total energy expenditure (Meehan *et al.* 2013a).

The measure of 'allocare' here is only proximity, and as a result the positive relationship between reproductive success and non-kin interactions may stem from other pathways them direct care. For instance, domestic tasks, cooperative food production and food sharing may occur with the same individuals who are proximate to dependent children. It is likely that having wide social networks including non-kin for food sharing and production is an important manner of reducing environmental unpredictability. Therefore, households with better ties with non-kin may be of 'higher quality' in terms of social position or relational wealth, and as a consequence have higher fertility and child survivorship rates.

Betweenness has also been associated with increased fertility in free-ranging chimpanzees, (*Pan troglodytes schweinfurthii*), albeit for different reasons; males with higher coalition network betweenness had increased rank and probability of siring offspring (Gilby *et al.* 2013). Male's preference for coalitions that were otherwise unconnected appeared to maximise connectivity in the network, with clear fitness implications, indicating the adaptiveness of third-party awareness in chimpanzees. Betweenness also appears important in other taxa; in terms of social transmission of ecological knowledge in bottlenose dolphins (Lusseau 2006) and in three tit species (*Paridae spp.* (Aplin *et al.* 2012)), as well as social position in long-tailed manakin (*Chiroxiphia linearis* (McDonald 2007)). Interestingly, among the long-tailed manakins it appeared that a male's betweenness earlier in life significantly predicted his social rise (McDonald 2007), a trend also noted in bottlenose dolphins (Stanton & Mann 2012) and humans (Giles 2005). Perhaps this sheds further light on the significant interaction between network position and age; if the fitness effects of social networks are a product of lifetime centrality then their effects may accumulate over the life course. Thus, mothers with consistently high betweenness will ultimately have the highest reproductive success. Furthermore, betweenness is associated with significant heritability; in a twin study Fowler and colleagues (2009) found that genetic factors account for 29% of the variability in betweenness, a finding further supported by Brent and colleagues (2013) research on rhesus macaques. As a result, it appears that given the fitness benefits, variability and heritability of betweenness, it is likely that such traits like third-party awareness, social intelligence as well as social network qualities could be considered targets of natural selection.

8.5.2 Betwixt between child quantity and quality (including the mother's)

It appears that both child BMI and haemoglobin levels decreased with rising levels of betweenness and non-kin allocare. One possibility is that non-kin allocare is of significantly lower quality. Certainly there is evidence among non-human primates, such as bonnet macaques (*Macaca radiata),* that forceful ('kidnapping') allocare of infants by mother's without offspring results in incompetent care and poor outcomes (Silk 1980). This reason, Hrdy (2011) suggests, may be a factor in the lack of allomothering in the other great apes and baboon species. In the case of the Agta it may be that non-kin allocare is also associated with meal sharing where non-related children are provided with less and/or lower quality foods resulting in a reduction of nutritional condition. Furthermore, maternal care would likely be of higher quality, and as non-kin allocare is associated with decreases in maternal interactions with a child, then perhaps it reduces a child's access to high quality childcare, particularly as the mother focuses on fertility (quantity) rather than quality. More in-depth data about the nature of allocare and provisioning is essential to explore the causal associations between child quality, betweenness and allocare. For instance, a second possibility is that mothers with more children simply do not provide active care for some children resulting in their poorer health outcomes, rather than non-kin allocare being necessarily negative. Nonetheless, it appears that allocare among the Agta may be an example of a maternal strategy of focusing on higher fertility, made possible by increased allocare and a reduction in workload, which results in lower quality offspring. Furthermore, this investment in fertility may simultaneously increase sibling competition resulting in further reductions in child quality (in this case BMI only). However, since child mortality is not increased by allocare or betweenness, this trade-off appears to pay-off in fitness terms.

Investment in quantity over quality makes 'life history sense' given the high morbidity, high mortality of the (particularly pygmy) hunter-gatherer lifestyle leading to faster life history strategies (Migliano *et al.* 2007). Our own data demonstrates that of 520 live births reported, the Agta experienced a childhood mortality rate of 388.5 per 1000. Therefore, following life history predictions (Charnov 1993), I would expect Agta mothers to invest in quantity rather than quality as they will experience diminishing returns on their investment given the high pathogen and morbidity rate (Quinlan 2007) as well as the increased likelihood of offspring dying before they reach reproductive maturity, making increased investment redundant. Further exploration into the quality and consistency of maternal care according to extrinsic risks is paramount to exploring this interpretation further.

There is little indication that allocare has any positive effects on survival or wellbeing. This is surprising since much of the literature on cooperative childcare suggests that allocarers have a greater influence on child nutritional status than maternal fertility (Sear *et al.* 2003; Strassmann & Gillespie 2002). However, as suggested above this may be related more to residence in a high risk, high pathogen and high mortality environment, rather than about the 'nature' of allocare and its consequences. Allocare simply frees up additional energy to be reinvested elsewhere. In a lower mortality environment allocare may be associated with increased child survival, however in a high mortality environment a mother may direct her energy to fertility instead. As with the variability in who helps according to context, it appears the consequences of this help are also dependent on the ecological and social conditions (Sear & Mace 2008).

Nonetheless, the data do reveal that the total amount of allocare received by a household from kin is associated with a significant decrease in self-reported sickness. Thus, allocare from kin may go some way to improve children's condition, boosting their immunological defences and nutritional condition, in agreement with cooperative breeding literature in general (Sear *et al.* 2002; Sear & Mace 2009; Sear & Mace 2008; Meehan *et al.* 2014; Hawkes *et al.* 1997; Gibson & Mace 2005). This may be related to the finding in section 6.5 which demonstrated that many types of kin increased the number of interactions a mother had with a child (including siblings, fathers, distant kin and paternal grandfathers). Therefore, children in receipt of more allocare from kin may be receiving more childcare overall, significantly improving their immunological condition. However, due to the focus on fertility and maternal network centrality I have not separated the developmental and health consequences of allocare from different type of kin (i.e. siblings, grandparents and aunts and uncles) nor looked at different age interactions (i.e. infancy, toddling and childhood). To truly explore these questions, these categories need to be separated as chapters 6 and 7 revealed that exactly *who* the allocarer is matters, as does the age of the child.

Interestingly, mothers with greater betweenness seem to suffer from more bouts of sickness. This finding is in line with much of the literature on disease transmission through networks which finds that 'brokers' in the network are both more likely to host a pathogen and transmit it widely throughout the network (Weber *et al.* 2013; Ueno & Masuda 2008; Corner *et al.* 2003; Hamede *et al.* 2009). As individuals with high betweenness are those who lie on central ties, it follows that much of the disease transmission flows through them (Hamede *et al.* 2009). However, it also seems in our sample that the mothers who report being sick the most are those with more children, though this may be a trade-off between fertility and somatic maintenance (Stearns 1992; Lawson *et al.* 2012) or a product of children acting as 'super-spreaders' of disease (Glass & Glass 2008; Keeling & Eames 2005).

8.5.3 The cost of social networks?

Contrary to others findings (McFarland & Majolo 2013; McFarland *et al.* 2015; Lehmann *et al.* 2015) degree has a significant negative relationship with fertility and reproductive success. Certainly, sociality comes at a cost of increased competition, risk of disease and social tensions (Krause & Ruxton 2002; Silk 2007b), thus being highly connected to a network may have negative consequences. This finding is demonstrated in research with female yellow-bellied marmots (*Marmota flaviventri*) in which social affiliation and neighbour overlap were negatively correlated with reproductive success (Wey & Blumstein 2012). Here, maternal BMI decreased with degree centrality, a likely factor impacting her fertility (Pike 2001; Lipson 2001; Ellison *et al.* 1993). This suggests that mothers with high degree have lower nutritional quality, perhaps related to the number of obligatory relationships they hold with others who compete for the same resources (Borgerhoff Mulder 2007; Sear 2008). This leaves unexplained why degree is positively correlated with child haemoglobin levels (but not BMI); if a high number of social ties due to resource competition has a negative effect on maternal BMI and fertility, then these individuals should also be in competition with the mother's offspring. This finding may be the consequence of uncontrolled relationships between degree and other predictors of child BMI, including the underlying causes of increased degree centrality. Or this may be the outcome of mothers with lower fertility increasing investment in child quality. These interpretations are mere speculation, therefore it is essential to expand these findings further to understand the effect of degree centrality on maternal and child outcomes.

8.5.4 Limitations

This study remains correlational and further research needs to be conducted into the processes underlying the relationship between degree and fertility and the relationship between betweenness and reported sickness. For instance, further exploration into the competition between individuals would be highly informative, as would observational data on the quality of allocare from different caretakers. Importantly, in this analysis I cannot distinguish whether more fertile mothers place themselves in a 'between' position to seek out more allocare to look after their offspring or whether mothers who are 'between' groups gain higher fertility due to the increased allocare from non-kin. However, this issue of causality makes no impact on the overall argument; both pathways demonstrate the advantages of network centrality. Perhaps more problematic, as argued by Gilby *et al.* (2013) is that betweenness may simply be a by-product of another trait which results in higher fertility. For instance, higher quality mothers may have higher betweenness. For this reason I explored the relationship with betweenness and allocare to understand these mechanisms (Brent 2015). However, future research should examine the role of social status and betweenness; individuals of high social status or relational wealth are known to have increased fertility (Chaudhary *et al.* 2015; Gurven & von Rueden 2010; Smith 2004; von Rueden *et al.* 2011; Borgerhoff Mulder & Beheim 2011). Finally, ethnographic and interview data exploring emic perspectives of social ties and how they vary across the life course will greatly aid our understanding of this complex (and abstract) relationships.

8.6 Conclusions

I have shown that individual's network centrality has important implications for fitness outcomes among Agta hunter-gatherers. This reveals how weak, strong, direct and indirect ties have important influences on Agta reproduction and cooperation. In particular, by exploring the emergent features of social networks, rather than focusing on 'who cares', I find that a mother's network position can be considered an extended phenotype given its importance in gaining access to a dispersed networks of allocare which significantly boost maternal reproductive success. The importance of a measure like betweenness may then lie with highly cooperative groups living in risky niches. Given the variable and unpredictable hunter-gatherer environment, on top of an existing childcare deficit (section 6.4), the ability to manipulate one's social network to ensure the household is buffered from care shortages may offer an important insight into the evolution of sociality and cooperation (Wey *et al.*

2013; Hill *et al.* 2009). This further reveals the evolutionary importance of third-party knowledge; if being a broker to disparate parts of the network is beneficial, it follows that individual's maintain an awareness of not only who they are friends with, but who are friends of friends (Brent 2015). Such dynamics take considerable social intelligence, and indicate one possible selective pressure for brain expansion in primates (Silk 2007a). These results are suggestive of the evolutionary importance of encephalisation in facilitating management of complex and diverse social networks since an individual's centrality depends not only on their direct ties but also indirect ties throughout the population (Formica *et al.* 2012). Further research using social network analysis to explore these indirect properties' influence on human fitness is essential, as they may play a major role in our social and behavioural evolution

Chapter Nine
Discussion and Conclusions

This thesis furthers our understanding of cooperation and life history in an extant foraging group. I have presented innovative ways to explore allocare and the fitness consequences of social networks in small-scale societies. I have robustly examined the role of kin selection and reciprocity in determining allocare, highlighting the importance of cooperation as a form of risk mitigation and presented an original study focused on examining within population variance and how this influences life history trade-offs. In this chapter I will briefly summarise the main findings from this research. Then I will offer some thoughts about the implications of my research for the wider literature on cooperative breeding and hunter-gather studies.

9.1 Overview of findings

In chapter six I demonstrated that fathers, siblings and non-kin are more significant allocarers than grandmothers by exploring who interacts with dependent children across a range of ages. This is in contradiction to Hawkes *et al.* (2000) hypothesis that the evolution of a prolonged post-menopause lifespan in humans is related to the beneficial role grandmothers play in cooperative breeding. However, this is supported by the majority of direct allocare studies among hunter-gatherers which find little investment by grandmothers (Kramer 2010; Kramer 2005; Crittenden & Marlowe 2008; Goodman *et al.* 1985; Hill & Hurtado 2009). Others have argued that grandmothers are a poor evolutionary strategy in foraging populations given their high mortality and flexible mobility (Hill & Hurtado 2009). My data supports this statement. The role of allocarer is context dependent and likely reactive to age-specific mortality schedules. Grandmothers may have had a smaller role in populations with high mortality and early first births, and perhaps grow in importance with slower life history strategies.

In chapter seven I presented the first detailed test of several hypotheses of why individuals provide costly allocare in the Agta. Competing explanations of kin and reciprocity are rarely examined in a multivariate analysis within the human literature, thus my conclusions have important implications for understanding the evolution of communal breeding. The results are supportive of the influence of both kin selection and reciprocity in communal breeding. Following increasing evidence supportive of the role of reciprocity (Nolin 2010; Allen-Arave *et al.* 2008; Jaeggi & Gurven 2013b; Kasper & Borgerhoff Mulder 2015; Alvard 2009) my work demonstrates that distant kin and non-kin provide a significant amount of proximity care predicted by contingency, benefits and costs. This brings this analysis of cooperative breeding in line with the larger cooperative literature which systematically explores the roles of B and C rather than simply varying r (Gurven 2004b; Hooper 2015; Kasper & Borgerhoff Mulder 2015; Jaeggi & Gurven 2013b). However, these dynamics are influenced by subsistence economy as increasing wealth and decreasing foraging emphasises the role of close kin over that of more distant and unrelated individuals. Recent research has focused on cooperation as forms of insurance against risk following need-based transfers (Aktipis *et al.* 2011; Hao *et al.* 2015). My work extends this by testing these hypotheses among the Agta, highlighting the usefulness of these perspectives.

Chapter eight demonstrated that communal breeding and maternal social networks have implications for reproductive success. Mothers with greater betweenness centrality had higher reproductive success and received more allocare from non-kin at the cost of poorer health for both the mothers and their offspring. Degree centrality on the other hand negatively influenced maternal reproductive success. Following literature from primatology and behavioural ecology, it appears then that the formation of social ties has implications for fitness, revealing that being aware of 'who is friends with whom' is an important behavioural strategy (Murphy *et al.* n.d.; Gilby *et al.* 2013; Brent 2015; McFarland *et al.* 2015; Lehmann *et al.* 2015; Stanton & Mann 2012). Chapter seven further revealed that cooperative breeding has an adaptive function as care from non-kin (who have been demonstrated to substitute maternal investment in chapter five) increases reproductive success. Contradictory to the majority of literature on human cooperative breeding it appears that Agta allocare is associated with increased fertility and decreased child quality. Future research should separate different types of kin, since it appears that grandmothers, aunts and uncles and cousins may not always be cooperative. Following this, the beneficial effects of betweenness may lay in the linking of disparate parts of the network which, from the risk buffering perspective, may have important implications for ensuring they are in receipt of care from non-kin when they have a care shortage.

9.2 Implications for cooperation, risk and hunter-gatherers

9.2.1 Moving beyond kin and their selection

The exploration of communal breeding in humans has been defined by the role of kin. Thus, anthropological and demographic literature has been particularly good at revealing the adaptive function of allocare between kin (Voland *et al.* 2005; Sear & Mace 2009; Sear & Mace 2008; Kramer 2005). Thus, rather than demonstrating that humans are cooperative breeders as cooperation subsides our rapid reproduction of costly infants (Mace & Sear 2005), the literature, by-and-large demonstrates that humans cooperatively breed *with kin* (Sear & Mace 2008; Snopkowski & Sear 2013; Tymicki 2004), which are theoretically speaking, two different things. Understanding humans to be communal, or plural breeders, opens up the door to cooperation not driven by relatedness but based on direct benefits. Without suppression of ovulation, mothers breed together and they (and their children) are able to assist based on reciprocity, allowing for unrelated individuals to cooperate within the inclusive fitness paradigm. Hunter-gatherers consistently reside in camps with a higher proportion of non-kin than kin (Dyble *et al.* 2015; Hill *et al.* 2011), and thus are less related to their group than other small-scale societies who do not practice foraging (Walker 2014). Therefore, given the fluidity of camp composition as individuals and households regularly move between groups (Kelly 2013), the most reliable and consistent 'group' of co-operators outside the household is likely unrelated. As a result, co-residence with non-kin in fluid groups produces an environment in which humans are hyper-cooperative with individuals they do not receive indirect fitness benefits (Burkart *et al.* 2014). Here, I have argued that this may be advantageous in evolutionary terms due to an increased ability to buffer risks in the environment when a population is mobile and lacks substantial wealth; a wide and dispersed social network produces multiple allocare options which are necessarily limited among kin. From this unique perspective I have produced analyses that highlight the importance of non-kin as they have a high number of interactions with dependent children, which significantly negatively correlates with maternal interaction, suggesting a pathway between non-kin interactions and increased fertility and offspring survivorship to age 16.

The primacy of kin in the literature has resulted in a void of research on allocare from non-kin and how allocare is maintained among 'selfish' individuals. I know of no other study which examines the question of communal breeding in this manner. However, in contrast the literature on food sharing and wider cooperation in small-scale societies is brimming with examples of robust, multivariate analysis of competing hypothesis exploring cooperation between both kin and non-kin (Jaeggi & Gurven 2013b; Kasper & Borgerhoff Mulder 2015; Alvard 2009; Nolin 2010). In particular, recent analysis has sought to break down the data and separate the confounding effects associated with costs and benefits (Hooper 2015), relatedness and proximity (Alvard 2009; Nolin 2010), reciprocity between kin and non-kin (Allen-Arave *et al.* 2008; Kasper & Borgerhoff Mulder 2015), and, by doing so, greatly furthers our understanding of the complex exchanges between individuals. By following the theoretical path set by the cooperative literature at large it is possible to understand the ultimate function of communal breeding and how it varies according to the individual and context. Previously, sample sizes and age controls have been poor in hunter-gatherer studies (Mace & Sear 2005), limiting the ability to conduct such explorations. However, hunter-gatherer studies have the benefit of often capturing the totality of interactions; communal breeding is the product of provisioning and food production, domestic help and direct care. Larger scale demographic studies struggle to capture these pathways which confound relationships. Consequentially, future work should focus on bringing these perspectives together, increasing the sample sizes of hunter-gatherer studies and explaining the totality of cooperative interactions. This approach might provide a better framework to under the diversity of results often apparent in the literature.

9.2.2 Relational wealth and its relation with risk

A second theme throughout this thesis surrounds the concepts of risk, its mitigation and the role of wealth. Borgerhoff Mulder and colleagues (Borgerhoff Mulder & Beheim 2011; Borgerhoff Mulder *et al.* 2009) developed a framework of expanding 'wealth' beyond the confines of maternal objects, into embodied or relational wealth. It is this relational wealth that I have discussed throughout this thesis; "the social ties on which an individual can draw, ties that derive from social position, trust, reputation, kinship and symbolic goods"(Borgerhoff Mulder & Beheim 2011: 345). Thinking about wealth in this manner offers, I believe, informative insights into how small-scale societies use behavioural strategies to adapt in any given environment. Given that this framework highlights the comparable roles of 'wealth in people' with 'wealth in things' it has direct relevance to hunter-gatherer research.

Traditionally hunter-gatherer research has often attributed behavioural strategies to residence in risky, unpredictable environments without wealth, thus their use of social insurance via cooperation was understood to mitigate unforeseen losses (Kelly 2013). Certainly Winterhalder's (1986) original model is robust and demonstrates that even among six to eight hunters, if returns are asynchronised, variability in food returns is effectively dealt with by food pooling. Theoretically, relational wealth appears to play an important role, leading Kaplan *et al.* (2009) to argue that risk-reduction strategies have major implications for the evolution of human social organisation. Due to large and variable package sizes being the 'basis' of foraging subsistence, cooperation produces reliable ties between households and non-kin, extensively broadening our social networks. I do not disagree with this theory, and believe that risk is an informative way of examining human cooperation. However, this theory is rarely tested, rather simply applied as an interpretation of results (as I have done in chapter 8). For instance, many studies imply that the ultimate *why* behind humans extensive cooperation, social capital, food sharing is due to survival in a risky foraging niche (Jaeggi & Gurven 2013a; Salali & Migliano 2015; Chaudhary *et al.* 2015; Gurven & Hill 2009). This is not problematic *ipso facto*; however, not all foraging environments are the same. Kelly (2013) warns about using 'hunting-gathering' as an explanatory variable, stating we should explore variability within and between populations to test these relationships. It is evident that there is significant variability in hunter-gatherer foraging returns, ranging from the Hadza who acquired meat on less than 3% of hunting trips (Hawkes 1991), to the Ache who faced a 60% failure rate (Hill *et al.* 1987) and as high as Agta fishing trips which were successful on 89% of trips. Surely then, such variability and range in package sizes (from the Hadza big game, Ache smaller jungle creatures to the small river fish consumed by the Agta) would be predicted to result in variability in cooperative strategies.

Consequently, future work should explore the relationship between cooperative behaviours, variability in returns and different types of risk environments, including disease risk (Sugiyama & Chacon 2000) and fitness outcomes. This would go further in exploring the adaptive value of cooperation. For instance, here I have argued that communal breeding and a high betweenness centrality is adaptive as it increases fitness. I speculate that this is due to betweenness allowing individuals to link to disparate parts of the social network ensuring that allocare remains constant in an environment when unpredictable shortfalls due to illness or foraging failure mean that childcare cannot be guaranteed within one 'exposure' unit. Care from non-kin is important as it can meet childcare demands when other kin cannot, particularly when there is little material wealth to buffer a household from risk. Howell (2010), in her work on the life history of the Dobe !Kung comes to a similar conclusion that a wide network of providers act as insurance, rather than simply 'kin as wealth'. However, these statements need further testing. For instance, future research should explore how the importance of 'betweenness' and non-kin allocare varies according to different measures of risk in the environment. Furthermore, I demonstrated that relational wealth holds the predicted relationship with material wealth, suggesting that different forms of risk mitigation, such as material accumulation and subsistence diversification, may mitigate the association between risk and cooperation. Therefore, do global properties of social networks change with ecology, risk and subsistence patterns? It is questions like these which will further our understanding of how groups behavioural strategies adapt to different environmental pressures.

9.3 Hunter-gatherers and human evolution

> "*Long before anthropologists arrived on the scene hunter-gatherers had already been given disease, shot at, traded with, employed and exploited by colonial powers or agricultural neighbors"* (Kelly 2013: 16)

It would be remiss of me not to discuss the role of hunter-gatherer studies in understanding human behavioural evolution. It is a contentious issue and the arguments for and against have been well rehearsed (O'Connell (1995) says the same and the debate remains by-and-large unchanged). However, in conclusion to this thesis I would like to offer my own interpretation of the issue. We have, of course, moved a long way from early anthropological thought, which saw present day foragers as analogous to our Palaeolithic ancestors (Wilson 1978; Kelly 2013). Predominantly, the study of human behavioural ecology has focused on the variability of foraging groups alive today, indicating that it is not possible to define a 'pure' or 'model' hunter-gatherer group. Certainty I would not attempt to do so for the Agta, but not because I believe they are any more or less of a 'foraging group' than any other population. Rather I argue that this line of argument leads to erroneous perspectives as it implies that hunter-gatherers were static before 150 – 200 years ago, so if we "carefully…account for the effects of contact on their way of life" (Lee 1979: 2) we can get at the 'reality' of foraging. Foragers have not lived in a world of only foragers since 13,000 – 6,000 (depending of course on geographic location (Diamond & Bellwood 2003)), and the archaeological, linguistic and genetic record is rife with evidence of significant amounts of interaction, trade, and stable periods of low-level food production (Smith 2001; Price & Gebauer 1995; Piperno & Pearsall

1998; Inomata *et al.* 2015; Bar-Yosef & Meadow 1995; Bollongino *et al.* 2013). As a result, it is unclear why or how one could 'remove' these influences which necessarily have shaped foragers behavioural strategies since their occurrence.

Consequently, I find Marlowe's (2005: 54) justification of the Hadza being 'model hunter-gatherers' as they have changed little in the last century since "all we can do is perhaps give extra weight to those with less contact" problematic. What about the centuries or millennia before this? Arguments by both Foley (1988) and Kuhn and Stiner (2001) point out the diversity in hominid and human evolution, respectively. Saying humans spent 99% of their history as hunter-gatherers lacks meaning given there is no one single time prior to the Neolithic revolution 10,000 – 13,000 years ago. Given that the Palaeolithic is marked by significant climatic changes, such as several glacial maxima, it is not surprising the archaeological record is one of considerable variability (Kuhn & Stiner 2001). Thus, what we consider to be the 'hunter-gatherer package' has not consistently been present, but is the product of adaptation to various selective pressures (Foley 1988; Kelly 2013). Consequently, even if we can infer that hunter-gatherers today are 'pre-Neolithic', then we are only representing "just a few late chapters in a long and complicated evolutionary story that began more than 2.5 million years ago" (Kuhn & Stiner 2001: 128). So where does that leave us - what meaning can we infer from extant hunter-gatherer studies about human and hominid prehistory and evolution?

Broadly speaking I am in agreement with the theoretical frameworks put forward by Kelly (2013), O'Connell (1995), Winterhalder and Kennett (2006) and Kuhn and Stiner (2001). Through the lens of human behavioural ecology we can understand behavioural strategies as optimising processes dependent on environmental, historical and social constraints (Kappeler *et al.* 2013). Thus, with the emphasis on individual decision-making and optimisation it is possible to develop and test predictions following inferences from archaeology. Rather than argue that one type of forager is 'ancient' or 'pure' we should be exploring how hunter-gatherers react to selective pressures, which may reveal parallels from prehistory. Thus, understanding individual decision-making following evolutionary principles adds new pathways of investigation to the study of archaeological periods (Winterhalder & Kennett 2006). Such approaches lie at the heart of behavioural ecology and should not be dismissed from understanding human evolution. As previously argued (Kelly 2013; Blurton Jones *et al.* 2002) hunter-gatherers today still must make allocation trade-offs based on their mode of subsistence, degree of mobility and social structures. Examining how this occurs and how this varies according to key variables provides a theoretical structure to exploring the behavioural ecology of human evolution (Kuhn & Stiner 2001). Therefore, I argue that it is by examining variability within a population, according to predictions from archaeology, that it is possible to reveal the roles of decision-making and optimisation, allowing human behaviour ecology to create a framework to understand human evolution. Under this framework, inferences about human behaviour from an evolutionary perspective are by no way limited to hunter-gatherers; in complete agreement with Nettle *et al.* (2013) if human behavioural ecology is how behaviour evolves in response to ecological conditions, then all societies tell us something about behavioural evolution.

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Appendices

Appendix A

Data collection documents

This appendix contains the English-language originals of the information sheets, consent form, data collection protocols and data collection forms used in this research.

Participant Information Sheet

Hunter-gatherer resilience: A project with University College, London

This project will be developed at University College London, by Dr Andrea Bamberg Migliano and participants of the "Hunter-Gatherer Resilience" project including PhD students and post-doctoral researchers.

The project aims to help us understand how hunter-gatherers live, and in what ways they are different from farmers. To help understand these differences, we will:

- Measure and weigh people to understand how people grow and change as they get older;
- Understand how the food people eat affects how they grow;
- Take sample of saliva to get DNA. DNA can tell us how you are related to other pygmies, why you are different from farmers, and why some people get sickness like malaria more often than others.
- Ask about recent illness and conduct medical tests to understand how healthy you and your family is;
- Collect information on who you and your children interact with;
- Ask about your family and way of life, to understand how you are related to each other.

Getting the sample of saliva is simple, and safe. If you agree to help us, after signing the consent form; you will be given a container in which to collect your own saliva. You will need to spit in it until it is half full, close it and return it to the researcher. The researcher will give it a number and date and take note of the number, your sex and village name.

This project is run through University College London, England, and is therefore in accordance with English Law. Data and any information will be treated as strictly confidential and handled in accordance with the provisions of the Data Protection Act, UK, 1998.

Participant Consent Form

Hunter-gatherer resilience: A project with University College, London

I have read (or, where appropriate, have had read to me) and understood the information above, and any questions I have asked have been answered to my satisfaction.

I agree to participate in the project, realising that I may physically withdraw from the study at any time and may request that no data arising from my participation are used, up to four weeks following the completion of my participation in the research.

I agree that research data provided by me or with my permission during the project may be included in a thesis, presented at conferences and published in journals on the condition that neither my name nor any other identifying information is used.

Name of participant: Date: ____/____/2014

Signature:

Name of authorised representative: Date: ____/____/2014

Signature:

Name of researcher: Date: ____/____/2014

Signature:

Field Protocols

Upon Arrival in Camp

1. Introduce ourselves and display/explain posters to everyone so they know; 1) Why it is interesting; 2) How we will collect the data; and 3) What we want to find out
    - Act this out ourselves first (1 person reads, other 2 act)
        - *Measurements;* 1) Why? See how you grow and develop, 2) How? Measure and weight each of you, 3) Find out? How growth is related to diet and health
        - *Saliva;* 1) Why? Everyone's saliva is different (like fingerprints), 2) How? Spit into pot, 3) Find out? How you are related to other people/populations, and why some people get ill and others don't (also doing genealogies to look at this)
2. Do community mapping with knowledgeable informant(s) in two stages
    - 1) Inter-community information (where other villages are (inc. size and distance), where non-Agta/Mbendjele reside (inc. size and distance), nearby resources, paths/roads)
    - 2) Intra-community information (number of households, size of households, names of everyone, approximate ages and life stages of all in camp)
3. At this time, we can also ask informant(s) for any important events which would be useful for aging (e.g., breakout of war, disease epidemics, other previous researchers)
4. Go around the camp introducing ourselves to everyone, taking pictures, and GPS coordinates (of both village and households – if resolution permits)
    - write names (inc. all aliases)/ID/village/age cohort on back of photo
5. Explain that we will give compensation for their time and cooperation (rice, coffee, etc.)
    - For measuring children, offer honey stick/biscuit/sweet treat

Order of Interviews

1) Repeat information again and get consent from everyone (for children, obtain consent from parents/guardians)
2) Genealogies
3) Relative Aging
4) Saliva Samples and Measurements/Questions

Genealogies

- **Step-by-step Guide**
    1. Explain what we are going to do/ask, and obtain informed consent from everyone by either a fingerprint or 'X' on sheet (parents can do this on behalf of their children)
    2. On A4 paper, begin with ego (or matriarch/patriarch of family if conducted in groups), and below symbol write ID, name (and other aliases), and age (if known)

3. Another person who has the booklet then notes extra information (date of birth/death, cause of death, village/clan, etc.)
4. Repeat process with spouse/previous spouses (begin with first spouse, and end with current/most recent spouse)
5. Ask who their first child is, then second, then third, etc. and get the same information
    a. **Probe** – To estimate the birth intervals, ask whether *x* was walking/crawling/talking when next child was born
6. After have all children, go over again and ask whether anyone died young/miscarried between each pair, or whether they forgot anyone
7. Continue down order of kin using the same method (first/second/third-born sister/maternal cousin/paternal second cousins, followed by checking for any gaps of forgotten/dead people)
    - **Order of questions**
        - 1) Ego and spouse (including previous spouses)
        - 2) Children and their offspring
        - 3) Siblings and their offspring
        - 4) Maternal relations (mother, mother's siblings, maternal cousins, maternal grandparents, etc.)
        - 5) Paternal relations (father, father's siblings, paternal cousins, paternal grandparents, etc.)

Accuracy, Consistency, and Detail Checks

- To check for accuracy/consistency, each night after completing genealogies compare them to other overlapping ones, to make sure info is similar
    - Any discrepancies can then be asked about the next day
- As more distant information is less likely to be accurate, best to try and find these distant kin and compare genealogies
    - If different, give more weight to closer relations
- Match photos to genealogies, to ensure we have all pictures

Relative Aging

- **First Stage – Approximate Groupings**
    1. Prepare photos of people in current camp and 2 or 3 of the nearest camps
        a. Doesn't apply to first camps, but can go back over them at the end
    2. Group photos into approximate ages based on rough age groupings (infant, child, teenager, young adult, middle-aged, old), or by approximate age (e.g., 0-5, 5-10, 10-15, 15-25, 25-35, 35-50, 50+)
        a. Knowledge individual(s) could assist this to begin with before interviews
- **Second Stage – Relative Aging**

1. Beginning with within-camp photos, get individuals (or groups) to arrange pictures in order of age centred around a target, one at a time
    - First comparison: 'Is *x* older or younger than you?'
    - Second comparison: 'Is *y* older or younger than you?', followed by, 'Is *y* older or younger than *x*?'
    - Continue until chain is built
2. Begin with within-camp comparisons, then add in between-camp comparisons after preliminary within-camp list has been made
    - Also include photos of people from birth camp
    - Need to make sure that Ego knows all of the targets
    - Add open question of "Is there anyone else you know and would like to add to this list?"
3. Once list has been finalised, transcribe order into booklet

- *Parents will make relative age lists of children, using the same method*

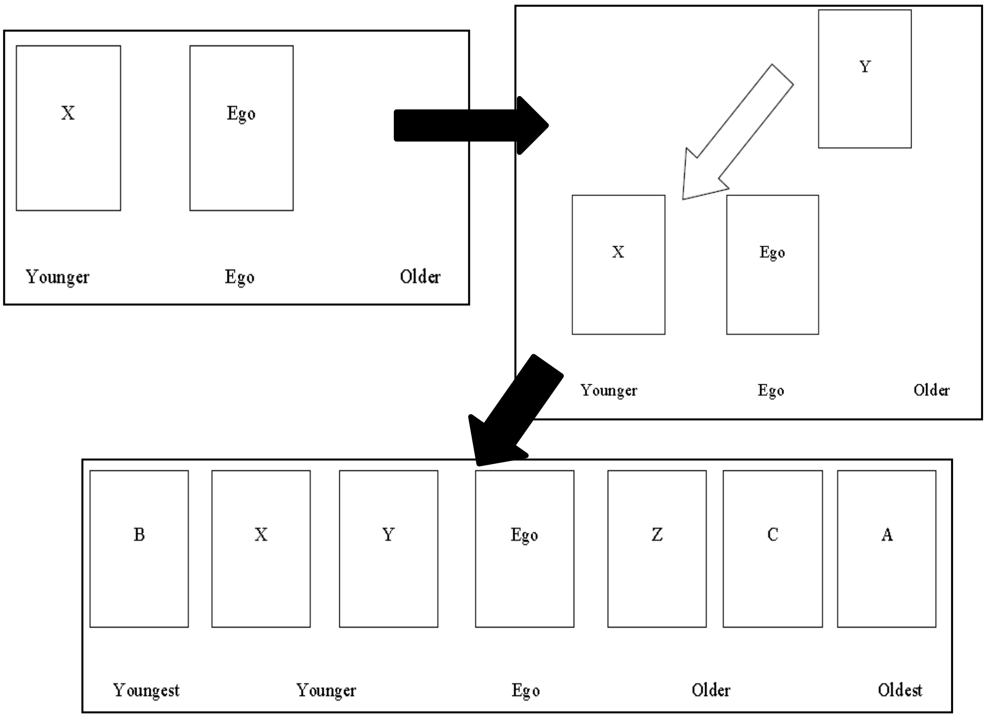

Figure 2: Example of relative aging process

Deceased Individuals

- Ask mother/siblings whether target was older/younger/contemporaneous with a known individual/event when they were born/died (Triangle method used in Ache)
    - E.g., *x* was born between *a* and *b*, and died around the same time *c* was born

Checking for Consistency and Accuracy

- *Consistency:* As with Ache method, could take the most common arrangement to be the most likely, while using the amount of disagreement to assess probability of order (e.g., if 9/10 say *a* > *b*, we can be fairly sure, but if only 6/10 say *a* > *b*, we are less sure)
- *Accuracy:* Need records which can be dated absolutely and show birth orders (which may not be possible)

Physical measurement protocols

Jed Stevenson, Jimma Child Development Study (2007 / 2008)

Weight

1. Put the scale on a flat place on the floor. Turn on the scale.
2. Enter the height, sex, and age of the person. The scale is now ready to weigh a person.
3. Ask the individual to stand on the scale. You will see the weight displayed in kilograms (e.g. 68.3). Body fat, body water, and bone mass will then scroll through
4. For infants, weigh the Mother alone, then Mother with child, and subtract the two to get infant's weight.

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 headboard. The child should look directly upward, and the crown of his/her head should touch the headboard.
    b. Another person should straighten the child's legs. The child's toes should point directly upwards.
3. Record the measurement in centimeters to the nearest 0.1 cm using the anthropometer/tape measure.

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 the child's head.
        i. Another person makes sure that the anthropometer is straight, and not tilted forwards or backwards.
5. Record the measurement in centimeters to the nearest 0.1 cm.

Data collection forms

Appendix A Table 1: To the following questions please answer always, sometimes or never true - *ask the mother*

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

Medical questionnaire

GASTRO-INTESTINAL DISEASE

How many times in the last week have members of your family suffered from diarrhoea?

Name	**Not at all**	**Once**	**3 – 4 times**	**Daily**
Mother				
Father				

For individuals with severe diarrhoea are there any additional symptoms (please circle):

1.vomiting nausea mucus blood bloating fever cramps
other:……………………………………………………………………………………………

2.vomiting nausea mucus blood bloating fever cramps
other:……………………………………………………………………………………………

3.vomiting nausea mucus blood bloating fever cramps
other:……………………………………………………………………………………………

4.vomiting nausea mucus blood bloating fever cramps
other:……………………………………………………………………………………………

Did you seek any treatment?……………………………………………………………………………
………
………

FLUS AND FEVERS

How many times in the last two weeks have members of your family suffered from fever/flu?

Name	**Not at all**	**Once**	**3 – 4 times**	**Daily**
Mother				
Father				

For individuals with recurrent fever are there any additional symptoms (please circle):

1.vomiting boils/wounds cough swollen gland disorientation cyclic
other:…………………………………..

2.vomiting boils/wounds cough swollen gland disorientation cyclic
other:………………………………………………………………………………..

3.vomiting boils/wounds cough swollen gland disorientation cyclic
other:………………………………………………………………………………..

4.vomiting boils/wounds cough swollen gland disorientation cyclic
other:………………………………………………………………………………...

Did you seek any treatment?...…………………
……
……………………………………………....…………………………………………………………
…………………………………………………………………

COUGHS

Do any of your family members suffer from recurrent or persistent coughs? Are they characterised by:

Name	Dry or cracking	Wet or phlegm	Wheezing or trouble breathing	Yellow or green phlegm	Blood	Chest or back pain	Thin	weak	Chronic (>2 weeks)
Mother									
Father									

Did you seek any treatment?...…………………
……
……………………………………………....…………………………………………………………
……
………..………………………………………………………………………………………………
……………………………………………

PARASITES

Do any of your family members suffer from the following:

Name	Swollen belly	Sore belly/indigestion	visual	Itchy anus	Pain urinating/blood	Anaemic or very pale/weak
Mother						
Father						

Did you seek any treatment?...…………………
……
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SKIN CONDITIONS

Do any of your family members suffer from the following:

Name	**Small itchy sores**	**Sores with pus**	**Boils**	**Large dark spots or patches**	**Swollen feet/hands/face**	**Rings which spread and itch**
Mother						
Father						

Did you seek any treatment?...

....

....

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MALNUTRITION

Signs of malnutrition:

Name	**Thinness**	**Potbelly**	**Wasting**	**Goitre**	**Vit A**
Mother					
Father					

Food diary

Mother			**Father**
What time did you last eat?			
Food 1		Collect/Give/Trade/Buy/Garden	Who?
Food 2		Collect/Give/Trade/Buy/Garden	Who?
Food 3		Collect/Give/Trade/Buy/Garden	Who?
What did you do today			
Mother	Fish/hunt/gather/garden/CL/None/ Sick	Details (i.e. weight):	
Father	Fish/hunt/gather/garden/CL/None/ Sick	Details (i.e. weight):	

Funding and ethics

This research and fieldwork was approved by UCL Ethics Committee (UCL Ethics code 3086/003) and carried out with permission from local government and tribal leaders in Palanan. Informed consent was obtained from all participants, and parents signed the informed consents for their children (after group and individual consultation and explanation of the research objectives in the Agta language). As part of the process, people identified as having any diseases, were provided with medical care, in partnership with the local government and field hospital.

Camp Scan form

A) Domestic Activities
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?

B) Childcare
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

C) Out of Camp
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)

D) Non-Work
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

Appendix B

Additional motes and aging methods from chapter three

This appendix presents data collection and analysis collected by other members of the hunter-gatherer team which was used in this thesis.

Motes: Software and data recovery

The embedded software developed in C and nesC for the experiment was written following an iterative process with many testing phases to adjust the parameters (frequency of messages, strength of wireless communications, length of phases of sleep to save battery and so forth) to their optimum values. In our application, each device sends messages every two minutes, receives messages from other devices within the programmed distance and stores them in a long-term memory. At the end of the experiment the device's memory can be downloaded to a computer via a PC side application written in JAVA. A message frequency of every two minutes was chosen due to the increased duration of the experiment of between five to six days (120 to 144 hours). We calculated that if each individual were in proximity to, on average, ten individuals then they would receive a maximum of 43,200 messages. At 12-bytes per message in our study this equates to 500 kilobytes or 25% of the 2MB capacity of the devices. This was a cautious estimate since we were unsure of the density of the camps. After the completion of the experiment we soon realised that we had only utilised on average 10-20% of the 2MB memory since individuals were in close contact with far fewer neighbours than we originally expected. Future deployments should include an altered parameter for messages to be sent and received each 30 seconds. Nonetheless, even with the message transmitted every two minutes, over the duration of a week we still collected an average of 3,150 message packets per individual, with a maximum of 20,876. Such fine-grained spatial social network data has never been collected previously, thus remains a significantly amount of data.

Once the data from each mote have been recovered and stored on a computer, the raw data was then run through a stringent data processing system written in Python and leveraging the filtering power of MySQL databases. This ensured that the used data was free from corruption due to devices shock damage or water exposure. As each mote was recording data from an origin of time set at its start-up, all messages had to be put back on the real timescale after the experiment. To do this we recorded the start and stop time of each device and characterised the linear clock drift arising from using a basic crystal oscillator in the device for time keeping purposes. Then, we analysed all the messages received by each device and when we detected a reboot - time reset at zero - we used the time of the motes communicating with the device which did not reboot during this period to re-synchronise the focal device. Where most motes did not have reboots in their recorded data, the ones that did usually had many as they are often created by permanent damage to the device creating electronic instability of the systems. Once the initial filtering of the raw data was conducted the data is matched with individuals' ID and each interaction between dyads recorded in a database. The latter is finally transformed into a matrix containing the frequency of interactions between each dyad that took part in the experiment.

Aging methodology

In the Gibbs sampling Markov chain Monte Carlo (MCMC) algorithm each individual is allocated with an *a priori* age distribution; such as no younger than *i* and no older than *u* and between these two points, all ages are equally probable. This seeks to generate a posterior age probability distribution per individual which allows downstream analysis to incorporate the uncertainties associated with point estimates. As each individual is given a random age within their bracket, inconsistency occur which mean they cannot be allocated. For instance, if a younger individual has been estimated an age of 3-7, and the algorithm thus places ego at 6 years old, but the next individual has an known age of 5.5 but considered as older, the list is now inconsistent and the run is discarded. This process is repeated millions of times until only the runs in which all individuals in an age rank are assigned as age are kept.

This procedure can generate as many samples as desired; the more reduce the sampling error and thus, better approximate the underlying distribution. From this it is possible to compute summary statistics for each individual's age (mean, median and mode), since the data for each individual originates from multiple relative age lists. In order to assess the efficiency of this Gibbs sampler age estimation method, we compared it with third-order (Blurton Jones et al. 1992) and fifth-order (Hill & Hurtado 1996) polynomial, and local regression approaches (**Figure 0.1**). We used a cohort of 65 Agta (Headland et al. 2011) for which we had both relative rankings and date of births.

The cohort was partitioned into z=5 partitions of w=13 randomly sampled individuals (so that w*z=65). Within one partition z_i, the date of birth of these 13 individuals were used to estimate the coefficients of the regression equations, where the date of births and the ranks were the independent and dependent variables, respectively. Once the equations had been obtained, the ages of the remaining v=52 individuals (where v=65-w) were determined using the equations on the v ranks. The same z partitions and random set of w individuals were used with the Gibbs sampler to estimate the ages of the remaining v individuals. These procedures were repeated for the z partitions, which provided z-1 age estimates for each individual. Since the dates of birth of the 65 individuals were known, we calculated the mean difference between the known and the estimated ages under each approach (three regression methods and the Gibbs sampler approaches). The best method would be the one that provides the lowest mean difference between the known and the estimated ages (Figure 1).

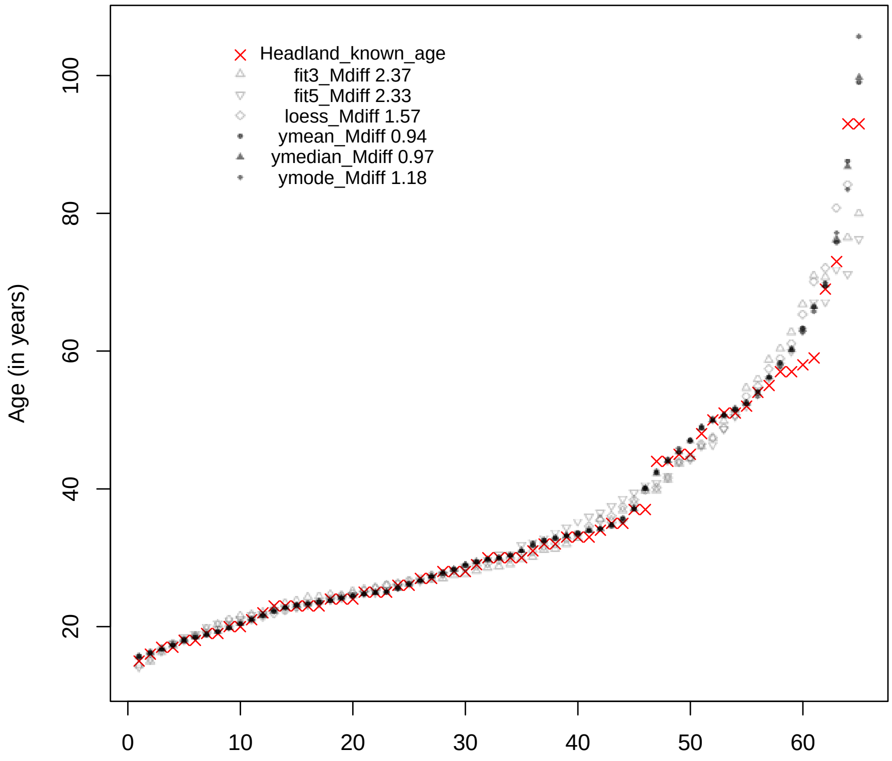

Figure 0.1: Quantification of aging techniques. Relationship between Headland's study population of known ages (red crosses) compared with previous methodologies of estimating ages in the literature (clear triangle pointing up, third-order polynomial regression; clear triangle point down, fifth-order polynomial regression; clear circle, local regression) and the Gibbs sampling method mean age (black circles). The mean difference between known and estimated ages for each of these methods is given in the top right-hand corner of the plot, being lowest (0.94) using the mean figure produced by the Gibbs sampler age model.

Appendix C

Model outputs for chapter seven: Betwixt and between.

Model results

In the following I have included models for null results not directly reported in the chapter. I have also included the intercept-only model for the computation of variance explained for each of the dependent variables. The proportion of variance which is attributed to each level is labelled VCP while the proportion reduction in variance comparative to the null-model is labelled as VAR. Significance values are given it z-scores; z-scores above 1.96 are taken as significant at $p = 0.05$, while a z-score of 2.58 represents $p = 0.01$ and a z-score of 3.33 or higher represents a p-value lower than 0.001 (Modelling 2015). The following models follow the order of results in the chapter: demographic results by centrality (fertility, reproduction and mortality); demographic results by kin and non-household care; mortality results by non-kin care; maternal haemoglobin levels, BMI and reported sickness by centrality; child haemoglobin levels, BMI and reported sickness by maternal centrality; allocare measures and child haemoglobin levels, BMI and reported sickness.

Centrality and reproductive success

Reproductive success Intercept-only model			
AIC	BIC		
90.1	95		
Random effects:			
Levels	Variance	SD	VCP
Camp	0.05492	0.2344	0.1
Residual	0.49338	0.7024	0.9
Fixed effects:			
	Estimate	SE	Z-score
(Intercept)	0.1001	0.153	0.654

Reproductive success EC model					
AIC	**BIC**				
92.100	100.300				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.042	0.204	0.081	0.242	
Residual	0.475	0.689	0.919	0.038	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	0.137	0.164	0.835	-0.228	0.548
EC	-0.191	0.133	-1.434	-0.468	0.077
Age	-0.001	0.007	-0.078	-0.015	0.014

Reproductive success strength model					
AIC	**BIC**				
91.400	99.600				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.054	0.233	0.106	0.009	
Residual	0.458	0.677	0.894	0.071	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	0.157	0.171	0.922	-0.222	0.593
Strength	-0.238	0.144	-1.648	-0.531	0.052
Age	-0.001	0.007	-0.153	-0.014	0.013

Centrality and fertility

Fertility Intercept-only model			
AIC	**BIC**		
90.100	95.000		
Random effects:			
Levels	Variance	SD	VCP
Camp	0.035	0.186	0.077
Residual	0.416	0.645	0.923
Fixed effects:			
	Estimate	SE	Z-score
(Intercept)	0.1581	0.1326	1.193

Fertility EC model					
AIC	**BIC**				
83.400	91.600				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.121	0.348	0.264	-2.502	
Residual	0.338	0.581	0.736	0.187	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	0.158	0.189	0.833	-0.277	0.648
EC	-0.232	0.126	-1.845	6.666	0.040
Age	0.005	0.006	0.897	-0.006	0.018

Fertility strength model					
AIC	**BIC**				
84.600	92.800				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.078	0.279	0.175	-1.257	
Residual	0.367	0.606	0.825	0.117	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	0.128	0.171	0.752	-0.269	0.580
Strength	-0.157	0.118	-1.328	-0.369	0.090
Age	0.006	0.006	0.919	-0.007	0.018

Centrality and mortality

Mortality EC model					
AIC	**BIC**				
120.1	133.2				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	
Residual	0.906	0.952	1.000	0.071	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	-0.306	0.552	-0.554	-1.415	0.804
EC	0.295	0.192	1.534	-0.092	0.681
Age	0.012	0.010	1.169	-0.008	0.030
Fertility	0.064	0.106	0.603	-0.149	0.277

Mortality Intercept-only model			
AIC	**BIC**		
115.700	120.600		
Random effects:			
Levels	Variance	SD	VCP
Camp	0.097	0.311	0.090
Residual	0.975	0.987	0.910
Fixed effects:			
	Estimate	SE	Z-score
(Intercept)	-0.024	0.210	-0.116

Mortality betweenness model					
AIC	**BIC**				
121.900	135.000				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	
Residual	0.951	0.975	1.000	0.024	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	-0.166	0.571	-0.290	-1.315	0.983
Betweenness	-0.115	0.180	-0.641	-0.477	0.246
Age	0.010	0.010	0.971	-0.011	0.031
Fertility	0.055	0.110	0.496	-0.167	0.277

Mortality Strength model					
AIC	**BIC**				
120.300	133.400				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	
Residual	0.951	0.975	1.000	0.024	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	-0.328	0.555	-0.591	-1.445	0.788
Strength	0.311	0.214	1.453	-0.119	0.741
Age	0.010	0.010	1.025	-0.009	0.029
Fertility	0.064	0.106	0.606	-0.149	0.278

Mortality degree model					
AIC	**BIC**				
121.800	134.900				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	
Residual	0.947	0.973	1.000	0.029	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	-0.242	0.562	-0.431	-1.372	0.888
Degree	-0.221	0.286	-0.772	-0.797	0.355
Age	0.011	0.010	1.063	-0.010	0.031
Fertility	-0.011	0.124	-0.087	-0.260	0.238

Allocare and mortality

Mortality non-kin model					
AIC	**BIC**				
97.500	109.700				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	
Residual	0.643	0.802	1.000	0.341	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	0.111	0.501	0.222	-0.900	1.122
Non-kin	0.067	0.155	0.430	-0.246	0.380
Fertility	0.034	0.090	0.381	-0.147	0.215
Age	-0.008	0.011	-0.735	-0.031	0.014

Mortality non-household model					
AIC	**BIC**				
97.200	109.400				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	
Residual	0.638	0.799	1.000	0.346	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	0.094	0.499	0.188	-0.914	1.102
non-household	0.104	0.154	0.677	-0.206	0.414
Fertility	0.031	0.089	0.348	-0.149	0.212
Age	-0.006	0.011	-0.542	-0.029	0.016

Mortality kin model					
AIC	**BIC**				
99.000	111.200				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	
Residual	0.673	0.820	1.000	0.310	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	-0.011	0.524	-0.021	-1.070	1.048
Kin	0.013	0.162	0.081	-0.314	0.341
Fertility	0.054	0.091	0.595	-0.129	0.237
Age	-0.008	0.011	-0.702	-0.030	0.012

Allocare and reproductive success

RS kin model					
AIC	**BIC**				
139.600	150.200				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	
Residual	2.352	1.534	1.000	0.049	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	0.226981	0.967173	0.235	-1.723465359	2.1774266
Kin	-0.004775	0.302004	-0.016	-0.613810207	0.6042607
Age	0.02811	0.01927	1.458	-0.0107572	0.06698053

RS non-household model					
AIC	**BIC**				
138.900	149.600				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	
Residual	2.306	1.519	1.000	0.068	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	0.19339	0.9418	0.205	-1.705879939	2.09266983
non-household	0.22106	0.28994	0.762	-0.363649636	0.8057778
Age	0.02743	0.01833	1.496	-0.01081878	0.06318491

Allocare and fertility

Fertility kin model					
AIC	**BIC**				
140.300	151.000				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	0.000	
Residual	2.401	1.550	1.000	0.005	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	-0.942	0.977	-0.964	-4.399	1.028
Kin	0.184	0.305	0.601	-0.432	0.799
Age	0.010	0.009	1.134	-0.007	0.027

Fertility non-household model					
AIC	**BIC**				
138.900	149.600				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	0.000	
Residual	2.343	1.531	1.000	0.029	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	-0.676	0.949	-0.712	-2.590	1.238
non-household	0.202	0.292	0.691	-0.387	0.791
Age	0.013	0.012	1.037	-0.012	0.037

Centrality and maternal sickness

Maternal sickness Intercept-only model			
AIC	**BIC**		
82.5	87.2		
Random effects:			
Levels	Variance	SD	VCP
Camp	0	0	0
Residual	0.49	0.7	1
Fixed effects:			
	Estimate	SE	Z-score
(Intercept)	0.8056	0.1167	6.905

Maternal sickness EC					
AIC	**BIC**				
82.400	95.000				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	0.000	
Residual	0.370	0.608	1.000	0.245	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	-0.942	0.977	-0.964	-4.399	1.028
EC	0.184	0.305	0.601	-0.432	0.799
Age	0.010	0.009	1.134	-0.007	0.027
Settled	0.184	0.305	0.601	-0.432	0.799
Household wealth	0.010	0.009	1.134	-0.007	0.027

Maternal sickness Strength					
AIC	**BIC**				
83.300	96.000				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	0.000	
Residual	2.343	1.531	1.000	0.029	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	0.291	0.367	0.794	-0.449	1.031
Strength	-0.083	0.139	-0.594	-0.363	0.197
Age	0.016	0.007	2.369	0.002	0.029
Settled	0.079	0.218	0.363	-0.359	0.517
Household wealth	0.056	0.167	0.332	-0.281	0.392

Maternal sickness degree					
AIC	**BIC**				
83.700	96.300				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	0.000	
Residual	0.383	0.619	1.000	0.218	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	0.268517	0.367034	0.732	-0.471627574	1.00865925
Degree	0.009108	0.152394	0.06	-0.297725897	0.31594147
Age	0.015843	0.00661	2.397	0.002533823	0.02915241
Settled	0.044457	0.210884	0.211	-0.380802247	0.46971545
Household wealth	0.036124	0.164903	0.219	-0.295896146	0.36814353

Centrality and maternal BMI

Maternal BMI Intercept-only model			
AIC	**BIC**		
179.500	184.500		
Random effects:			
Levels	Variance	SD	VCP
Camp	0.000	0.000	0.000
Residual	5.008	2.238	1.000
Fixed effects:			
	Estimate	SE	Z-score
(Intercept)	18.266	0.358	50.970

Maternal BMI EC					
AIC	**BIC**				
182.800	196.100				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	0.000	
Residual	4.217	2.054	1.000	0.158	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	16.620	1.189	13.977	13.202	19.106
EC	-0.192	0.409	-0.470	-1.014	0.630
Age	-0.045	0.021	-2.086	-0.087	-0.002
Settled	1.008	0.702	1.436	-0.402	2.417
Household wealth	0.273	0.547	0.499	-0.826	1.372

Maternal BMI Strength					
AIC	**BIC**				
182.600	195.900				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	0.000	
Residual	4.193	2.048	1.000	0.163	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	16.672	1.190	14.007	14.277	19.279
Strength	-0.304	0.452	-0.672	-1.211	0.604
Age	-0.045	0.021	-2.118	-0.088	-0.002
Settled	1.044	0.701	1.489	-0.365	2.452
Household wealth	0.305	0.549	0.555	-0.798	1.407

Maternal BMI betweenness					
AIC	**BIC**				
83.700	96.300				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	0.000	
Residual	4.229	2.057	1.000	0.184	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	16.512	1.189	13.885	14.122	18.901
Betweenness	0.124	0.374	0.331	-0.628	0.875
Age	-0.043	0.022	-1.995	-0.087	0.000
Settled	0.971	0.694	1.399	-0.423	2.365
Household wealth	0.215	0.540	0.398	-0.870	1.300

Centrality and maternal haemoglobin

Maternal RBC Intercept-only model			
AIC	**BIC**		
179.500	184.500		
Random effects:			
Levels	Variance	SD	VCP
Camp	12.900	3.591	0.018
Residual	724.200	26.911	0.982
Fixed effects:			
	Estimate	SE	Z-score
(Intercept)	107.526	4.761	22.59

Maternal RBC EC					
AIC	**BIC**				
345.8	350.6				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	
Residual	627.500	25.050	1.000	0.134	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	87.84935	15.24165	5.764	57.1614172	118.5372843
EC	1.77594	5.12868	0.346	-8.5502775	12.1021631
Age	-0.37339	0.27081	-1.379	-0.9186441	0.1718738
Settled	-2.72238	8.80246	-0.309	-20.4454848	15.0007259
Household wealth	11.47289	6.84307	1.677	-2.3051285	25.2509083

Maternal RBC Strength					
AIC	**BIC**				
349.000	361.700				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	
Residual	610.000	24.700	1.000	0.158	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	86.628	15.022	5.767	56.383	116.873
Strength	6.012	5.586	1.076	-5.235	17.258
Age	-0.357	0.267	-1.336	-0.895	0.181
Settled	-4.438	8.746	-0.507	-22.048	13.172
Household wealth	10.506	6.792	1.547	-3.168	24.181

Maternal RBC betweenness					
AIC	**BIC**				
350.100	362.800				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	
Residual	628.100	25.060	1.000	0.133	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	89.028	15.261	5.834	58.302	119.754
Degree	-1.423	4.779	-0.298	-11.044	8.198
Age	-0.387	0.276	-1.403	-0.942	0.168
Settled	-2.513	8.728	-0.288	-20.086	15.061
Household wealth	11.785	6.785	1.737	-1.875	25.445

Maternal RBC Degree					
AIC	**BIC**				
349.200	361.800				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	
Residual	612.000	24.740	1.000	0.155	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	88.593	14.950	5.926	58.492	118.693
Degree	6.239	6.136	1.017	-6.115	18.593
Age	-0.345	0.269	-1.283	-0.886	0.196
Settled	-2.496	8.483	-0.294	-19.576	14.584
Household wealth	11.279	6.716	1.679	-2.243	24.802

Centrality and child haemoglobin

Child RBC Intercept-only model			
AIC	**BIC**		
733.000	742.600		
Random effects:			
Levels	Variance	SD	VCP
Camp	0.000	0.000	0.000
Household	69.460	8.334	0.150
Residual	392.460	19.811	0.850
Fixed effects:			
	Estimate	SE	Z-score
(Intercept)	110.08	2.735	40.25

Child RBC Strength					
AIC	**BIC**				
669.300	696.800				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	

Child RBC EC					
AIC	**BIC**				
669.100	696.600				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	
Household	0.000	0.000	0.000	1.000	
Residual	403.300	20.080	1.000	-0.028	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	103.133	18.668	5.525	64.940	141.025
Maternal EC	4.258	4.036	1.055	-3.868	12.417
Age	0.948	0.759	1.250	-0.559	2.456
Maternal RBC	-0.196	0.122	-1.605	-0.439	0.047
Child sex	6.007	4.998	1.202	-3.919	15.934
Settlement	7.719	5.421	1.424	-3.047	18.484
Dependents	0.689	1.955	0.353	-3.193	4.571
Household wealth	4.441	3.527	1.259	-2.563	11.445

Household	0.000	0.000	0.000	1.000	
Residual	404.100	20.100	1.000	-0.030	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	108.155	19.404	5.574	68.825	146.709
Maternal strength	4.061	4.137	0.982	-4.155	12.277
Maternal BMI	-0.225	0.131	-1.721	-0.485	0.035
Child age	0.955	0.760	1.257	-0.554	2.465
Child sex	6.057	5.006	1.210	-3.884	15.998
Settlement	7.346	5.638	1.303	-3.890	18.547
Dependents	0.237	1.790	0.132	-3.318	3.934
Household wealth	4.569	3.516	1.300	-2.413	11.551

Centrality and child BMI

Child BMI Intercept-only model			
AIC	**BIC**		
222.300	232.300		
Random effects:			
Levels	Variance	SD	VCP
Camp	0.164	0.405	0.228
Household	0.000	0.000	0.000
Residual	0.553	0.743	0.772
Fixed effects:			
	Estimate	SE	Z-score
(Intercept)	0.093	0.184	0.506

Child BMI EC					
AIC	**BIC**				
227.600	257.800				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.074	0.273	0.127	0.546	
Household	0.000	0.000	0.000	0.000	
Residual	0.509	0.713	0.873	0.079	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	-1.118	0.910	-1.228	-2.968	0.748
Maternal EC	0.015	0.128	0.114	-0.240	0.270
Maternal BMI	0.109	0.042	2.611	0.026	0.191
Settlement	-0.350	0.312	-1.122	-1.015	0.554
Child sex	-0.145	0.166	-0.875	-0.473	0.184
Child age	-0.025	0.024	-1.012	-0.073	0.024
Dependents	0.063	0.066	0.956	-0.082	0.196
Household wealth	-0.098	0.151	-0.650	-0.447	0.335

Child BMI Strength					
AIC	**BIC**				
227.500	257.600				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.070	0.265	0.121	0.570	
Household	0.000	0.000	0.000	0.000	
Residual	0.509	0.714	0.879	0.079	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	-1.206	0.909	-1.327	-3.059	0.655
Maternal strength	0.056	0.128	0.439	-0.199	0.312
Maternal BMI	0.113	0.042	2.673	0.029	0.197
Settlement	-0.385	0.309	-1.249	-1.040	0.508
Child sex	-0.145	0.166	-0.877	-0.473	0.184
Child age	-0.024	0.024	-0.977	-0.073	0.025
Dependents	0.073	0.062	1.174	-0.064	0.198
Household wealth	-0.121	0.152	-0.799	-0.469	0.314

Child BMI Degree					
AIC	**BIC**				
227.600	257.700				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.067	0.260	0.116	0.588	
Household	0.000	0.000	0.000	0.000	
Residual	0.511	0.715	0.884	0.075	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	-1.144	0.901	-1.270	-2.947	0.740
Maternal degree	0.037	0.158	0.233	-0.081	0.414
Maternal BMI	0.111	0.043	2.565	-0.016	0.203
Child age	-0.365	0.298	-1.225	0.000	-0.219
Child sex	-0.131	0.175	-0.749	-0.149	0.219
Settlement	-0.025	0.024	-1.028	-0.060	0.015
Dependents	0.062	0.055	1.137	-0.042	0.170
Household wealth	-0.104	0.143	-0.728	0.000	-0.034

Centrality and child reported sickness

Child sickness Intercept-only model			
AIC	**BIC**		
194.500	221.400		
Random effects:			
Levels	Variance	SD	VCP
Camp	0.103	0.322	0.175
Household	0.011	0.105	0.019
Residual	0.477	0.691	0.806
Fixed effects:			
	Estimate	SE	Z-score
(Intercept)	0.093	0.184	0.506

Child Sickness EC					
AIC	**BIC**				
196.400	225.700				
Random effects					
Levels	Variance	SD	VCP	VAR	
Household	0.000	0.000	0.000	1.000	
Camp	0.000	0.000	0.000	1.000	
Residual	0.445	0.667	1.000	0.067	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	1.145	0.343	3.343	0.466	1.825
Child age	-0.015	0.024	-0.622	-0.061	0.032
Maternal EC	0.049	0.120	0.411	-0.189	0.288
Maternal sickness	0.419	0.133	3.159	0.156	0.681
Settlement	0.268	0.167	1.603	-0.063	0.599
Child sex	-0.090	0.156	-0.579	-0.399	0.219
Dependents	0.013	0.064	0.198	-0.114	0.139
Household wealth	-0.246	0.106	-2.324	-0.456	-0.036

Child Sickness Betweenness					
AIC	**BIC**				
196.500	225.800				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	
Household	0.000	0.000	0.000	1.000	
Residual	0.446	0.668	1.000	0.065	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	1.174	0.335	3.500	0.509	1.839
Maternal betweenness	0.011	0.085	0.126	-0.158	0.180
Maternal sickness	0.414	0.136	3.042	0.144	0.683
Child age	-0.014	0.024	-0.598	-0.061	0.033
Settlement	0.295	0.158	1.863	-0.019	0.608
Child sex	-0.094	0.156	-0.601	-0.403	0.216
Dependents	-0.003	0.054	-0.060	-0.110	0.104
Household wealth	-0.234	0.102	-2.297	-0.435	-0.032

Child Sickness Strength					
AIC	**BIC**				
196.400	225.800				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	
Household	0.000	0.000	0.000	1.000	
Residual	0.445	0.667	1.000	0.066	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	1.162	0.337	3.452	0.495	1.830
Maternal strength	0.037	0.115	0.323	-0.191	0.265
Maternal sickness	0.414	0.133	3.108	0.150	0.677
Child age	-0.015	0.024	-0.616	-0.061	0.032
Settlement	0.274	0.166	1.645	-0.056	0.603
Child sex	-0.089	0.156	-0.569	-0.399	0.221
Dependents	0.008	0.061	0.124	-0.113	0.128
Household wealth	-0.245	0.107	-2.281	-0.458	-0.032

Child Sickness Degree					
AIC	**BIC**				
195.100	224.400				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	
Household	0.000	0.000	0.000	1.000	
Residual	0.438	0.662	1.000	0.081	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	1.225	0.332	3.690	0.567	1.883
Maternal degree	-0.154	0.127	-1.215	-0.407	0.098
Maternal sickness	0.427	0.132	3.238	0.165	0.688
Child age	-0.015	0.023	-0.626	-0.061	0.032
Settlement	0.318	0.157	2.029	0.007	0.628
Child sex	-0.160	0.164	-0.974	-0.485	0.166
Dependents	-0.018	0.054	-0.333	-0.126	0.090
Household wealth	-0.243	0.101	-2.401	-0.443	-0.042

Child RBC kin care					
AIC	**BIC**				
703.100	731.400				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	
Household	11.800	3.435	0.033	0.515	
Residual	342.500	18.510	0.967	0.105	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	99.061	17.340	5.713	63.216	133.701
Kin care	-1.104	2.614	-0.422	-6.293	4.314
Maternal RBC	-0.092	0.119	-0.775	-0.337	0.156
Child age	0.820	0.690	1.188	-0.528	2.193
Child sex	4.530	4.521	1.002	-4.562	13.652
Settlement	9.020	4.849	1.860	-1.106	18.964
Household wealth	3.820	3.417	1.118	-3.127	13.102
Dependents	-0.013	1.520	-0.009	-3.029	3.150

Allocare and child RBC

Child RBC household care					
AIC	**BIC**				
690.100	718.100				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	
Household	0.000	0.000	0.000	1.000	
Residual	375.100	19.370	1.000	0.020	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	99.585	17.452	5.706	64.626	134.191
Non-household care	-5.796	2.577	-1.249	-11.006	0.053
Maternal RBC	-0.169	0.115	-1.466	-0.398	0.060
Child age	0.968	0.722	1.342	-0.464	2.400
Child sex	5.636	4.722	1.194	-3.737	15.008
Settlement	13.848	5.054	2.740	3.816	23.879
Household wealth	6.655	3.413	1.950	-0.121	13.431
Dependents	0.324	1.485	0.218	-2.623	3.270

Allocare and BMI

Child BMI non-household care					
AIC	**BIC**				
210.900	240.300				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.000	0.000	0.000	1.000	
Household	0.000	0.000	0.000	1.000	
Residual	0.514	0.717	1.000	0.069	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	-0.981	0.790	-1.243	-2.547	0.584
Non-household care	-0.282	0.090	-1.147	-0.460	0.014
Maternal BMI	0.117	0.039	2.969	0.039	0.196
Child age	-0.019	0.025	-0.771	-0.069	0.031
Child sex	-0.131	0.170	-0.770	-0.468	0.206
Settlement	-0.428	0.175	-2.445	-0.775	-0.081
Household wealth	-0.222	0.111	-2.003	-0.441	-0.002
Dependents	0.066	0.049	1.352	-0.031	0.162

Child BMI kin care					
AIC	**BIC**				
222.200	251.900				
Random effects					
Levels	Variance	SD	VCP	VAR	
Camp	0.056	0.236	0.096	0.659	
Household	0.000	0.000	0.000	1.000	
Residual	0.523	0.723	0.904	0.054	
Fixed effects					
	Estimate	SE	Z-score	Lower CI	Upper CI
(Intercept)	-0.878	0.887	-0.990	-2.718	0.899
Kin care	-0.067	0.098	-0.682	-0.281	0.138
Maternal BMI	0.100	0.042	2.392	0.063	0.166
Child age	-0.032	0.025	-1.263	-0.070	0.008
Child sex	-0.130	0.170	-0.767	-0.247	0.177
Settlement	-0.438	0.280	-1.563	-1.042	0.010
Household wealth	-0.151	0.142	-1.059	-0.498	0.304
Dependents	0.060	0.056	1.080	-0.068	0.174