The behavioural ecology and evolutionary implications of hunter-gatherer social organisation

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

Abstract

Much that is remarkable about human behaviour relates in some way to our advanced social cognition. Understanding why this advanced social cognition evolved benefits from an understanding of the kind of social organisation that is promoted by hunting-and-gathering, the dominant mode of subsistence throughout most of human evolutionary history. In this thesis, I explore the social organisation of hunter-gatherers in general and of the Palanan Agta in particular. In chapter four, I present data that demonstrate that, like many small-scale hunter-gatherer societies, the Agta live in small groups of fluid composition in which a large number of unrelated individuals co-reside. I present the results of a model that simulates the process of camp assortment and which suggests that sex equality in residential decision making may serve to constrain group relatedness. In chapter five, I challenge traditional biological conceptions of relatedness, arguing that under conditions of stable pair-bonding, individuals can derive inclusive fitness benefits through aiding affinal kin. In chapter six, I explore multilevel social organisation among the Agta and argue that it serves to provide individuals with access to the range of social relationships required to overcome both short-term variability in foraging returns and long-term energetic deficits resulting from the demands of having an energetically expensive life-history strategy.

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Chapter 1: Introduction

1.1 Human sociality

Even before the advent of agriculture, humans had colonised nearly every corner of the planet and demonstrated the ability to survive in habitats to which we are poorly suited, at least from a physiological point of view (Armitage et al. 2011; Groucutt et al. 2015). This success is likely due, in large part, to our intense sociality and ability to communicate using language, understand each other's mental states, and share cultural and technological innovations. Even among the intensely social haplorrhine primates, humans are outliers in both the intensity and extent of our sociality. How can we explain this? Firstly, we ought to acknowledge that however remarkable humans may be, we are, like all species, a product of our evolutionary history. Humans are, as Foley (1987) states, '*another unique species*'.

Is there a particular derived trait to which we can attribute our biological success? Perhaps language, encephalization, technology, or bipedalism? Brief consideration of any one trait soon reveals it is inextricably connected to others. For example, the use of technology clearly relies on the greater intelligence allowed by encephalization which itself requires an extended period of brain growth related to increased infant dependency, creating an energetic burden which must be solved through food sharing and provisioning. Thus, although many traits can be argued to be *necessary* in the course of human evolution, none are *sufficient*. Simple hypotheses soon become part of a dense web of co-evolved human traits.

Although not necessarily a *prime mover* in human evolution, many of our distinctive behavioural and physiological traits have been argued to have co-evolved with some aspect of our sociality and social organisation, including our larger brains (Dunbar 2003; Dunbar 2009; Kaplan et al. 2000), language (Dunbar 1993), cumulative culture (Pradhan et al. 2012; Hill et al. 2014; Tennie et al. 2009) and life history (Kaplan et al. 2000). Indeed, hypotheses have abounded about unique human social adaptations including the 'cultural intelligence' (Herrmann et al. 2007), 'social brain' (Dunbar 1998; Dunbar 2009), 'human cultural niche' (Boyd et al. 2011; Derex & Boyd 2015), and 'cognitive niche' (Pinker 2010) hypotheses. In most cases these hypotheses focus on the cognitive abilities which underlie human sociality and behaviour – for example social learning (Dean et al. 2012; Muthukrishna et al. 2014; Herrmann et al. 2007), theory of mind (Frith & Frith 2005; Tomasello & Carpenter 2007; Searle 1983), and language (Dunbar 1996; Pinker 2010). Together, these specialised and derived aspects of human social cognition allow the flexible behavioural responses required to survive in difficult environments and therefore underlie the biological success of *Homo sapiens*. Explaining why this advanced social cognition evolved is the overarching question of this thesis. I aim to understand how the readily observable features of human social organisation (for example the size and structure of our groups, pair-bonding, and the recognition of kinship) may be related to each other and may have provided the selective context for human social and cognitive evolution.

Given the focus on 'social organisation' in this thesis, it is worth defining briefly what I mean by the term. Although social organisation, social structure, and social system are often used inter-changeably, there has, at least in the primatological literature, been some discussion of how these terms ought to be used (Struhsaker 1969; Rowell 1993; Kappeler & van Schaik 2002; Hinde 1979; Gowlett 2011). Kappeler and van Schaik (2002) define the social system as the product of (*a*) the *social organisation* which is the "size, sexual composition, and spatio-temporal cohesion of a society" (p709), (*b)* the *social structure* which is the "pattern of social interactions and the resulting relationships among members of a society" (p710), and (*c*) the *mating system,* which is the sub-set of social interactions among mating couples. According to this definition, I explore all three aspects of the social system of hunter-gatherers in this thesis.

What features characterise human social organisation? Given the enormous cross-cultural variation, is this even a reasonable question to ask? Although there is, of course, much variation, attempts to compile lists of human universals have been undertaken (e.g. Brown 1991; Brown 2000) and structuralist anthropologists such as Levi-Strauss (1969) have attempted to determine core features of human sociality. We should also not assume that variation represents noise - the diversity we see is not completely random. Indeed, a large body of theoretical and empirical work in the field of human behavioural ecology has sought to develop an evolutionarily informed framework for understanding diversity in human behaviour (see section 1.2 below for an introduction to the field). Within this paradigm, cross-cultural diversity in social organisation can be seen as the product of adaptive responses by individuals to their social and ecological situations (Borgerhoff Mulder & Schacht 2012; Laland & Brown 2011). Accordingly, if we want an insight into social organisation in human evolutionary history, the most appropriate models are contemporary hunter-gatherers since they potentially face similar environmental and ecological pressures.

Although there is enormous cross-cultural variation in human social organisation, humans are capable of having a social system that is derived in form relative to the other great apes in several ways. To my mind, these are best summarised by Chapais (2008, 2011) who suggests that humans exhibit six important and derived characteristics: (*i*) multilevel structure, where individuals are part of a nested series of social groups, (*ii*) stable pair bonds, (*iii*) flexible residence systems, (*iv*) the maintenance of relationships between dispersed kin, (*v*) recognition of bilateral consanguines, and (*vi*) recognition of affinal kin. Chapais holds that pair-bonding is necessary for all of these traits, hence his proposition that "pair-bonding gave birth to human sociality" (2008). Although the features of social organisation outlined by Chapais (2008) may be universal features of human social organisation, there is still a great deal of diversity and variation in social organisation cross-culturally. Although much of this variation can be associated with particular economic modes of production (pastoral, horticultural, foraging, agricultural etc.), there is also considerable variation within these groups.

Complex hunter-gatherers

Among foragers, there is a division between two classes of hunter-gatherers often described as 'simple and 'complex' (Kelly 2013; Keeley 1988). Keeley (1988) explores socio-economic complexity among 94 hunter-gatherer populations and argues that there are few societies who fall between these two types. Complex hunter-gatherers tend to live in larger, more sedentary, and more densely populated groups, have greater political and economic inequality, greater occupational specialisation, and are more likely to have resource ownership, bounded territories, and inter-group warfare (Kelly 2013). Complex hunter-gatherers include (historically, at least) the Kwakiutl and other groups of the Pacific northwest (Arnold 1996; Williams 1987; Ames & Maschner 1999), the Ainu of Japan (Watanabe 1968), Californian coastal groups (Gamble 2008), and several peoples of New Guinea (Roscoe 2006). Most complex foraging societies exploit coastal habitats and have the technology and knowledge required to preserve surplus foods. They can therefore, in Woodburn's (1982) scheme, be considered as having a 'delayed-return' economy.

Why does social complexity emerge among foragers? One explanation, proposed by Hayden (1995), is that abundant and predictable resources allow the accumulation of surplus by individuals who can then engage in 'aggrandising behaviours' such as the Kwakiutl potlatch, using such occasions to accumulate political and economic advantages. An alternative, advocated by Ames (1985), is that political hierarchies emerge to solve the scalar stresses encountered by foraging societies who experience population growth. Kelly (2013) suggests that increasing population density, and the sedentism which results drove the emergence of complexity, potentially through the kind of runaway evolutionary process described by Boyd and Richerson (1988). Kelly's argument is one which utilises methodological individualism - it reasons political complexity up from the decision making of individuals trying to increase their fitness rather than relying on society-wide functional benefits such as scalar stress. Whatever processes can account for the emergence of political complexity in foraging societies, the wide gulf in the political and economic lives of simple versus complex hunter-gatherers ought to serve as a warning about generalising hunter-gatherers as a single cultural type.

1.2 Theoretical perspectives

1.2.1 Contemporary hunter-gatherers as models of the past

Humans, like all species, are a product of our evolutionary history. For humans, all but the most recent 12,000 years of that evolutionary history was spent as hunter-gatherers. Evidence of 'behavioural modernity', however, stretches back much further, perhaps even deep into the African middle stone age (Henshilwood et al. 2002; McBrearty & Brooks 2000; d'Errico & Banks 2013; Marean & Assefa 2005). It is understandable, therefore, that evolutionary anthropologists should look to contemporary hunter-gatherers for insights into the social and economic context in which humans evolved. An understanding of the lives of contemporary hunter-gatherers has also been important in informing understanding of archaeological site formation (e.g. Binford 1980; Binford 2001; Enloe 2003), and in the development of theory in evolutionary psychology (Barkow et al. 1992; Cosmides & Tooby 1997), and evolutionary medicine (Gluckman et al. 2009; Williams & Nesse 1991; Nesse & Williams 1996). How far are we justified, however, in drawing direct analogy from contemporary hunter-gatherers to the human evolutionary past?

The extent to which contemporary hunter-gatherers represent a good model of the human past has been argued to depend on the extent to which they have continuous cultural tradition, something that has been the subject of a fierce and long-standing debate within anthropology. This debate has become known as the 'Kalahari debate', owing to the fact that much of the debate focused on interpretations of the cultural history of the San, hunter-gathers from the Kalahari of southern Africa (Barnard 1992; Sadr 1997). The debate has been between the 'traditionalists' who believe that contemporary hunter-gatherers do have a continuous cultural history as hunter-gatherers (Lee & Guenther 1991) and 'revisionists' who believe there to be little cultural continuity among contemporary foragers who are instead a product of their interactions with neighbouring groups and represent, in many cases, an underclass of the wider society (Wilmsen 1989). In other words, the debate was about whether contemporary hunter-gatherers are 'genuine or spurious' (Solway & Lee 1992; Kent 1992). Some groups were suggested to be 'respecialised' foragers (i.e. having non-foraging ancestors) (Layton 2001). The extent to which contemporary hunter-gatherers represented a consistent enough 'cultural type' to make the establishment of commonalities a worthwhile project also came under criticism (Ingold 1991). The debate reached a crescendo in the late 1980s and early 1990s. The eminent anthropologist Richard Lee even declared a "crisis in hunter-gatherer studies" (Lee 1992).

What does this debate mean for research on hunter-gatherers within evolutionary anthropology? For behavioural ecologists, the 'crisis' in hunter-gatherer studies does not undermine theory to such an extent as it does in disciplines which rely on more direct ethnographic analogy. This is because human behavioural ecologists see contemporary hunter-gatherers less as '*living fossils*' and more as '*natural experiments*' (Hawkes et al. 1997, p29). As Hawkes et al. 1997, say "If modern people who forage for a living are constrained by features of local ecology, then variation in these constraints, the behavioural trade-offs they impose, and the solutions adopted by individuals differing in age, sex and reproductive status are open to direct ethnographic observation" (p29). In other words, human behavioural ecology is not in the business of wholesale ethnographic analogies but rather in developing a general body of theory which expects different adaptive solutions to different selective pressures. From this general theory, predictions about the evolutionary past can be made. This is not to render the consideration of the issues mentioned above unnecessary. As I will describe in chapter three, while the Agta do live largely by foraging they also have significant interactions with their non-farming neighbours. A careful theoretical approach is therefore required. In the following section, I outline in more detail the various sub-fields of evolutionary anthropology, including human behavioural ecology as mentioned above.

1.2.2 Why do we do what we do?

This is the question that is asked, one way or another, by most social scientists or researchers in the humanities. For the most part, focus is on proximate levels of explanation and, for the most part, we take it as a given that people will want to do things such as maximise value, increase their political power, or care for their family. But *why* should we want to do these things in the first place? What explains human behaviour at a more *ultimate* level? Evolutionary thinking provides a framework for addressing the question of why we do what we do at an 'ultimate' level by exploring how our behaviour may have been shaped by our evolutionary history. This is not to say that explanations at different levels are incompatible or contradictory. A useful framework for thinking about different kinds of '*why*' questions was set out by the ethologist Niko Tinbergen with his 'four whys' (Tinbergen 1963). Tinbergen outlined a division between dynamic and static questions on one hand and between proximate and ultimate levels of explanation on the other (see Table 1-1).

Table 1-1: The four classes of explanation of behaviour outlined by Tinbergen (1963) and known as ‘Tinbergen’s ‘four questions’.

	Dynamic	**Static**
Proximate	**Ontogeny** How did a trait develop from DNA to current form?	**Mechanism** How does a particular trait operate?
Ultimate	**Phylogeny** What is the history of a trait over generations?	**Adaptation/function** What adaptive benefit does the trait serve?

Although Darwin himself was greatly interested (and often theoretically troubled) by social behaviour (1859; 1871), biology from the turn of the 20th century onwards was, by and large, interested in mechanistic rather than adaptive questions (Clutton-Brock et al. 2009). From the 1930s onwards, however, ethologists such as Lorenz, von Frisch, and Tinbergen (who all went on to win the 1973 Nobel Prize for Physiology or Medicine) began to develop theoretical accounts of the functional significance of animal behaviour. In many cases, however, thinking still focused on behaviours as being for the ‘good of the species’ (Wynne-Edwards 1962).

From the 1960’s onwards, however, there was a rapid development of theory led by biologists such as Bill Hamilton (1964) who combined a broad knowledge of animal behaviour with an understanding of the population genetics of Fischer (1930) and Haldane (1932). This new body of theory was summarized in E.O. Wilson’s influential (and controversial) 1975 book ‘Sociobiology: The New Synthesis’. In subsequent decades, research under the umbrella of socio-biology split into a number of distinct fields (Laland & Brown 2011). Arguably, there are five species within the socio-biology genus although I would suggest that only three of these maintain healthy populations: human behavioural ecology, evolutionary psychology, and gene-culture co-evolution (also known as duel-inheritance theory). As with biological species, some people are epistemological ‘lumpers’, who would argue that pigeonholing of academic disciplines is unproductive, while others remain ‘splitters’, arguing that distinctive research programmes do exist and ought to be recognised. Although I am personally more inclined toward ‘lumping’ than ‘splitting’, I review these three main fields briefly below.

Evolutionary Psychology

Evolutionary psychology (EP) researchers are interested in how psychological and cognitive processes in contemporary humans have been shaped by our evolutionary history. Often this posits a ‘mismatch’ between our ‘stone age minds’ (Cosmides et al. 1992; Cosmides & Tooby 1997) and modern environments. EP is therefore not directly interested in explaining human diversity and focuses on cognitive processes, rather than behaviour itself. Evolutionary psychologists are interested in hunter-gatherer lifestyles in-so-far as they inform our understanding of the environment of evolutionary adaptation (EEA), to which they argue our psychology is adapted (Cosmides & Tooby 1997). How critically assumptions about the EEA are examined, however, has attracted criticism (Foley, 1996; Irons, 1998). Similarly, evolutionary psychology has been attacked for its over-extension of the computational metaphor (Panksepp & Panksepp, 2000), and reliance on ‘massive modularity’ (Buller & Hardcastle, 2000).

Gene-culture co-evolution

Gene-culture co-evolution (also known as duel-inheritance theory, or cultural evolution) explores the process by which culture evolves both in its own right, and in tandem with our genetic endowment (Cavalli-Sforza & Feldman 1981; Richerson & Boyd 1978; Laland & Brown 2011; Durham 1991). The field is interested in the processes underlying the transmission of culture including various transmission biases (Boyd & Richerson 1988; Henrich & Gil-White 2001) and also interested in cultural phylogenetics and cultural gene-cultural co-evolution at a macro level, over human history (Holden & Mace 2009; Mace et al. 2003; Currie et al. 2010; Currie & Mace 2011; Fortunato & Jordan 2010; Opie et al. 2014).

Human Behavioural Ecology

Finally, we have human behavioural ecology (HBE) which, as the main paradigm employed in this thesis, I will explore in more depth. HBE has its roots in ethology and the study of animal behaviour more generally and views humans as flexible decision makers, adopting behavioural strategies which increase fitness returns depending on their social and ecological context (Cronk 1991; Smith & Winterhalder 2003; Borgerhoff Mulder & Schacht 2012; West & Burton-Chellew 2013).

In its sources of theoretical inspiration, behavioural ecology is an omnivorous field, influenced a great deal by models from neo-classical economics and game theory as well as evolutionary theory. HBE balances modelling and theoretical work on one hand with empirical hypothesis testing on the other and holds the neo-Darwinian view of selection largely at the level of gene and individual rather than the group. HBE also applies methodological individualism – the view that group level phenomena are emergent from strategic choices made by individuals (Smith & Winterhalder 1992; Smith 1988; Elster 1982). HBE tends to focus on readily observable phenomena such as food production and sharing, inheritance and marriage patterns, and territoriality (Borgerhoff Mulder & Schacht 2012). Although the focus has largely been on traditional and natural fertility populations, models from HBE have also been applied to post-industrial and contraceptive using populations (Colleran et al. 2015; Borgerhoff Mulder 1998).

Of the four 'whys' outlined in Table 1-1 above, human behavioural ecology focuses almost exclusively on adaptive function. In fact, human behavioural ecologists often remain agnostic about the historical and mechanistic reasons why behaviours are manifested, employing what is known as the 'phenotypic gambit' (Laland & Brown 2011; Borgerhoff Mulder & Schacht 2012). Although evolutionary psychology, for example, may engage more with proximate mechanisms, many of the mechanistic hypotheses are out of touch with our understanding of neuroscience (Panksepp & Panksepp 2000). Although at some point it is important to try to understand the proximate and historical reasons why the behaviours we see are expressed, it is perhaps better to assume too little than too much. Human behavioural ecology, however, like neo-classic economics, has been criticised for assuming that agents have perfect information (Borgerhoff Mulder & Schacht 2012), an assumption to that behavioural economics and cognitive neuroscience are increasingly challenging (Gigerenzer & Todd 1999; Goldstein & Gigerenzer 1999).

A broader epistemological framework

It has been argued that thought in the humanities and social sciences falls, explicitly or implicitly, on a spectrum from idealism to materialism. Materialism would hold that economic and environmental conditions are what drive changes in human society and thought, while idealist interpretations would hold the reverse - that human ideas, beliefs, and values shape social organisation and economy. For example, was the protestant reformation motivated by the existing religious doctrine being at odds with a changing economy? Or that the emergence of Protestant ideas and the 'protestant ethic' paved the way for engagement in a new kind of economy (Weber 1904)?

In addition to materialism and idealism, I would argue that a third tradition is present – *naturalism*. Naturalism holds that individuals are not 'blank slates' but are endowed with some sort of 'human nature', be it an evolved psychology, Freudian subconscious, or non-specific kind of Hobbesian brutishness. With this three-way division between materialism, idealism and naturalism we can perhaps have a framework into which we can place the three fields which deal with evolutionary approaches to human behaviour. Where does each lie? In the sense that it posits a 'mismatch' between adaptations and modern environments, Evolutionary Psychology (EP) is strongly naturalistic but is, on the whole, not especially interested in the material or cultural circumstances in which individuals find themselves. The fields of human behavioural ecology (HBE) and gene-culture co-evolution (GCCE) also assume an evolved human psychology but are interested in its interaction with ecological conditions and ideas/culture respectively (Figure 1-1).

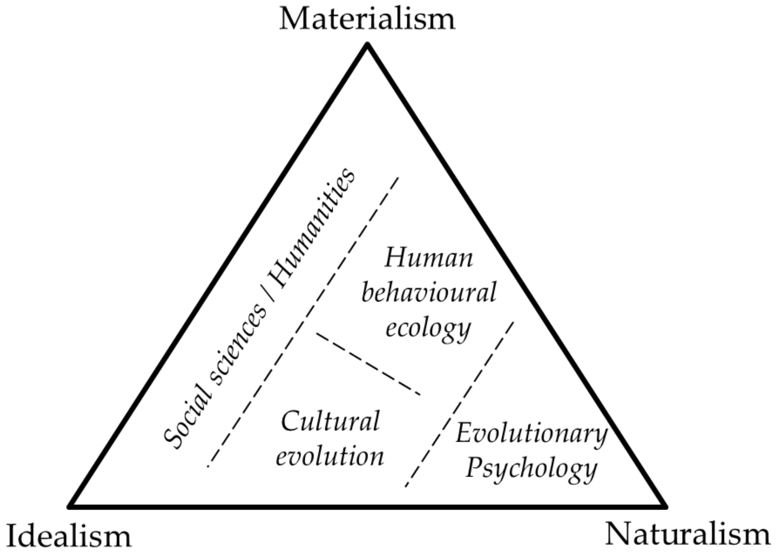


Figure 1-1: Situation of the 'three fields' of evolutionary anthropology discussed in section 1.2.2 above as well as the social sciences and humanities within the broader epistemological context.

1.3 Overview of thesis

In this thesis I explore the social organisation of hunter-gatherers, with particular reference to the Agta, hunter-gatherers from the northern Philippines with whom I conducted ethnographic fieldwork in 2013-14. The thesis is concerned with three main dimensions of social organisation. The first is *empirical* – what is size, composition, and structure of Agta communities, and how do these compare the groups of other small scale hunter-gatherers? The second is *functional* – how does group structure activities such as food sharing and foraging? The third dimension is *evolutionary* – if the kind of social organisation we see among the Agta and other contemporary foragers was typical of foragers in human evolutionary history, how might this have related to the evolution of other derived human traits? While the majority of the thesis is directly related to addressing these concerns, I also explore some related broader issues underlying the study of social organisation such as biological conceptions of relatedness.

The thesis is structured as follows. In chapter two, I provide an overview of the fieldwork methods employed to collect quantitative ethnographic data on the Agta. Many of the methods I employed are relatively straightforward, following procedures used by previous researchers. In some places, however, myself and colleagues on the Hunter-gatherer Resilience project have introduced some important methodological innovations – most notably in the statistical analysis of relative ageing data (section 2.3.2) and the use of 'motes' to collect data on behavioural associations (section 2.3.4).

In chapter three, I provide an ethnographic account of the Agta, hunter-gatherers who live in the mountainous and coastal regions of north-eastern Luzon, Philippines and with whom I conducted ethnographic research over nine months in 2013/4. I provide an introduction to the demography, social organisation, subsistence, and economy of the Agta using both quantitative and qualitative data.

In chapter four, I explore the community composition of hunter-gatherers in general and of the Agta in particular. I demonstrate that the Agta, like many contemporary hunter-gatherers, live in camps containing a large proportion of distantly related, or unrelated individuals and have a multi-local residence system with men and women equally as likely to be living with kin. I then discuss the results of a model I created in order to understand how group-level community relatedness emerges from decisions made at the individual level. My modelling suggests that even when there is strong preference toward living with kin at the individual-level, community relatedness is reduced if both men and women have influence over camp composition.

In chapter five, I critically examine the way in which evolutionary anthropologists typically think about relatedness, arguing that in pair-bonded species such as humans, affinal kin can derive inclusive fitness benefits through aiding each other, despite being unrelated by common descent. I argue that biological conceptions of relatedness ought to be reckoned *forward*, through common reproductive interest, rather than *backwards*, through common descent. I propose an alternative coefficient of relatedness that is based on shared reproductive interest. I provide the results of an agent-based evolutionary model which demonstrates that investment in affinal kin is adaptive, and also show that my alternative coefficient of relatedness is a better predictor of behavioural interactions among the Agta than is the 'standard' coefficient of relatedness.

In chapter six, I explore the functional significance of multilevel social organisation through the analysis of networks of inter-household food sharing in six Agta camps. I find that Agta households tend to have strong food sharing relationships with a sub-set of the other households in their camps, and that there exists an important (if ephemeral) social unit larger than the household but smaller than the band. I describe this unit as the 'residential cluster'. I suggest that the 'multilevel' social structure in which individuals are situated within households within clusters, within the wider camp allows them access to the range of social relationships with spouses, extended kin, and unrelated individuals needed to facilitate the exchange of food required to meet the energetic inter-dependence to which humans are committed because of our risky foraging niche and energetically expensive life history.

Finally, in chapter seven, I provide an overview of the findings of this thesis and explore potential directions for future research. Taken together, my results emphasise that hunter-gatherers inhabit complex social worlds in which individuals negotiate relationships with spouses, extended family (including affinal kin), as well as a large pool of unrelated individuals.

Chapter 2: Methods

2.1 Summary

In this chapter I provide an overview of the methods used to collect the quantitative ethnographic data described and analysed in the 'data' chapters of this thesis (chapters four to six) as well as in the ethnographic chapter (chapter three). As outlined in section 2.2 below, I conducted two seasons of fieldwork with the Agta in the municipality of Palanan, north-eastern Luzon, Philippines in 2013-14. With my colleagues, I collected a broad range of data relating to the fertility, mortality, body size, and age of individuals as well as the relatedness and interactions between them. I outline the methods used to collect this core data in section 2.3. I also collected data on foraging, food production, and sharing, as outlined in section 2.4.

2.2 Timeline of fieldwork

I conducted two seasons of fieldwork with the Agta: April to June 2013 and February to July 2014.

2.2.1 April-June 2013

In April-June 2013, I conducted, along with my PhD colleagues Abigail Page and Daniel Smith, a ten-week fieldwork season in Palanan with the aim of (*a*) collecting a database of basic demographic, anthropometric, and genealogical data on the Agta which would provide a solid foundation and rich source of data for our later work, and (*b*) establishing the contacts and local knowledge required to make our long-term 2014 fieldwork a success.

For the majority of the 2013 trip we were based just outside of a small fishing village in San Isidro barangay on the north-eastern-most part of Palanan, not far from the Agta community of Diago (~20minutes walk) and a two hour trip by boat from Palanan town ('Bayan'). From San Isidro we could walk to five Agta camps: Dimatog (~20mins), Diago (~20mins), Didikeg (~80mins), Dipaguiden (~70mins), and Dimelmel (90mins) (camps 65, 66, 67.2, 67.1, and 68 on the in map in Figure 2-1 respectively). Visiting these camps occupied the first five weeks of our trip. Once the camps within walking distance had been visited, we organised a week-long trip to Kanaipang (74), a two hour boat trip south from San Isidro. After Kanaipang, we rented an apartment in Palanan town. From here we could take motor-tricycles and then walk to a number of inland Agta camps including Simento (54), Culasi (64), and Dibungco (59). We took a short trip to Disokad (50) in southern Divilacan (the next municipality north of Palanan). In total, the 2013 season was very productive, and we collected genealogical, genetic, and anthropometric data on around 600 people.

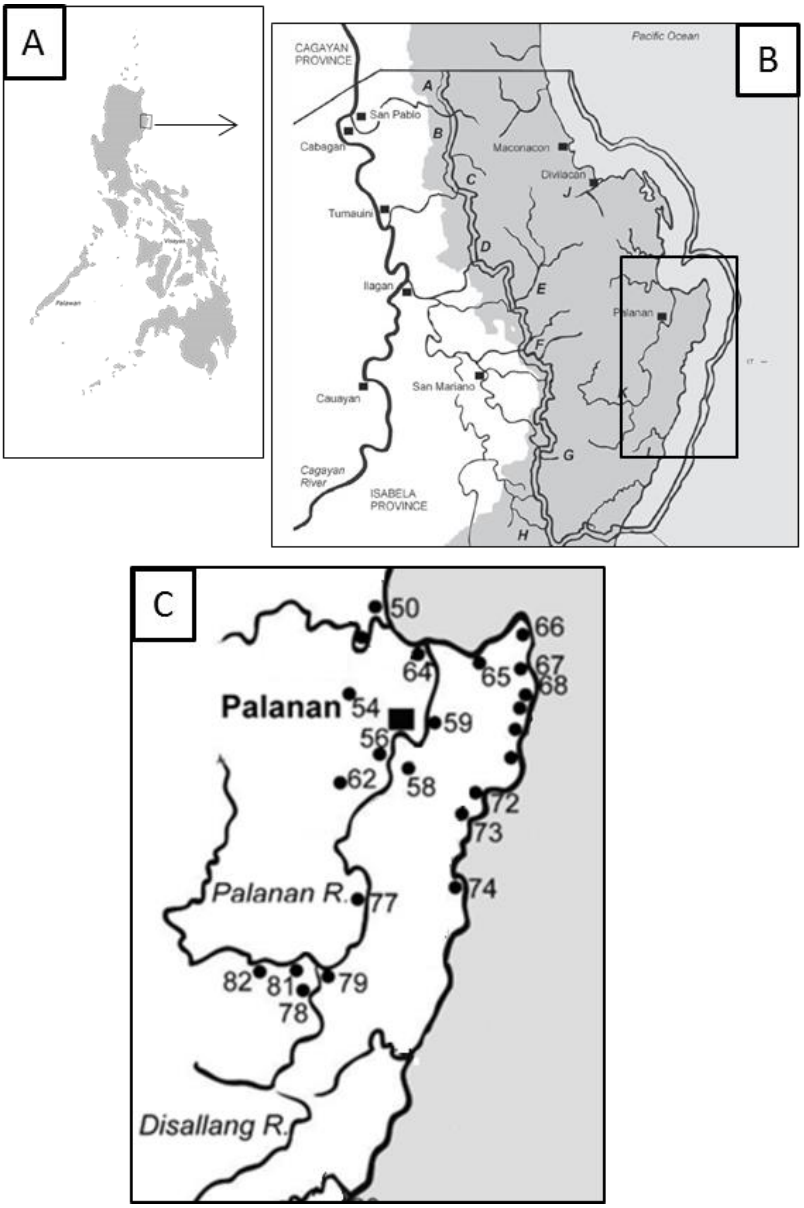


Figure 2-1: Situation of Palanan. (A) Location of the study area within the Philippines; (B) situation of Palanan within the wider province of Isabela and Sierra Madre Natural Park. The double line represents the park boundaries. Adapted from Minter (2008); (C) Location of our study camps within Palanan. Modified from Minter (2008). I use the community numbers on this map in order to have a common system of community identification between our study and Tessa Minter's. See Table 2-1 for corresponding camp names.

Table 2-1: List of the Agta communities I visited in 2013-14. Numbers refer to map locations in Figure 2-1. *The barangay is the smallest administrative division in the Philippines – Palanan has sixteen. Camp numbers refer to those used by Minter (2008) and used in the map of Palanan above (Figure 2-1).

Number	Community	Barangay*	Years visited
50	Disokad	Dimapnat (Divilacan)	2013
54	Simento	Dialomanay	2013, 2014
56	Dicabayo	Centro West	2014
58	Dikente	Marikit	2014
59	Dibungku	Marikit	2013
62	Dinipan	Bisag	2014
64	Sabangan	Culasi	2013, 2014
65	Dimatog	San Isidro	2013
66	Diago	San Isidro	2013, 2014
67.1	Dipaguiden	San Isidro	2013, 2014
67.2	Didikeg	San Isidro	2013, 2014
68	Demelmel	San Isidro	2013, 2014
72	Cacawayanan	Didadungan	2013
73	Dicobeyan	Didadungan	2013
74	Kanaipang	Didadungan	2013, 2014
77	Diambarong	Didian	2014
78	Magtaracay	Didian	2014
79	Dipgsangan	Didian	2014
82	Lukban	Didian	2014
84	Diabbut	Dialomanay	2014
85	Apap	Didian	2014
86	Disibulig	Didian	2014

2.2.2 February to July 2014

My 2014 field season lasted from February to July. During the trip, we aimed to (*a*) visit those camps in Palanan we had not visited in 2013 to continue to collect the basic 'census' data and (*b*) to collect the longer-term behavioural data in selected Agta camps (e.g. relating to food production and sharing). The general pattern of the 2014 trip was to spend around ten days staying with one Agta camp before returning to Palanan town for a few days to buy food and organise the next trip. The camps I visited in 2014 are outlined in Table 2-2 below.

Table 2-2: The main Agta communitites visited during the 2014 fieldwork season. The numbers in brackets after the camp names refer to the codes used by Minter (2008) and referenced in the map of Palanan above (Figure 2-1) .

Camp (Map Code)	*Dates*	*Approx. families*	*Conditions*
Diabbut (84)	3-19th March	8	Rainy, muddy, cold
Simento (54)	24th March – 1st April	4	End of rainy season
Dipaguiden/Didikeg (67)	21st April- 2nd May	4/5	Hot, summer, dry
Kanaipang (74)	6th May-17th May	22	Hot, summer, dry
Diago (66)	2nd May- 30th May	13	Hot, summer, dry
Dipagsangan (79)	7th June-17th June	5	Hot summer, storms
Diambarong (77)	22nd June-1st July	4	Hot summer, storms

2.2.3 Translators and interviews

Before going to Palanan I was unable to speak Paranan, the language spoken by both Agta and non-Agta in Palanan for which no resources are available in English. I could also only speak a very limited amount of Tagalog (Filipino), the national *lingua franca* of the Philippines. Although I spent a total of nine months in Palanan, I would most likely have needed to spend at least that amount of time again to have sufficient Paranan to conduct productive interviews without a translator. Luckily, there are a significant minority of non-Agta in Palanan who can speak both English and Paranan. We therefore employed a number of translators across the two fieldwork seasons. In both field trips we worked with Gurly Curampez, who had previously worked for the NCIP (National Commission on Indigenous Peoples), her husband Amai and, in 2014, Aima Curampez. In 2014 we also worked with Christie Cabaldo, an Agta lady from Maconacon.

2.3 Core data collection

As mentioned above, I conducted my field research in 2013 and 2014 as part of a small team of researchers. Although we each had a distinct research topic (in my case, food production and sharing) we all contributed to the collection of core data sets using the protocols outlined in this section.

2.3.1 Genealogies

An understanding of how individuals are related to each other is a basic requirement for most studies in human behavioural ecology and is one of the major objects of study in my research. When visiting a new camp and whenever we met adults we had not previously met, we conducted genealogical interviews with them. In these interviews we attempted to establish (*a*) the extent of their knowledge about ancestral, collateral, and affinal kin, and (*b*) details of their reproductive histories. Paternity was assumed to be as reported. When interviewing, for example, the sibling of someone we had already interviewed, we would consult the notes from their sibling's interview and ask 'fact checking' questions to verify the previous account and to fill in details that were missing, rather than repeat the whole process again. For each individual mentioned in a genealogy, we would try to record the following, if known:

1. Birth order within their sibling set;
2. Current and previous marriages and children from these;
3. Current location;
4. Location of birth;
5. If dead, as much as is known about the location, cause, and date of death.

Genealogical interviews typically took around half an hour although when an individual's family history was completely unknown to us and they were an obliging interviewee, it could take more than an hour. The data collected in these interviews were also a source of information on ages – both relative and absolute, and provided an opportunity to 'triangulate' ages. For example, we might ask questions about birth orders, and whether various life history events (births, deaths, first child, weaning) occurred before or after events with known dates (e.g. hurricanes or fights between the NPA communist guerrillas and the Philippine army in Palanan). This helped provide many of the 'anchors' important to the production of age estimates (see section 2.3.2 below).

Since interviews were recorded free-form and on paper, digitising them when back from the field represented a major undertaking. Between three people we spent at least a month doing this. What made this process so time consuming was trying to verify connections between families. Much time was spent cross-checking interviews to establish whether, for example, the 'Dede' and 'Ita' mentioned as cousins of person A were the same people as the 'Dedeng' and 'Eva' noted as being the siblings of person B's wife. To store this data we used the genealogical software 'GRAMPS'. From this I could produce a simple list of all individuals, with their own ID numbers and the ID numbers of their parents and spouses. From this list I could use genealogical packages in 'R' such as pedigree (Coster 2012) and kinship2 (Therneau et al. 2014) as well as my own scripts to compute the closest dyadic relatedness of individuals in our sample. In total, we collected a dataset of 1,381 living individuals of which we had a good amount of data, and an additional 1,743 people who were either dead or who we knew only as names within the genealogies of others.

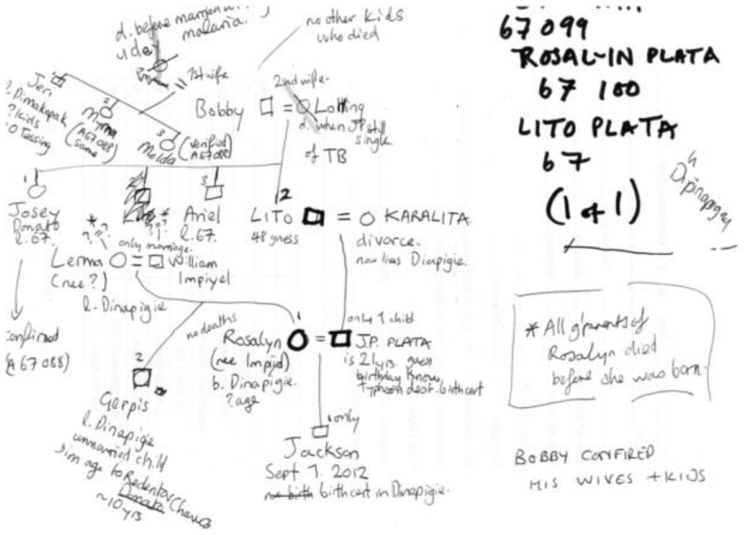


Figure 2-2: Example of notes from a genealogical interview made with Lito Plata and his daughter Rosalyn Plata in Dipaguiden, 2013. As in standard anthropological kinship diagrams, squares are males and circles are females. The double hyphen represents marriages, vertical ties represent parenthood, and horizontal brackets represent sibship.

2.3.2 Age

Several of the analyses presented in this thesis require estimates of the age of individuals. Given that the Agta are, by and large, unaware of their own absolute ages, obtaining these estimates is a difficult task. When asked if they were known, birth dates were often inconsistent with birth order and sometimes totally implausible. On one occasion I asked a man if he knew the birth dates of his children, not realising that one of my colleagues had already asked this a few days earlier. On both occasions he had confidently given exact dates but none of these matched up. Faced with similar challenges, some researchers have resorted to simple visual estimates of age or have averaged across the estimates of several researchers. Although the latter approach may reduce inter-observer error, the group of researchers as a whole may still be making systematic over- or under- estimates of age as can easily be the case for populations of, for example, shorter stature, such as the Agta.

How, then, can we derive accurate age estimates for individuals who do not know their own age? The answer lies in utilising what they do know which is their age relative to family and friends with whom they grew up. In order to help in obtaining accurate age estimates, we endeavoured to collect data on relative ages using a protocol inspired by one outlined by Kim Hill and Hillard Kaplan in their book ‘Ache life history’ (1996). This involved compiling a ‘relative age list’.

Compiling a relative age list – the card ranking exercise

Using a digital camera, we took photos of everyone we hoped to age and, using a small polaroid 'USB' printer, printed passport-size photos of all individuals. We initially split up individuals into the following age groups based on our visual estimates: less than four years, 4-8 years, 9-12 years, 13-18 years, 19-45 years, and over 45 years. We then sat down with as many people as possible to try to construct a 'relative age list' of photo cards.

We would begin the age ranking with ego's own photo and explain to them that we wanted to place people younger than them to the left of their photocard and people older than them to the right of their photocard. We would randomly draw a photo card from the age group pile and ask '*do you know this person?*'. We would have written the name of the person on the back of the card in order to verify this. If they didn't know the person in question, we would not include them in the age ranking. If they were uncertain about the person's name but recognised their face, we would also exclude them on the basis that they probably did not know them sufficiently well to know their relative age. If they were known to ego, we would ask '*who is older, you or this person*?'. Once we had a ranking of several people, we would ask the '*who is older?*' question as many times as it took to locate the photocard in the relative age list. After a few photocards had been placed, participants often understood the concept well enough to start placing photocards themselves. Sometimes the participant would say that they were 'age mates' with the person in question, or that two others were 'age mates' in which case we would put the photos on top of each other to show they are a similar age. The widely understood concept of 'age mates' (those who lived together as children) proved useful in this exercise. For the youngest age groups, we asked parents to order the cards.

Figure 2-3: Conducting a relative age listing in Diago, 2013 in the home of Sammy Donato (*left*).

Splitting up the photo cards into rough age groups sped up this process by concentrating effort on similar age individuals. If an individual was ranked as the youngest within their age class, we would also include them in the younger age group ranking, and where relative age lists challenged the rough age categorisations we had made, we would move individuals into the appropriate list. Thus, these age categories were only a rough starting point and were modified with time. Where participants were willing and were confident in the procedure, we would introduce photo cards of individuals from neighbouring camps. Although it took some time, most people were keen to take part and enjoyed seeing the photographs, especially of people from other camps they may not have seen for some time.

As a result of conducting 214 of these card ranking exercises, we had an extensive amount of relative age data. From questions asked about dates of births and deaths during the genealogical interviews (see section 2.3.1), we also had a number of individuals whose age was known with enough confidence to treat them as an 'anchors'. We were also aided in the establishment of 'anchors' by the data sets of Tessa Minter and Thomas Headland who have conducted censuses with the Agta and who knew a number of key dates of birth. Tessa Minter, having worked in Palanan most recently, was a source of important data on more recent events, while Headland's database was of use in ageing some of the older individuals who had previously lived further south, in his study area of Casiguran and who are included in his publicly available demographic database - a rich source of demographic data collected during more than forty years with the San Ildefonso Agta.

Deriving age estimates from our raw data

In summary, then, we have two kinds of ageing data: relative age ranks, and absolute age estimates. In both cases, we have more confidence in our relative and absolute estimates for some individuals than for others. How could we integrate all this (sometimes contradictory) data into a coherent set of age estimates? In order to do this we used an algorithm developed by Mark Thomas and colleagues at UCL which employs the Gibbs sampler Markov chain Monte Carlo method (Geman & Geman 1984) to integrate all information on absolute and relative ageing to produce a probability distribution for the age of each individual in the sample. I used the median value from each individual's probability distribution as their estimated age.

2.3.3 Camp Scans

During the 2014 field season, we conducted 'camp scans' at regular intervals during the day in which we recorded a snapshot of the activities of individuals. This has become common practice for many researchers in quantitatively minded anthropology (Wood & Marlowe 2013; Hames & McCabe 2007; Gurven et al. 2000). How much data is collected, and how often scans are made, however, varies depending on purpose. Minter (2008), for example, recorded the main activity each individual was involved in each morning and afternoon. Other researchers (e.g. Gurven et al. 2000; Wood 2013; Hames & McCabe 2007) conducted scans every hour. We opted for an intermediate strategy, conducting a camp scan every 3 hours throughout the day and varying the start time systematically from 6:30 to 9:00am and taking turns between available researchers to conduct scans. In each scan we collected data on:

(A) *Activity*. The activity each individual was engaged in. We used a modified set of categories from Minter (2008). Most of the 'in-camp' categories were straightforward reflections of what we saw people doing, for example 'A1: Cooking' and 'D6: Sleeping'. Out of camp activities often required us to ask around as to what activity out-of-camp individuals were engaged in. Where individuals were involved in more than one activity, we recorded all that applied.

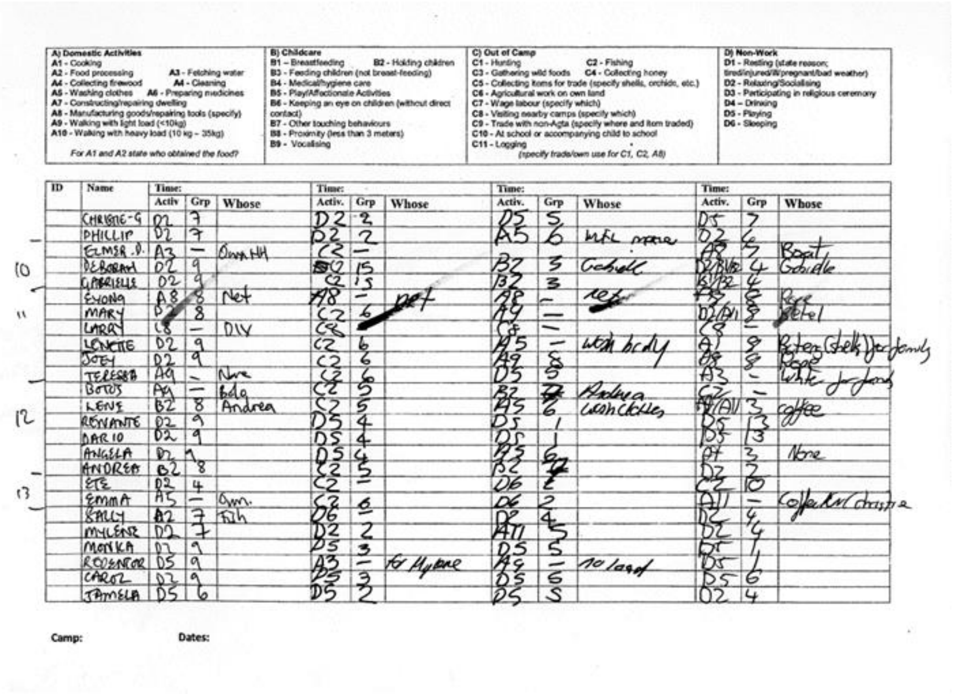
(B) *Proximity*. In addition to the activity that each individual was engaged in, we recorded who they were in close proximity to at that time. To define proximity we adopted the rule-of-thumb of whether individuals would be able to hear each other when speaking without shouting.

(C) *Details*. For some activities, we recorded additional details. For example, if a baby was being held (code B2), we would record which baby this was, or if someone was visiting a neighbouring camp (code C8), we would note which camp this was.

Although recording proximity as well as activity allowed us to add a valuable social dimension to camp scans, this made data collection more time consuming. In the smaller camps, this did not matter so much - camp scans could be completed in less than five minutes and represented an easy way to collect an accurate snapshot of camp life - we could look around, take notes, and maybe ask a few questions if necessary. In small camps, scans were a relatively inconspicuous form of data collection. In larger camps, however, scans became more time consuming. For example in Kanaipang (the largest camp visited) scans took up to 45 minutes to complete. With this comes the difficulty of individuals moving between proximity groups and changing activities, creating dilemmas about which activity we ought to record them as engaging in. Generally, we would take the first activity we saw them doing. But sometimes they might become critical to the activity of another individual. For example, a woman walking across camp may be recorded as walking without load (A9) but we may see them a few minutes later carrying a small child (B2). The point is, in large camps, scans become something of a headache. Trekking around a large camp in the midday sun was not an enjoyable task and one I was close to abandoning on several occasions. In general, however, camp scans were an efficient way to collect a large amount of valuable data. In total, we recorded activity and proximity group at more than 11,500 person time points (see Table 2-3 for a breakdown by camp). As with genealogies, entering this data was a time consuming task.

Table 2-3: Overview of camp scan dataset. Map codes refer to those used in Figure 2-1.

Camp (Map code)	*Days*	*Scans*	*Individual time points*
Diabbut (84)	9	31	1,023
Simento (54)	6	24	561
Kanaipang (74)	9	36	3,951
Diambarong (77)	7	32	838
Dipagsangan (79)	8	28	1,054
Diago (66)	13	49	2,677
Dinipan (62)	7	24	805
Magtaracay (78)	6	24	779
TOTAL	65	248	11,688



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

ID	Name	Time:			Time:			Time:			Time:		
		Activ	Grp	Whose	Activ.	Grp	Whose	Activ.	Grp	Whose	Activ.	Grp	Whose
	CHRISNE-G	D2	7		D2	2		D5	5		D5	7	
	PHILLIP	D2	7		D2	2		A5	6	MFL mama	D2	6	
	ELMER.D.	A3	—	Own HH	C2	—					A8	5	Boat
10	DEBORAH	D2	9		B2	15		B2	3	Gabrielle	D2/B1/B2	4	Gabrielle
	GABRIELLE	D2	9		C2	15		B2	3		B1/B2	4	
	EYONA	A8	8	Net	A8	—	net	A8	—	ref	A8	8	Rope
11	MARY	D2	8		C2	6		A9	—		D2/A11	8	Betel
	LARRY	C8	—	DIV	C8			C8	—		C8	—	
	LENETTE	D2	9		C2	6		A5	—	wash body	A1	8	Beter (shells) for family
	JOEY	D2	9		C2	6		A9	8		A8	8	Rope
	TERESITA	A9	–	None	C2	6		D5	5		A3	–	White for family
	BOTOS	A9	—	Bdg	C2	5		B2	7	Andrea	C2	—	
	LENIE	B2	8	Andrea	C2	5		A5	6	wash clothes	A11/A11	3	coffee
12	RENANTE	D2	9		D5	4		D5	1		D5	13	
	DARIO	D2	9		D5	4		D5	1		D5	13	
	ANGELA	D2	9		D5	4		A5	6		A1	3	None
	ANDREA	B2	8		C2	5		B2	7		D2	2	
	ETE	D2	4		C2	—		D6	2		C2	10	
13	EMMA	A5	—	Own.	C2	6		D6	2		A11	—	Coffee for Christina
	SALLY	A2	7	Fish	D6			D2	4		D2	4	
	MYLENE	D2	7		D2	2		A11	5		D2	4	
	MONIKA	D2	9		D5	3		D5	5		D5	1	
	ROSENDOR	D5	9		A3	—	for Mylene	A9	—	10 load	D5	1	
	CAROL	D2	9		D5	3		D5	6		D5	6	
	JAMELA	D5	6		D5	2		D5	5		D2	4	

Camp: Dates:

Figure 2-4: Example of a camp scan data collection sheet in Diago, 2014. For each individual in each scan we listed the activity they were engaged in according to the codes at the top of the sheet, the group they were in, and any relevant additional details.

2.3.4 "Motes" – Portable wireless sensing technology

During the 2014 fieldwork trip we conducted a series of experiments in which we asked participants to wear 'motes'. Motes are small electronic units with low-energy sensors that send and receive radio signals to and from other units. These are small enough to fit in a wristband or on a belt and they were used in order to collect data on the frequency of interaction between individuals. In seven camps we asked all families willing to participate to wear the motes during daytime for a period of four to nine days. Throughout this time, motes would send out signals every two minutes and record from which other motes they received signals. Signals were received and saved from all other motes in a radius of around three metres. We kept only the data received between 5am and 8pm.

In order to protect the motes from water damage and to make them comfortable to wear, we wrapped each one in cling film and a small plastic bag and sealed them into either a wristband or belt, depending on preference. Each mote had a unique identifying number and, in order to reduce the number of times people swapped motes by accident, we regularly asked to check they were wearing the correct mote and also tried to give each one a distinguishing feature such as a marker pen design or coloured ribbon. Any swaps which did occur were noted and taken into account when processing the data. The motes do not provide any information in 'real time' – to collect the data they must be given back and the data downloaded and processed.

Data from the motes were processed using a script written in C++ by Sylvain Viguier, who also designed both the hardware and software of the motes. The output of this data was a table of raw frequencies of signals received between each dyad of motes. Using code initially written by myself, we converted this raw data into (*a*) the actual proportion of time which each dyad spent together and (*b*) the proportion of each ego's time that was spent with each alter.

2.3.5 Additional data collection

In addition to the methods outlined above, I also contributed to the collection of a range of other data which I do not use directly in this thesis. Below, I briefly outline what these additional datasets were.

Household questionnaires

During the 2014 fieldwork season, we conducted a brief 'household survey' with at least one adult from each household. In this survey, we asked questions about mobility, housing type, possessions, and access to education and health.

Anthropometric data

During the 'census' phase of our research we collected anthropometric data on almost all individuals. We used a Harpending anthropometer to measure height, hip width, and shoulder width and used electronic scales to measure weight. We also collected head circumference for children.

Genetic data

When conducting the 'census' part of our fieldwork, we collected saliva samples from all adults willing to provide one. We used ORAgene saliva sample kits to do this which required the participant to salivate, rub their cheeks with the teeth a little, and spit into the container.

2.4 Production and sharing data

The methods described in the section above were those used by myself, Abigail Page, and Daniel Smith to compile our 'shared' dataset. Beyond this shared data collection, we divided our labour, each collecting data on one or more specific themes. I collected data on foraging, food production, and food sharing. Although food production and sharing require different data collection procedures and will be part of different data sets, they can be thought of as part of one *chaîne opératoire* of decisions and actions relating to food acquisition (Figure 2-5). First in this chain, individuals must decide how much time and energy to invest in foraging (foraging effort). The amount they produce while out foraging is a function of this foraging effort, skill, and luck. They then face the decision of how much of a resource to bring back to camp, and how much to consume prior to returning. Out-of-camp eating has often been overlooked, and a recent paper by Collette Berbesque has shown it is extensive among the Hadza (Berbesque et al. 2016). Once they have brought food back to camp, a 'primary distribution' may occur, where the producer distributes food shares between households. Once in the household, food may be distributed further once it has been prepared and/or cooked and may also be shared by inviting members of other households to eat with you. This distribution has described as the 'secondary distribution' (Wood and Marlowe 2013).

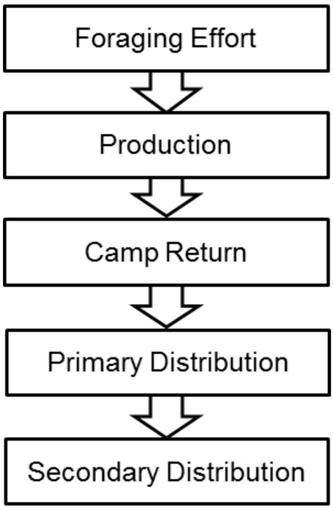


Figure 2-5: The *chaîne opératoire* of food production and sharing from foraging effort to the secondary distribution of food.

Ideally, one would conduct an observational study where all aspects of the *chaîne opératoire* are observed, such that food can be traced from foraging to the mouths it feeds. How would one do this? Should we follow households, individuals, or the food package itself? Whatever the method, a single researcher would be sure to miss important data and even for a small team of researchers, this would be logistically challenging. A trade-off must therefore be made between data quality and comprehensiveness. In the sections below I briefly review the methods used in previous research as well as my own.

2.4.1 Food Production

Research on food production has been conducted by evolutionary anthropologists for a number of reasons. The primary objective for some has been to quantify the foraging returns of a large number of individuals with the intention of exploring between individual differences in productivity. For others, however, the process of food production itself has been of primary interest. In particular, there has been great interest in testing the applicability of models derived from optimal foraging theory on human foraging (e.g. Smith et al. 1983; Smith 1991; Hawkes et al. 1982; Hill & Hawkes 1983). Unsurprisingly, different data collection methods accompany these different research questions.

If one is interested in the actual process of foraging, then focal follows (where the researcher accompanies people on foraging forays) are a necessity. For those interested largely in the relative productivity of individuals, however, it is more effective simply to wait for individuals to return to camp and to weigh all food they bring back with them. This can yield much more data. This is because the researcher can potentially collect data on the productivity of all members of camp every day, while focal follows restrict the researchers to one person-observation-day each day. That said, the 'stay-in-camp' method should be supplemented with at least a few focal follows in order to explore the proportion of food that is being eaten outside of camp, if any. In my research, I endeavoured to strike a balance between focal follows and stay-in-camp production data collection.

2.4.2 Focal follows

The aim of focal follows is simply to accompany an individual on a foraging trip and systematically record what happens. This includes collecting data on:

(a) *Changes in activity.* I would try to make a note of the time when certain activities occurred. So for example, on a fishing trip, I might record the time at which we left camp, stopped walking, swum across a river, took a cigarette break, started fishing and so on.

(b) *Foods produced and consumed;* Foods eaten while out of camp, the amount of food returned to camp once the trip was over and, where possible, it's weight;

(c) *GPS*. Focal follow notes were taken in my field notebook and were sometimes associated with GPS points, although the GPS signal was limited when in deep forest. I carried either a Garmin GPS or a small 'i-gotU' unit.

During the 2014 field season, I conducted 36 focal foraging follows. These ranged in length from quick twenty-minute fishing trips in the river adjacent to a camp to ten hour hunting trips deep into the forest. The mean size of foraging parties I accompanied was 2.31 individuals (SD = 1.84) *versus* 1.45 (SD = 1.84) for those I did not accompany. The average duration was 155 minutes (SD = 105) *versus* 228 minutes (SD = 308) for trips I did not accompany. As indicated by these discrepancies, the focal follows I conducted were not necessarily a representative sample of foraging trips in general. This is largely because one goes on the trips one is invited on, and this is not necessarily a representative sample for a number of reasons outlined below.

Firstly, it took a while to establish a reputation as being fit enough to accompany people on fishing or hunting trips without holding them back. Thankfully, I passed this test and established a reputation for being '*mabilis*' (fast), a reputation which, by the end of summer 2014, had made its way to camps ahead of me. To begin with, however, I first had to first prove my abilities by accompanying teenage boys foraging and perhaps go a short trip with the men before being invited on longer trips. Secondly, I felt it may have been seen as inappropriate for me to accompany women on solitary foraging trips and most of my sample of female foraging was therefore with groups (although, that said, group foraging tends to be the norm among women anyway). Thirdly, planned trips often failed to materialise. On several occasions I was invited on to trips which would 'leave as soon as so-and-so arrived'. Unsurprisingly, on many occasions this never happened and by this point I had missed the opportunity to go out foraging with others. Finally, I could never assume that I was a completely neutral observer on foraging trips. While I might have been fit enough to keep up with them, and endeavoured not to interfere, the people I was observing are never going to pretend I was not there. On one trip, for example, it transpired that we had been taken on a long detour so that I could be shown a particularly scenic waterfall (see
Figure 2-6).

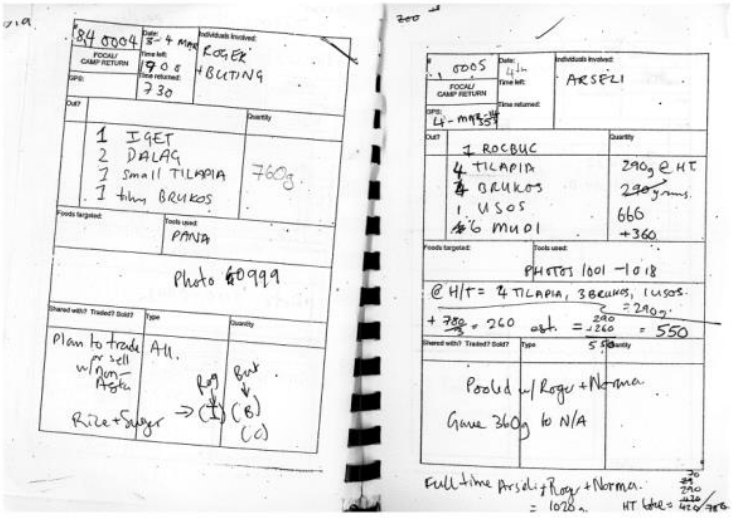
Figure 2-6: Detour from a hunting trip to see a waterfall. Simento, spring 2014. "Eddie" Chavez (left) with his bow, Nonoy Villeta (right) with his air rifle and small dove.

2.4.3 'Stay-in-camp' production

As mentioned above, a well-established method for capturing camp-return production is simply to weigh, count, or visually estimate all foods brought back to camp (Wood & Marlowe 2013) and this is a method which I used to collect food production data throughout my fieldwork in 2014. For each foraging trip, I would record (*a*) a unique trip ID, (*b*) the date and time of departure from camp and date and time of return, (*c*) the names of the participants, (*d*) a description of the foods returned and, their weight, if recorded, (*e*) the primary distribution of the food package returned (if observed), and (*f*) any extra details such as identifying GPS codes, tools used, and photo numbers. These details were recorded in a booklet made for this purpose (see Figure 2-7, for example).

I weighed food brought back to camp using one of two Pescola spring scales (I had one for 0-500g and another for 0-20kg). Of the 498 foraging trips in which a food package was returned to camp, I was able to weigh the food myself in 263 (53%) instances. In 34 (7%) of cases I relied on my own visual estimates because I did not have my scales to hand or because the food was distributed or processed in some way before I could weigh it. In 201 (40%) cases I did not get a chance to weigh or visually estimate the food package and had to rely on self-report estimates from the producers. This occurred for a variety of reasons. In some cases, I was out on focal foraging trips or otherwise engaged - one cannot be totally omnipotent. In some cases, the food had been sold or traded with non-Agta before the foragers returned to camp. Luckily, self-report estimates for packages of known weight were, by and large, fairly accurate. Given most Agta sell fish and other goods on a regular basis, they have a good eye for how many kilos of fish they have caught. In some camps, the Agta had small scales which had been given to them by an NGO with the aim of empowering them to getting a fair price when selling their goods.

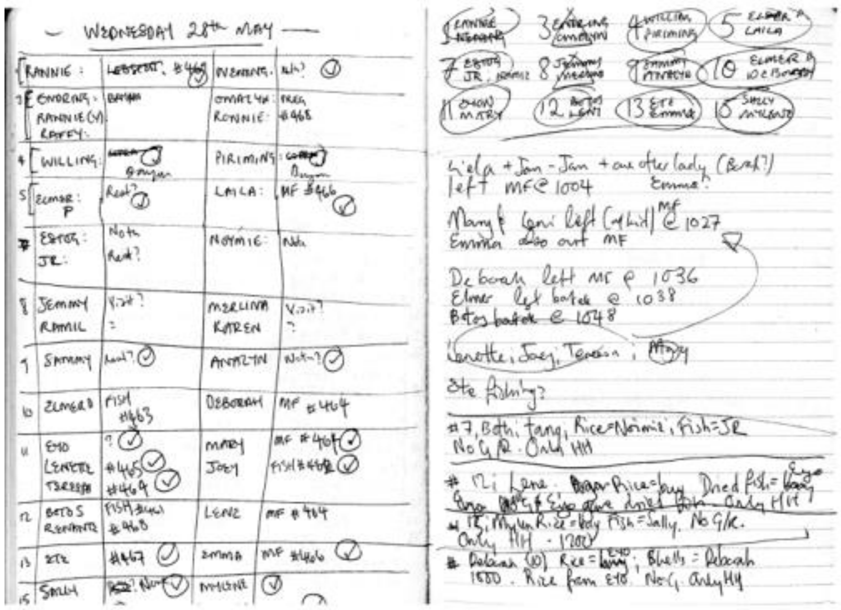
People's patience is a finite commodity and when we are collecting data on all manor of things I did not want to annoy people by asking them too many questions, especially if they had just returned from a long foraging trip. Nonetheless, where possible, I would ask questions about where people had been foraging and what tools or techniques they had used. Where appropriate I also asked foragers to identify the names of the species they had collected and cross-referenced the Agta species names with the lists of scientific names complied by Minter (2008), Linnebank (2001), and Goslinga (2009).



84 0004
Date: 3-4 Mar
Individuals involved: ROGER +BUTING
FOCAL/ CAMP RETURN
Time left: 1905
Time returned: 730
GPS:
Out?
Quantity
1 IGET
2 DALAG
1 small TILAPIA
1 tiny BRUKOS
760g
Foods targeted:
Tools used: PANA
Photo 60999
Shared with? Traded? Sold?: Plan to trade or sell w/non-Agta
Type: All.
Quantity:
Rice+Sugar → (I) (B) (C)
Rog But

0005
Date: 4th
Individuals involved: ARSELI
FOCAL/ CAMP RETURN
Time left:
Time returned:
GPS: 4-mar-14 357
Out?
Quantity
1 ROCBUC
4 TILAPIA
4 BRUKOS
1 USOS
6 MUOI
290g @ HT
~~290~~ grams.
666
+360
Foods targeted:
Tools used:
PHOTOS 1001 -1018
@ H/T = 4 TILAPIA, 3 BRUKOS, 1 USOS = 290g.
+ 780 - 260 est. = 290 + 260 = 550
Shared with? Traded? Sold?
Type
Quantity
Pooled w/ Roger + Norma
Gave 360g to N/A
Full time Arseli + Roger + Norma = 1028 g.
HT total = 420/786

Figure 2-7: Example of a foraging trip/production data sheet from Dialomanay, March 2014. Each trip is given a unique ID code and details are provided of the date and time of the trip, the participants, the food returned including its weight (if available), and various other details such as the tools used and the reference numbers of any associated photographs.



— WEDNESDAY 28th MAY —

	RANNIE:	LEBBERT. #469 ✓	WENNING.	Nh? ✓
1	ENDRING: RANNIE (Y) RAFFY:	BAGAN	EMALYN: RONNIE:	PREG #468
4	WILLING:	~~[illegible]~~ ✓ Bagan	PIRIMING:	~~[illegible]~~ ✓ Bagan
5	ELMER: P	Rest? ✓	LAILA:	MF #466 ✓
7	ESTOR: JR:	Nth Rest?	NOYMIE:	Nth
8	JEMMY RAMIL	Visit? ?	MERLINA KAREN	Visit? ?
9	SAMMY	Rest? ✓	ANNALYN	Nth? ✓
10	ELMER D	FISH #463	DEBORAH	MF #464
11	EMO LENETTE TERESA	? ✓ #465 ✓ #464 ✓	MARY JOEY	MF #464 ✓ FISH #462 ✓
12	BETOS RENANTE	FISH [illegible] #463	LENE	MF #464
13	ETE	#467 ✓	EMMA	MF #466 ✓
15	SALLY	[illegible]? Nth ✓	MYLENE	✓

1 RANNIE WENNING
3 ENDRING EMALYN
4 WILLING PIRIMING
5 ELMER & LAILA
7 ESTOR JR, RAMIL
8 JEMMY MERLINA
9 SAMMY ANNALYN
10 ELMER & DEBORAH
11 EMO MARY
12 BETOS LENE
13 ETE EMMA
15 SALLY MYLENE

Leila + Jan-Jan + one other lady (Beth?) Emma?
left MF @ 1004

Mary & Leni left (w/ kid) MF @ 1027
Emma also out MF

Deborah left MF @ 1036
Elmer left batek @ 1038
Betos batek @ 1048

Lenette, Joey, Teresa, Mary

Ete fishing?

#7, Both, fang, Rice=Noimie, Fish=JR
No G/R. Only HH

12; Lene. ~~Bagan Rice=buy Dried fish=Eyo~~ ~~[illegible] Eyo gave dried fish. Only HH~~

15; Mylene Rice=buy Fish=Sally. No G/R.
Only HH - 1200

Deborah (10) Rice = buy; Shells = Deborah
1500. Rice from Ete. No G. Only HH

Figure 2-8: Example of food production notes, Diago, May 2014. The notes made on these pages provide an overview of the adults in camp and the activities they were involved in that day. Reference numbers listed next to the names of individuals on the left hand side refer to the ID numbers of particular foraging trips.

In order to establish the calorific value of food brought into camp I used estimates derived from the nutritional database of the USDA (United States Department of Agriculture) Nutrient Data Lab that is publicly available online (US Department of Agriculture, Agricultural Research Service 2015). An accurate estimate of the calorific value of a food package would require that (*a*) I was able to accurately weigh the food package, (*b*) I was able to correctly identify the species harvested, and (*c*) that this exact species is listed in the USDA database. In many cases, one or more of these requirements was not met, especially in the case of fish, where a multitude of species are harvested. At any rate, even with the best estimates in the world, reducing all food to calorific value is problematic since these values do not recognise micro- or macro-nutrient differences. I therefore made some simple assumptions about the calorific value of some resources. For example, for all marine fish for which species-specific nutritional data are not available, I used the values provided for mullet. Full details are provided in appendix A.

2.4.4 Food sharing data

A wide variety of methods have been used to collect data on food sharing among small-scale societies and researchers often employ several methodologies in tandem. The major methodological division is between data collected through observation and through interviews. Of the observational methods, three main protocols have been used: block observations, resource follows, and scans. Block observations involve the researcher observing a small number of nearby households for a set period of time. This method was used by Kaplan and Hill (1985), Allen-Arave et al. (2008), Gurven et al (2000) and Gurven et al. (2002) among the Ache. Resource follows involve waiting for foods to be brought into camp, weighing them, and then attempting to follow and weigh the portions received by each household. This method was used by Hawkes et al. (2001) and Wood and Marlowe (2013) among the Hadza. In some cases, the researcher themselves will have been on the foraging trip and so this 'resource following' becomes an extension of their focal foraging follow (Wood and Marlowe, 2013). Finally, some researchers have conducted scans at regular intervals throughout the day where individuals who are eating are asked who had originally produced the food (O'Connor et al. 2011; Gurven et al. 2002; Hames & McCabe 2007; Koster et al. 2015; Kaplan & Hill 1985; Gurven et al. 2000).

Of those studies using interviews to collect food sharing data, there are two main kinds. Some researchers conducted interviews on a daily or weekly basis about the food sharing which had occurred during that time. For example, Koster and Leckie (2014, 2015), who studied food sharing among lowland Nicaraguan horticulturalists, conducted interviews with households every morning about the food they had consumed the previous day, and who had given them these foods. Similarly, Hooper et al. (2015) and Gurven et al. (2012) conducted interviews with Tsimane households roughly twice a week. This is in contrast to those who conducted a single interview with one member of each household about their long-term sharing relationships with all other households. Nolin (2010, 2012), for example, asked each household in Lamalera which households they had given and received food from "…more than just once" in the previous season, while Patton (2005), who studied sharing among horticulturalist-foragers in the Ecuadorian amazon, asked participants to rank all other households by the amount of food they had received from them over an indefinite timeframe.

Early on in my 2014 fieldwork I had tried to rely only on observational data on food sharing using mainly the 'resource follow' method described above. In the relatively small camps of Diabbut and Simento, this was not too challenging a task. In the larger camps such as Dipaguiden, Diago, and Kanaipang, however, it became difficult to keep track of all foraging trips and I therefore supplemented my observations with daily interviews with each household. At dusk each day I would go to each household and ask the following questions:

1- *When did you last eat?*
2- *What foods did you eat?*
3- *Who foraged these foods?*

4- *What food did you collect today?*
5- *Did you give food to any other household?*
6- *Did any households give food to you?*
7- *Did you share meals with any other households?*

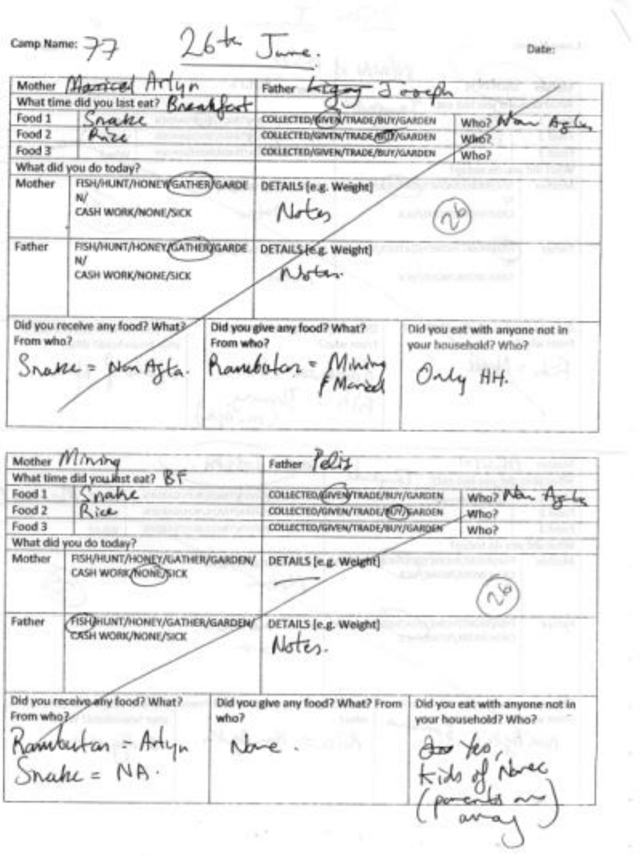
The critical questions here were numbers five and six. The others were primarily asked in order to solicit more accurate responses to questions five and six. This was necessary because some people would either have forgotten who they had shared with, or were shy to say so. The answers to questions 1-4, in addition to my own observations of food sharing in camp during the day, allowed me to ask more specific questions such as '*did you give any of that octopus to anyone?*' and '*who gave you the shells you had this afternoon*?'. Questions 1 and 2 also proved useful in providing a dataset on meal composition. When asking these questions in the evening, we tried to do so at the time when people were eating their evening meals. In total, I was able to collect data on the composition of 831 meals across seven camps.

As with all ethnographic fieldwork it is worth considering what impact the presence of researchers may have on the phenomenon being investigated (Atkinson & Hammersley 1994). There are two main ways in which my presence may have influenced food sharing. Firstly, interviewing individuals about food sharing every evening could potentially serve to reinforce norms relating to sharing or cause individuals to reflect on their food sharing more than they might usually do. Secondly, myself and the other members of the research team would frequently be offered food by the Agta and had ourselves bought a large amount of food into camp. To counter these potential problems, I aimed to conduct interviews as privately as possible, did not buy or take shares of food from the Agta, and gave gifts of food only once we were leaving camp. At all times we aimed to be self-sufficient, not relying on the Agta for food. Although these ideals were occasionally compromised to avoid offense to to help families in need, I believe that, overall, the data represent an accurate picture of Agta food sharing.

As discussed in section 2.4, I estimated the weight and calorific value of all food packages entering camp. Although my food sharing observations and interviews allowed me to identify the households to which these food packages were distributed, in most cases I have no estimates of the size or calorific content of individual household shares. My food sharing dataset, therefore, consists of counts of the number of food shares exchanged between each dyad of households.

Table 2-4: Summary of food sharing data collection locations. * Due to high mobility of household, camp composition often fluctuated during each study period.

Camp (Map Code)	Approx. number of households*	Observation days	Methods employed
Diago (66)	14	26	Observational & daily interviews
Diabbut (84)	6	13	Observational only
Simento (54)	4	8	Observational only
Kanaipang (74)	18	14	Observational & daily interviews
Didikeg (67.2)	7	24	Observational & daily interviews
Dipaguiden (67.1)	6	24	Observational & daily interviews
Diambarong (77)	5	9	Observational & daily interviews
Dipagsangan (79)	7	11	Observational & daily interviews



Camp Name: 77 26th June. Date:

Mother Maricel Artyn		Father Liggy Joseph	
What time did you last eat? Breakfast			
Food 1	Snake	COLLECTED/[✓ GIVEN]/TRADE/BUY/GARDEN	Who? Non Agta
Food 2	Rice	COLLECTED/GIVEN/TRADE/[✓ BUY]/GARDEN	Who?
Food 3		COLLECTED/GIVEN/TRADE/BUY/GARDEN	Who?
What did you do today?			
Mother	FISH/HUNT/HONEY/[✓ GATHER]/GARDEN/ CASH WORK/NONE/SICK	DETAILS [e.g. Weight] Notes	(26)
Father	FISH/HUNT/HONEY/[✓ GATHER]/GARDEN/ CASH WORK/NONE/SICK	DETAILS [e.g. Weight] Notes.	

Did you receive any food? What? From who?	Did you give any food? What? From who?	Did you eat with anyone not in your household? Who?
Snake = Non Agta.	Rambutan = Mining & Maricel	Only HH.

Mother Mining		Father Peliz	
What time did you last eat? BF			
Food 1	Snake	COLLECTED/[✓ GIVEN]/TRADE/BUY/GARDEN	Who? Non Agta
Food 2	Rice	COLLECTED/GIVEN/TRADE/[✓ BUY]/GARDEN	Who?
Food 3		COLLECTED/GIVEN/TRADE/BUY/GARDEN	Who?
What did you do today?			
Mother	FISH/HUNT/HONEY/GATHER/GARDEN/ CASH WORK/[✓ NONE]/SICK	DETAILS [e.g. Weight] —	(26)
Father	[✓ FISH]/HUNT/HONEY/GATHER/GARDEN/ CASH WORK/NONE/SICK	DETAILS [e.g. Weight] Notes.	

Did you receive any food? What? From who?	Did you give any food? What? From who?	Did you eat with anyone not in your household? Who?
Rambutan = Artyn Snake = NA.	None.	Yes, kids of Norec (parents are away)

Figure 2-9: Example of a food sharing data collection sheet, completed in Diambarong, Didian, June 2014. Details are provided on the individuals in the household, the composition of their most recent meal, the food they had produced that day, and the food they had given to or received from other households.

2.5 Computational modelling

In chapters four and five of this thesis I present the results of agent based models. Agent based models (ABMs) are computational simulations that allow for the exploration of social and evolutionary dynamics (Miller & Page 2009; Page 2008; Gilbert 2008). In an ABM, a system is seen as a collection of independent decision-making agents who interact both with each other and with their environment. Typically, each agent is given a predetermined set of rules which govern how they will behave in relation to the environment and to other agents. Recent advances in computing also make it possible for ABMs to incorporate sophisticated computational learning techniques and neural networks (Bonabeau 2002).

The major benefit of ABMs is that they are able to capture emergent phenomena. In other words, they allow us to explore how changes in decision making at the micro or individual level can result in patterns at the macro or societal level. This is especially important where emergent phenomena can result in outcomes opposite to those desired by individual agents. This is provided useful for the exploration of scenarios in which intuition alone may be a poor guide to group-level dynamics such as pedestrian and traffic movement (Helbing et al. 2001), flows of crowds in panic situations (Helbing et al. 2000), stock markets (Palmer et al. 1994), and company organisation (Prietula et al. 1998). ABMs also have the advantage of easily incorporating differences in behaviour between individuals and nonlinear individual behaviours such those contingent on a threshold being met (Bonabeau 2002).

Conceptually, ABMs are well suited for behavioural ecologists who also see human behaviour as contingent on our social and environmental context and who seek to explain group level phenomena as the product of individual level decision making (in behavioural ecology, this is known as *methodological individualism* - see section 1.2 for further discussion). ABMs have been used to great effect in hunter-gatherer behavioural ecology to explore, for example, demography (White 2014), the effect of 'walking-away' on cooperation (Lewis et al. 2014), and the transition from foraging to farming (Gallagher et al. 2015). On a pragmatic level, ABMs may also be more tractable than analytical models for researchers who are familiar with statistical modelling software but without a background in mathematics. As Page (2008, p2) says, "agent based models occupy a middle ground between stark, dry rigorous mathematics and loose, possibly inconsistent descriptive accounts".

Agent-based modelling is also easily amenable to modelling evolutionary dynamics, with agents reproducing and passing genes to the next generation (e.g. Rasteiro et al. 2012). Where these 'genes' govern how the agents make decisions, the evolutionary dynamics of behavioural strategies can be modelled. While analytical solutions may be able to prove that an equilibrium exists in behavioural strategies (such as the equilibrium between aggressors and pacifists in the famous 'Hawk-Dove' game (Smith 1982; Smith & Price 1973)), this is not the same as showing that such an equilibrium can emerge and be maintained.

In this thesis I present the results of two agent-based models. Both were created using the open source 'R' software (version 3.1.1) (R Core Team 2014) and are computationally thrifty enough to be run on a standard PC.

Chapter 3: The Palanan Agta

3.1 Chapter Summary

In this chapter I provide an ethnographic account of the Agta hunter-gatherers of the northern Philippines – a population of hunter-gatherers with whom I lived and conducted fieldwork in 2013-14. I provide quantitative and qualitative data on demography and health, subsistence and economy, and social organisation. In doing so, I hope to provide not only the ethnographic background required to contextualise findings reported in the remainder of this thesis but also to make a valuable contribution to the wider anthropological literature on the Agta.

3.2 Situation

Island Southeast Asia is not necessarily a region that people immediately associate with hunter-gatherers. In fact, the vast majority of the 350 million inhabitants of maritime southeast Asia are the descendants of agriculturalists who expanded into the region at least 4,000 years ago as part of the Austronesian expansions out of Taiwan which eventually resulted in the most geographically dispersed language family in the world, ranging from Madagascar to Easter Island (Gray & Jordan 2000; Currie et al. 2010). Nonetheless, across southeast Asia are a number of indigenous hunting-and-gatherer populations including the Batek of southern Malaysia (Endicott 2008), Maniq of southern Thailand (Kricheff & Lukas 2015), Onge and Jarawa of Andaman Islands (Pandya 1999), and the Agta, Aeta, Ata, and Batak of the Philippines (Shimizu 2001; Headland 1984; Rai 1985; Griffin 1996) (see Figure 3-1). Although the genetic history of these peoples are still to be fully understood (Lipson et al. 2014; Jinam et al. 2013; Migliano et al. 2013), they may be descendants of a much earlier population expansion into the region up to 40,000 years ago. Due to their striking phenotypic similarities including small body size, curly hair, and dark skin (Migliano et al. 2007; Stock 2013; Stock & Migliano 2009), these populations have been described collectively by the Spanish term 'Negrito' (Endicott 2013; Higham 2013), a term which remains in use despite its derogatory connotations, largely for want of a better alternative.

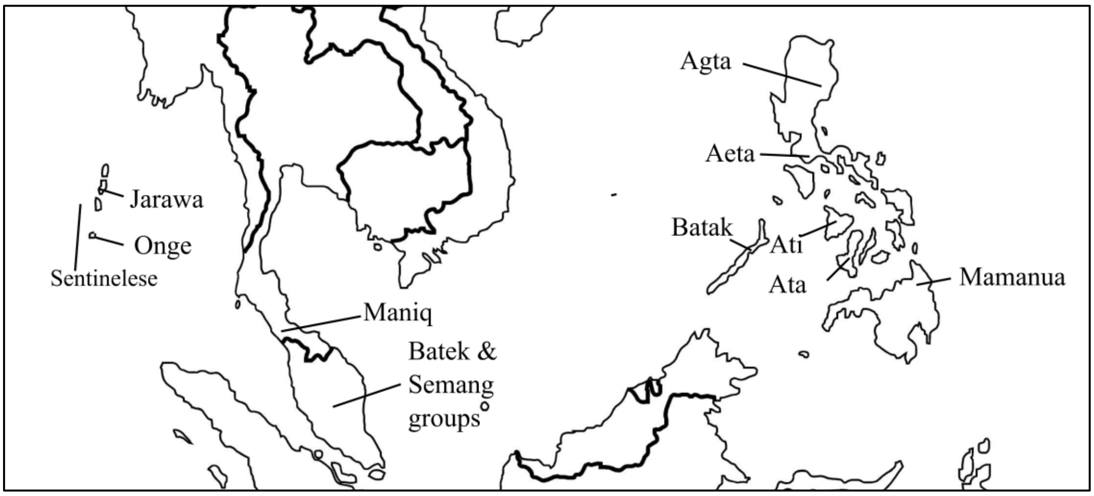


Figure 3-1: Location of contemporary SE Asian 'Negitro' populations.

The Philippine Negritos

The Philippine archipelago is composed of over 7,000 islands – with two main large islands – Luzon in the north and Mindanao in the south. While representing only a small fraction of the total population of the Philippines, Negrito populations are distributed widely across the country (see map Figure 3-2). The two largest groups are the Agta and Aeta who live on Luzon and, according to number around 10,000 and 15,000 people respectively (all population estimates are as reported by Reid (2007:7)). Although the Agta are less numerous than the Aeta, they occupy a much larger geographic range of over 700km. The Aeta, in contrast, are concentrated around Mount Pinatubo. Understandably, many Aeta were displaced by the eruption of Pinatubo in 1991

(Shimizu 2001). Also on Luzon live three smaller groups - the Atta (1,500 people) and Alta (650 people). Groups outside of Luzon include the Batak of Palawan (~400 people) and Mamanua of Mindanao (~1,000 people), and the Ati and Ata of Panay and Negros (both <1,000 people) (see Figure 3-2 for locations).

The total population of Filipino Negritos numbers around 31,000 – less than 0.05% of the population (Early and Headland 1998, p4). Early and Headland (1998) estimate that this population has declined in both absolute and relative terms in the last 400 or so years from a population of around 100,000 in 1600 which would have represented about 10% of the population of the Philippines, estimating from Spanish colonial records. All the contemporary groups are thought to have had historic trade links with farming populations, as evidenced by their adoption of Austronesian languages (Headland 1986; Reid 1987). Linguistic studies suggest that the languages spoken by Negrito populations of the Philippines are no more closely related to each other than the languages of non-Negrito Filipinos (Headland 1986).

Figure 3-2: Map of the Philippines with the approximate locations of Negrito populations. The long coastal range of the Agta in the Luzon corresponds to the length of the Sierra Madre mountain range which separates the Pacific coast of Luzon from the rest of the island.

The Agta

Of the Negrito foraging populations of the Philippines, by far the most engaged in foraging are the Agta, with whom I conducted ethnographic fieldwork in 2013 and 2014. During this time, I visited more than twenty Agta camps and met almost one thousand people. This represents almost the entire Agta population of Palanan, a small coastal municipality in the province of Isabela. Below, I provide a brief sketch of the Agta in Palanan, exploring their demography, livelihood strategies, social organisation, engagement with neighbours, and other subjects required to provide a balanced portrait and to contextualise the rest of this thesis.

The Agta live largely along the mountainous coastal regions of north-eastern Luzon and have a total population of around 10,000 individuals (Headland & Griffin 1997).

Although this region is of much lower population density than the rest of Luzon, the Agta still remain a small minority. In Palanan, for example, Minter (2008, p50) estimated that Agta make up 728 of the 15,317 inhabitants recorded in 2000-2005 (just under 5% of the total population). Although migrants from other parts of Luzon are increasing the non-Agta population of this coastal region, living alongside farmers is something the Agta and their ancestors may well have been doing for at least 3,000 years, and many Agta families have longstanding trade relationships with farming families (Headland et al. 1989; J. Peterson 1981; Peterson 1978a).

The most detailed anthropological, demographic, and linguistic research with the Agta has been conducted by Headland (Headland & Griffin, 1997; Headland et al., 2013; Headland, 1990), Rai (Rai 1982; Rai 1990; Rai 1985), Griffin and Estioko-Griffin (Griffin 1996; Griffin P. Bion 1997), Persoon, and Minter (2008, 2009), Warren and Jean Peterson (Peterson 1978b; J. Peterson 1981; W. Peterson 1981), and Reid (Reid 1994; Reid 1987). While all of these researchers spent some time in Palanan, it was not a focal study region for all. The most recent and detailed work in Palanan, the municipality where the majority of my research was conducted, was by Tessa Minter (Minter 2008; Minter 2009; Minter & Ploeg 2014; Persoon et al. 2004) who has provided a wealth of data on the Palanan Agta and whose PhD thesis and papers were an invaluable resource in the planning of our fieldwork.

Palanan is a coastal municipality currently unconnected by road to the interior (although plans to build a road have been on the horizon for some time). Indeed, Palanan is so isolated from the rest of Luzon that the locals describe the land to the other side of the Sierra Madre range as the ‘mainland’. Despite its isolation from the rest of Luzon, Palanan and the Palanan Agta have not escaped involvement in the major political events of Filipino twentieth century history. For example, Palanan has seen the last stand of the first Philippine republic in the American-Philippine war (1899-1902), the retreat of the Japanese army in 1945 (an event some elderly Agta claim to remember) and, most recently, Army operations against communist guerrillas of the 'New People's Army' (NPA) who still operate in the region.

The municipality of Palanan falls within the boundaries of the 'Northern Sierra Madre Natural Park' (NSMNP), the largest protected area in the Philippines and an area of important biodiversity (Abate 1992). It was established in 1997 and is governed by the Department of Environment and Natural Resources (DENR). Although the Agta are given special provision within the park (Persoon et al. 2004), it complicates the process by which they can be given an Ancestral Domain Title in the area (Minter & Ploeg 2014). The small town marked as 'Palanan' in Figure 2-1, and locally known as 'Bayan' (Tagalog: *centre*) is the largest town in the NSMNP and is the point of entry into the region either by sea or air.

3.3 Demography and health

Based on the ageing protocols described in section 2.3.2, we were able to produce age estimates for our sample of 914 Agta and to use these to produce a population pyramid. The Agta have a typical natural fertility and 'pre-transition' population pyramid (Table 3-1,

Figure 3-3). Just over half of the total population of our sample are under the age of 15 years, a result consistent with Minter's (2008, p48) sample of 1,725 Agta living in the NSMNP. Our sample includes a noteworthy sex bias, with 417 females to 497 males, a male to female sex ratio of 119:100. Among people of reproductive age (here defined as 20-40years), however, the sex ratio is balanced, with 103 men to 103 women.

Table 3-1: Population of the Palanan Agta* by age and sex of 914 individuals. *These data also include those individuals we met in Disocad, Divilican in 2013 who, despite living in southern Divilican, speak Paranan Agta.

Age	Male		Female		Total		
	Count	*%*	*Count*	*%*	*Count*	*%*	*Cum %*
<5	104	20.9	75	18	179	19.6	19.6
5-10	81	16.3	73	17.5	154	16.8	36.4
10-15	78	15.7	61	14.6	139	15.2	51.6
15-20	46	9.3	44	10.6	90	9.8	61.4
20-25	43	8.7	46	11	89	9.7	71.1
25-30	27	5.4	20	4.8	47	5.1	76.2
30-35	16	3.2	19	4.6	35	3.8	80
35-40	17	3.4	18	4.3	35	3.8	83.8
40-45	16	3.2	14	3.4	30	3.3	87.1
45-50	17	3.4	13	3.1	30	3.3	90.4
50-55	20	4	21	5	41	4.5	94.9
55-60	9	1.8	6	1.4	15	1.6	96.5
60-65	8	1.6	1	0.2	9	1	97.5
65-70	10	2	2	0.5	12	1.3	98.8
70+	5	1	4	1	9	1	99.8
Total	497	100	417		914	100	

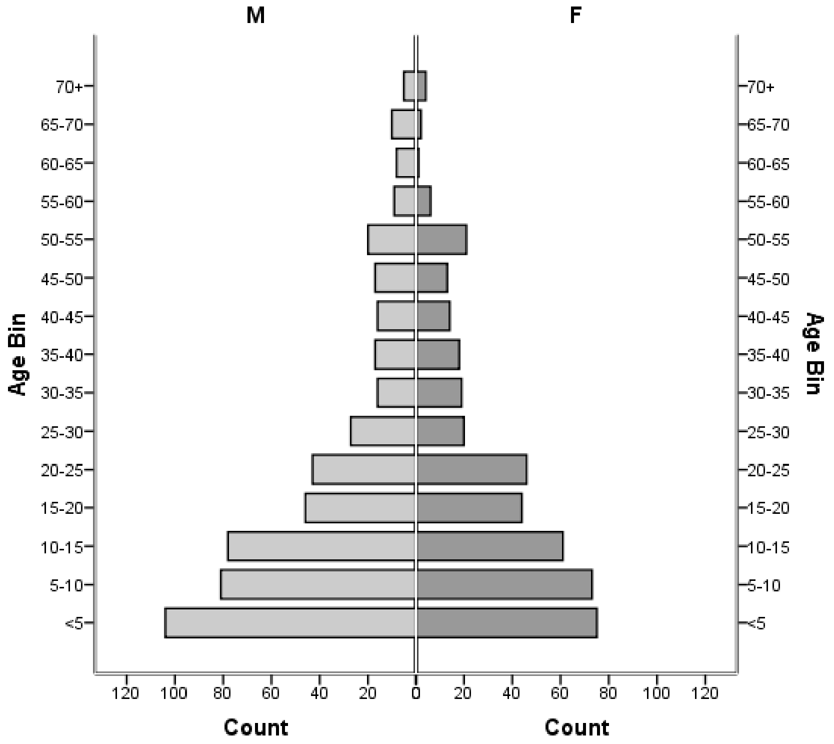


Figure 3-3: Population pyramid of the 914 Palanan Agta listed in Table 3-2 above. Light grey bars on the left represent males, dark grey bars on the right represent females.

Our population estimate for those Agta living in Palanan is 914. Although this includes one community from Divilican, we did potentially miss an equivalent number of Agta households in Palanan from one part of the coast we did not visit. This compares to a population estimate of 728 for the year 2000 (Minter and Ranay, 2005), and 669 in 1990 (Rai, 1990;176). It is hard to say whether this population change has resulted from changes in fertility and survivorship or from mobility between Palanan and neighbouring municipalities. It is clear, however, that the population of Agta in Palanan, as in the region more generally, has declined in relative terms as a result of net migration into the region from Ilocano and other groups from west of the Sierra Madre. According to Minter's (2008,51) figures based on National Statistics Office (NSO) figures, the population of Palanan in 2000 was 15,317 non-Agta and 728 Agta (a total population of

16,445). According to other NSO figures collated by Minter, this total population was up from 13,220 in 1995, 8,930 in 1975, 5,599 in 1960, and 2,410 in 1918. According to National Economic Development Authority (NEDA) figures, the population of Palanan is expected to double in the twenty years from 2010 to 2030 to 31,908 (NEDA 2006; Minter 2008).

3.3.1 Fertility

The Agta are a 'natural fertility' population with high fertility rates. I explored the sample of women who are (*a*) over the age of 45 years, and (*b*) with whom we conducted a reliable reproductive history interview - a total of 40 women. On average, these women had 7.4 pregnancies (SD = 2.9), of which an average of 6.9 live births had resulted (SD = 2.5) (see Figure 3-4 for full distribution), and 5.0 living offspring remained alive at time of interview (SD = 2.2). Of these 40 women, one had never given birth and two had had only one child. Of those who had given birth at least twice, the mean age of first birth was 22.9 years (SD = 4.8), mean age of last birth was 40.7 years (SD = 5.9), and the mean time between first and last birth was 17.9 years (SD = 6.1).

Of the equivalent sample of 43 men over the age of 45 years, the data was fairly similar. Men reported having fathered an average of 6.3 live births (SD = 3.0) (see Figure 3-4) and had an average of 4.6 living children (SD = 2.5). Only one man had never had a child. Men reproduced slightly later with a mean age of first birth of 24.5 years (SD = 6.0), mean age of last birth of 42.0 years (SD = 8.8) and with a mean period of 17.5 years (SD = 8.0) between first and last birth, similar to that reported for women. The variance in male reproductive success in this sample is, therefore, only slightly greater than seen among women, as expected among a monogamous population. That men stop reproducing at a similar age to women is a pattern seen among other contemporary foragers (Vinicius et al. 2014).

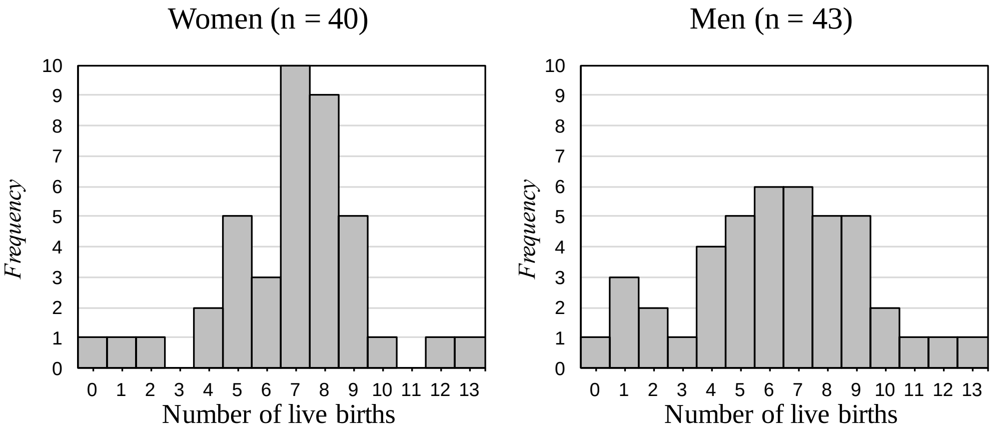


Figure 3-4: Histograms of number of live births for women (left) and men (right) who are (a) over the age of 45 years, and (*b*) with whom we conducted a reliable reproductive history interview.

3.3.2 Mortality

The Agta are said to have one of the lowest life expectancies at birth of any population in the world, with Early and Headland (1998) estimating a life expectancy of 25 years among the San Ildefonso Agta in Casiguran. Although Minter (2008) is of the opinion that the Agta living in the NSMNP have better health than those in San Ildefonso/Casiguran where Early and Headland worked, it is still poor in absolute terms. Minter (2008) estimated that 137 of 1,000 Agta babies die within a year, that 283 of 1,000 die before they are five, and around one in three die before they reach puberty.

Through our genealogical interviews, we were able to establish the reported cause of death for 160 Agta. This includes both adults and children though is not necessarily a representative sample. Causes of death are also difficult to ascertain through interview, especially since both the person being interviewed and the translator are unfamiliar with the ‘western’ medical names for conditions that we were ultimately trying to establish. Those which were known were often given as a catch-all. For example, a whole range of respiratory infections including TB and pneumonia were commonly described as asthma. The causes of death in our sample of 160 deaths (see Table 3-2) are not dissimilar to those reported by Minter (2008) and by Early and Headland (1998: 104) in so far as infectious diseases are the major cause of death (Early and Headland (1998) estimate that 86% of deaths in San Ildefonso can attributed to infectious diseases). Sadly, respiratory infections, measles, malaria and diarrhoea are all common among the Agta, as are other gastro-intestinal and parasitic infections. In a medical study conducted by Abigail Page (*in prep*), the majority of individuals had multiple parasitic infections. The rate of infectious disease is likely due in part to the drinking of untreated water contaminated by farming communities upstream, the absence of sanitary facilities, and lack of immunization. Outside of infectious disease, maternal deaths are sadly common (Early and Headland (1998) reported 352 maternal deaths per 10,000 live births, one of the highest known maternal mortality rates). Accidental deaths are also relatively common – especially drowning, either at sea or during typhoons. Homicides are rare but not unheard of.

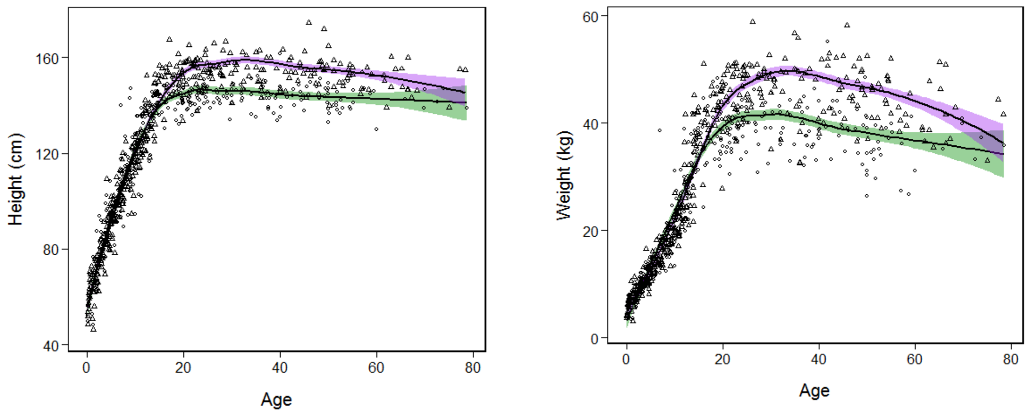
Table 3-2: Causes of death for 160 Agta as recorded in our genealogical interviews.

	< 1 year		1-5 years		6-15 years		> 15 years		Total		
	F	M	F	M	F	M	F	M	Count	%	Cum %
Unknown/Conflicting	9	7	3	3	1	4	0	0	27	16.9	16.9
Respiratory	10	3	1	3	1	3	2	1	24	15.0	31.9
Measles	2	2	2	8	3	4	1	0	22	13.8	45.6
Malaria/Fever	1	4	1	4	5	2	1	1	19	11.9	57.5
"Subi-subi"	7	6	3	1	0	0	0	0	17	10.6	68.1
Accident	0	1	1	5	2	2	1	2	14	8.8	76.9
Gut	0	3	2	2	1	2	0	0	10	6.3	83.1
Infection	4	2	0	0	0	0	0	0	6	3.8	86.9
Hepatitis A	0	0	1	2	2	0	0	0	5	3.1	90.0
Diarrhoea	1	0	2	0	0	0	0	0	3	1.9	91.9
Childbirth	0	0	0	0	0	0	3	0	3	1.9	93.8
Witchcraft	0	1	0	1	0	0	0	1	3	1.9	95.6
Head/Stroke	0	0	0	0	0	0	1	1	2	1.3	96.9
Ulcer	0	0	1	0	0	0	0	0	1	0.6	97.5
Body swelling	0	0	0	0	1	0	0	0	1	0.6	98.1
Heat	0	0	0	0	0	1	0	0	1	0.6	98.8
Alcohol related	0	0	0	0	0	1	0	0	1	0.6	99.4
Homicide	0	0	0	0	0	0	0	1	1	0.6	100.0
Total	34	29	17	29	16	19	9	7	160		

3.4.3 Anthropometric data

As outlined in above, we collected anthropometric data during the ‘census’ phase of our fieldwork. Compared to non-Agta Filipinos, the Agta are particularly small, a trait which they share with many hunter-gatherer populations (Migliano et al. 2007; Perry & Dominy 2009; Migliano 2005). By some standards, the Agta have a ‘pygmy’ phenotype, potentially as a consequence of an accelerated life-history strategy (Stock & Migliano 2009). Among the individuals included in our sample, the mean height of adult women (n = 156) was 143.5cm (SD = 4.72), their mean weight was 38.7kg (SD = 4.75), and mean BMI was 18.8 (SD = 2.1). For adult men (n = 162), mean height was 153.6cm (SD = 6.3), mean weight was 45.4kg (SD = 5.2), and mean BMI was 19.2 (SD = 1.5).

(a) Height by age *(b) Weight by age*



(c) Height vs. weight *(d) Adult BMI by age*

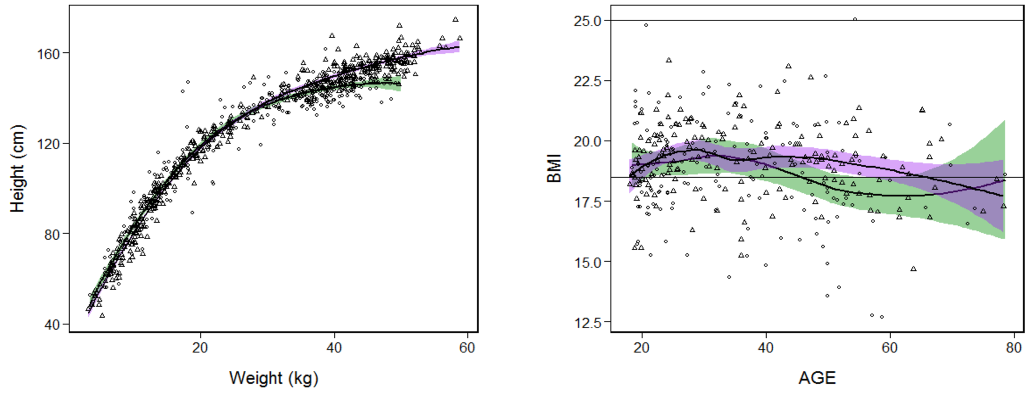


Figure 3-5: Anthropometric data of (*a*) weight by age, (*b*) height by age, (*c*) height vs. weight, and (*d*) adult BMI by age. Lines are loess lines plus SE where green is female and purple is male. Triangles are males, circles are females. The two horizontal lines in panel

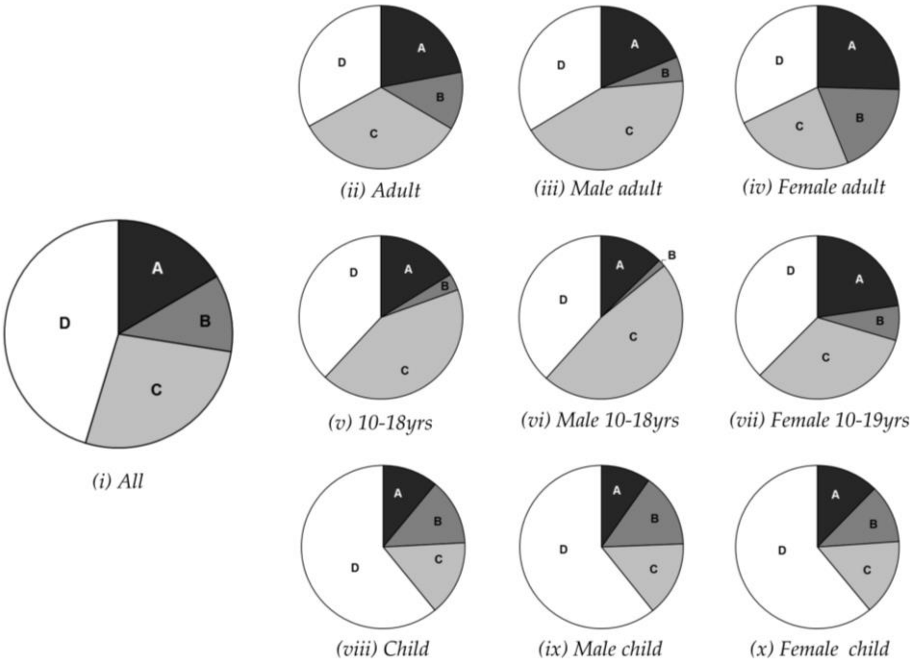
(*d*) which intercept the y-axis 18.5 and 25 represent the thresholds below or above which individuals are regarded as 'underweight' and 'overweight' respectively.

3.4 Subsistence and Economy

3.4.1 Time budgets

As outlined in section 2.3.3, one of the core data collection protocols in the 2014 fieldwork season involved conducting 'camp scans' in which we recorded, at regular intervals through the day, what activities individuals were engaged in, and who they were in close proximity too. Although we recorded only four scans a day, over the course of several days we could build up a reasonable number of data points for each individual. When aggregated across age and sex classes, we can begin to build up a picture of changes in 'time budgets' through the life course for men and women. Time is one of the central constraints in behavioural ecology and time budget data has proved a useful tool for understanding the relationships between group size and ecological constraints among primate societies (Dunbar & Lehmann 2014; Dunbar et al. 2009; Korstjens et al. 2010; Dunbar 1993).

In our camp scans, we recorded four main classes of activities. Group A corresponds to domestic activities, group B to childcare activities, group C to foraging and non-household economic activities (including wage labour and trade), and group D to social activities, rest, and sleep (see section 2.3.3 for more details on data collection). We collected only daytime data. The summary data in Figure 3-6 and in Table 3-3 provide a breakdown of activities by sex across the following age groups: children (<10years), older children and young adults (10-18years), and adults (>18years). Children (pie charts *vii* to x in Figure 3-6), spend around 60% of their time playing, sleeping, and relaxing, and show no sex differences in this. Much of the time that the children are recorded as engaging in childcare is as the recipient of it (i.e. infants being held or breastfed), although older children do actively care for infants. Among 10-18 year olds and adults, we see more of a sex difference in activity budgets emerging, with young men spending less time on childcare and more time on economic and foraging activities, although young women still spend more time foraging than engaged in childcare. These sex differences are even more pronounced among adults. Interestingly, however, group D activities (resting, socialising, relaxing, and playing) occupied a similar proportion of time for men and women, even though men were out of camp for a much large proportion of time. Both men and women spent around a third of their time doing these activities.



(ii) Adult (iii) Male adult (iv) Female adult

(i) All

(v) 10-18yrs (vi) Male 10-18yrs (vii) Female 10-19yrs

(viii) Child (ix) Male child (x) Female child

Figure 3-6: Time allocation budgets across all individuals (i), adults (ii-iv), 10-18 year olds (v-vii), and children (viii-x). Pie charts represent the proportion of camp scans in which individuals were taking part in the following activities: A) domestic, B) childcare, C) economic, and (D) socialising or resting.

Table 3-3: Time allocation data for male and female Agta of different ages (n = 386 individuals total). The activity categories are as follows: A) domestic, B) childcare, C) economic, and (D) socialising or resting.

			Activity type (% of time)			
	N individuals	N observations	A	B	C	D
Adult	169	4398	22.0	11.4	33.6	32.9
Male	89	2268	18.8	4.8	42.8	33.6
Female	80	2130	25.4	18.5	23.8	32.2
10-18yrs	69	1539	16.2	3.3	42.4	38.1
Male	41	1001	12.7	1.4	47.6	38.4
Female	28	538	22.7	6.9	32.9	37.5
<10yrs	148	4216	11.0	13.2	14.9	60.9
Male	81	2210	9.8	14.6	14.8	60.8
Female	67	2006	12.3	11.6	15.1	61.0
All	386	10153	16.5	10.9	27.2	45.3

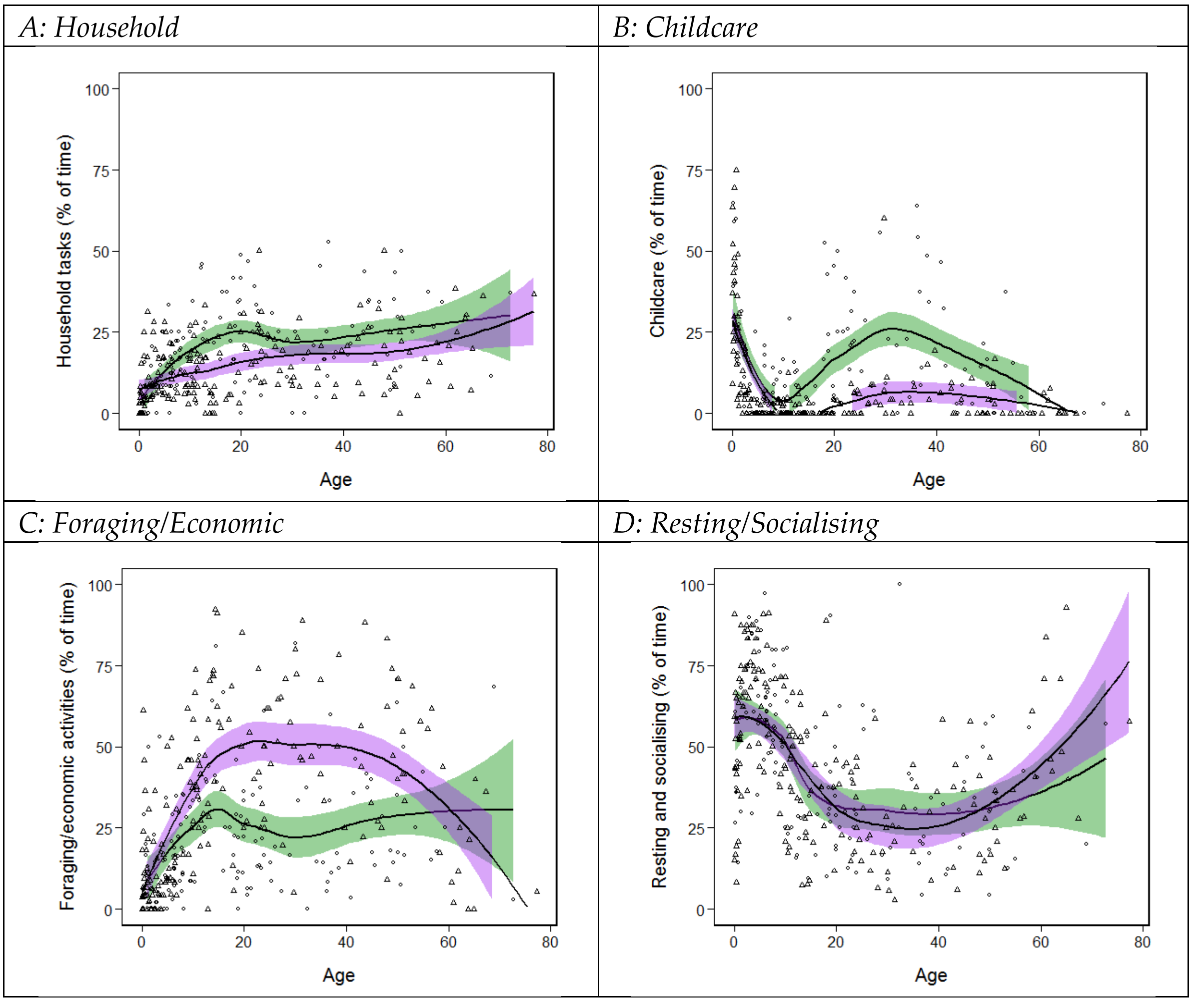


Figure 3-7: Activity budget data by age and sex. Lines are loess lines plus SE where green is female and purple is male. Triangles are males, circles are females.

As can be seen from the data in both Table 3-4 and Figures 3-4 and 3-5, there is a noteworthy difference in the amount of time than men and women spend foraging and on other out-of-camp economic activities (42.8% vs. 23.8% of total day time respectively). Although such a division of labour is typical of foraging societies in general (Kelly 2013; Ember 1975) there is, in fact, a clear inverse relationship between effective temperature and men's contribution to subsistence activities (Waguespack 2005; Hiatt 1970). In well-studied equatorial foraging populations such as the Hadza, Mbuti, and Ju/'hoansi, male contribution to the diet (in calories) has been estimated to be less than 50% (Hiatt 1970; Kelly 2013).

While differences may exist in the time spent foraging by men and women, this is not to say that there is a sex difference in the total amount of work done by men and women. Waguespack (2005) demonstrated that as female contribution to the diet declines, the time spent performing other tasks increases (such as weaving, basketry, pottery, firewood collection, and other domestic tasks). This also appears to be the case among the Agta – as the data in Table 3-4 show, while women spent significantly less time foraging than men, their overall 'resting' time was very similar to that of men (32.3% for women, 33.6 for men). Why, in general, should there be a division of labour between men and women? General explanations have focused on the incompatibility of childcare, pregnancy, and breastfeeding with hunting and the fact that, compared to hunting, gathering is more easily interrupted, is often done closer to camp, and rarely requires overnight stays (Brown 1970; Burton et al. 1977).

3.4.2 Freshwater foraging

All of the inland Agta communities in Palanan live in close proximity (<5mins walk) to the Palanan river or one of its tributaries. These cool mountain streams contain a number of fish species caught by the Agta. As Minter (2009) points out, fishing is seasonally dependent. During the summer months the cool mountain streams offer pleasant respite from the heat and are rarely of dangerous velocity. Fishing in the summer is often good fun, as well as an important part of subsistence. Trips sometimes last all day, with frequent breaks. Unlike many rivers in tropical forests, the water is often clear enough in the summer to see larger fish in mid-stream from the shore. During the cooler 'winter' months, however, the rivers swell greatly after heavy rain and become deep, murky, and fast.

The majority of freshwater fishing requires only a simple 'pana' spear made of a small sharpened metal spoke, rubber band and home-made goggles. When fishing at night or in deep and murky parts of the river, a waterproofed torch is used. The fishing returns from the rivers are not as great as from marine fishing, partly due to diminished fish stocks as a result of illegal dynamite and electro-fishing by non-Agta, and invasive species such as Nile Tilapia (*Oreochromis* Sp). As well as Tilapia, commonly caught freshwater fish species include Paleleng (Gobi; *Gobididae* sp.), Iget (Giant mottled eel; *Anguilla marmorata*), Mori (Largesnout goby; *Awaous melanocephalus*), Burukos (Celebes goby, *Glossogobius celebius*), and Banag (Mullet, *Mugilidae* sp). The Agta also collect Udang (Fresh water shrimp, *Macrobrachium lar*). Names are in Paranan. English and scientific species names are based on Minter (2008) and Linnebank (2001).

On four occasions during my fieldwork, I witnessed the occurrence of 'saret' fishing. Saret fishing involves around ten people fishing cooperatively. A saret is a long cord of vines and banana leaves which is dragged just below the river surface and spooks fish in such a way as to make them easier to catch. In order to make a saret, several thick vine leaves are tied together so that they are long enough to stretch across the river. The longest I saw was perhaps thirty meters long. A banana stem is then cut and the long onion-like layers are separated and cut into lengths of around a metre. These are then tied perpendicular to the vine at intervals of around a metre. At regular but more distant intervals, additional short vines are tied to the long vine at one end and to a small rock of maybe 500g-1kg at the other. From start to finish, this takes around an hour for two or three people to make. When fishing, the saret is dragged by two people on either bank. It does not physically trap the fish but creates a shadow and disruption to the water which causes them to swim away from it (I saw a saret used both upstream and downstream to equal effect). As many as ten people would fish behind the saret, using *pana* (elastic and an arrow) to catch fish. Men, women, and children were all involved often from across the community, although on one occasion an entire nuclear family (two parents and eight children) did this. People would be communicating the whole time saret fishing is taking place about the location of fish. Some people would stand further back, behind the fishers, throwing rocks and creating an additional scare for the fish.

With a sample of four occasions, I do not have the power to test whether this was a more effective form of fishing than lone spearfishing, but it certainly appeared to be so, especially the occasion where this technique was used to drive fish into a net – a trip that produced 31 fish with a total weight of 3.5kg in just over two hours. Although the saret must be weakened by use, I never saw one break and was surprised that something which took so long to make was discarded at the end of the fishing foray and not used again.

Figure 3-8: Making a *saret*, near Simento, March 2014.

3.4.3 Marine fishing/foraging

Unsurprisingly, the main marine foraging activity is fishing. Marine fishing is largely, although not exclusively, the domain of men and trips are, by and large, conducted alone or in pairs. Most commonly, homemade spear guns are used with a wooden shaft and handle, strong elastic band, and sharpened metal spear. Children tend to use a smaller handheld 'pana', as used in river fishing. Marine fishing requires men to be strong swimmers and divers and be able to hold their breath while diving for up to two minutes, an impressive feat of athleticism.

Marine fishing yields a much more diverse range of species than does riverine fishing. Goslinga (2009) conducted a survey of fish species among the Agta from Kanaipang and documented the use of more than 110 fish species. Although I did not ask the names of fish species returned from every fishing trip, I did so with regular enough frequency to get an impression of the more commonly caught species. These include Malabad (surgeonfishes; *Acanthuridae* sp), Malade (rabbitfish; *Siganidae* sp), Omipos (chubs; *Kyphosidae* sp), Mahagta (lined bristletoot; *Tenochaetus stratus*), Igat (Moray eel; *Gymnothorax eurostus*), Sahungen (Blue spine unicornfish; *Naso unicornis*), Mul-mul (wrassers; *Labridae* sp), Lapu-lapu (groupers; *Serranidae* sp), and Kugita (octopus (*Octopodidae* sp). Names are in Paranan. English and scientific species names are based on Minter (2008) and Goslinga (2009). Occasionally, turtles are caught although the Agta are wary of discussing this – hunting turtles is illegal in the Philippines. I saw, however, four turtles caught during the summer of 2014, and the number of turtle shells seen discarded just outside of camp suggested this was not uncommon. So far as I could tell, all were green turtles (*Chelania mydas*) although loggerhead turtles (*Caretta caretta*) are also caught, according to Minter (2008, p130).

In addition to fish, the inter-tidal coastal areas, particularly the coral flats along much of the Palanan coast, provide abundant resources at low tide including shrimps, lobsters, crabs, shells, molluscs and octopi. These are collected by hand or using knives or metal rods used to prize crabs, shells from rock or coral and to spear hiding octopi. Marine foraging groups usually have a broader participation than fishing trips and include women and children. In some cases, these foraging trips will take place on the coral flats adjacent to where men are spearfishing in the sea.

3.4.4 Hunting

The Agta hunt a large number of species. Mammalian species include the Philippine warty pig (*Sus philippinensis*), brown deer (*Cervus mariannus*), long tailed macaque (*Macaca fascicularis*), and various fruit bat species (*Pteropodidae* sp). They also hunt birds including hornbills (*Buceros hydrocorax* and *Penelopides panini),* civits *(Paradoxurus hermaphroditus and Viverra tangalunga*), and various pigeons (*Columbidae* sp.) as well as monitor lizards (*Varanus salvator* and *Varanus olivaceus*) and, occasionally pythons (*Python reticulates*) (Minter 2008; Headland & Greene 2011) (Species names from Minter (2008, p102)). With the exception of the python, which 25% of Agta men claim to have been attacked by (Headland & Greene 2011), and to some extent the warty pig, these are not dangerous species to hunt. A variety of tools are used in Agta hunting practices. Largely, hunters use bow and arrows, self-made match guns, airguns, snares, and dogs.

Generally, hunting trips take longer than fishing trips and are less likely to be solitary trips (see Table 3-4). Most hunting trips are day-trips from camp although the party might spend at least an hour or so walking deep into the forest before beginning hunting in earnest. During 2014, some of the more westerly communities (those with kinship ties in San Mariano on the other side of the mountains such as Diabut and Dipagsangan) would go on week-long hunting trips in which they would set traps on the way to San Mariano, visit family, and check their traps on the way back, hunting and fishing as they went. Hunting occurs much more often during the wet season (Minter 2008), especially among the coastal groups who did very little hunting during the dry season, as my data attests too. The gender division in hunting is an important issue to note. Famously, Estioko-Griffin and Griffin (Estioko-Griffin & Griffin 1981; Estioko-Griffin 1985) reported female Agta hunting in Diangu. However, Griffin and Griffin (2000) note that this practice was rare by 1985. Minter (2008) heard no current reports of female hunting and neither did we. Unlike fishing, which is generally learnt through trial-and-error learning with age peers, boys are actively brought along by men on hunting trips (Hagen 2015).

Figure 3-9: Buting Fernandez removing the skin of a lizard (*Varanus* sp.) prior to cleaning using fire and a knife. The lizard was caught by the dogs of Dede Alvarez while in the forest west of Diabut.

3.4.5 Tubers, honey, and other forest foods

Tubers

The extent to which the Agta and other tropical-rainforest foragers exploit wild tubers or USOs (underground storage organs) has been a key part of the 'wild yam' debate about whether foragers could survive in tropical rainforest without being able to trade with farmers for domesticated carbohydrates (Headland 1987b). Although wild tubers are not consumed as often as domesticated rice bought or traded with farming neighbours, I would agree with Minter (2008, p151) that they represent an important part of the diet, providing an alternative source of carbohydrates either simply to diversify the diet (they are quite tasty both boiled and roasted) or as a necessary alternative when rice in unavailable or expensive, as it was in February to April 2014 after a poor rice harvest in Palanan. Minter (2008, p151) lists eight species of tubers listed by Rai (1982) and Allen (1985) as exploited by the Agta. Of these, the two I witnessed being consumed were Ilos

(*Dioscorea filiformis*) and Sigig (*Dioscorea cf esculenta*). I only, however, witnessed the collection of Ilos, the species said to be tastiest but also the deepest in the ground. I only ever saw women collecting Ilos and they did so using a knife and *sag-sag* – a long bamboo pole split at the end which, when forced into the ground from a crouching position, can pick up large clods of earth. Ilos plants have surprisingly few leaves above ground and a single long root connecting tubers and leaves.

Honey

Honey is, in many ways, the ultimate prize the forest can offer. It represents a sweet, dense, and highly calorific resource which often comes in very large package sizes. It is, however, difficult to obtain. Firstly, it is difficult to find. Sometimes dedicated honey scouting trips will occur while other times honey will be noticed when traveling through the forest or collecting other forest products. If a small amount is discovered, it may be collected alone. Typically, however, the location will be remembered for the future when a group trip can be organised to collect it. Honey is a demanding resource to collect. First, one or two bails of leaves must be tied up and lit to provide the smoke needed to partly protect the climber from bees. One or two men will then climb the tree (sometimes as high as 10 meters) carrying the smoking bale. Once at the nest they will almost certainly be stung many times despite the smoke. They will then use a machete to either cut off the branch the honey is on or to take pieces of honey comb and place them in a purpose-made pack on their backs. They then make their way down the tree quickly and, on some occasions, run from angry bees.

The Agta collect three kinds of honey: giyaw, pitukan, and paleg (Rai, 1982;93). Attributing who is seen as the producer of honey is difficult. After seeing the bravery, prowess and effort required by men to get honey I had assumed that they would be seen as the 'producer' by others, if such a status is given. When I asked a lady in Dipagsangan whether Jorning (the man who had climbed the tree for honey) had given her a share she insisted that it was her who had given some to him, since she was the one to originally see the honey in the forest to begin with.

Figure 3-10: Small part of a large honey haul. Forest near Dipagsangan, June 2014.

Other forest foods and resources

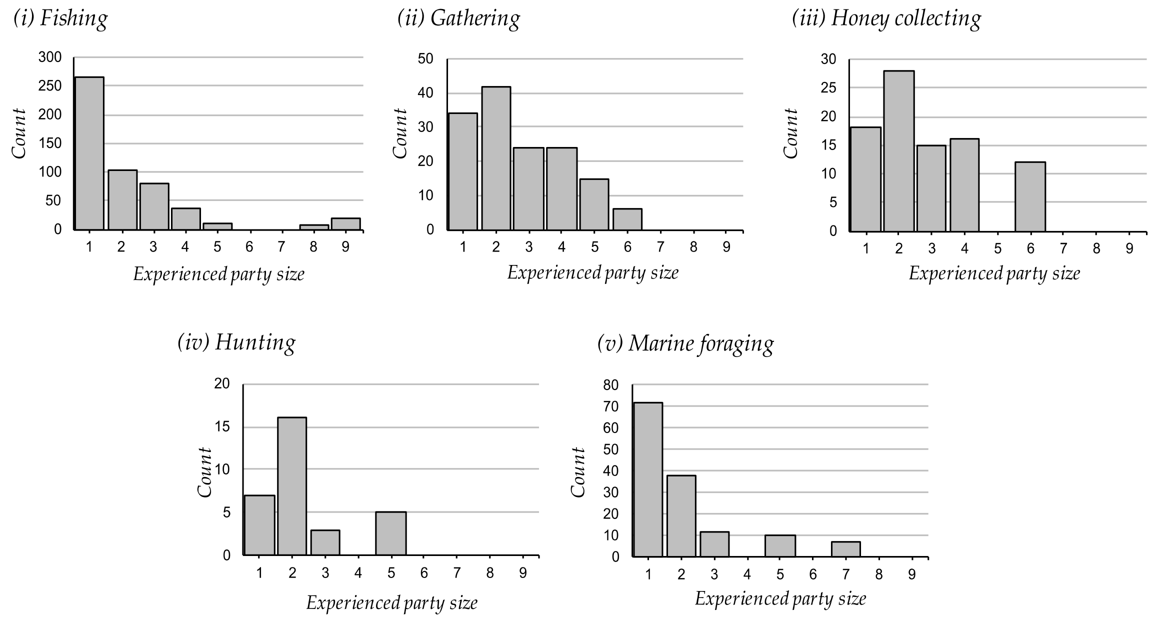
In summer, Rambutan trees (*'Bulala'* in Paranan) yield vast amounts of sweet and easy to extract fruits. Some trees provide upwards of 25kg of fruit, one quarter of which was rambutan flesh, by my estimates. Rambutan fruits would often provide a quick snack when out collecting honey or hunting but were also collected *en masse* when whole trees came into fruit. Generally, rambutan was not collected according what would be assumed to be a 'sustainable' strategy, with whole trees often being felled using a machete (which often took quite some time). Perhaps this was not so unsustainable in the long-run, however, since, during rambutan season, trails in the forest would be strewn with the large pips of rambutan fruits. Most Agta chew betel nut (*Areca* sp) which they collect wild in the forest, usually opportunistically. Many people will carry a pouch with betel nut plus the litlit leaves (*Piper* sp) and a white powder of lime from crushed mollusc shells which they chew in combination with it. Together, these can produce a powerful light-headedness.

3.4.6 Foraging group size

As might be expected, there were differences in duration, party size, and calorific returns between the main foraging types explored above. While fishing, gathering, and marine foraging all returned food on more than 80% of trips, honey collecting and hunting were less successful, with 41% and 65% of trips returning food respectively (see Table 3-4). That said, honey collecting and hunting returned food packages of greater calorific value (see Table 3-4). Experienced group size for fishing, gathering, honey collecting, hunting, and marine foraging trips are provided in Figure 3-11. Experienced party size is a weighted mean, and more representative of individual experience. If a sample consisted of ten solitary foraging trips and one group trip of ten people, for example, the mean foraging group size would only be 1.82, whereas the mean experienced foraging group size would be 5.5.

Table 3-4: Descriptives relating to the number, success rate, mean calorific return, and duration of fishing, gathering, honey collecting, hunting, and marine foraging trips.

	N trips	N successful	Calorific return (successful trips) kcal±SD	Mean duration of trip (minutes ± SD)
Fishing	350	306 (87%)	1911±3460	219±350
Gathering	73	65 (89%)	2062±3017	109±121
Honey collecting	17	7 (41%)	5864±6677	347±135
Hunting	17	11 (65%)	4729±6750	358±412
Marine foraging	98	79 (81%)	1602±1607	202±249


(i) Fishing

(ii) Gathering

(iii) Honey collecting

(iv) Hunting

(v) Marine foraging

Figure 3-11: Experienced group size for (*i*) fishing, (*ii*) gathering, (*iii*) honey collecting, (*iv*) hunting, and (*v*) marine foraging trips.

3.4.7 Non-foraging activities, resilience, and change

The Agta communities with whom I conducted detailed research in 2014 were all engaged in fishing, hunting, and gathering wild foods. Many of them, however, also engaged in more market integrated activities, such as smallholding, commercial foraging, and wage-labour (Griffin, 2012; Minter 2008). They also varied in their association with local farmers, with whom they trade forest products for rice. Although the extent of market integration is largely a function of proximity to farming or fishing villages, in some cases (such as at Diago (66) and Kanaipang (74)) evangelical missions had encouraged the community to build more permanent houses, churches, and, in the case of Diago, establish a communal garden.

As shown in Figure 3-12, camps differed in the extent to which they engaged in non-foraging activities. The data shown in Figure 3-12 are only available for those camps in which we conducted camp scans and represents the relative amount of time that individuals from that camp were engaged in each activity. Across the eight camps, non-foraging economic activities (brown shaded blocks in Figure 3-12) accounted for 27% of time in economic activities. In Simento, Dinipan, and Diabut, engagement in non-foraging activities was much higher than other camps. In Simento and Diabut, this is a reflection of the seasonal demand for labour during the rice harvest in late March and early April when we visited these camps. During the time in Dinipan, people were concentrating on gathering wild rattan in the forest to sell.

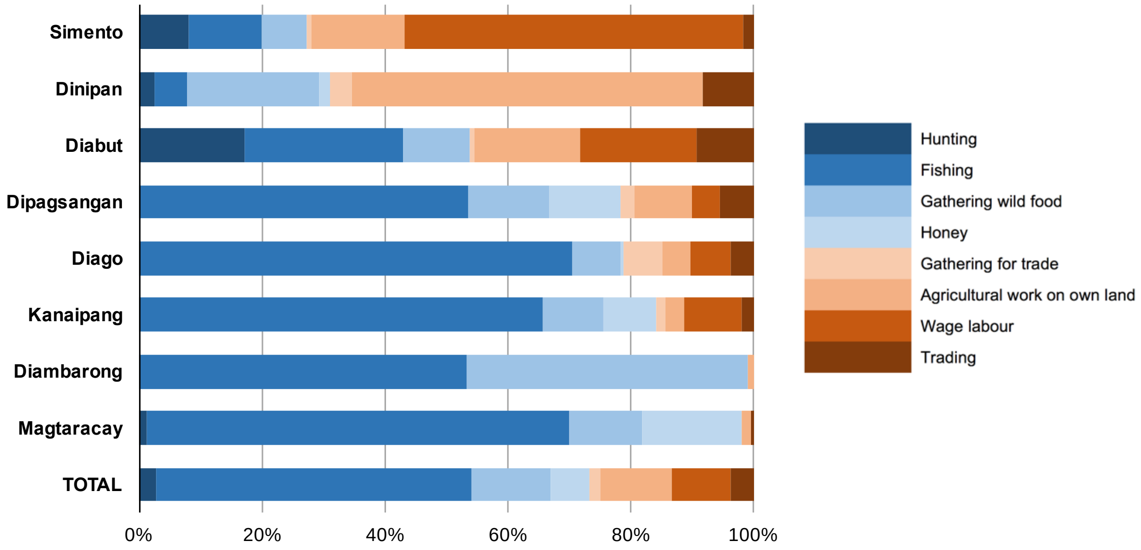


Figure 3-12: Proportion of economic activities in foraging (blue) vs. non-foraging (brown) spheres across eight Agta communities.

Although the 'trade' category in Figure 3-12 does not take up a large proportion of time (a total of only 4%), trade with farmers has a significant effect on the diet of the Agta. Essentially, while the Agta engage in more foraging than non-foraging activities, non-wild foods, especially rice, represent a significant part of their diet and in all camps was consumed as part of the majority of meals (Table 3-5). This can be clearly seen from the composition of afternoon meals across seven camps provided in Table 3-5. The majority (81.6%) of afternoon meals contained rice, and 21.3% of meals consisted of only rice. Around half of all meals contained fish.

Table 3-5: Composition of afternoon meals in seven camps.

Camp (Map code)	N (meals)	*Proportion of meals containing:* Rice	Only rice	Animal protein	Fish
Diago (66)	271	89.7	17.0	57.2	40.2
Dipaguiden (67.1)	73	90.4	34.2	61.6	56.2
Didikeg (67.2)	122	96.7	25.4	56.5	42.6
Diambarong (77)	34	79.4	14.7	58.8	47.1
Kanaipang (74)	215	62.3	25.1	58.6	47.9
Magtaracay (79)	63	63.9	19.7	55.7	49.2
Diabut (84)	54	92.5	5.6	79.6	79.6
TOTAL	830	81.6	21.3	59.3	47.5

Table 3-6: Indicators of market integration across Agta camps.

Dist. to town (rank)	Camp Name	Area	Families	% received immunisation	Church
1	Dibunkgo (59)	Inland	26	0.49	Y
2	Semento (54)	Inland	6	0.44	N
3	Culasi (64)	Coast	12	0.47	Y
4	Diabut (84)	Inland	7	0.03	N
5	Dinipan (62)	Inland	5	0.03	N
6	Djago (66)	Coast	13	0.38	Y
7	Kanaipang (74)	Coast	24	0.23	Y
8	Diambarong (77)	Inland	6	0.04	N
9	Dipaguiden (67.1)	Coast	6	0.09	N
10	Didikeg (67.2)	Coast	9	0.05	N
11	Dipagsanghan (79)	Inland	10	0.17	Y
12	Magtaracay (78)	Inland	8	0.01	N

Most ethnographers who have worked with the Agta have made socio-economic change a focus of their work (see Peterson (1982; 1984), Griffin (1985; 1991; 1989), Rai (Rai 1990), Headland (1989; 1986)). Bennagen (1977) even issues a "rallying call to save a Filipino group from cultural extinction". Arguably, however, it is neither fair nor productive to cast the Agta as a people whose way of life is facing inevitable extinction (see Minter's

(2008) discussion of the 'tribal extinction paradigm'). In Palanan and the NSMNP, the Agta face challenges from the net migration of non-Agta into the area, environmental degradation, discrimination, and the threat of a road being built from the 'mainland'. Land inside the NSMNP which the Agta should have ancestral domain rights to are also rumoured to be being bought - apparently by wealthy provincial politicians hoping to build beach resorts if the road opens. Although not always put into practice, the Philippines does also have progressive legislation with regards to Indigenous People and the Agta are, for example, involved in the NSMNP management board (although their voice are not necessarily heard above those of more powerful political agents). Therefore, while the Palanan Agta are facing uncertainty and change, I would agree with Minter (2008) that they demonstrate remarkable resilience and flexibility in the face of the socio-economic change.

3.5 Social organisation

Kinship and marriage

The Agta have a bilateral kinship system (Rai 1990; Early & Headland 1998; Headland 1987a). Griffin also suggests that the Agta have cognatic descent groups (Griffin 1996) whereby groups trace their shared ancestry to a deceased but tangibly recent ancestor (two or three generations ago). Marriages between those who call each other by kinship terms (including affinal terms) are said to be prohibited and this generally matches what we see in our genealogical data - there were no first cousin marriages reported, for example. Although Griffin (1996) mentions a few cases of polygyny, we encountered only monogamous marriages. Marriages were generally open, with only a few cases of sibling set marriages (where multiple children of one set of a parents marry multiple children of another set of parents). As suggested by the mean ages at first birth given above, men tend to marry when slightly older than women. When couples marry they will generally set up their own household, even before they have children, and are regarded as an autonomous unit.

Most marriages occur with neighbouring groups and young unmarried men are often seen away from their families touring around communities, in part with the hope of meeting young ladies. Although some parents have suitable spouses in mind, young adults have a degree of free-choice in marriage and may begin living together before any 'official' marriage. As documented by Early and Headland (1998) and Minter (2008), we heard reports of bride service, where a young husband is asked to prove his worth to the parents of his new wife for up to a year. However, in most cases it seemed like this was a token gesture, rather than a serious several month long service. Marriage parties can occur in the area of either the husband or wife's parents and the marriage will only occur once all the important kin are in attendance (Minter 2008).

Housing and settlement types

The most basic kind of Agta settlement is the lean-to, a simple windshield woven from wooden branches and dried palm leaves (Figure 3-13). These are easy to construct and make ideal temporary dwellings on the beach during summer fishing trips. A more permanent structure is used in the rainy season which has a roof made in the same way as the lean-to but built on a wooden platform made of bamboo or, if available, wooden planks (Figure 3-14). In a few inland Agta camps in Palanan, families were given corrugated metal roofs after a particularly bad hurricane. Most families sold these soon after, although some kept theirs and constructed a more permanent dwelling with wooden plank walls.

Figure 3-13: Example of a lean-to shelter. Magtaracay, Didian (2014)

Figure 3-14: Example of a more permanent house. Diambarong, Didian (2014)

Politics and social relations

Social relations among the Agta are relatively egalitarian. Personal autonomy is highly valued and there are no clear hierarchies within communities. Most of the larger and established camps had a nominal leader, although this seemed to be a position which involved representing the group to outside agencies who assume a leader exists rather than to organise camp life. Social relationships are, for the most part, relaxed and the mood in camps is jovial. Impromptu parties sometimes began when men returned from a big fishing or hunting trip. Such parties might occur at any time of day, including early morning if this happened to be when men returned! This is not to say that hostile relations and conflicts do not occur from time to time. The few conflicts we witnessed, however, were, at worst, verbal shouting matches which resulted in one household leaving camp. Stories of violence were rare and those we did hear about were often linked to alcohol, a bigger problem in some camps than others. Some individuals who have a reputation for being volatile or heavy drinkers were generally avoided by most families – one man on the coast was a rather fierce individual at times and lived only with his two or three most closely related households. Residential flexibility gives people the chance to move away from hostilities and avoid social friction and, in the evolutionary anthropology literature, has been posited as a potentially important mechanism in the maintenance of cooperation (Aktipis 2011; Lewis et al. 2014)

Residential mobility

The Agta have, in general, a flexible pattern of residence where households move regularly between camps and areas (a feature of their organisation which is of critical importance to my analysis of co-residence patterns in chapter 4). Generally, however, it would be unusual to move to an area in which the households had no kinship connection. This usually restricts households to camps around one or two rivers or to one stretch of coast (Minter 2008). It is important to note that in the case of the Agta, as for many other hunter-gatherer groups (Kelly, 2013), residential mobility is of households between residential locations, rather than of residential camps between areas. In other words it is not the case (in our experience, at least) that whole camps will decide to move *en masse*. There are a large number of sites which will be occasionally occupied for seasonal foraging activities and others which are almost always occupied but have a regular turnover in composition. In both my experience and that of Minter

(2008) and Rai (1990), mobility is highest during the summer. For inland camps the reason for this is obvious – heavy rains soon result in fast and deep rivers that make moving dangerous and unpleasant.

The Agta move for a number of reasons including seasonal foraging opportunities, visiting family or friends, and to take advantage of wage labour opportunities. From my recording of data on food sharing I was able to provide a rough estimate of Agta mobility of a move every ten days during the summer, although many of these moves represented 'visits' rather than resettlements. Another rough estimate of mobility comes from the household interviews (see section 2.3.5) where we asked adults to list all the barangays they had lived in (the barangay is the smallest administrative division in the Philippines and in Palanan typically represents an area of around 4-5km^2). Adults had reported living in 2.50 (SD = 1.09) barangays in their lifetime.

Although it is said to not have occurred for at least a generation in Palanan, the Agta are said to have a history of inter-group raiding (*ngayaw*). According to Rai (1990), raiding parties consisted of ten or so men armed with bows. Although this practice is said to have stopped with martial law in 1972 (Minter 2008: p86), the practice is still discussed among the Agta. On one occasion in Dipagsangan, two young men from a neighbouring camp turned up dressed in the typical *ngayaw* costume of a red g-string and arm bands with bows and dogs making a lot of noise (see Figure 3-15). Needless to say, this was taken to be the joke it was intended to be and the whole camp was greatly amused. If raiding did take place, it is unclear what motivated it – from a theoretical point of view, the resources exploited by the Agta are neither densely or predictably distributed enough for stable territorial groups to be expected (Smith 1988; Dyson-Hudson et al. 1978).

Figure 3-15: A joke *ngayaw* raiding party. The men are with their dogs and hold bows and arrows. Dipagsangan 2014

Sub-groups

There is an open question about the extent to which the Agta form distinct sub-groups. Although Minter (2008) and Rai (1990) both propose sub-group boundaries, the creation of such divisions are disputed by Griffin (1996). Minter (2008) suggests that three sub-groups exist within those Agta living in the NSMNP: one group living along the coast, and two inland groups (these are labelled A, B, and C in Figure 2-1). Minter's proposed boundary between the two inland groups falls north of my sample population and therefore I cannot comment on it with any authority. I would support the proposed division, however, between the coast and inland Agta in Palanan. The inland Agta tended to have more kinship ties with Agta in San Mariano than with the coast, with the exception of a number of ties between Kanaipang on the coast and those Agta camps in southern inland Palanan. As well as kinship relations, these boundaries may reflect differences in foraging specialisation between riverine and marine foraging. When I asked him if he could fish in the sea, one man from an inland camp laughed and said he wouldn't swim in the sea and was worried he would drown! Divisions between the coast and island Agta are clear from the common use of the term 'ebukid' used by the coast-dwellers to describe the inland camps. Ebukid means ‘wild’ or ‘of the mountains’ (Estioko & Griffin 1975) and was generally used in the context of warnings to us when visiting new camps – “don’t visit the Agta in Dipagsnagan, they are *ebukid*”.

3.6 Summary

The Palanan Agta are a population of small-scale foragers who fish, hunt, and gather wild food and honey. Like many contemporary hunter-gatherers, the Agta also supplement their foraging activities with more ‘market integrated’ activities and trade with farming neighbours. The Agta have a social organisation typical of ‘simple’ hunter-gatherers, with individuals living in highly mobile households within small residential bands within which social interactions remain relatively egalitarian. In the next chapter, I unpack this social organisation in more detail, exploring, among other questions, how closely related individuals are to their campmates.

Chapter 4: What explains the low relatedness of hunter-gatherer bands?

4.1 Chapter Summary

One of the most striking features of human sociality is our ability to live and cooperate with individuals to whom we are unrelated and with whom we may never have interacted before, a capacity that is clearly evident in modern post-industrial cities and nation-states. Is this ability to interact with unrelated individuals only allowed by the social institutions of complex society? Or is it something that is characteristic of human society more generally? In this chapter I show that the Agta, like many contemporary hunter-gatherers, live in groups in which both sexes may disperse their natal community and in which a large proportion of campmates are distantly related or unrelated to one another. I then present the results of an agent-based model that suggests that sex equality in residential decision making (as characterised by a bilocal or multi-local dispersal system) significantly reduces group relatedness. The low relatedness of hunter-gatherer bands has important implications because if groups of such low relatedness were the norm in human evolutionary history, this could have provided the selective context for the evolution of our capacity for cooperation with unrelated individuals, facilitated through mechanisms including reputation, exclusion, punishment, mobility, partner choice, reciprocal interactions, and social norms. The work presented in this chapter is published as a research paper in the journal *Science* entitled "Sex equality can explain the unique social structure of hunter-gatherer bands" (Dyble et al. 2015). A copy of this paper is provided in appendix B.

4.2 Introduction

*Like the chimpanzee [humans were] violent, mobile, intensely suspicious of strangers, and used to hunting and fighting in bands of close relatives. Yet now… [*with the development of agriculture and complex societies*]…the same shy, murderous ape that had avoided strangers throughout its evolutionary history was now living, working and moving among complete strangers in their millions.*

Seabright (2010, p5)

Is Seabright right? Did hunter-gatherers in human evolutionary history live in small, kin-based groups, wary of outsiders? If they did, this would have profound implications for our understanding of the evolution of human social cognition. For one, cooperation within the band would likely be driven by kin selection, and the complex cognition required for cooperation through reputation, punishment, social norms, and reciprocity would not be so important. Although Seabright's portrait of the human social past is somewhat hyperbolic, it is an example of the kind of assumptions often made about hunter-gatherer sociality. How justified are such assumptions? The most recent and comprehensive survey of group relatedness among contemporary hunter-gatherer populations comes from Hill and colleagues (2011) who compiled data on the residence patterns of 32 contemporary foraging societies. They found that contemporary hunter-gatherer groups are often of surprisingly low relatedness, with around half of co-resident dyads being either distantly related or unrelated to each other. Walker (2014) found that hunter-gatherer bands are less closely related than those of Amazonian horticulturalists.

The low relatedness of hunter-gatherer bands has important implications because if groups of such low relatedness were the norm in human evolutionary history, this could have provided the selective context for the evolution of our capacity for cooperation with unrelated individuals, facilitated through mechanisms including communication, exclusion, punishment, mobility, partner choice, reciprocal interactions, and social norms (Lewis et al. 2014; Trivers 1971; Clutton-Brock 2009; West et al. 2007). More fluid and expansive social groups may also provide the context for cumulative cultural evolution (Kempe & Mesoudi 2014; Lee 1979; Pradhan et al. 2012; Powell et al. 2009).

What about dispersal patterns among contemporary small-scale hunter-gatherers?[1] In the first half of the twentieth century, the dominant paradigm was that of the 'patrilocal band' as advocated by Stewart (1955), Sahlins (1959), Owen (1965), and Service (1962), and taking inspiration from Radcliffe-Brown's (1931) 'patrilineal horde' with an emphasis on territoriality and male co-operation as underling patrilineality/patrilocality. Service (1962) did recognise that some hunter-gatherers appeared to have more flexible residence systems but saw this as representing a degradation from an original 'social core' due to contact with the modern world, a hypothesis also proposed by Ember and Ember (1983) .

As with many aspects of hunter-gatherer studies, the *Man the Hunter* symposium of 1966 cast fresh light on anthropological understandings of hunter-gatherer residence patterns. Lee and DeVore (1969) argued that patrilocality was "certainly not the universal form… that Service thought it was" (p8) and instead described more flexible, mobile, and

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[1] Terms of residence are typically used to describe where a newly married couple typically reside. The most common distinction is between residence with the family of the husband (patrilocality/virilocality) versus family of the wife (matrilocality/uxorilocality). While patrilocality and matrilocality are the more commonly used terms, virilocality and uxorilocality are more etymologically accurate since the Latin roots refer to husband and wife, rather than father and mother (Adam 1947). Other systems include neolocality where the couple reside away from both their natal communities, bilocality (or ambilocality) where the couple can live with the community of either the husband or wife (or, indeed, alternate between them), and duolocality where the couple live with their natal communities and have a 'walking marriage', as seen among the Mosuo of central southern China (Ji et al. 2013; Wu et al. 2013). Among highly mobile foragers, where households move often between camps containing family of either or neither, Marlowe (2004) suggests use of the term multi-locality, a term I use in this chapter.

bilateral residence systems in which either men or women could reside with their kin after marriage. Although specific ethnographic accounts emphasised this bilocal residence, cross-cultural analyses such as compiled by Ember (1978) continued to suggest that patrilocality was the most common residence pattern across foraging societies. In Ember's sample, 62% of foraging groups were classified as patrilocal and only 16% as bilocal.

The quality of the data used in Ember's analysis, however, was challenged by Alvarez (2004) who reanalysed the data, finding that once poor quality data are removed, around 40% of the remaining groups were bilocal, 22.9% were matrilocal, and 25% were patrilocal. Similar findings were described by Marlowe (2004) with data on 186 societies from the standard cross-cultural sample. Marlowe (2004) advocated the use of the term 'multi-local' to describe hunter-gatherer residence on the grounds that the common pattern is not only that couples may reside with the family of either the husband or wife (bilocality) but also that households move frequently between camps containing both and, in some cases, neither. As mentioned above, Hill and colleagues (2011) analysed actual co-residence data from 32 hunter-gatherer societies, finding that multi-locality is more common than patrilocality or matrilocality.

Ethnographic evidence, then, has led to a widespread rejection of the patrilocal band model and recognition that hunter-gatherer residence is often fluid, multi-local, and that unrelated individuals often co-reside. It is worth noting, however, that there are some researchers such as Knight and Power (Knight 2008; Knight & Power 2005) who invoke the late nineteenth century work of Morgan (1877) and Engels (1884) in arguing that matrilocality and matrilineality were the norm in human evolutionary history, despite being rare among contemporary hunter-gatherers (Hill et al. 2011; Ember 1978; Marlowe 2004; Alvarez 2004; Dyble et al. 2015). Knight and Power perhaps see the debate about the history of human social organisation less as an empirical issue and more as an "ideological battleground" (Knight and Power 2005, p81) where, at least in the capitalist world, a "pro-family, anti-communist ideology overrode scholarship" (p81). Such language is in keeping with Knight's descriptions of collectivised childcare, menstruation as sex strike and human revolution (Knight et al. 1995; Knight 1991).

While patterns of hunter-gatherer residence may have important implications for our understanding of human social evolution, a key question remains unanswered – *why* do hunter-gatherers live in groups of such low relatedness? Indeed, can we even say that hunter-gatherer groups do have low relatedness? What constrains group relatedness? It seems clear, for example, that group relatedness must be limited to some extent by exogamous marriage which introduces unrelated spouses into the group (Walker & Bailey 2014). These are questions I seek to address in this chapter. In particular, I aim to test the hypothesis that the adoption of multi-local dispersal in which both men and women can leave their natal communities places a constraint on how closely related hunter-gatherer communities can be.

4.3 Methods (Ethnographic data)

The first aim of this chapter is to establish the relatedness and dispersal systems of Agta groups. I aim to establish this through exploring quantitative data on the relatedness of co-resident dyads, rather than from normative, qualitative assessments. What is required, therefore, is to classify how all co-resident individuals in my sample are related to each other. In small camps, where individuals may be closely related, this is a task that is possible to do 'by hand' through consulting notes from genealogical interviews. In larger camps, however, this soon becomes a monumental task. For example, while a camp of 12 individuals contains a relatively manageable 132 dyads, a camp of 80 individual contains some 6,400 dyads. A computational solution is therefore required, and is described below.

Genealogical data used in this study

The genealogical data presented in this chapter were collected according to the procedures set out in chapter 2.3.1. Relatedness between individuals in the sample analysed in this chapter are established using all genealogical data collected during fieldwork in 2013-14. The camp compositions used in this chapter, however, are as we found them during our short fieldwork season in 2013. I use this data because the 2013 fieldwork season involved brief stays at each camp visited. Our data from this year therefore represent a more concise 'snapshot' of residence patterns. In contrast, over the more prolonged fieldwork season in 2014 I often encountered the same families living in different camps and camp composition often changed during the stay in each camp.

Comparative data

Although in this chapter I focus mainly on Agta co-residence data, my counterparts working in the Congo collected equivalent data which I analysed in the same way and which was included in the short format journal article version of this paper (Dyble et al. 2015). In some of the figures below, I show this alongside the Agta data. I also compare this with data from the Ju'/hoansi and Ache provided in the supplementary material of Hill et al. (2011). In addition to these data from hunter-gatherer societies, I collected a smaller sample of co-residence patterns among three Paranan communities, farming neighbours of the Agta. For the Paranan farmers, I used an abbreviated protocol to collect relatedness data where I specifically asked how each individual in the community was related to each other as opposed to collecting as deep a genealogy as possible as was done for the Agta. This was both for expediency and because I was not collecting the other demographic data which are made available when 'complete' genealogies are collected.

Defining relatedness

Many analyses of community relatedness focus only on the average coefficient of relatedness between individuals as defined by Wright (1922) which reflects the probability of the genes of two individuals being identical by descent (e.g. Nolin 2010; Gurven 2004; Chagnon & Bugos 1979; Walker 2014; Apicella et al. 2012). In focusing only on relatedness through common descent (pedigree) and disregarding affinal kinship, studies are (*a*) missing important social relationships and (*b*) missing relationships between individuals who have a common reproductive interest and therefore, according to inclusive fitness theory, can derive fitness benefits through cooperation (I expand on this point at length in chapter five). I therefore wanted to define relatedness categorically and in such a way as to include both affinal and consanguineal ties. For the sake of having results comparable to those reported for other populations, I classified dyadic relatedness according to a scheme set out by Hill and colleagues (2011) in their analysis of hunter-gatherer residence patterns mentioned above. This scheme classifies relatedness into nine categories, set out in Table 4-1.

Kinship as a network

Although I wanted to define categorical relatedness using the same scheme as Hill et al. (2011) I did not have access to the computer scripts they used in their classifications. Classifying dyadic relatedness categorically therefore required some computational innovation. The solution I reached involved recognising relatedness, both conceptually and computationally, as a network. Networks are composed of vectors connected by edges. In the case of kinship, we can conceptualise people as vectors, and kinship ties as edges. Of course, kinship ties differ in their strength. So in order to take account of this, in my network, edges represent either primary kinship ties or marriages. From the ego's point of view, primary kinship ties are those with parents, siblings, and children (those who share a Wright's (1922) coefficient of relatedness of $r = 0.5$). Primary kinship and marriage ties are arguably the core building blocks of kinship and kinship terminology. For example, we may have a single word for 'cousin' in English but we can also express 'cousin' as the product of three primary kinship components, for example, mother's brother's son or father's sister's daughter. In some cases, ego and alter will be related through several different genealogical pathways. For example, ego and alter could be married but also be cousins. In these cases, the relationship involving the shortest number of genealogical steps was used (in this example, their marriage tie represents one genealogical step, while their cousinship represents three genealogical steps: from ego to parent to sibling to child).

By creating a network of kinship we are able to make use of the various packages and computing functions designed to analyse networks such as ‘Kinship2’ (Therneau et al. 2014) and ‘Pedigree’ (Coster 2012). These can quickly tell us, for example, the length of the shortest path between any two individuals. These tools are very helpful in categorising relatedness into the categories set out in Table 4-1. Admittedly, information is also lost when creating the matrix, since we lose information about generations (a tie with a parent looks exactly the same as a tie between siblings in a primary kinship network, for example). For the purposes of the work presented in this chapter, however, this approach sufficed. For other analyses such as those reported in chapter five, a more detailed output was produced which can classify more specific relationships (for example, mothers, fathers, and various grandparents rather than just ‘primary kin’, ‘distant kin’ and so on).

Table 4-1: Defining relatedness according to dyadic network characteristics. L(*prim*) is the shortest path length between nodes in the network containing only primary kinship ties, L(*aff*) is the shortest path length between nodes in the network containing only marriage ties, and L(*kin*) is the shortest path length in between nodes in a network containing both primary kinship and marriage ties.

Relatedness	**Relatedness to ego**	**Definition from networks**
Primary kin	The parents, children, and siblings of ego.	L(*prim*) = 1
Distant kin	All consanguineal kin of between two and five primary kin 'steps'.	L(*prim*) = 2-5 and L(*prim*) < L(*aff*)
Spouse	Ego and alter are, or were, married	L(*aff*) = 1
Spouse's primary kin	The parents, children, or siblings of ego's spouse.	L(*kin*) = 2, L(*prim*) > 2, and where the tie between ego's spouse and alter is L(*kin*) = 1
Primary kin's spouse	The spouses of ego's primary kin (as set out above)	L(*kin*) = 2, L(*prim*) > 2, and where the tie between ego's spouse and alter is L(*kin*) ≠1
Spouse's distant kin	Consanguineal kin of ego's spouse of up to four genealogical steps.	Where the tie between ego's spouse and alter is L(*kin*) < 5, L(*kin*) < 6 and L(*prim*) > 5
Other Affines	Individuals connected to ego by five or fewer genealogical steps who are not classified in one of the above categories.	L(*kin*) < 6 but not included in the above
No Relatedness	Individuals more than five genealogical steps from ego.	L(*kin*)>5

4.4 Results (Ethnographic data)

4.4.1 Sample sizes

Among the Agta I collected data on co-residence patterns for 191 adults living in eleven camps, a total of 4,055 dyads. Mean experienced camp size across the sample was 21.23 adults (SD = 8.61)[2]. The comparative data set on Paranan farmers consisted of 49 adults across

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[2] Experienced camp size is a mean weighted by the number of individuals in each camp and is therefore a better reflection of the experience of individuals. For example, if we found one camp

three camps containing a total of 1,048 co-residence dyads. The comparative data set on Mbendjele hunter-gatherers consisted of 103 adults across nine camps, containing a total of 1,863 co-residence dyads. Mean experienced camp size was 21.41 adults (SD = 9.32) among the Paranan and 18.09 adults (SD = 8.62) among the Mbendjele.

4.4.2 Sex differences in relatedness to the group

As stated above, I sought to use quantitative data on co-residence to establish the extent to which residence patterns were sex biased (i.e. whether the Agta and other populations can be said to be unilocal, multi-local, or somewhere in between). For the Agta, Mbendjele, and Paranan I calculated the average number of co-resident dyads of different relatedness for all adults in my sample. As reported in Table 4-1 and Figure 4-1, there were no significant differences in the average number of co-resident individuals of any category between men and women among either the Agta or Mbendjele, suggesting that neither population can be said to have a sex biased residence system. In other words, both populations, like most other contemporary foragers (Hill et al. 2011), have a bilocal or multilocal residence system. In contrast to the unbiased residence patterns of the Agta and Mbendjele, Paranan farmers (n = 49 adults, 1,049 dyads) demonstrate a significant male bias in residence, with men living with a larger number of primary kin (n = 23, mean = 2.65, SD = 2.29) than women (n = 26, mean = 1.27, SD = 2.05; t=2.23 p = .031).

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of 10 individuals and another of 100 individuals, the average camp size of 55 would be much smaller than the average experienced camp size of 91.8 individuals.

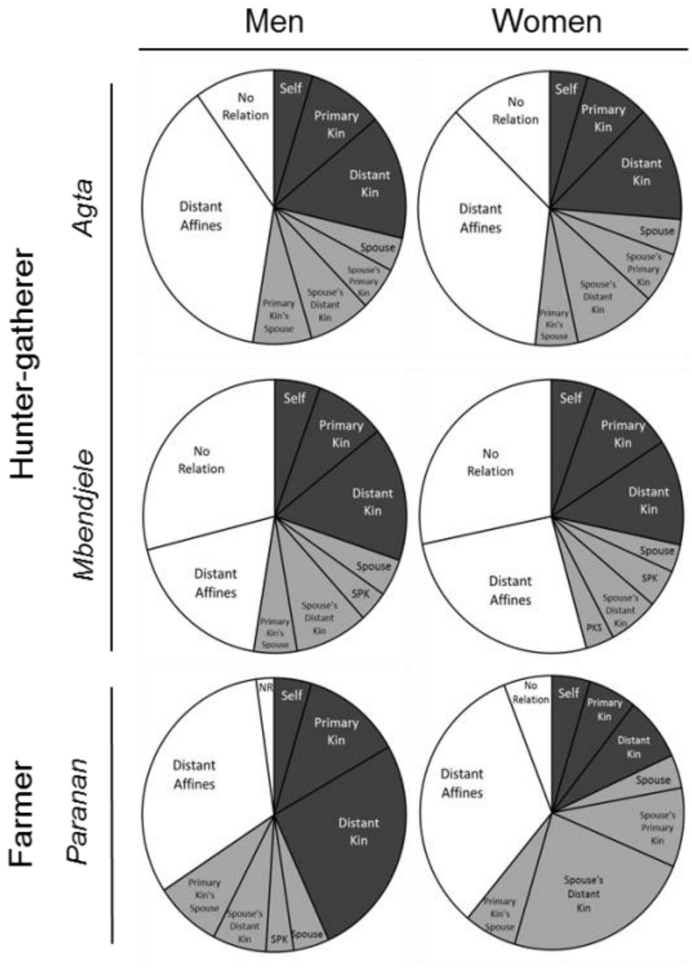


Figure 4-1: Observed co-residence patterns for males and females among the Paranan, Agta, and Mbendjele. Chart area represents the proportion of all co-resident dyads which fall into each of the nine categories described by Table 4-1.

Table 4-2: Mean number of co-resident dyads for men and women across nine relatedness categories among the Agta, Mbendjele, and Paranan. Mean number of dyads per adult +/- SD. Independent samples t-tests comparing men with women in each population, *p < .05, **

	Agta		Mbendjele		Paranan	
Relatedness Category	Men (*n* = 99)	Women (*n* = 92)	Men (*n* = 44)	Women (*n* = 59)	Men (*n* = 23)	Women (*n* = 26)
Primary kin	1.94 ±1.63	1.70 ±1.62	1.57 ±1.56	1.88 ±1.79	2.65 ±2.29*	1.27 ±2.05*
Distant kin	3.09 ±4.00	2.93 ±4.00	2.86 ±2.62	2.27 ±2.82	5.78 ±4.44***	1.62 ±3.44***
Spouse	0.84 ±0.37	0.90 ±0.30	0.80 ±0.46*	0.59 ±0.50*	0.96 ±0.21	0.85 ±0.37
Spouse's primary kin	1.08 ±1.43	1.28 ±1.53	0.66 ±0.91	0.81 ±0.86	0.74 ±1.54*	2.00±1.98*
Spouse's distant kin	1.60 ±2.39	2.16 ±2.89	1.61 ±1.59	1.12 ±1.60	1.43 ±3.47**	4.96 ±4.65**
Primary kin's spouse	1.52 ±1.51	1.12 ±1.29	0.95 ±1.41	0.63 ±1.07	1.78 ±2.00	1.00 ±1.79
Distant affines	7.91 ±5.10	7.63 ±4.86	3.32 ±3.65	4.73 ±4.42	7.00 ±3.67	7.08 ± 4.10
No relation	2.07 ±2.90	2.71 ±3.11	5.20 ±5.90	5.14 ±5.80	0.48 ±1.16*	1.27 ±1.46*

4.4.3 Low group relatedness

Among the Agta, as well as among the comparative Mbendjele sample, around 25% of co-resident dyads were consanguineal kin, 25% were close affinal kin, and around 50% were distant affinal kin or unrelated individuals (Figure 4-2, Table 7). These results are similar to those reported for the Ache and Ju/'hoansi by Hill and colleagues (14); see Figure 4-2. Despite having a comparable group size of 21.4 adults (*SD* = 9.30). Paranan farmers live with fewer unrelated individuals than the hunter-gatherer groups, (4.2% vs. 16.7%; $\chi^2 = 108.93$, $p < .001$) (Figure 4-2).

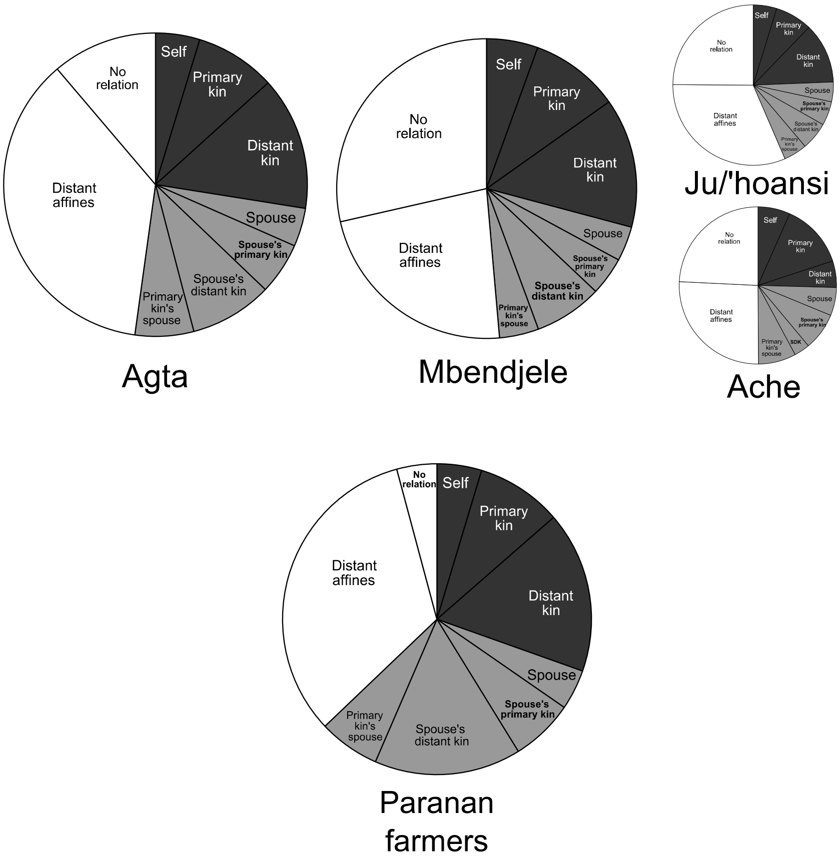


Figure 4-2: *Top*: observed co-residence patterns among four multilocal hunter-gatherer groups (from *left* to *top right*: the Agta, Mbendjele, Ache, and Ju/'hoansi). Ache and Ju/'hoansi charts are based on data provided in Hill et al. (2011). *Below*: Observed co-residence among the patrilocal Paranan farmers.

Table 4-3: Observed numbers of co-resident adult dyads across nine relatedness categories among the Agta, Mbendjele, and Paranan farmers.

	Agta		Mbendjele		Paranan Farmers	
	N	%	N	%	N	%
Self	191	4.7	103	5.5	49	4.7
Primary kin	348	8.6	180	9.7	94	9.0
Distant kin	576	14.2	260	14.0	175	16.7
Spouse	166	4.1	70	3.8	44	4.2
Spouse's primary kin	225	5.5	77	4.1	69	6.6
Spouse's distant kin	357	8.8	137	7.4	161	15.4
Distant kin's spouse	253	6.2	79	4.2	67	6.4
Distant affines	1485	36.6	425	22.8	345	32.9
No relation	454	11.2	532	28.6	44	4.2
Total dyads	4055	100	1863	100	1048	100

4.4.4 Comparison with random assortment

Later in this chapter I present a model which tests the hypothesis that sex equality in residential decision-making and multi-local residence reduces relatedness at the group level despite a preference to live with kin at the individual level. A simple alternative hypothesis, however, is that individuals are not motivated to live with kin at all and, instead, randomly assort into camps. Under such conditions, the low relatedness we see in communities would simply be the result of a widespread indifference toward living with kin. The data, however, do not support this hypothesis since the frequency of primary kin co-residence was significantly higher than would be expected if adults assorted randomly across camps (Mbendjele, $\chi^2 = 451.62$, $p < .001$; Agta, $\chi^2 = 982.00$, $p < .001$). In other words, people actively assort with kin.

4.5 Methods (Model)

The ethnographic data presented above suggest that the Agta and Mbendjele are similar to other contemporary hunter-gatherers (as reported by Hill et al. 2011) in so far as they live in groups of low relatedness, with multi-local residence. Although the low relatedness of hunter-gatherer groups represents a striking *pattern*, it is not clear what *process* reduces the relatedness of hunter-gatherer groups. Surely, if individuals are to avoid inbreeding, then some unrelated individuals must co-reside. I aim to test the hypothesis that sex equality in residential decision making reduces group relatedness. In order to do this, I created an agent-based model that simulates the process by which individuals assort into camps. By using an agent-based model, I can explore how decision making at the individual level can lead to particular patterns at the group level. As Smith (1988, p227) states:

> *"Individual actions have many unintended consequences… Such consequences are not the goals of the actor who produce them, though they may have a considerable or even critical effect on the collectivity. More important, there are strong theoretical and empirical reasons for expecting that individual preference is often thwarted or constrained by the preferences and power of others. As a consequence, one needs specific theoretical tools to follow the often twisted path between individual intention and social outcome."*

Model design

The model begins with an initial population of two "married" but otherwise unrelated individuals - a wife and husband. In the first round, one of them is randomly selected as a 'draw agent' who chooses one adult primary kin to join the camp – an 'incoming agent'. The relationship of the incoming agent to the draw agent is chosen with the following probabilities: sibling (50%), adult offspring (25%), and parent (25%). These probabilities approximate the relative number of living kin of these categories for adults in our observed hunter-gatherer populations. The model assumes exogamous monogamy and, as such, each incoming agent is accompanied by an unrelated spouse.

Thus, in each turn of the model, two agents are added to the fictional camp, and a new draw agent is randomly selected from the pool of existing camp members. The model proceeds until the camp reaches a specified size (Figure 4-3). The model could therefore be thought of as simulating the occupation of an empty camp by actors who have a simple set of preferences about who they want to live with. If we imagine this process taking place in different camps until all individuals are allocated, further assortment would imply a balance between incoming and outgoing couples that does not alter levels of relatedness in each camp. For this reason, the model is also a simulation of the effects of household mobility on camp relatedness. I ran two main versions of this model: an 'egalitarian' and 'non-egalitarian' version. In the 'egalitarian' version, both the draw agent and incoming agent can be either male or female. In the 'non-egalitarian' model, the draw agent is of one sex only, and can only select an incoming agent of the same sex as them (resulting either in a patrilocal or a matrilocal residential pattern). In essence, this is a 'pen and paper' model and the above, if I have explained it clearly enough, can be replicated through drawing a fictional genealogy. However, in order to run the model many times, a script was necessary, and was written in R 3.1.1. For both versions of the model, I ran 100 replications of the model at eight camp sizes ranging from 10 to 80, simulating and classifying a total of more than 4 million dyadic relationships.

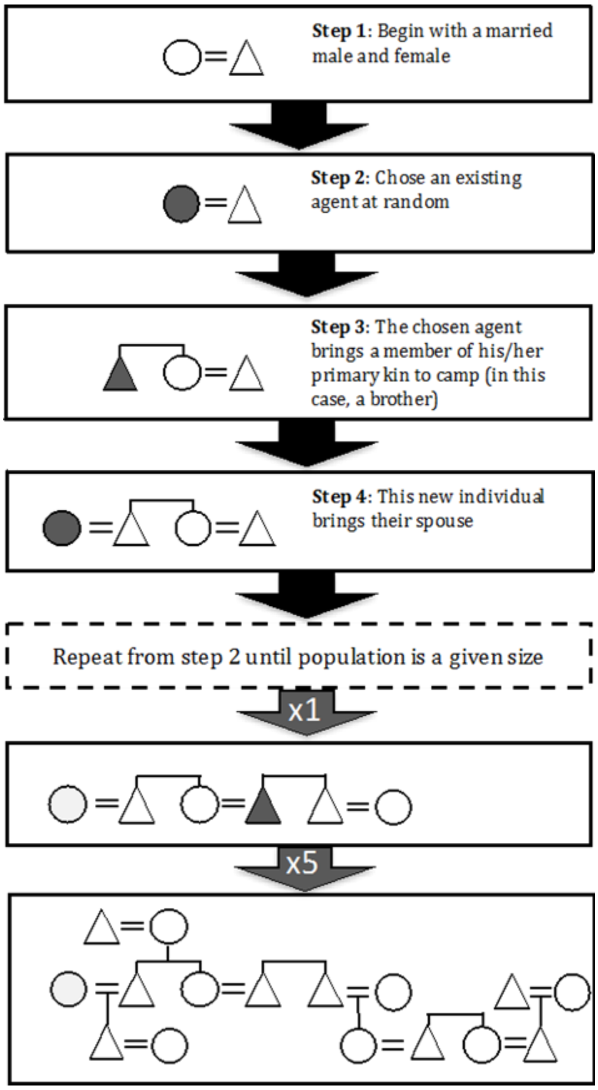


Figure 4-3: Flow chart of the egalitarian model, simulating the process of camp assortment. Triangles are male, circles are female. A double hyphen represents marriage, horizontal ties represent siblingship, and vertical ties represent parenthood. In the non-egalitarian model, step 2 involves choosing from existing agents of one sex only, and step 3 involves choosing a primary kin of the same sex.

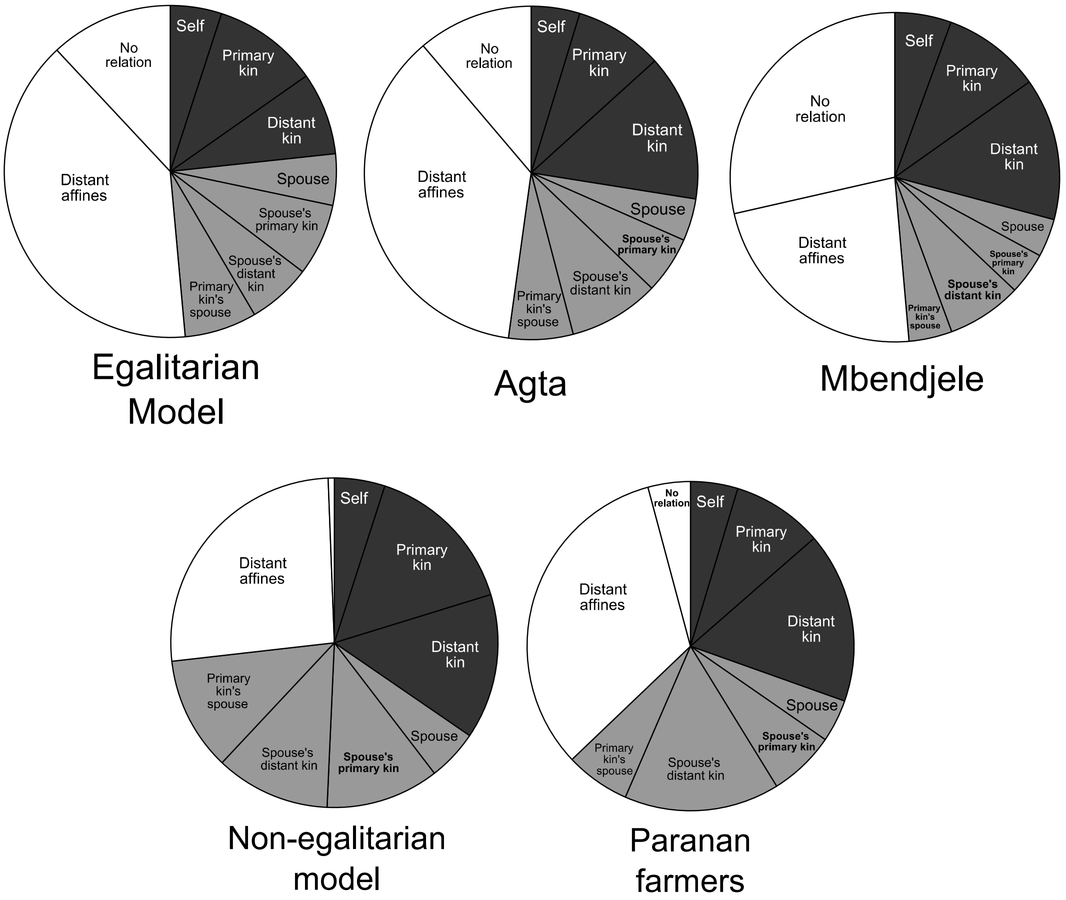
Polygyny

The 'standard' egalitarian and non-egalitarian models described above assume monogamous pair-bonds in the modelled populations. It is possible, however, that polygyny may have an influence on the relatedness of groups. Although we did not observe polygyny among the Agta, it does occur occasionally among the Mbendjele (Chaudhary et al. 2015). I therefore ran an additional set of simulations in which men were polygynous (or, indeed, women could be polyandrous) with a fixed probability. Simulations were run in which polygyny was either sororal or non-sororal. In the standard egalitarian and non-egalitarian models, each marriage introduces an unrelated individual into the camp. It therefore follows that the introduction of polygyny, and especially of non-sororal polygyny, would reduce group relatedness relative to a monogamous comparison. Introducing polygyny, however, results in a skewed sex ratio since the camps created would include more women than men (or men than women if polyandrous). To maintain a balanced sex ratio, I ran a further set of simulations in which men had no wife with the same probability that they had two.

4.6 Results (Model)

4.6.1 Egalitarian vs. non-egalitarian model

The primary aim of the model described above was to compare simulated camp composition under 'egalitarian' and 'non-egalitarian' conditions. In the 'egalitarian' condition, both men and women can influence camp composition. In the non-egalitarian condition, only one sex can influence camp composition. These two conditions result in striking differences in group composition. Across 100 simulations at a population size of 20 adults, for example, there were a significantly larger proportion of unrelated dyads in the modelled egalitarian camps (12.0% ± 8.4) compared to the non-egalitarian, single-sex dispersal camps (0.6% ± 1.5) ($\chi^2 = 4372.36$, $p < .001$; Figure 4-2). In both versions of the model, relatedness decreased with group size although modelled egalitarian camps show higher proportions of unrelated individuals irrespective of camp size (Figure 4-5).


Egalitarian Model

Agta

Mbendjele

Non-egalitarian model

Paranan farmers

Figure 4-4: Modelled and observed co-residence patterns for egalitarian (*top*) and non-egalitarian (*bottom*) populations. Mean camp sizes for the modelled population is n = 20 agents. Mean are 21.23±8.61 for the Agta, 18.09±8.62 for the Mbendjele, and 21.41±9.32 for the Paranan farmers.

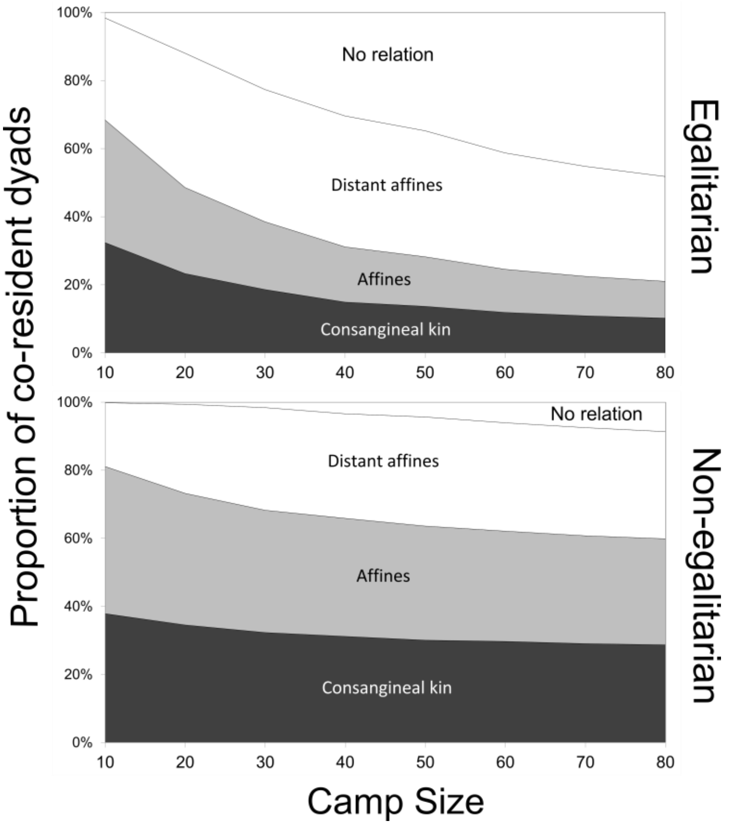


Figure 4-5: Results of the egalitarian model (*top*) and non-egalitarian model (*bottom*) at camp sizes between 10 and 80. Area represent the proportion of co-resident dyads that fall within each of the following four categories: consanguineal kin, affines, distant affines, and no relation.

Table 4-4: Modelled camp composition across nine relatedness categories for the egalitarian version of the model. Values represent the average percentage of dyads in the category +/- SD over 100 simulations.

	Population size							
Relatedness Category	10	20	30	40	50	60	70	80
Self	10.0±0.0	5.0±0.0	3.3±0.0	2.5±0.0	2.0±0.0	1.7±0.0	1.4±0.0	1.3±0.0
Primary kin	15.4±3.2	10.2±1.9	7.5±1.4	5.9±1.0	4.9±0.8	4.2±0.6	3.7±0.6	3.3±0.4
Distant kin	7.0±5.0	8.1±4.6	7.7±4.7	6.5±3.4	6.8±3.2	6.0±2.5	5.8±2.6	5.6±2.2
Spouse	10.0±0.0	5.0±0.0	3.3±0.0	2.5±0.0	2.0±0.0	1.7±0.0	1.4±0.0	1.3±0.0
Spouse’s primary kin	10.3±1.8	7.0±1.5	5.3±1.2	4.3±0.9	3.5±0.7	3.1±0.5	2.7±0.5	2.4±0.4
Spouse’s distant kin	5.4±3.3	6.2±3.3	6.0±3.3	5.2±2.6	5.6±2.6	4.9±2.0	4.8±2.1	4.7±5.9
Primary kin’s spouse	10.3±1.8	7.0±1.5	5.3±1.2	4.3±0.9	3.5±0.7	3.1±0.5	2.7±0.5	2.4±0.4
Other affines	30.0±8.2	39.5±5.8	38.8±6.7	38.5±6.5	37.0±6.3	34.2±5.9	32.3±6.3	30.8±5.9
No relation	1.6±2.8	12.0±8.4	22.6±11.5	30.4±10.0	34.7±10.5	41.3±9.3	45.2±9.7	48.2±7.9

Table 4-5: Modelled camp composition across nine relatedness categories for non-egalitarian model. Values represent the average percentage of all dyads in the category +/- SD over 100 simulations.

	Population size							
Relatedness Category	10	20	30	40	50	60	70	80
Self	10.0±0.0	5.0±0.0	3.3±0.0	2.5±0.0	2.0±0.0	1.7±0.0	1.4±0.0	1.3±0.0
Primary kin	19.4±4.4	15.3±3.4	12.2±2.6	10.8±2.6	9.4±2.5	8.1±2.8	7.3±1.9	6.7±1.9
Distant kin	8.6±5.2	14.3±4.8	16.8±3.4	17.9±3.4	18.7±3.4	19.9±3.5	20.3±2.6	20.7±2.3
Spouse	10.0±0.0	5.0±0.0	3.3±0.0	2.5±0.0	2.0±0.0	1.7±0.0	1.4±0.0	1.3±0.0
Spouse’s primary kin	13.2±3.5	11.2±3.3	9.3±2.5	8.5±2.6	7.5±2.5	6.6±2.8	6.0±1.9	5.5±1.9
Spouse’s distant kin	6.9±3.5	11.3±3.3	14.1±2.5	15.3±2.6	16.5±2.5	17.6±2.8	18.3±1.9	18.8±1.9
Primary kin’s spouse	13.3±3.5	11.2±3.3	9.3±2.5	8.5±2.6	7.5±2.5	6.6±2.8	6.0±1.9	5.5±1.9
Distant affines	18.8±4.5	26.2±3.1	30.2±2.7	30.7±3.5	32.1±4.8	31.8±4.5	31.8±6.2	31.5±6.3
No relation	0.1±0.3	0.6±1.5	1.6±2.2	3.4±3.9	4.3±4.9	6.0±5.0	7.5±6.7	8.6±7.0

4.6.2 Comparing modelled and observed co-residence patterns

The modelled co-residence patterns closely mirror our observed data. The proportion of unrelated dyads in the model at a comparable group size ($n = 20$ agents) (12.0% ± 8.4) was not significantly different from the observed proportion of unrelated co-residency among the Agta (11.2%, $\chi^2 = 1.98$, $p = .016$). Although the Mbendjele had significantly larger numbers of unrelated individuals in the camps (28.6%) than predicted by the model ($\chi^2 = 440.76$, $p < .001$) this was in the direction consistent with our hypothesis. While the observed proportion of unrelated dyads among the Paranan (4.2%) was larger than the modelled proportion (0.6% ± 1.5, $\chi^2 = 183.41$, $p < .001$), it was lower than either of the observed hunter-gatherer populations or the egalitarian model ($\chi^2 = 58.65$, $p < .001$). The central question of this chapter was why hunter-gatherer camps have such low relatedness. The results of my model suggest that pair-bonding and sex equality in residential decision-making act together to constrain the overall relatedness of groups, leading to the co-residence of individuals unrelated through either genetic or affinal ties.

4.6.3 Introduction of polygyny

The introduction of polygyny to the model had little influence on group relatedness. As demonstrated in Table 4-6 and Table 4-7, if 15% of men have two wives rather than one, community relatedness is modestly reduced in both the egalitarian and non-egalitarian model. As stated above, however, the introduction of polygyny in this way skews the male to female ratio. If we maintain a balanced sex ratio by allowing a man to have no wife at the same frequency of having two wives, relatedness increases again (Table 4-6 and Table 4-7). The same is true when polygyny is sororal (the two wives are sisters) (Table 4-8). Even when 30% of men are polygynous, the effects remain relatively modest (Table 4-9)

Table 4-6: Modelled camp composition across nine relatedness categories for the egalitarian model with varying levels of monogamy, polygyny, and non-marriage. Values are the mean percentage ± SD across 99 simulations.

	Egalitarian		
	100% monogamy	15% non-sororal poly; 85% monogamy	15% non-sororal poly; 15% no spouse; 70% monogamy
Self	5.00 ±0.00	5.12 ± 0.15	5.08 ±0.18
Primary kin	10.25 ±1.90	8.60 ±1.97	9.96 ±2.45
Distant kin	8.10 ±4.67	4.63 ±3.58	6.46 ±3.97
Spouse	5.00 ±0.00	5.69 ±0.30	5.12 ±0.41
Spouse's primary kin	7.06 ±1.53	7.04 ±1.78	7.51 ±1.82
Spouse's distant kin	6.23 ±3.37	4.09 ±3.06	5.67 ±3.29
Primary kin's spouse	7.06 ±1.53	7.04 ±1.78	7.56 ±1.82
Distant affines	39.37 ±5.85	42.03 ±6.43	41.93 ±6.49
No relation	11.93 ±8.45	15.79 ±10.96	10.70 ±8.43

Table 4-7: Modelled camp composition across nine relatedness categories for the non-egalitarian model with varying levels of monogamy, polygamy, and non-marriage. Values are the mean percentage ± SD across 99 simulations.

	Non-egalitarian		
	100% monogamy	15% non-sororal poly; 85% monogamy	15% non-sororal poly; 15% no spouse; 70% monogamy
Self	5.00±0.00	5.07±0.15	5.13±0.17
Primary kin	15.29±3.47	13.66±3.07	14.55±4.44
Distant kin	14.25±4.82	12.42±4.15	11.97±5.57
Spouse	5.00±0.00	5.39±0.31	5.15±0.38
Spouse's primary kin	11.20±3.37	11.25±3.11	11.50±4.00
Spouse's distant kin	11.30±3.37	11.26±3.12	10.84±4.00
Primary kin's spouse	11.20±3.37	11.25±3.11	11.50±4.00
Distant affines	26.14±3.18	29.33±3.61	28.44±5.03
No relation	0.61±1.56	0.38±0.92	0.92±2.53

Table 4-8: Modelled camp composition across nine relatedness categories for the non-egalitarian model with varying levels of monogamy, sororal polygamy, and non-marriage. Values are the mean percentage ± SD across 99 simulations.

	Non-egalitarian		
	100% monogamy	15% sororal polygyny; 85% monogamy	15% sororal polygyny; 15% no spouse; 70% monogamy
Self	5.00±0.00	5.13±0.16	5.12±0.16
Primary kin	15.29±3.47	14.21±2.92	15.30±4.30
Distant kin	14.25±4.82	12.55±4.18	13.43±4.84
Spouse	5.00±0.00	5.47±0.26	5.16±0.37
Spouse's primary kin	11.20±3.37	11.22±3.02	11.26±3.32
Spouse's distant kin	11.30±3.37	11.30±3.04	11.28±3.45
Primary kin's spouse	11.20±3.37	11.22±3.02	11.26±3.32
Distant affines	26.14±3.18	28.44±3.70	26.63±4.72
No relation	0.61±1.56	0.45±1.19	0.58±1.14

Table 4-9: Modelled camp composition across nine relatedness categories for the non-egalitarian model with varying levels of monogamy, polygamy, and non-marriage. Values are the mean percentage ± SD across 99 simulations.

	Non-egalitarian		
	100% Monogamy	30% non-sororal polygyny; 70% monogamy	30% non-sororal polygyny; 30% No spouse; 60% monogamy
Self	5.00±0.00	5.09±0.18	5.06±0.19
Primary kin	15.29±3.47	12.87±3.31	13.55±4.17
Distant kin	14.25±4.82	9.76±4.25	10.61±4.57
Spouse	5.00±0.00	5.68±0.34	5.25±0.54
Spouse's primary kin	11.20±3.37	12.34±3.59	11.53±3.57
Spouse's distant kin	11.30±3.37	10.02±3.67	10.91±3.72
Primary kin's spouse	11.20±3.37	12.34±3.59	11.53±3.57
Distant affines	26.14±3.18	31.45±4.50	30.93±5.12
No relation	0.61±1.56	0.45±0.95	0.63±1.29

4.7 Discussion

The Agta live in small bands in which around half of all co-resident dyads are either distantly related or unrelated to each other. Although this pattern of low relatedness has been found among many simple contemporary hunter-gatherers (Hill et al. 2011), why this low relatedness occurs is not well understood. In this chapter, I described an agent-based model that demonstrates that groups of low relatedness can emerge even when there is a strong preference to co -reside with kin at the individual level, so long as all individuals, both male and female, have an equal influence over camp composition. If only one sex can influence camp composition, however, much more closely related groups emerge. In other words, my model suggests that sex equality in residential decision making places a constraint on the relatedness of groups. My simulations therefore provide a solution to the apparent contradiction between individual-level preferences for living with kin and group-level co-residence with non-kin and establish a link between multi-local residence and low community relatedness.

That small-scale hunter-gatherer populations have (*a*) fluid residence, (*b*) groups of relatively low relatedness, and (*c*) generally egalitarian political relations between men and women has been the standard paradigm within hunter-gatherer studies since the late 1960s (Lee & DeVore 1969). With co-residence with many unrelated individuals and no sex bias in relatedness to the camp, the Agta appear to have a social system typical of this small-scale hunter-gatherer type (Hill et al. 2011). The main contribution of this chapter, therefore, is not only to provide further evidence of these traits among contemporary hunter-gatherers but to elucidate the causal links between them.

Evolutionary Implications

If multi-local residence and groups of relatively low relatedness were the norm in human evolutionary history, this may have had many important consequences for human social evolution. Firstly, cooperation with unrelated individuals cannot be explained in terms of inclusive fitness benefits and may require the negotiation of cooperation through more cognitively demanding processes such as the monitoring of reputation, the development and maintenance of social norms, and the application of punishment. Secondly, fewer kin *in* camp means that there are more kin *out of* camp. This may have allowed individuals to extend their social networks, buffering environmental risk and promoting levels of information exchange required for cumulative culture (Kempe & Mesoudi 2014; Lee 1979; Pradhan et al. 2012; Powell et al. 2009).

A good example of the consequences of a fluid/open sociality comes from work by Hill and colleagues (2014) who estimate that Hadza and Ache men witness around 300 others making tools during their lifetime, while adult chimpanzees interact with around only 20 other adult males in their lifetime. The differences in the breadth of social interactions may reflect the difference between the relatively fixed group composition seen among chimpanzee troops, and the more fluid and mobile groups of hunter-gatherers (Lehmann et al. 2014; Manson & Wrangham 1991).

Group thinking

Within the paradigm of human behavioural ecology, individuals are assumed to be rational decision makers, aiming to increase their reproductive success and making decisions that are contingent on their socio-strategic context. The size, structure, and relatedness of groups provides the socio-strategic 'landscape' within which such decisions are made. Understanding group composition is therefore an important first step in understanding social dynamics. Groups are not, however, passively imposed – their size and composition is also the result of socio-strategic decision making. This is especially relevant among highly mobile foraging groups. With some notable exceptions (Smith 1981; Smith 1985; Boone 1992; Alvarez 2004; Chagnon & Bugos 1979), the process of group formation has received less attention from anthropologists than the activities that go on within these groups. I hope that the work presented in this chapter provides an important demonstration of the merits of agent-based modelling as a tool for exploring how group composition emerges as a result of individual-level preferences.

Sex equality?

Given the generally egalitarian nature of interactions between men and women among the Agta, it seems reasonable to argue that the equal frequency of residence of a household with kin of the husband and of the wife represents the compromise of two parties both wanting to reside with their kin. In other words, it is the outcome of sex equality in residential decision-making. It is possible, however, that multi-locality does not have to imply sex equality in residential decision-making. It could represent, for example, a tug-of-war between the interests of a woman's husband and her brother (or, indeed, between a man's wife and his sister). It could also be that one sex makes all residence decisions but recognises the advantages of residing with his or her spouse's kin.

4.8 Summary

Like many contemporary small-scale hunter-gatherers, the Agta live in small residential camps containing a large proportion of distantly related or unrelated individuals. They also have a multi-local residence system in which both men and women can leave their natal community and where households are highly mobile, moving regularly between camps. This kind of fluid, multilevel social system may provide a social context within which individuals must negotiate social interactions with a large pool of unrelated individuals. It may also allow individuals access to the expansive interaction networks required for cumulative cultural transmission. I created an agent-based model that suggests that even if all individuals in a community seek to live with as many kin as possible, within-camp relatedness is constrained if men and women have equal influence in selecting camp members. Simulated camp compositions closely approximate observed patterns of co-residence among Agta and Mbendjele BaYaka hunter-gatherers. My results suggest that pair-bonding and greater residential flexibility in human evolutionary history may have had a transformative effect on human social organisation. In the next chapter I explore affinal kinship, arguing, in part, that the ability to recognise affinal kinship allowed the more flexible residence systems seen among contemporary hunter-gatherers.

Chapter 5: Human evolution and affinal kinship

5.1 Chapter summary

According to inclusive fitness theory, organisms can derive fitness benefits through aiding related individuals (Hamilton 1964). As such, we might expect natural selection to have endowed organisms with the ability to recognise related individuals and to interact with them in ways that increase their inclusive fitness. Humans, with our ability to recognise extensive networks of kinship, could be said to have kin recognition *par excellence*. Not everyone that we recognise as kin, however, is related to us by common descent. Human kinship also includes ties through marriage (affinal kin or '*in-laws*'). How, within the standard inclusive fitness framework, could altruism directed toward affinal kin be adaptive? And what significance does the recognition of affinal kinship have for human social evolution? In this chapter, I outline a means of calculating relatedness through common reproductive interest. I then present the results of an agent-based model which demonstrates proof of concept for this new coefficient and shows that where paternity certainty is high and pair-bonds are stable, individuals can yield inclusive fitness benefits through aiding affinal kin. I also show that this alternative coefficient of relatedness better predicts behavioural interactions among the Agta. In short, I argue that investment in affinal kin can be an adaptive strategy and that the recognition of affinal kinship may have had a transformative effect on human social and behavioural evolution, paving the way for a further expansion of social life in which interactions with unrelated individuals became increasingly frequent and important.

5.2 Introduction

In chapter four, I examined how contemporary hunter-gatherers, including the Agta, live in small groups of relatively low relatedness and fluid composition, a sociality in contrast to the more closed groups typical of chimpanzees (Mitani & Watts 2005; Wilson & Wrangham 2003; Lehmann et al. 2014). If hunter-gatherers today have a social structure that represents past populations, and if these 'closed' chimpanzee-like groups were also characteristic of the human-chimpanzee last common ancestor (LCA), then what facilitated the transition in humans to a more open social system? According to the model of human social evolution advanced by Chapais (2009), the evolution of pair-bonding in humans was vital in expanding groups since it allowed the recognition of shared reproductive interest between unrelated males who are the spouses and brothers of dispersing females. This meant that women could become 'appeasing bridges' between communities (Chapais 2009, p226), facilitating the creation of a supra-group or 'tribal' level of social organisation. This hypothesis is similar to the 'Alliance Theory' ideas of Lévi-Strauss (1969) and earlier theories of Edward Tylor (1889).

Of course, the formation of stable pair-bonds also represents the creation of a stable sub-unit within social groups which, in the primatological literature, is referred to as a 'one male unit' (Guo et al. 2015; Grueter, Matsuda, et al. 2012). Furthermore, in allowing greater certainty of paternity, pair-bonding also allows the recognition of bilateral kinship ties (i.e. consanguineal kinship through both the mother and father), facilitating the recognition of extended kinship. Thus, in allowing the recognition of both bilateral consanguines and affines, pair-bonding may have played a pivotal role in the formation of several levels of human social organisation, leading to the formation of what have been described as 'multilevel' societies (see section 6.1 for full discussion of this). This is the crux of Chapais's (2009) argument that '*pair bonding gave birth to human society*'.

In the hypothetical pair-bonded and patrilocal system explored by Chapais (2009), if unrelated males exchange a female in a kind of reciprocal system (similar to that outlined by Lévi-Stauss in his seminar work '*The Elementary Structures of Human Kinship*' (1969)), it is clear why both parties would have an interest in the woman - the brother of the woman shares a genetic interest with her through common ancestry, while the husband has a common genetic interest with her in the next generation. Intuitively, this makes sense from the point of view of inclusive fitness theory (Grafen 2009; Hamilton 1964) – while affinal kin may be unrelated by common descent, their reproductive success is inextricably linked.

Estimation of whether an action is of net fitness benefit to an individual can be defined, with a few assumptions about population structure aside, using 'Hamilton's rule', which holds that an action has a net fitness benefit when:

$$c < rb$$

[Equation 5-1]

Where c is the cost to ego, r is the relatedness of ego and alter, and b is the benefit to alter. Thus, relatedness (r) is a necessary condition for the realisation of inclusive fitness benefits (Figure 5-1).

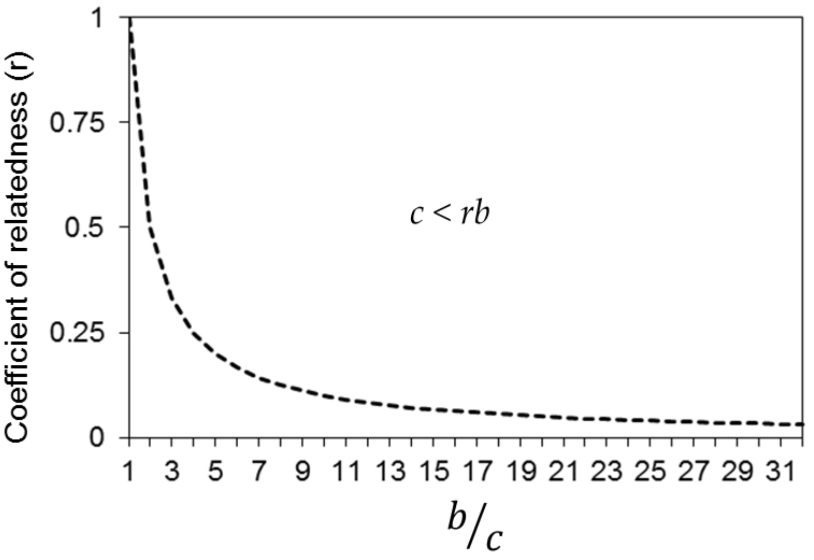


Figure 5-1: The conditions under which altruistic acts will be fitness enhancing according to the basic formulation of 'Hamilton's rule'. As in equation 5-1 above, c represents the cost to the donor and b represents benefit to the recipient.

How is relatedness defined? Estimations of relatedness are most often (at least in evolutionary anthropology) quantified using Wright's (1922) 'coefficient of relatedness' which provides an estimation of the probability that alleles at the same loci in the two individuals in question will be identical by descent (IBD). This is defined as below where p represents all paths connecting A and B with a unique common ancestor and where L(p) represents the length of these paths.

$$\sum_{p_{AB}} 2^{-L(p_{AB})}$$

[Equation 5-2]

So, for example, full siblings are related to each other through two paths of $L(p) = 2$ and therefore are related by ¼ + ¼ = ½. Thus, according to Wright's coefficient of relatedness, in a haploid species, individuals are related to their parents, children, and full siblings by $r = 0.5$, to their aunts, uncles, grandparent and grandchildren by $r = 0.25$, and to their cousins by $r = 0.125$.

The ubiquity of both Wright's coefficient of relatedness and Hamilton's rule in evolutionary anthropology and behavioural ecology more generally should not lull us into a false sense of security. Indeed, both remain theoretical concepts in a state of flux. As Grafen (2009) says, "we are not quite sure what inclusive fitness is in any but very simple circumstances, and relatedness might be more complicated than we think" (Grafen 2009, p3135). For example, other means of calculating relatedness have been outlined in which relatedness between ego and alter is estimated relative to relatedness between ego and an average member of the wider population (Queller 1994; Grafen 1985)[3]. Such nuances are important in understanding the evolution of altruism in viscous populations in which related individuals may also be competitors (West et al. 2002).

Reckoning relatedness: 'forward' versus' backward'

The standard framework for quantifying relatedness in evolutionary biology, then, is constructed around the estimation of common ancestry – a reflection of past reproductive events. In this scheme, there is no room for affinal kinship – affinal kin are classified as 'unrelated' individuals unless they have some shared ancestry. Fitness, however, is realised not backward but forward, through future reproductive events. In a pair-bonded species, where individuals can have some confidence in who they and others will reproduce with, they can begin to recognise common reproductive interests, and potential fitness enhancing benefits of directing investment toward affinal kin.

This argument, that relatedness ought to be reckoned, forward rather than backwards was made by Austin Hughes in his 1988 book *Evolution and Human Kinship*. He argues that: "marriage creates a genetic common interest between two groups that were previously unrelated or distantly related – the common interest in the offspring of the

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[3] Although this could be framed as an alternative means for calculating relatedness it is, strictly speaking, an additional consideration required in order to make predictions about the spread of an altruistic gene among a viscous population - it does not invalidate or undermine standard calculations of identity by descent outlined above.

marriage" (Hughes, 1988, p78). Thus, common reproductive interest is the product not only of *descent* but also of *alliance*. These two forces – descent and alliance – have been at the heart of twentieth century anthropological thought relating to kinship and social organisation (Radcliffe-Brown & Forde 1950; Fox 1967; Evans-Pritchard 1951; Lévi-Strauss 1969; Needham 2004).

Why do biological conceptions of relatedness only deal with descent, and not with alliance or marriage? In doing so they overlook not only affinal kinship in humans but one of the most important relationships in nature more widely – that between individuals in breeding pairs. Within evolutionary anthropology, affinal relatedness has often been neglected by omission, with authors not mentioning affinal ties. Tucker (2004), however, explicitly states that the large amount of food distribution between affinally related Mikea foragers is "inconsistent with kin selection" (p43). Exceptions to the general neglect of affinal kinship include a paper by Alvard (2009) which notes the importance of affinal ties in explaining Yanomamo group formation[4] and a paper by Burton-Chellew and Dunbar (2011) in which they compare the emotional closeness felt by participants toward their consanguineal and affinal kin, finding that affinal kin were treated more like consanguineal kin than non-kin. However, their scheme for calculating relatedness relies on equating affines with their consanguineal opposite numbers, defining brothers-in-law as having a relatedness of r = .5, for example. In other words, while their argument is similar to that set out here, they do not offer a generalizable formula for the estimation of common reproductive interest. They also do not test whether investment in affinal relationships bring indirect fitness benefits.

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[4] Alvard (2009, p 409) notes that "affinal marriage alliance has not attracted the attention of human behavioural ecologists interested in cooperative relationships".

5.3 A new method for quantifying common reproductive interest

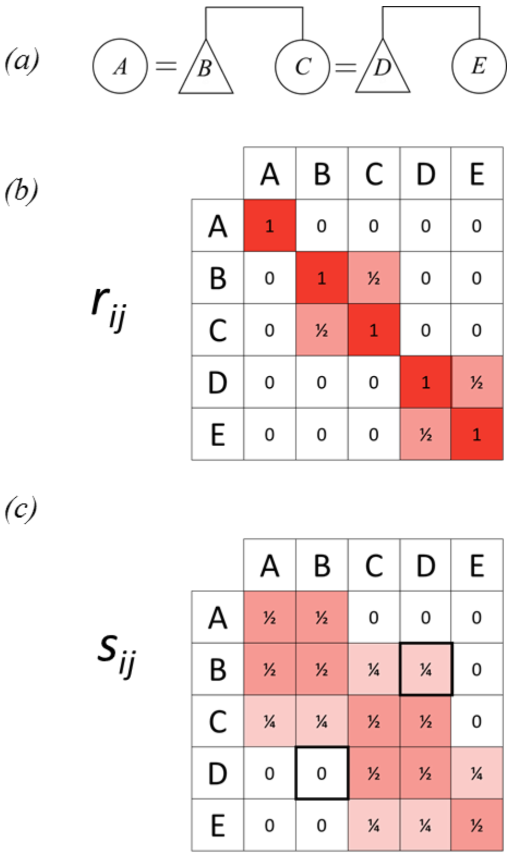
As stated above, my concern with Wright's coefficient of relatedness is that it reckons relatedness *backwards*, through common descent, rather than *forwards*, through common reproductive interest. As outlined above, under conditions of long-term pair-bonding, individuals unrelated by common descent but with an affinal kinship tie may have a common reproductive interest in the next generation and therefore could, in theory, derive inclusive fitness benefits through aiding each other even though they share no common ancestry. How can we incorporate such relationships into our means of quantifying relatedness? In order to quantify common reproductive interest, I propose the 'coefficient of common reproductive interest' (s) below (between A and B where C is the spouse of B):

$$s_{AB} = \frac{\sum_{p_{AB}} 2^{-L(p_{AB})} + \sum_{p_{AC}} 2^{-L(p_{AC})}}{2}$$

[Equation 5-3]

What this coefficient measures is simple – rather than the relatedness between ego and alter, it calculates the relatedness between ego and the hypothetical offspring of alter should they reproduce with their current reproductive partner. So, for example, the relatedness between pair-bonded partners would be S = ½ and between ego and their sibling's spouse would be S = ¼. Of course, unlike the standard coefficient of relatedness, ego's relatedness to themselves is not 1 but ½ since that will be their relatedness to their own child (I am assuming a diploid population here). This must be taken into consideration when calculating relative fitness returns. In other words, we must make explicit the ego's relatedness to themselves implicit in Hamilton's rule.

It should be noted that in some cases this relationship is asymmetrical such that s_{AB} does not equal s_{BA}. For example, while you would have a genetic stake in the offspring of your sister's husband, he would not have a genetic stake in your own offspring (this applies to the relatedness between individuals B and D in the example given in Figure 5-2).



r_{ij}

	A	B	C	D	E
A	1	0	0	0	0
B	0	1	½	0	0
C	0	½	1	0	0
D	0	0	0	1	½
E	0	0	0	½	1

s_{ij}

	A	B	C	D	E
A	½	½	0	0	0
B	½	½	¼	¼	0
C	¼	¼	½	½	0
D	0	0	½	½	¼
E	0	0	¼	¼	½

Figure 5-2: Relatedness between individuals in genealogy (a) according to Wright's coefficient of relatedness (b) and coefficient of common reproductive interest (c).

In a sexually reproducing species, individuals are obliged to recombine their genetic material with another. Thus, the coefficient of relatedness outlined in equation 5-3 above represents the true relatedness of ego to the offspring of alter. Future reproductive events, however, cannot always be predicted with certainty. Thus, as a behavioural heuristic, we should add a probability term (*i*) to the coefficient above such that:

$$s_{AB} = \frac{\sum_{p_{AB}} 2^{-L(p_{AB})} + i\left(\sum_{p_{AC}} 2^{-L(p_{AC})}\right)}{2}$$

[Equation 5-4]

5.4 An evolutionary model of kinship recognition

In order to provide proof of concept for the alternative means of reckoning relatedness outlined in section 5.3, I created an evolutionary agent based model in which agents can choose to act altruistically toward each other by donating the units of energy required to reproduce. Agents invest in others according to Hamilton's rule such that they will donate energy units if the costs to themselves is less than the benefit to the recipient moderated by the coefficient of relatedness between them. The way in which agents evaluate relatedness, however, is genetically determined. There are several variants (alleles) of the 'kin detection' gene such that some individuals will evaluate relatedness based on the standard coefficient of relatedness while other will do so according to the alternative coefficient of relatedness outlined above (there are, in fact, four possible alleles, as described below). When successful individuals reproduce, they can pass on their gene to the next generation such that we are able to trace the change in allele frequencies in the population through time. By varying parameters such as pair-bond stability and extra-pair mating, we can estimate the 'parameter space' under which investment in the recognition of affinal kinship and investment in them would be fitness enhancing.

5.4.1 Model design

This model was produced in R 3.1.1 (R Core Team 2014) and uses functions from the pedigree (Coster 2012), kinship2 (Therneau et al. 2014), and igraph (Csardi & Nepusz 2006) packages. This is an 'agent-based' model in which simple agents are able to assess their relatedness to each other, interact with each other to share resources, and reproduce. I begin with a population containing three generations of *n* individuals. Although agents vary in their reproductive success, the population is in demographic equilibrium (it neither grows nor declines) – there are always three generations of *n* individuals. For consistency with the results presented in Figure 5-2 let us say that *n* = 40, so that the total population is 120 agents. A schematic overview of the model process is given in Figure 5-3, with a description of each stage of the model below.

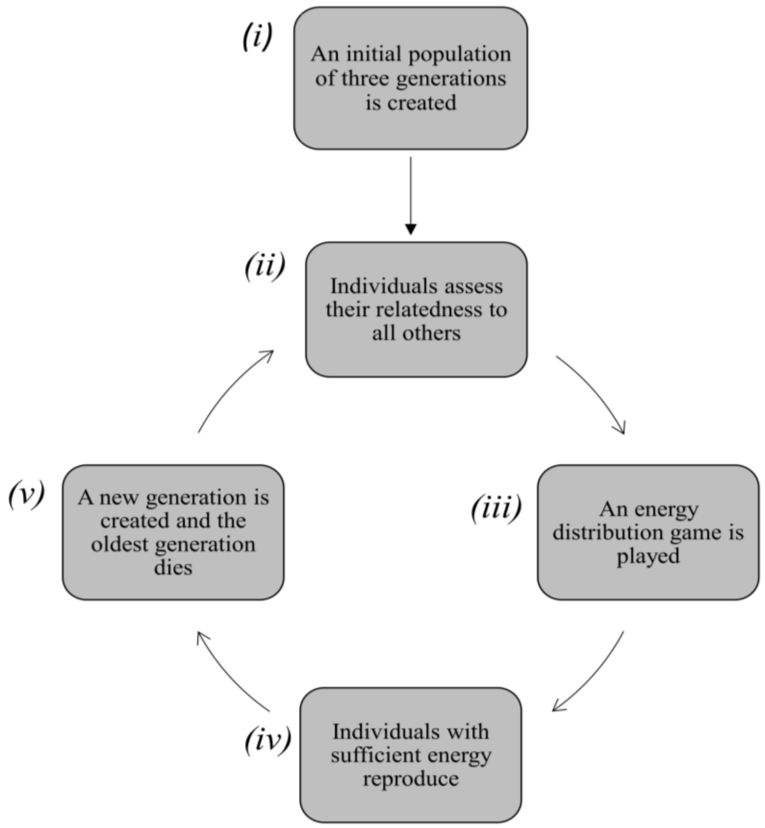


Figure 5-3: Schematic representation of the agent-based model each box refers to one of the five main phases of the model described in section 5.4.1.

(i) An initial population is created

An initial population of three generations of 40 agents is created. Half are male, half are female, and each is given an allele of the 'kin recognition' gene in equal number (the function of these are explained below). The males and females in each generation 'marry' exogamously, avoiding marriage with individuals related through common ancestry.

(ii) Assessment of relatedness

Individuals assess their relatedness to all other individuals according to one of the four 'genetically determined' rules. Individuals can trace back ancestry through a maximum of three generations. The four rules are as follows:

- Agents with allele 'A' recognise no relatedness to any others and therefore never act altruistically by gifting resources;
- Agents with allele 'B' recognise relatedness through matrilineal ancestry only;
- Agents with allele 'C' recognise relatedness through both matrilineal and patrilineal ancestry;
- Agents with allele 'D' recognise relatedness according to the coefficient of common reproductive interest outlined above.

(iii) The energy game

In each generation, agents play a series of 'energy games'. In each of these games, agents are given a random number of energy units, ranging between 1-20. These energy units have a marginal value such that each additional unit is worth less than the previous one. In the standard model, the value of the first energy unit is 1, and each additional unit is worth 0.05 less than the previous, such that the value of the nth energy unit is:

$$1 - 0.05(n - 1)$$

[Equation 5-5]

And the cumulative value of n energy units is therefore:

$$n - 0.05\left(\frac{n(n-1)}{2}\right)$$

[Equation 5-6]

Agents are chosen in a random order to evaluate the cost to themselves of losing one unit of energy. They compare this with the product of their coefficient of relatedness to every other agent multiplied by the benefit every other agent would derive from having additional energy units. For those agents for whom a donation is estimated to be fitness enhancing (i.e. $rb > c$), one unit of energy will be given to the agent with the maximum relatedness moderated benefit. This process is repeated for each agent until there are no other agents for whom $rb > c$. We then iterate through the next donor agent who makes decisions based on the amount of energy held by all agents at that point in time (i.e. they take into account the donations of previous agents). In the 'standard' model, thirty rounds of this energy game are played in each generation.

(iv) Reproduction

Once the game has been played thirty times, the value of the resources held at the end of each round of the game are summed. The 40 agents who have accumulated the largest number of energy units each reproduce once. The remaining 80 agents do not reproduce in this generation.

(v) Creation of a new generation

Forty new agents are 'born' to the successful agents described above, and the oldest generation dies. The new generation 'marry' exogamously but otherwise randomly. Agents are monoploid, and each new agent therefore inherits a single gene either from their mother or father.

I start the model with equal frequencies of all four alleles (25% of agents have each) and continue until one allele reaches fixation or 100 generations elapse. Critically, I repeat this process with varying levels of pair bond stability and paternity certainty. This allows us to explore the conditions under which investment in affinal kin would be adaptive and therefore explore the conditions under which human kinship recognition may have evolved.

Pair-bonding and affinal kinship

In the basic version of the model described above, all agents have a 'spouse' with whom they reproduce exclusively. Thus, the basic model simulates a social system in which there are monogamous pair bonds with certain paternity and with no extra-pair mating. However, since stable pair bonds are hypothesised to be a necessary condition for kin recognition (Chapais 2009), I wanted to explore the conditions under which various degrees of kin recognition would evolve. I therefore added to the model the possibility of extra-pair mating and pair-bond instability. The difference between these two is as follows –paternity certainty is a misallocation of paternity –holding an erroneous belief about who your father is. In contrast, I define pair-bond instability as an individual agent reproducing with an individual who is not their original spouse but where all other agents know that this change has occurred (in human terms we could say that they have divorced and remarried rather than secretly 'cheated' on their spouse).

In the model, paternity uncertainty is added in stage (*v)* as the probability that the 'gene' the new agent may inherit from their father comes from a random other male in the population. Pair-bond instability is added in stage (*iv*) where the reproducing individual does not reproduce with the spouse they had previously been allocated but with a random other individual. However, in this case, this other male becomes the reproducing agent's new spouse and is recorded as the father of the new 'offspring'.

5.5 Model Results

5.5.1 Basic results

Before going on to use this model to compare the alternative ways of reckoning relatedness outlined above, it is worth demonstrating that this model can provide a proof of concept for more fundamental principles. In particular, will a standard 'identical by descent' coefficient of relatedness be selected over a heuristics which cause agents to (*a*) be totally selfish or (*b*) randomly direct investment? In other words, is investing according to Hamilton's rule a more successful strategy than random investment?

'Selfish' vs. Wright's coefficient of relatedness

In the first model, I ran 20 simulations over 100 generations in a population of 120 individuals, with 30 energy games per generation and under conditions of stable pair-bonding and no extra-pair mating. I began the model with 50% of agents having the 'selfish' allele of the gene, and 50% having the bilateral kinship recognition allele. In other words, half my agents were completely selfish, ignoring all relatedness to others and thus never donating in the energy games, and half reckoned relatedness through common descent (Wright's *r*). In all twenty simulations, the 'bilateral kinship' allele had reached fixation before 100 generations had elapsed (see Figure 5-4), providing a strong demonstration that the framework of my model is indeed one in which kin nepotism can be adaptive.

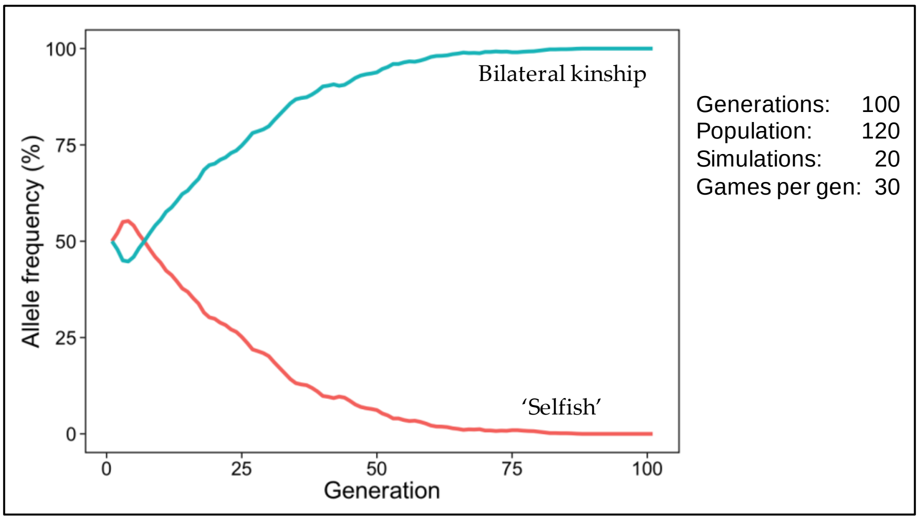


Figure 5-4: Simulated frequencies of the bilateral kinship (blue) and selfish (red) genes over 100 generations, at a population size of 120. Lines represent the average across 20 simulations.

Random investment vs. bilateral kinship recognition

What if, rather than being 'selfish', we compare the bilateral kinship allele against a 'random investment' strategy in which agents do invest in others but do so regardless of relatedness to them. In order to test this, I created an additional allele in which agents calculate their relatedness by descent to all others, but then randomise the individual to whom these relatedness values are associated. This means that agents with the 'random investment' gene are, importantly, going to be donating resources to others with a similar frequency to those with the 'bilateral kinship' allele such that the difference in strategies is about who they donate resources to, rather than how often they donate resources. I ran twenty simulations in which half of agents in the initial population had the 'random investment' allele, and half had the 'bilateral investment' allele. Other parameters were the same as above. As shown in Figure 5-5, the random investment allele was selected against even faster than the 'selfish' allele. With the bilateral kinship allele reaching fixation before 25 generations had elapsed in every simulation. The fact that selfishness is a better strategy than random investment is further confirmed in simulations comparing these two strategies directly (Figure 5-6).

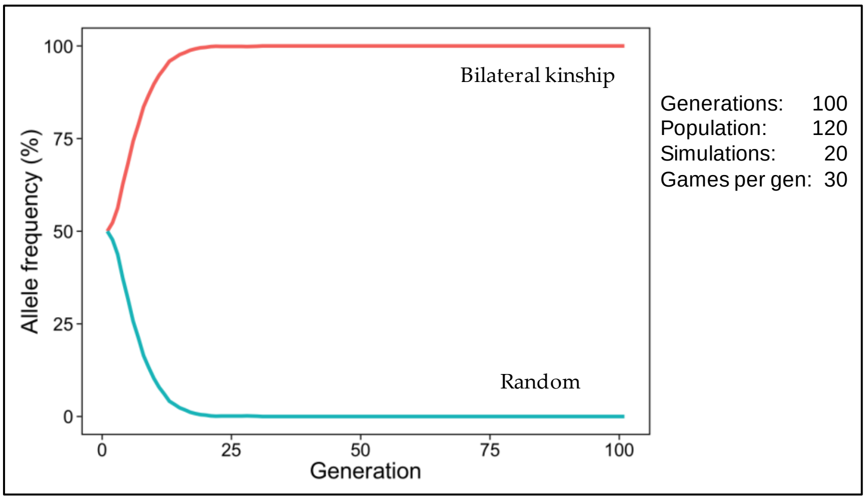


Figure 5-5: Simulated frequencies of the bilateral kinship (red) and random (blue) genes over 100 generations, at a population size of 120. Lines represent the average across 20 simulations.

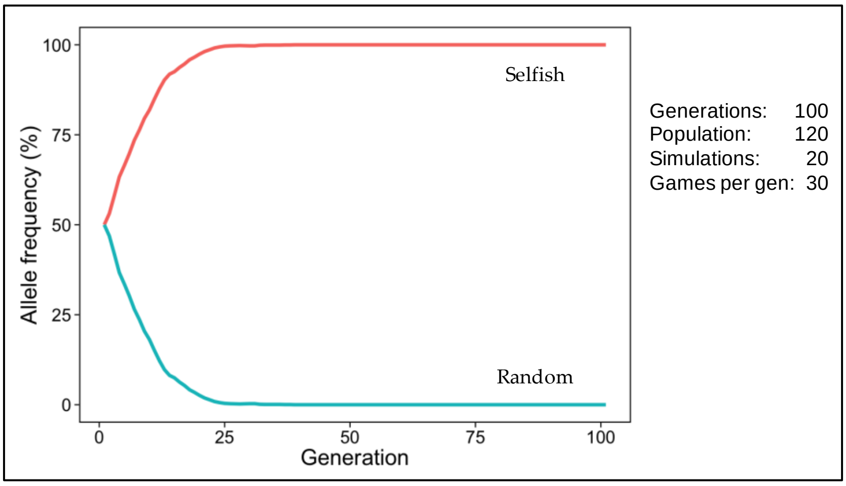


Figure 5-6: Simulated frequencies of the random (blue) and selfish (red) genes over 100 generations, at a population size of 120. Lines represent the average across 20 simulations.

5.5.2 Can investment in affinal kin increase inclusive fitness?

To provide a test of my hypothesis that investment in affinal kinship is adaptive, I ran 100 simulations at a population of 120, with 100 generations and 30 games per generation. I began the model with 50% of agents having the 'full kinship' allele (i.e. they recognised both affinal and consanguineal ties) and 50% of agents having the bilateral kinship allele (i.e. they recognise all consanguines but no affines). In all simulations, the affinal kinship recognition allele had reached fixation by 100 generations (Figure 5-7).

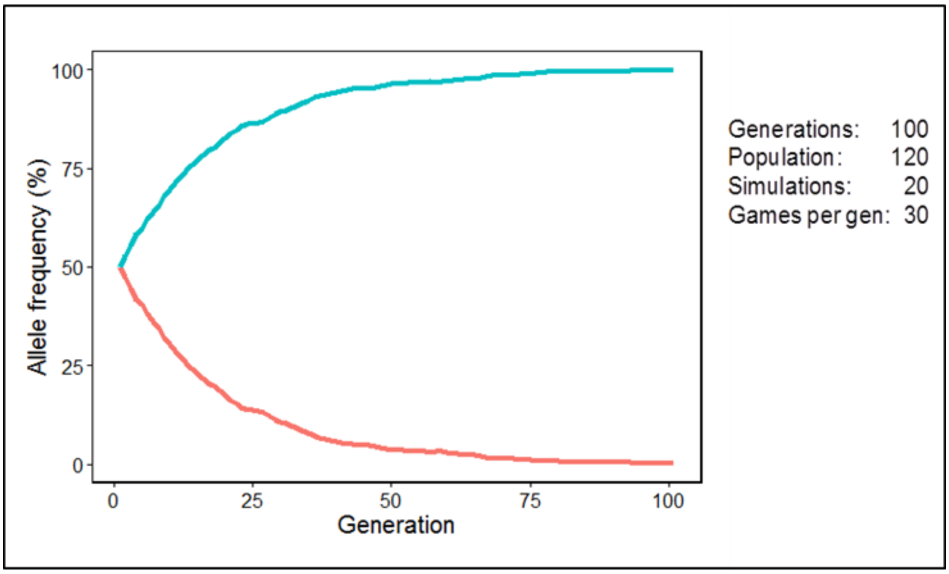
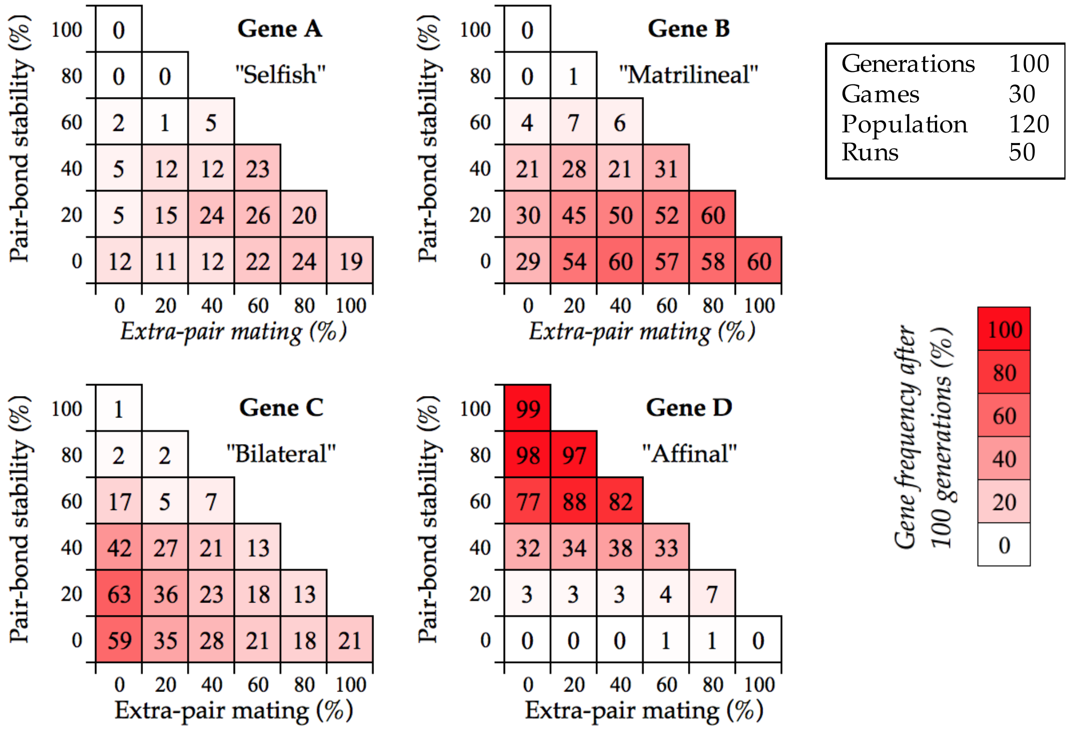


Figure 5-7: Simulated frequencies of the full kinship (blue) and consanguineal kinship only (red) genes over 100 generations, at a population size of 120. Lines represent the average across 20 simulations.

5.5.3 Did "pair-bonding give birth to human sociality"?

Although Figure 5-7 demonstrates that affinal kinship recognition can be adaptive, this is under conditions of no extra-pair mating and enduring pair-bonds. In other words, under conditions in which agents have perfect information about past and future reproductive events. What happens when we vary this? In what 'parameter space' is investing in affinal kin adaptive? In order to explore these questions, I ran 60 simulations of the model at a population size of 60 where each simulation continued until 100 generations had elapsed. In each generation, the 'investment game' was played 25 times. The model began with 25% of agents having each of the four alleles described above. I then tracked the changing frequency of alleles over 100 generations. I ran this set of 60 simulations across a range of extra-pair mating and pair-bond stability conditions. Since pair-bonding is unlikely when extra-pair mating is so high I did not model the parameter space in which the probability of extra-pair mating was greater than pair-bond stability. For each simulation, I recorded the frequency of each allele after 100 generations, averaging over the 60 simulations.

The results of this model are summarised in Figure 5-8 and clearly demonstrate that gene D (in which carriers evaluate relatedness according to common reproductive interest, and therefore include affinal kin) is the dominant strategy when pair-bond stability is greater than around 50%. When both pair-bond stability and extra-pair mating are low, gene C (recognition of bilateral descent) was selected for most strongly. Where pair-bond stability was low but extra-pair mating was high (obscuring paternity certainty), recognition of matrilineal kinship was selected most strongly. These results suggest that recognition of, and investment in, paternal kin is only adaptive when paternity uncertainty is low, a fairly intuitive finding. Gene A, which caused agents to be totally selfish, not investing in any others under any circumstance was the least successful allele, although it was not strongly selected against when paternity certainty was high and pair-bond stability was low. Under no conditions was the 'selfish' gene found, on average, at significantly greater frequencies than its starting point of 25%.



Gene A "Selfish"

Pair-bond stability (%)						
100	0					
80	0	0				
60	2	1	5			
40	5	12	12	23		
20	5	15	24	26	20	
0	12	11	12	22	24	19
Extra-pair mating (%)	0	20	40	60	80	100

Gene B "Matrilineal"

Pair-bond stability (%)						
100	0					
80	0	1				
60	4	7	6			
40	21	28	21	31		
20	30	45	50	52	60	
0	29	54	60	57	58	60
Extra-pair mating (%)	0	20	40	60	80	100

Gene C "Bilateral"

Pair-bond stability (%)						
100	1					
80	2	2				
60	17	5	7			
40	42	27	21	13		
20	63	36	23	18	13	
0	59	35	28	21	18	21
Extra-pair mating (%)	0	20	40	60	80	100

Gene D "Affinal"

Pair-bond stability (%)						
100	99					
80	98	97				
60	77	88	82			
40	32	34	38	33		
20	3	3	3	4	7	
0	0	0	0	1	1	0
Extra-pair mating (%)	0	20	40	60	80	100

Generations	100
Games	30
Population	120
Runs	50

Figure 5-8: Heat maps representing the gene frequency of alleles A, B, C, and D after 100 generations of the model where population was 120, and 30 investment games were played per generation. Results are the average across 60 simulations. Dark red represents a large proportion, white represents a low proportion. The x-axis of each heat map represents the likelihood of extra-pair mating. The y-axis represents pair-bond stability.

These results provide support for Chapais's (2009) argument that pair-bonding is a necessary condition for the emergence of human kinship and also provide proof of concept for my alternative coefficient of relatedness – in the appropriate social context, the recognition of, and investment in, affinal kin increases inclusive fitness.

5.5.4 General conclusions of the model

My model provides a framework within which agents can derive inclusive fitness benefits through aiding related individuals. Agents equipped with the ability to donate resources to others when the condition of Hamilton's rule are met have higher fitness than agents who are entirely 'selfish', never investing in any other agents. In other words, the model provides proof of concept for standard inclusive fitness theory (*sensu* Hamilton 1964), whereby individuals assess their relatedness to others according to the extent of their shared ancestry. The model also shows, however, that investment in affinal kin can be fitness enhancing when pair-bonds are stable and paternity certainty is high. This provides proof of concept for the 'coefficient of common reproductive interest' outlined in section 5.3. I also show that when past paternity is known but current pair-bonds are likely to dissolve, the dominant strategy is to invest in bilateral consanguines but not in affines. Finally, when pair-bonds are stable and paternity certainty is high, the dominant strategy is to invest in both bilateral kin and affines (i.e. in common reproductive interest).

5.5.5 Exploring model parameters

How robust are the results of my model? In order to show that my results have broad relevance, I need to demonstrate that they hold across a broad parameter space. Doing so is not only good practice in modelling but it allows the identification of the conditions necessary for our results to emerge.

Population size

In order to explore the effect of population size on results, I ran the model at population sizes ranging from 60 to 300. As demonstrated in Figure 5-9, population size made little difference to the strength of selection. After 25 generations had elapsed, the positively selected allele (in this case the common reproductive interest allele) was found at similar frequencies at all population sizes[5].

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[5] My original motivation for running the model at the relatively small populations sizes of 60 and 180 described above was to reduce the time it takes to run the model. Several parts of the model

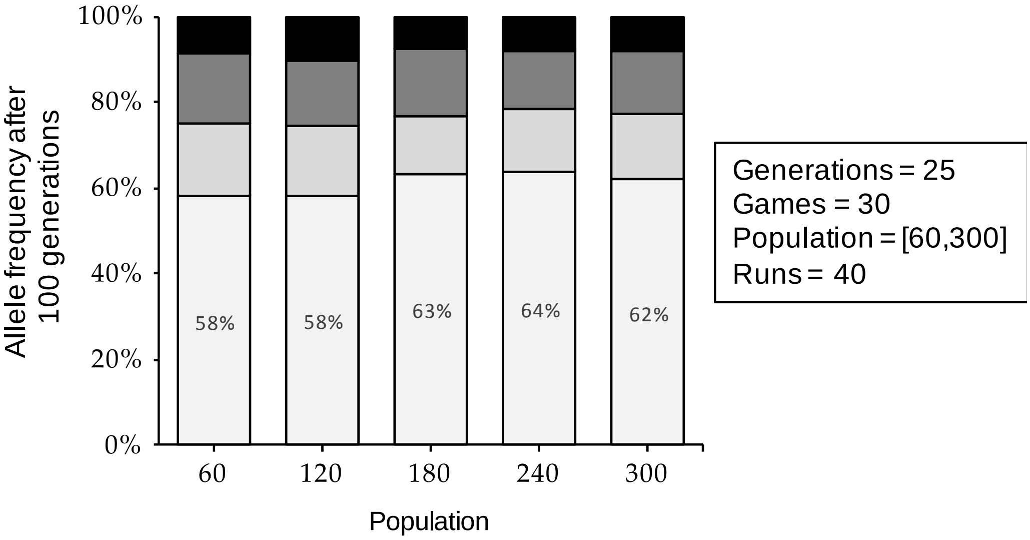

Figure 5-9: Mean allele frequency over 40 simulations after 100 generations and 30 games per generation with a varying population size. From bottom to top and lightest to darkest are (1) affinal and bilateral kinship, (2) bilateral kinship, (3) matrilineal kinship, (4) 'selfishness'.

The number of 'energy games' played

As outlined above, agents invest in others during the 'energy game' phase of the model in which agents are assigned a random number of energy units which they can donate to others if doing so is adaptive given their understanding of relatedness. In each generation, the 'energy game' is played several times. In each game, agents are randomly assigned between 1 and 20 energy units. If we imagine only one game being played per generation, then the energy units held by each agent will be more a function of luck than of the investment received from others. As we play more rounds, stochasticity decreases, and the importance of investment from others increases. To explore the effect of this on model results, I ran forty simulations with the 'standard' parameters but varying the number of energy games played between 10 and 40. As can be seen from Figure 5-10, the

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require iteration through all dyads, such that a doubling of population size results in a fourfold increase in computing time.

more games were played per generation, the more strongly the positively selected allele was selected.

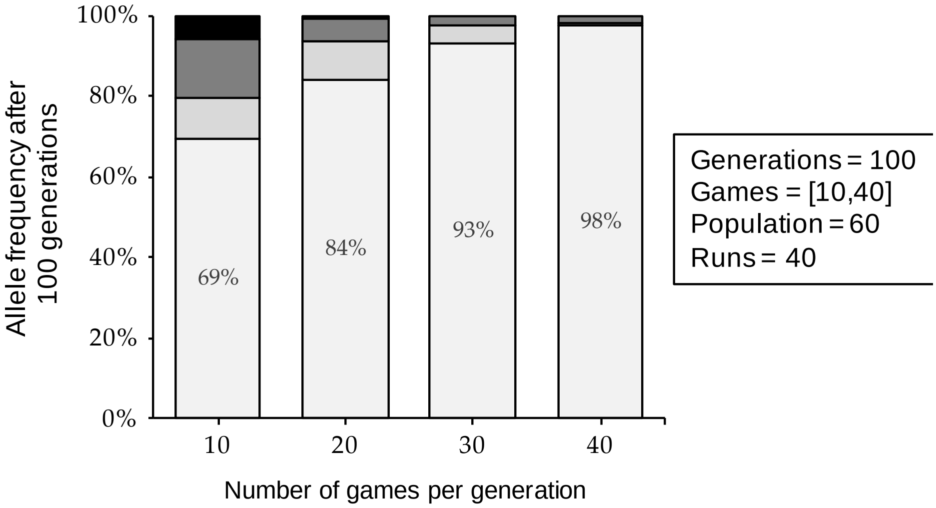

Figure 5-10: Mean allele frequency over 40 simulations after 100 generations and a population of 60 agents with a varying number of games per generation. From bottom to top and lightest to darkest are (1) affinal and bilateral kinship, (2) bilateral kinship, (3) matrilineal kinship, (4) 'selfishness'.

Only one generation

The game presupposes a human-like scenario in which three generations are alive at the same time. This allows individuals access to both lineal and collateral kin. Perhaps it is only in such a situation that affinal kinship recognition might be adaptive? In order to test this, I created a version of the model in which there was only one generation of agents in the game at any one time. However, as the results in Figure 5-11 demonstrate, affinal kinship recognition was positively selected for, even in this context.

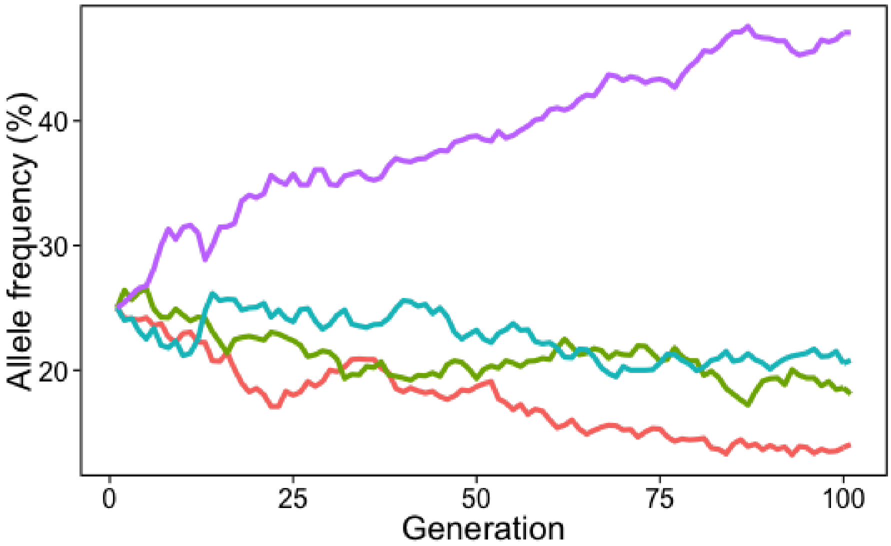

Figure 5-11: Simulated frequencies of the bilateral kinship (blue), matrilineal kinship (green), affinal and bilateral kinship (purple), and 'selfish' (red) genes over 100 generations at a population size of 60 with 30 games per generation where there was only one generation in the model (and therefore no inter-generational affinal ties existed).

No investment in spouses

Are the benefits of affinal kinship actually realised through investment in children-in-law, siblings-in-law and the like? Or is it simply a function of individuals being able to invest in their spouses? In order to establish this, I ran a version of the model where investment in spouses was prohibited. As shown in Figure 5-12, selection for the 'common reproductive interest' allele (purple) was still positively selected for when investment in spouses was prohibited, although selection was slower than it is when spouse investment is permitted Figure 5-13.

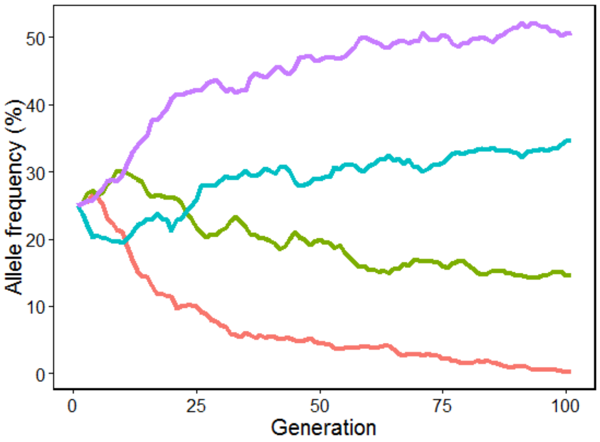

Figure 5-12: Simulated frequencies of the bilateral kinship (blue), matrilineal kinship (green), affinal and bilateral kinship (purple), and 'selfish' (red) genes over 100 generations at a population size of 60 with 40 games per generation where investment in spouses was prohibited.

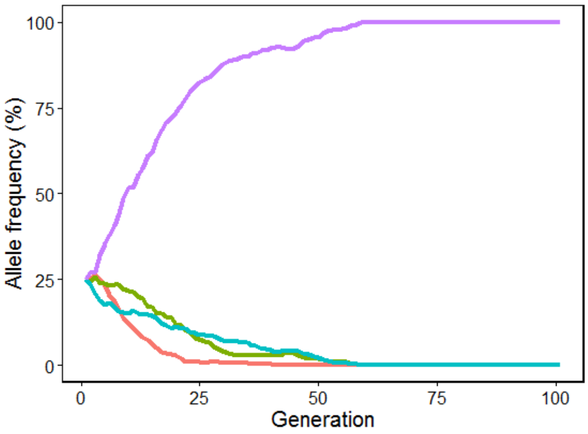

Figure 5-13: Simulated frequencies of the bilateral kinship (blue), matrilineal kinship (green), affinal and bilateral kinship (purple), and 'selfish' (red) genes over 100 generations at a population size of 60 with 40 games per generation where investment in spouses was not prohibited.

Curve of marginal means

In the 'energy game' part of the model, individuals assess not only their relatedness to all others but also the costs and benefits of surrendering resources. The costs may only outweigh the benefits because energy units have a diminishing value, such that the second unit is less valuable than the first. Since asymmetries in value are necessary for donations in the 'energy game' to occur, it is worth exploring what influence different marginal value functions have on the strength of selection in the model.

I therefore ran the 'standard' version of this model with four different energy value functions (*i* to *iv*). Function (*i*) has no diminishing value - each unit of energy has a value of 1. In functions (*ii*) and (*iii*), the first energy unit has a value of 1, and each additional energy unit is worth 0.025 and 0.05 less than the previous unit, respectively. Function (*iii*) is the one used for all models presented above. In function (*iv*), the value of each additional unit is 85% of the previous one. The formulae for the cumulative value and value of the nth unit are provided in Table 5-1. Graphs of the unit and cumulative values are provided in Figure 5-14.

Table 5-1: Definitions of the four energy value functions plotted in Figure 5-14.

Function	Value of nth unit	Cumulative value
i	1	n
ii	$1 - 0.025(n-1)$	$n - 0.025\left(\frac{n(n-1)}{2}\right)$
iii	$1 - 0.05(n-1)$	$n - 0.05\left(\frac{n(n-1)}{2}\right)$
iv	$0.85^{(n-1)}$	$\sum_n 0.85^{(n-1)}$

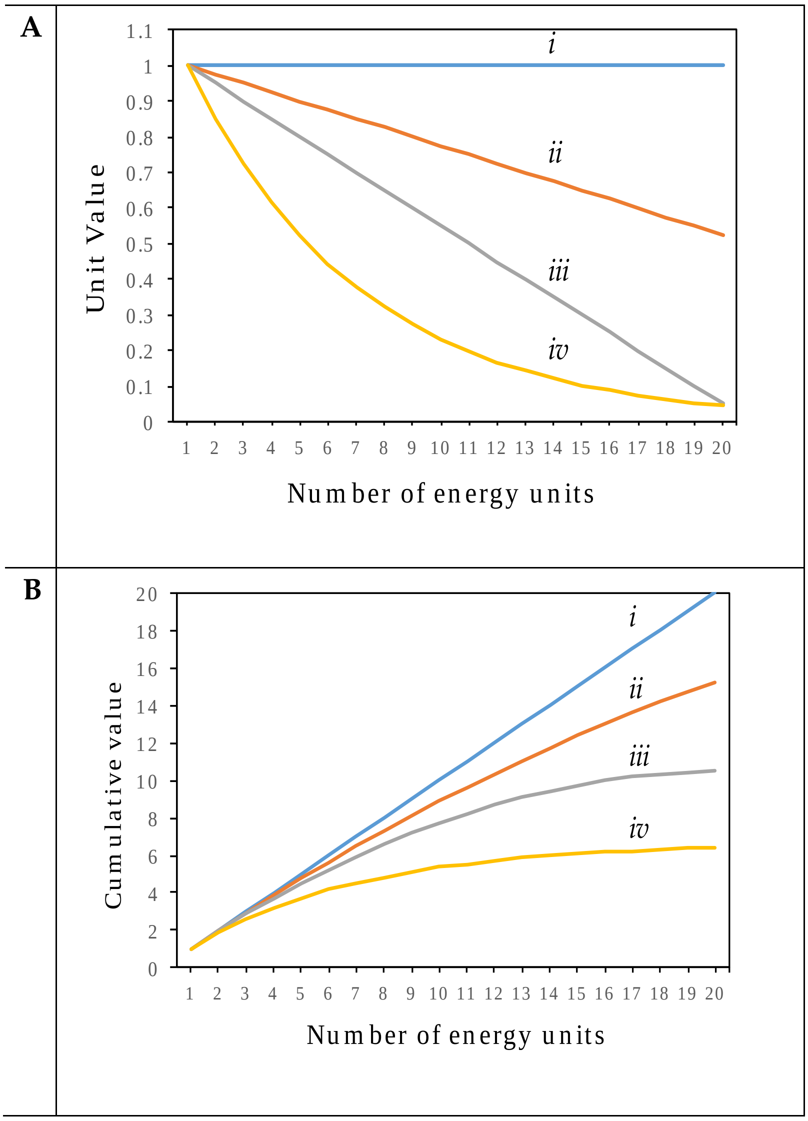

Figure 5-14: Unit values (*panel A*) and cumulative values (*panel B*) for the four functions defined in Table 5-1.

Using each of the four value functions defined above, I ran 40 simulations at a population size of 60, over 100 generations, with 30 energy games played per generation. As shown in Figure 5-15, while functions (*iii*) and (*iv*) created the necessary asymmetries in value required for energy sharing to be fitness enhancing, functions (*i*) and (*ii*) did not, leading to patterns that imply either very weak selection or randomly drifting allele frequencies.

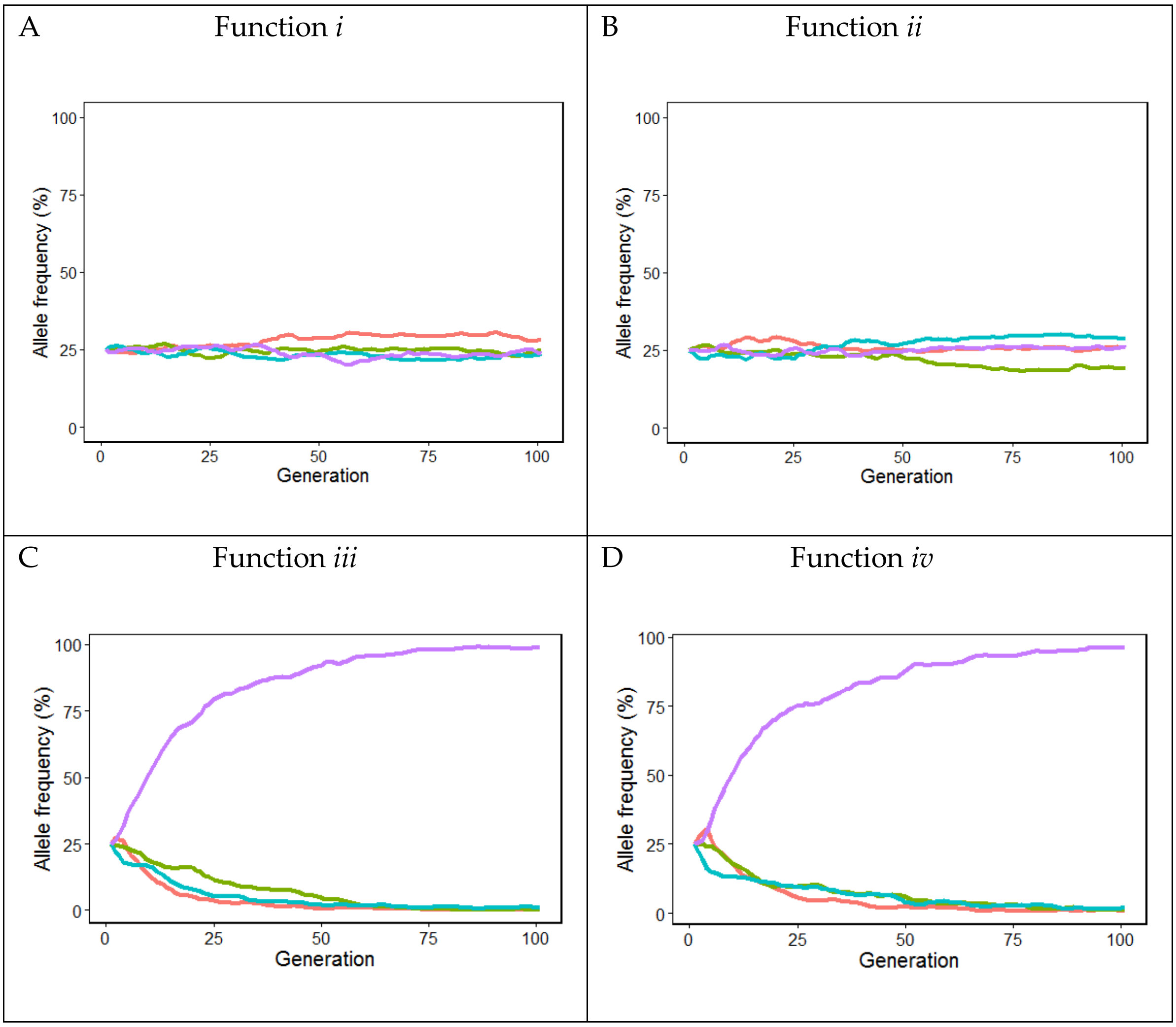

Figure 5-15: Allele frequencies over 100 generations and 40 simulations using each of the four value functions defined above. Blues lines represent bilateral kinship, green lines matrilineal kinship, purple lines represent the recognition of both affinal and bilateral kinship, and red represents non-investment (selfishness).

5.6 Behavioural observations

The modelling presented above provides proof of concept for the coefficient of common reproductive interest and suggests that it would be positively selected over the reckoning of relatedness through common descent under conditions of low extra-pair mating and high pair-bond stability. The next test of this coefficient is its explanatory power of observed behavioural interactions ‘on the ground’. In this section, I present the results of analyses in which I explore how well the ‘coefficient of common reproductive interest' outlined in section 5.3 predicts behavioural interactions among the Agta. Critically, I seek to compare the relative explanatory power of the coefficient of common descent with the coefficient of common reproductive interest.

5.6.1 Methods

Along with my colleagues in the field, I collected data on behavioural interactions among five Agta camps: Diago, Didikeg, Dinipan, Simento, Dipaguiden, and Diabbut. In each community, we collected data on the frequency of contact between all individuals in a series of communities using 'motes', an electronic device which sends and received radio signals at regular intervals. Full details of this data collection are described in section 2.3.4 above. For each dyad included in the motes experiments, I estimated the proportion of time spent together and, for each camp, generated a matrix of behavioural associations. I take behavioural associations as a proxy for willingness to engage in altruistic or cooperative behaviours. I then generated, using scripts based on those used in the previous chapter and described in section 4.3, (a) the coefficient of relatedness between these dyads, and (b) the coefficient of common reproductive interest, as defined in equation 5-3 above.

The aim of the analyses presented below was to compare the explanatory power of these two coefficients of relatedness in predicting frequency of interaction between campmates. In order to do this, I used a function available in the 'sna' package for 'R' to perform a linear regression of the matrix of dyadic relatedness between individuals onto a matrix of the frequency of interactions between individuals. The function then tests the resulting fits and coefficients against a null hypothesis derived from 1,000 random iterations using a Quadratic assignment problem (QAP) permutation test (Krackhardt 1988). This procedure tests whether a relationship we see between relatedness and frequency of interaction is greater than we would expect by chance. I produced two models in each camp. In model 1 I regressed the proportion of time that each dyad spent together with their coefficient of relatedness by common descent (i.e. Wright's coefficient). In model 2, I regressed this same dyadic interaction data against the coefficient of reproductive interest outlined above.

5.6.2 Results

Behavioural associations

The results of the two models for each of the six Agta camps are presented in Table 5-2. Both coefficients of relatedness were significant predictors of behavioural associations. In five of six camps, the R-squared value of model 2 was greater than that of model one, suggesting that behavioural interactions among the Agta are better explained by shared genetic interest in the next generation than by shared ancestry.

Table 5-2: Results of QAP models across six Agta camps that evaluate the power of the standard coefficient of relatedness (Model 1) and the coefficient of common reproductive interest (Model 2) in predicting overserved dyadic interactions based on 'motes' data. * *p* <. 05; ** *p* <. 01; *** *p* < .001

	Diago	Didikeg	Dinipan	Simento	Dipaguiden	Diabbut
N individuals	39	48	33	18	26	36
Model 1 (coefficient of relatedness)						
Intercept	.032**	.01	.04	.04**	.07**	.048*
Relatedness	.24***	.34***	.31***	.12**	.36***	0.41***
R^2	.21***	.28***	.19***	.08***	.18***	.21
Model 2 (coefficient of common reproductive interest)						
Intercept	.028***	.01	.04	.04*	.06**	.046**
Relatedness	.37***	.53***	.37***	.18**	.59***	.56***
R^2	.31***	.38***	.17***	.12***	.28***	.25***

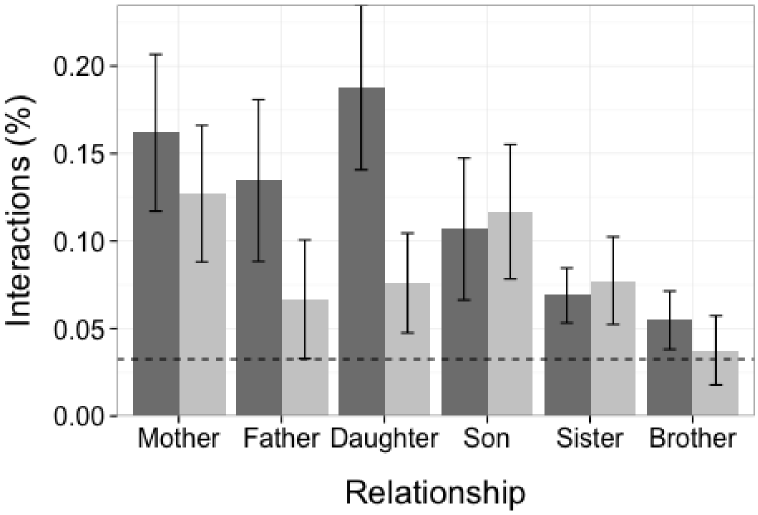

Figure 5-16: Proportion of time in the motes experiment that individuals interacted with kin of different kinds. Dark grey bars represent time spent with consanguineal kin, and light grey bars represent time spent with the equivalent affinal kin (for example, on far left, the dark grey bar is interactions with mothers, and light grey is with mothers-in-law). Error bars represent standard deviation.

5.7 Discussion

In so far as humans have the ability to classify large and complex webs of kinship, it could be said that we have kin recognition *par excellence.* Almost all systems of human kinship, however, recognise affinal as well as consanguineal ties. That is, they recognise both marriage *and* descent. As well as an important part of human social lives cross-culturally, affinal kinship may have had a transformative effect on human sociality, ameliorating between-group hostility and facilitating the emergence of the 'tribal' supra-group level of social organisation (Chapais 2009; Lévi-Strauss 1969). Going back to first principles, however, we ought to ask why, from an inclusive fitness point of view, individuals would be interested in their affinal kin. This is an especially pertinent question since standard biological conceptions of relatedness focus only on shared ancestry, overlooking affinal ties entirely.

In this chapter, I argue, as Hughes (1988) and Burton-Chellew and Dunbar (2011) have done, that relatedness ought to be reckoned *forward*, rather than *backwards*. I propose a variation on Wright's (1922) coefficient of relatedness that estimates relatedness based on shared reproductive interest in the next generation, rather than shared ancestry. In doing so, I incorporate both affinal and consanguineal kinship into estimations of relatedness. I describe this as the 'coefficient of common reproductive interest' (*s*). I show, using an agent-based evolutionary model, that this coefficient of common reproductive interest represents an adaptive behavioural heuristic when pair-bond stability is high and extra-pair mating is infrequent. This is, to be frank, demonstrating the obvious - it should not be surprising that stable-pair bonds are a pre-requisite for affinal kinship – this is true almost by definition. What is more important is the demonstration that investment in affinal is fitness enhancing even under the kind of conditions of pair-bond stability typical of humans [6]. In my model, agents able to reckon relatedness forward realise greater inclusive fitness benefits than those only able to recognise relatedness through shared ancestry.

What new insights can we gain from reckoning relatedness through shared genetic interest? It should be noted that, unlike relatedness by descent, reproductive interest is not always symmetrical. For example, a man will share genes with the child of his sister's husband but not with the child of this wife's brother. Asymmetries may also exist between a mother-in-law and daughter-in-law, with the former being related to the children of the latter but not *vice versa*. Cant and Johnstone (2008) argued that this

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[6] Of course, there is considerable cross-cultural variation in the stability of pair-bonds, the reproductive skew, marriage practices, family structure, and understanding of paternity (Flinn & Low 1986; Fox 1967; Ellsworth et al. 2015; Murdock & White 1969; Walker et al. 2015). Although systematic comparison of this diversity is difficult (Veneziano 2000; Ember & Ember 2000), a recent paper by Ellsworth and colleagues (2015) suggests that pair-bond stability and male reproductive skew can be estimated from genealogies by considering the relative proportion of full siblings, paternal half sibling, and maternal half siblings. They find that across available genealogies from 80 societies, 61% of siblings were full siblings, 27% were paternal half-sibs, and 13% were maternal half-sibs.

asymmetry in relatedness to the next generation may underlie the evolution of female reproductive senescence. They argue that in a female-dispersing system, a migrating woman moves into a camp in which she will be unrelated to the children of the other women. For example, she would have no genetic interest in her husband's mother's children. The husband's mother, however, will have a genetic stake in her offspring (they will share a relatedness of r = 0.25). As a result, "a younger female will have an advantage in reproductive competition with older females because she is insensitive to the costs she inflicts on an older female by breeding and because older females have more to gain by helping" (p5334). Cant and Johnstone suggest that when the younger female starts to reproduce, the stable strategy is for the older woman to invest in 'helping' her daughter-in-law. This, of course, requires a patrilocal residential system which, in chapter four, I argue is not representative of contemporary hunter-gatherers and therefore may not have been as common as assumed in human evolutionary history. Nonetheless, Cant and Johnson's model of the evolution of menopause makes use of the idea of common reproductive interest, even if they do not generalise its calculation.

As mentioned in section 5-2, the recognition of affinal kin and, in particular, the ability for unrelated males to recognise their shared interests as brothers and husbands of 'exchanged' females is at the heart of the 'Alliance Theory' outlined by structuralist anthropologists and most notably by Claude Levi-Strauss in his 'Elementary Structures of Human Kinship' (1969). For Levi-Strauss, the reciprocal exchange of sisters between groups allowed the amelioration of hostile between-group relations and the formation of the tribal unit of social organisation. Chapais (2009) also draws on similar ideas in his discussion of the importance of pair-bonding in the expansion of human social groups. Although it assumes a patrilocal residential system, strict reciprocal exchange of females does allow affinal relationship to be symmetrical since one's sister's spouse is also one's spouse's brother, meaning that all parties have shared reproductive interests in the next generation.

Why did affinal kinship recognition evolve?

I would argue that three conditions are necessary for affines to be recognised and to be worth maintaining relationships with. The first condition, as demonstrated by my model, is enduring pair-bonds. This is, of course, true by definition since you can't have in-laws without marriage. The second condition is the cognitive capacity to recognise third-party relationships. The cognitive capacities required to conceptualise kinship almost certainly require the kind of shared intentionality and theory of mind argued to underpin human social intelligence (Frith & Frith 2005; Tomasello & Carpenter 2005; Call 2009). Arguably, complex kinship also requires the kind of recursive thinking required for human language (Pinker & Jackendoff 2005; Hauser et al. 2002). Milicic (2013) argues that "kinship terms could have been the original nucleus of human language" (p1). Indeed, the importance of kinship in human cognitive evolution was suggested almost 150 years ago by Lewis Henry Morgan (1871) who wrote that "A formal arrangement of the more immediate blood kindred into lines of descent, with the adoption of some method to distinguish one relative from another, and to express the value of the relationships would be one of the earliest acts of human intelligence" (p10). Although interest in kinship within evolutionary and quantitative anthropology is experiencing, in the words of Shenk and Mattison (2011), something of a 'rebirth', questions remain about the relationship between kinship and grammar (Jones 2004; Jones 2010; Kemp & Regier 2012) and the extent to which humans have an innate capacity for kinship detection (Lieberman et al. 2007).

Finally, pair-bonding and advanced social cognition may be necessary for affinal kinship recognition but they do not necessarily make affines important, or worth maintaining relationships with. What makes affines so important in so many human societies? As I will argue in the following chapter, humans have evolved an energetically demanding life-history strategy. This means that humans are evolutionarily committed to energetic inter-dependence. In recognising affinal kin, we can expand the pool of individuals who can provide the provisioning required to meet the costs of our derived life history.

5.8 Summary

What is the significance of the work presented in this chapter? Firstly, to clarify, it is not a reformulation of Hamilton's rule– it falls entirely within the scope of inclusive fitness theory. What it does require, however, is that we conceptualise relatedness as reckoned *forward*, through common reproductive interest, rather than *backwards*, through shared descent. Such a framework should not be challenging to evolutionary biologists – fitness returns must always be realised through future reproductive events. In reckoning kinship forward, we realise that the two building blocks of human kinship – consanguinity and affinity - both represent routes through which individuals can derive inclusive fitness benefits. Thus, at least from the point of view of evolutionary anthropology, by incorporating affinal kinship into estimations of relatedness, this work provides an important bridge between biological and social conceptions of kinship. This chapter also emphasises the importance of pair-bonding in human social evolution. I argue that pair-bonding not only allows for the inter-sexual provisioning required to balance the long-term energetic deficits faced by forager mothers but, by allowing individuals to recognise affinal kinship, opens up an additional pool of individuals who recognise a shared interest with you in the next generation.

Chapter 6: How does multilevel sociality structure cooperation?

6.1 Summary

In this chapter, I explore patterns of inter-household food sharing across six Agta camps, finding that food sharing is highly concentrated within 'clusters' of households that, along with the household and camp, form a three-tiered multilevel social organisation. I explore patterns of relatedness, co-foraging, and food production across the household, cluster, and camp. I argue that multilevel sociality (see definition in 6.2 below) allows individuals access to the range of social relationships required to mitigate against both the day-to-day variability in foraging success inherent in the human foraging economy (McElreath & Koster 2014; Winterhalder 1986) and the long-term inter-personal dependency to which humans are committed due to our costly life-history niche (Kaplan et al. 2000; Mace 2000).

6.2 Hunter-gatherer multilevel social organisation

In the previous chapters I described a social organisation among both the Agta and contemporary hunter-gatherers more generally in which individuals belong to a series of nested social groupings: stable households, within extended families including both bilateral consanguines and affinal kin, within camps that are themselves fluid sub-sets of the wider population. This kind of social organisation has been described as a 'multilevel' organisation (Anderson 1983; Grueter, Chapais, et al. 2012). As outlined in section 1.1, Chapais (2008, 2011) argues that this multilevel social organisation is the product of pair-bonding which creates both a core social group (the household) and allows individuals to recognise the kinship ties required for the existence of meta-groups. Foley and Gamble (2009) argue that the evolution of both supra-communities and infra-group structure in the hominin lineage to be the product of a series of ecological, technological, and behavioural transitions.

Multilevel sociality, however, is not exclusive to humans. The most inclusive definitions of multilevel sociality include any social system in which individuals are recognisably part of a group of which all members are part of a wider group. This would, for example, include both the fission-fusion communities seen in chimpanzees (Goodall 1986; Wakefield 2008; Lehmann et al. 2014), as well as the aggregations of 'one male units' found in many papion species (Patzelt et al. 2014; Swedell & Plummer 2012; Hongo 2014; Anderson 1983; Crook & Gartelan 1966). Others, such as Grueter et al. (2012), however, have a more restricted definition in which the smallest social unit of a social system must include "single-male-multi-female core units nested within larger social bands" (p1002) as most clearly seen among the papionins, colobines, and hominins (see

Table 6-1 for a full list and citations). In other words, Grueter et al. (2012) argue that truly multilevel societies must be what Lehmann and colleagues (2014) describe as ‘molecular’ and ‘bottom up’ groups in which individuals belong to stable groups within a wider meta-group. This is in contrast to ‘atomistic’ or ‘top down’ groups in which individuals are found in fluid sub-groups of the wider meta-group (see Figure 6-1). Humans groups can be described as molecular/bottom-up, while chimpanzees societies are atomistic or top-down.

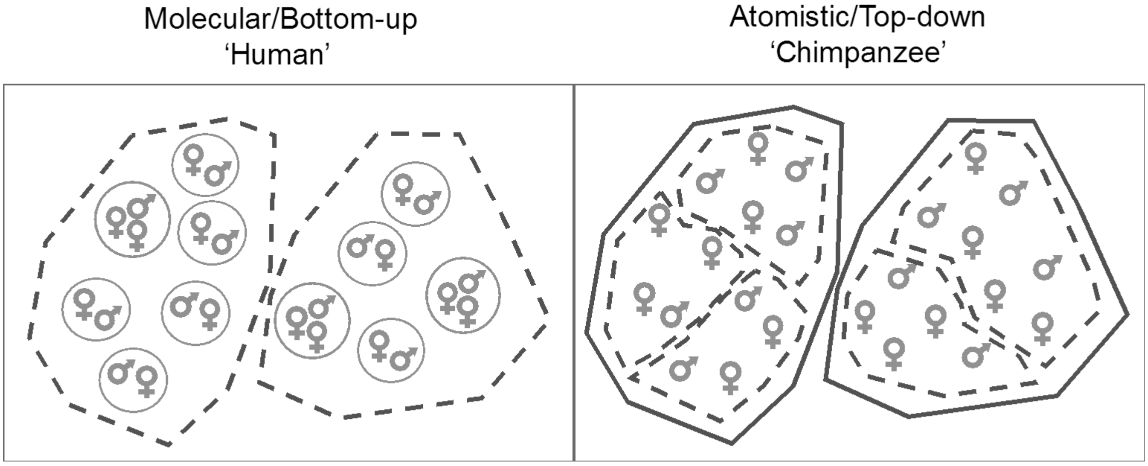

Figure 6-1: Schematic representation of ‘bottom-up’ or ‘molecular sociality (*left*) and ‘top-down or ‘atomistic sociality (*right*). Solid lines represent social groups of stable membership, dotted lines represent groups of fluid membership.

6.2.1 Multilevel sociality in non-human mammals and primates

In recent years, there has been much interest in multilevel social organisation with, for example, a special edition of the *International Journal of Primatology* dedicated to it in 2012 (including many of the papers listed in Table 6-1). Among primates, multilevel sociality in the strict ‘bottom-up’ sense defined above has been described largely among papionins (baboons, madrills, geladas), colobines (snub-nosed monkeys), and humans (see Table 6-1 for a full list and citations). How many levels do these groups have? Among hamadryas and gelada baboons, individuals have been described as part of a one-male ‘harems’, within a ‘team’ of two or three harems, within a band, within a community (Lehmann et al. 2014, p246). Among Guinea baboons, Patzelt and colleagues (2014) describe a similar organisation with one-male units situated within parties, within gangs, within communities.

Outside of the primates, multilevel social organisation has been described among cetaceans, elephants, and a number of other taxa (see Table 6-1). In some cases, however, questions must be asked about how units of social organisation ought to be defined. For example, in a recent study of sperm whales by Cantor and colleagues (2015), three units of social organisation are described – “individuals, within social units, within vocal clans” (p3). Firstly, describing individuals as a level of social organisation is questionable. Secondly, the vocal clans are defined on similarities in vocalisations, rather than actual behavioural interactions. Although methodologically challenging to collect data on behavioural interactions in many species (especially whales), social groups should ideally be defined based on social interactions, rather than proxies of it.

Table 6-1: Non-human mammalian societies described as have a multilevel social organisation (broadly defined).

Taxon	*Species*	*Citation*
Papions	Hamadryas Baboons (*Papio hamadryas*)	(Schreier & Swedell 2012; Swedell & Plummer 2012; Anderson 1983)
	Baboon Group (*Papio anubis × P. hamadryas*)	(Bergman & Beehner 2004)
	Guinea baboon (*Papio papio*)	(Patzelt et al. 2014; Maciej et al. 2013)
	Mandrills (*Mandrillus sphinx*)	(Hongo 2014)
	Geladas (*Theropithecus gelada*)	(Snyder-Mackler et al. 2012; Crook & Gartlan 1966)
Colobines	Yunnan snub-nosed monkeys (*Rhinopithecus bieti*)	(Ren et al. 2012)
	Golden snub-nosed monkeys (*Rhinopithecus roxellana*)	(Guo et al. 2015; Qi et al. 2014)
Other primates	Peruvian Red Uakaris *(Cacajao calvus ucayalii)*	(Bowler et al. 2012)
	Common chimpanzee *(Pan troglodytes)*	(Goodall 1986; Wakefield 2008)
	Spider monkeys (*Ateles belzebuth*)	(Suarez 2001)
Non-primate mammals	Reticulated giraffe (*Giraffa camelopardalis*)	(VanderWaal et al. 2014)
	Asian elephants (*Elephas maximus*)	(de Silva & Wittemyer 2012)
	African elephants (*Loxodonta sp*)	(Wittemyer et al. 2005; Moss & Poole 1983; Hill et al. 2008)
	Sperm Whales (*Physeter microcephalus*)	(Whitehead et al. 2012; Cantor et al. 2015; Whitehead et al. 1991)
	Brown Bats (*Eptesicus fuscus*)	(Willis & Brigham 2004)
	Spotted hyaena (Crocuta crocuta)	(Smith et al. 2008)
	Wild horses (Equus caballus)	(Linklater et al. 2000)
	Prairie dogs (*Cynomys ludovicianus*)	(Hoagland 1995)
	Bottlenose dolphins (*Tursiops truccatus*)	(Baird et al. 2009)
	Plains zebra (*Equus quagga*)	(Rubenstein & Hack 2004)
	Orca (*Orcinus orca*)	(Hill et al. 2008)

6.2.2 Multilevel sociality in humans

That human communities live in a series of concentric, hierarchical social groups is not a particularly novel observation. In his classic 1940 ethnography of the Nuer pastoralists of southern Sudan, for example, Evans-Pritchard describes the Nuer as living in huts, within homesteads, within hamlets, within villages, within tertiary, secondary, and primary tribal sections, within the wider Nuer tribe (Evans-Pritchard 1940). Among hunter-gatherers, anthropologists have long been discussing important units of social organisation with concept such as Birdsell's (1958) definition of the community level of social organisation of around 500 individuals being much discussed (Marlowe 2005; Layton & O'Hara 2009; Kelly 2013; Lehmann et al. 2014). Although the fluidity of hunter-gatherer camps implies that individuals have social networks that stretch beyond the residential camp, whether these individuals are all part of a bounded group is unclear.

Of the more recent descriptions of multilevel sociality in humans, two particularly important papers are by Zhou and colleagues (2005) and Hamilton and colleagues (2007). Zhou and colleagues (2005) compile data on the size of layers of personal social networks and conduct a fractal analysis which allows them to identify a "discrete hierarchy of group sizes with a preferred scaling ratio close to three" (p439). In other words, their analyses suggest that rather than a continuous range of group sizes, groups are more likely found of around 3-5, 9-15, 30-45 and 150 individuals. This latter group size is the maximum size of human social group suggested by Dunbar (1992) based on extrapolations from the general trend between brain size and group size seen in primates (Dunbar 1998; Dunbar 2003). Hamilton et al. (2007) conducted a similar analysis to Zhou et al. (2005) using data on social group sizes from 339 hunter-gatherer societies compiled by Binford (2001). Although they report a scaling ratio between social units of closer to four than the ratio of three reported by Zhou et al., a subsequent reanalysis of their data by Lehmann et al. (2014) demonstrated that this difference is due to the inclusion of individuals as a unit of social organisation. The scaling ratios of 3-4 have, interestingly, also been found among elephants, gelada baboons, hamadryas baboons, and orcas in a study by Hill et al. (2008). Multilevel social organisation has also been described in archaeological record (Grove 2010a; Grove 2010b), and online communities (Fuchs et al. 2014)

6.2.3 From *form* to *function*

I think it would be fair to summarise the existing literature on human multilevel sociality by saying that we have a good idea of its *form*, but a poor understanding of its *function* (if it is functional at all). What might account for the structure of hunter-gatherer groups? To my mind, there are three bodies of literature which should be brought to bear on this question. The first relates to understanding the evolutionary history of human sociality (Foley & Gamble 2009; Chapais 2013; Foley 2001). The second is that relating to cognitive constraints on group size. The social brain hypothesis (Dunbar 2003; Dunbar & Shultz 2007; Joffe & Dunbar 1997) suggests that the encephalization seen across the haplorrhine primates was driven by selection for increased social intelligence. This hypothesis is well supported by strong correlations between various measures of brain size and group size across haplorrhines (Dunbar 1992; Aiello & Dunbar 1993). One implication of this work is that social intelligence is limited by brain size. Indeed, there is evidence of positive correlations between personal network size and grey matter density in relevant brain regions both in humans (Lewis et al. 2011; Powell et al. 2012; Spitzer 2012; Sutcliffe et al. 2012), and non-human primates (Sallet et al. 2011). Extrapolating from the relationship between brain size and group size, Dunbar (1998) suggests a maximum human group size of around 150 individuals, a number that has become popularly known as 'Dunbar's number' and has received empirical support across a range of social contexts (Dunbar 1993; Hill et al. 2003; Grove 2010a; Barrett et al. 2002). Based in part on the work by Zhou et al. (2005) and Hamilton et al. (2007), it has also been suggested that cognitive constraints act not only on the maximum group size but on the size of smaller social units within this, such as the 'support clique' and 'sympathy group' (Dunbar & Spoors 1995).

Finally, there is a large amount of work, both theoretical and empirical, relating to ecological determinants of group size, both in humans and primates more generally. In primates, the size and composition of social groups is shaped by food distribution, predation pressure, and infanticide (Crook & Gartlan 1966; Wrangham 1980; van Schaik 1989). In the general socioecological model, these three pressures determine female distribution which, in turn, determines male distribution (Wrangham 1980; Foley & Gamble 2009). Group size, then, is the result of a compromise between cooperation and competition, patch depletion, travel time, and predation. Fission-fusion systems may allow individuals to benefit from the best of both worlds, allowing individuals, for example, to feed in small groups during the day (reducing competition and travel time) but aggregating at night to avoid predation (van Schaik 1983; Cowlishaw 1997). What about multilevel societies? Hamilton and colleagues (2007) hypothesize that "the general pattern of hierarchical [multilevel] organisation reflects the… underlying cohesive and disruptive forces that govern the flow of material resources, genes and non-genetic information within and between social groups" (p2195).

The aim of this chapter is to test the hypothesis that multilevel social organisation among the Agta serves to facilitate the food sharing required to buffer individuals against the short-term variability inherent in the foraging economy as well as the long-term energetic deficits that result from our energetically expensive and derived life-history.

6.3 Introduction to hunter-gatherer food sharing

Anthropologists have long been interested in systems of hunter-gatherer food sharing, and much work has focused on the political, ethical, cultural, and psychological dimensions of sharing and, in many cases, food sharing is inextricably linked with the egalitarian politics and cosmology of hunter-gatherers (e.g. Bird-David 1990; Lewis 2014; Woodburn 1998). Within the framework of behavioural ecology, however, explaining one proximate phenomenon in terms of another is logically incomplete since it lacks methodological individualism. A more complete explanation of food sharing therefore ought to (*a*) outline the ecological conditions under which sharing is potentially advantageous to individuals, and (*b*) propose mechanisms by which individual and group interests are reconciled (if, indeed, they are at odds). In the sections below, I argue that food sharing is advantageous to foragers since it solves two main problems. These problems are as follows. Firstly, hunting-and-gathering is a risky economy, with foragers encountering day-to-day variability in returns. Secondly, humans have evolved a demanding life-history strategy in which we have slow growing and energetically expensive offspring born at relatively short intervals (Kaplan et al. 2000). Below, I outline these two problems more fully before exploring the mechanisms by which food sharing may be maintained despite the temptation to be a 'free-rider' who takes from a communal pot but does not contribute to it themselves.

6.3.1 Problem one: variable foraging returns

Hunter-gatherers are faced with a great deal of variation in how resources are distributed through space and time over both the short and long term. In thinking about this variability in returns, it is useful to consider the distinction between risk on one hand and uncertainty on the other. Stevens and Charnov (1982) define risk as stochastic variation in the returns gained from a particular action, and uncertainty as a lack of information about the potential returns of different decisions. To put this into context, a hunter tracking a deer may be faced with *uncertainty* as to where the deer might be in the forest, while a hunter shooting an arrow at a deer is faced with the *risk* of missing. Foraging is therefore not only a *risky* business but an *uncertain* one too.

While risk and uncertainty are useful concepts in thinking about foraging, in food sharing our main concern is actually with how variable resource acquisition is. The most straightforward metric of resource acquisition is the success rate – the proportion of foraging trips on which food is successfully procured. This of course varies between populations and between types of foraging, with gathering almost always being more dependable than hunting. In hunting, return rates of 23% have been reported for the Ju/'hoansi (Lee 1979), 27% among the Hadza (Hawkes 1991), 59% among the Batek (Endicott 1981) and, according to Griffin and Griffin (2000), 63% among the Palanan Agta. Among my sample of Agta foraging trips, 87% of fishing trips, 89% of gathering trips, and 65% of hunting trips were successful (see section 3.4 for more details).

At a group level, a strategy to mitigate against the vicarious returns of foraging would be for all members of a group to pool resources, and take from a communal pot. Stated more formally, since the value derived from a perishable good has diminishing returns, a second portion is less valuable than the first (Figure 6-2). This can be modelled as a sigmoid curve with a range of α to β and a mean of $\bar{x}$. Individuals who rely only on resources they procure themselves will have mean of $\frac{V(\alpha+\beta)}{2}$ while individuals in a group who collectively pool resources and take an equal share will have a higher mean return of V($\bar{x}$). This sharing not only reduces variation but increased mean value.

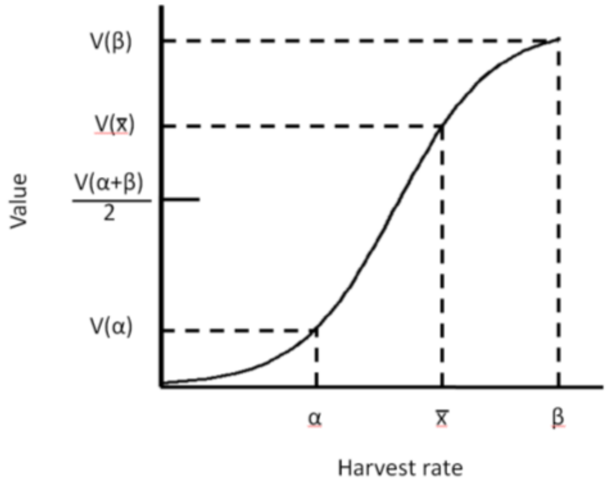

Figure 6-2: Food value in relation to availability. Based on Smith (1988).

Although Figure 6-2 demonstrates the benefits of pooling risk, it does not indicate how many foragers need to share to mitigate against different levels of risk. Winterhalder (1986), however, provides a model in which variation in post-foraging returns is a function of the average net acquisition rate of an independent forager (S), the number of individuals who are sharing (N), and the average between-forager correlation in foraging returns (R) such that:

[Eq. 2]

$$\sigma = S\left[\frac{1 + (N - 1)R}{N}\right]^{0.5}$$

An example of variation in returns after sharing where S = 0.35 is provided in Figure 6-3.

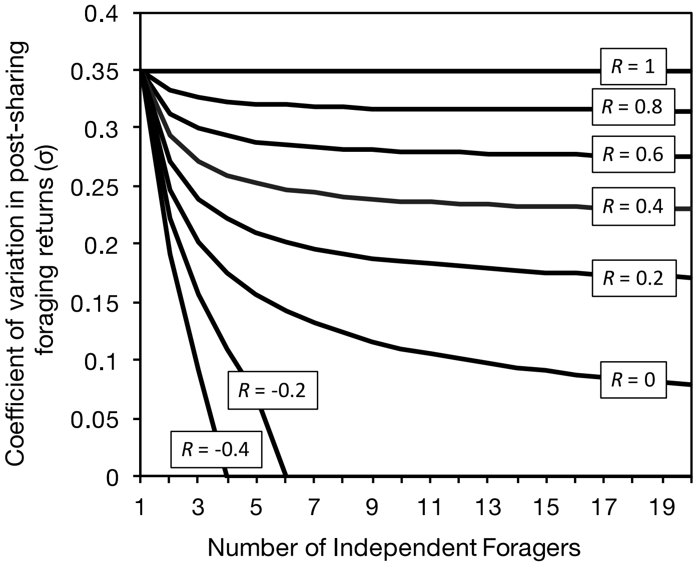

Figure 6-3: The coefficient of variation (c.v.) for net acquisition rate achieved by sharing foragers, as defined in Equation 2. In this case, S = 0.35. Redrawn from Winterhalder (1986).

The reduction of risk, then, provides a functional explanation of food sharing. If independent foragers with similar acquisition rates share, all will be better off. From the point of view of the individual, however, the temptation arises to 'free-ride' on the productivity of others. Individuals with a large package size are also, of course, still better off keeping it all for themselves, at least in the short-term. Why are individuals motivated to share food in spite of the temptation to free-ride on the production of others? Several hypotheses have been advanced and tested, and are discussed in section 5.2.3 below. First, however, I outline the second major problem encountered by foragers –expensive human life-history.

6.3.2. Problem two: humans have an expensive life-history

Compared to chimpanzees, humans live longer, start and finish reproducing later, and have heavier offspring (see Table 6-2) (Kaplan et al. 2000; Mace 2000). We also have large and expensive brains that contribute 16% of our total basal metabolic rate despite representing only 2% of total body weight (Aiello & Wheeler 1995). Although partly offset by a reduction in gut size (Aiello & Wheeler 1995), our large brains are still energetically expensive to grow and to maintain (Aiello & Wells 2002). Aiello and Key (2002) estimate the daily resting metabolic rates of 1,448kcal for a 56kg human female and 1,694kcal for a human male. With additional energetic expenditure, a daily energetic requirement of 1,930 kcal is estimated for women. Crucially, gestation increases energetic costs by 25% and lactation increases total costs by 39% over the baseline (Aiello & Key 2002). Even after weaning, offspring remain energetically dependent until their late teenage years (Kaplan et al 2000, Kaplan 1994, Gurven and Walker 2006). Most of the traits mentioned above are characteristic of what is described as a slow life history strategy (Stearns 1992; Charnov 1993). Most mammalian species that have adopted slow life-history strategies also tend to have fewer offspring. In other words, species tend to either compromise quantity for quality or *vice versa*. Humans, however, do not seem to have made this compromise and, in fact, have shorter inter-birth intervals than chimpanzees despite the increased costs of offspring (see Table 6-2). Humans, therefore, are in the unique position of having a life history strategy that is both fast and slow. So far as life history is concerned, we both have our cake and eat it.

Table 6-2: Life history parameters of humans and chimpanzees. *Agta results based on data collection protocols described in chapter 2. Ages are +/- 3 months for 5years olds n=26, for 10 years olds n = 21. Interbirth interval is a crude estimate based on mean time between first and last reproduction divided by mean live births minus one. †human forager data is the average of Ache, Hadza, Hiwi, and !Kung data reported in (Kaplan et al. 2000). ‡Chimpanzee data is the average for Bossou, Gombe, Kibale, Mahale, and Tai reported also reported in (Kaplan et al. 2000).

	Agta*	Human foragers†	Chimpanzees‡
Probability of survival to age 15	NA	0.6	0.35
Expected age of death at 15	NA	54.1	29.7
Mean age at first reproduction	22.9	19.7	14.3
Mean age at last reproduction	40.7	39	27.7
Mean IBI (months)	36.5	41.3	66.7
Mean weight age 5 (kg)	13.3	15.7	10
Mean weight age 10 (kg)	22.4	24.9	22.5

While the ability to have higher quality offspring born at shorter intervals is of clear evolutionary advantage, it also imposes a large energetic burden on mothers. The demands of our energetically expensive offspring have been linked to the evolution of other distinctive human traits such as pair-bonding (Lovejoy 1981; Chapais 2009; Washburn & Lancaster 1968; Gurven & Hill 2009) and the long post-reproductive lifespan of women (Hawkes et al. 2000; Hawkes et al. 1989; Hawkes 2003) (Interestingly, even though they are able to reproduce, men in many hunter-gatherer societies stop reproducing at the same age as women (Vinicius et al. 2014)). A recent model has linked the evolution of pair-bonding and grandmothering (Coxworth et al. 2015). Whether provisioning and care of offspring comes from fathers, grandmothers, other kin, older children, or unrelated individuals, the central point is that in the course of human evolution we have forfeited our energetic independence, and could therefore be argued to be committed to cooperative breeding (Hrdy 2009; Sear & Mace 2008).

6.3.3 Food sharing and the 'free-rider' problem

As outlined above, foragers are faced with energetic shortfalls in the short term due to variability in foraging returns and in the long term due to the costs of our expensive offspring. In facilitating the transfer of energy from those in surplus to those in deficit, food sharing could be regarded as a solution to these problems. Food sharing, however, also represents a problem in its own right since, at an individual level, the temptation exists to free-ride, taking from a communal pot without contributing. How is this problem solved? Below, I outline the four main evolutionary hypotheses advanced to explain why individuals might be motivated to produce and share food.

Kin Nepotism

Even if the act of food sharing is costly to the donor, it could yield indirect fitness benefits if the recipient is related to the donor by common descent (Hamilton, 1964), or if recipient and donor have a shared genetic interest in the next generation (Hughes 1984; Hughes 1988) (see also chapter 5). If there is asymmetry in the value of the resource, then the inclusive fitness benefits of sharing might be greater than the benefits of retaining the resource. This is modelled simply as 'Hamitlon's rule', where *all else being equal*, if the cost of the 'altruistic' act is less than the benefit to the recipient discounted by relatedness ($c > rb$), then the act is fitness enhancing (Hamilton, 1964).

Some caveats must be recognised here since all else rarely *is equal*. There are additional considerations such as the reproductive potential of the recipient and donor (Hughes, 1988), the degree of competition between kin (Frank 1998; Queller 1994), the certainty of paternity (Euler & Weitzel 1996), and the amount of shared genetic interest (Hughes, 1988, chapter 5). In short, deriving 'on the ground' predictions from kin selection theory is not as simple as Hamilton's rule might suggest. That said, kin selection has been a powerful explanation for much human behaviour including the provision of childcare (Bereczkei 1998; Judge 1995; Pennington & Harpending 1993), alliance formation (Chagnon & Bugos 1979; Dunbar et al. 1995; Johnson & Johnson 1991), survivorship in life-threatening circumstances (Grayson 1993; McCullough & Barton 1991), and investment patterns (Madsen et al. 2007; Dyble, van Leeuwen, et al. 2015; Curry et al. 2012; Burton-Chellew & Dunbar 2011). Predictions derived from kin selection theory have also been borne out in experimental studies (Burnstein et al. 1994; Kruger 2003; Webster 2008).

The preferential sharing of food with kin has been documented in a number of hunter-gatherer populations including the Inupiaq (Magdanz et al. 2002), the Achuar (Patton 2005), the Mer (Bird & Bird 1997), and more sedentary camps of Ache (Gurven et al., 2002). Nolin (2012) also found significant kin nepotism in self-reported patterns of food sharing among the Lamalera. Marlowe (2003) found that Hadza men with young children put in greater foraging effort. In other cases, however, food shared in camp is distributed widely and equally, with little or no bias toward kin (as among the forest Ache (Kaplan & Hill, 1985), Kung San (Lee & DeVore 1969), Hadza (Hawkes, 1993), and Hiwi (Gurven et al. 2000)). Of course, the work on co-residence presented in chapter four ought to be considered here too. If within-camp food sharing is not directed preferentially toward kin but individuals actively assort into camps with kin to begin with, can we truly rule-out kin nepotism?

Tolerated theft/Tolerated scrounging

In Figure 6-2 above we can think of a resource as having two 'portions' – the first from α to $\bar{x}$ and the second from $\bar{x}$ to β. To the hungry individuals A and B, the first portion is valued equally (V($\bar{x}$)-V(α)) If A were to consume the first portion, however, the second portion would be less valuable to A than it is to B for whom its value would be V($\bar{x}$)-V(α) (to A, the value would be V(β)-V($\bar{x}$)). If we introduce the possibility of contest for the resource, the asymmetries in value between A and B mean that, at some point, the cost of defending the food will be greater than the value derived from consuming it, and its theft should be 'tolerated' by the individual with less to lose. The costs of a potential contest for the resource depend on what Blurton-Jones (1984) describes as the 'resource holding potential' of the individuals involved. All else being equal, individuals with greater holding potential are more likely to be able to retain a resource they hold, or be ceded a resource from another. Tolerated theft is the dominant model for food distribution in several non-human species, including chimpanzees (McGrew & Feistner 1995; Jaeggi & M Gurven 2013). For such tolerated theft to occur, the resource in question needs to be of large enough package size to share, such as a big-game carcass (Winterhalder, 1996).

In observed patterns of food sharing, it is difficult to detect the presence of tolerated theft as compared to other hypothesis for food sharing. Food sharing as a result of tolerated theft would predict that resources coming in larger package sizes would be shared more widely. While this is certainly a general trend across hunter-gatherer populations (Gurven 2004a) it is also consistent with the expectations of reciprocal altruism, and to some extent, kin selection, since asymmetries in value are also critical to both of these. Tolerated theft would also predict a general lack of producer control. Again, while this prediction is borne out in some populations (Hawkes et al., 2001; Wiessner, 2002) it begs the question as to why producers would accept the cost of transporting food back to camp (Allen-Arave et al., 2008; Nolin, 2010). A third prediction based on a model of tolerated theft would be a lack of reciprocity in resource exchange. This prediction has been borne out in a number of populations, such as with turtle meat sharing among the Meriam (Bird & Bird 1997), and honey sharing among the Mikea, where literal theft often occurs (Tucker 2004) as well as other groups (Hames & McCabe 2007; Schnegg et al. 2005).

Costly Signalling

Hawkes (1993) noted that in a context of widespread tolerated theft, food essentially becomes a public good and thus susceptible to free-riders who can bully others out of food while producing little or no food themselves. Thus, Hawkes (1993) argues that if food sharing represents tolerated theft and can be modelled as a public good, then the salient question is not *'why share food?'*, but *'why hunt?'*. Hawkes and colleagues suggested that individuals forage and share food because they derive *non-consumptive* benefits from doing so. The acquisition of food, especially big-game and marine resources, requires a degree of skill and physical prowess which cannot be 'faked' and is therefore an 'honest signal' of the fitness of the producer. If such a signal of fitness can attract mates, alliance partners, or social capital, then, even if it is an otherwise costly or sub-optimal behaviour, it could still have net fitness benefits. Such a behaviour has been described as being a 'costly signal'. Costly signalling has been invoked to explain why Hadza men engage in big-game hunting when alternative foraging strategies (such as small-game hunting) could yield greater caloric returns, and when extensive food sharing means that men and their families do not receive the consumptive benefits of the food he produces any more than any other family (Hawkes, 1993).

As well as explanation for high-risk foraging strategies, costly signalling has also been advanced as an explanation of the act of food sharing itself (Alexander 1987; Frank 1998; Gurven et al. 2000). Several authors (Gurven et al. 2000) have stressed the importance of drawing a division between these two forms of signalling. They could be characterised as signalling *quality* versus *intent*. For food sharing to be signalling as *intent*, there must be *producer control*. In other words, the individual responsible for sourcing the food package must have the ability to preferentially direct shares of food to particular individuals or households. Separating this kind of signalling as intention from reciprocal altruism is difficult, both empirically and conceptually. They both involve a short-term cost in order to attract a benefit in the future and contain the risk of non-reciprocation.

There have been two main strands of support for the costly signalling hypotheses. The first are demonstrations that individuals engage in foraging strategies which are sub-optimal but showcase ability and skill. Turtle hunting among the Meriam (Bliege Bird et al. 2001; Smith, 2004) and torch fishing on Ifaluk (Sosis 2000) are strong candidates for such a behaviour, although they are small part of a wider portfolio of foraging which is not overtly sub-optimal. Hawkes et al (1991) argued based on test hunts that Hadza men are pursuing a broadly sub-optimal foraging strategy by engaging in so much big game hunting. A more recent analysis of a newer and more complete dataset on Hadza production does not support this, however (Wood and Marlowe, 2013). Other tests of costly signalling have looked at correlations between the proposed costly behaviour and reproductive success (Smith, 2004; Wiessner, 2002b), offspring survivorship (Hill & Hurtado, 1996), more productive wives (O'Connell et al. 2001), and age at first marriage (Alvard & Gillespie, 2004). These correlations could be, however, the result of phenotypic correlation and are not inconsistent with other hypotheses for food sharing that also predict a correlation between sharing and reproductive success. Finally, as is the case with many attempts to gain prestige or wealth in hunter-gatherer societies, levelling mechanisms may exist to check the ambitions of those seeking to increase their status from costly signalling (Wiessner 1996).

Reciprocal altruism

Like tolerated theft, reciprocal altruism relies on asymmetries in ego and alter's valuation of a resource. Rather than ceding the resource to avoid the costs of defending it, however, the resource holder cedes portions where they evaluate the expected value of a future return transfer to be greater than that of the currently held portion (Trivers 1971). Reciprocal altruism is especially relevant for foods which have large package size (and therefore contain several 'portions'), and is unpredictably distributed (Winterhalder, 1990).

The main prediction of reciprocal altruism would obviously be reciprocation (also termed 'contingency' in the literature) in sharing through time such that A is more likely to give to B if B gave to A previously. In an analysis of food sharing data from eight hunter-gatherer populations, Gurven (2004) finds strong levels of contingency, even among the Hadza who have previously been said to have low producer control

(Hawkes, 1993). There is also evidence of contingency in food transfers among a number of other populations (Magdanz et al., 2002; Nolin, 2010b; Patton, 2005a; Tucker, 2004). However, it should be noted that kin altruism and even tolerated theft could produce patterns of contingency in food transfers (Nolin, 2010). Also, at a proximate level, if food sharing were motivated by reciprocal altruism, we might expect strong social norms relating to reciprocity, and examples of ostracism and punishment. In this regard, hunter-gatherer populations are very variable. Gurven (2004) reports that while ostracism and punishment are clear in some populations, in others, individuals have been reported to respond to unreciprocated exchanges with indifference.

6.3.4 Testing these hypotheses

The four hypotheses outlined above represent theoretically distinct pathways to cooperation. But how can we detect them from quantitative data on food sharing *on the ground*? The hypotheses make two sets of predictions. The first are related to observed patterns of food sharing, while the second relate to correlations between production, sharing, and fitness outcomes.

Predictions in food sharing

Taken in isolation, kin selection would predict that food will be shared when doing so increases the fitness of related individuals. Reciprocal altruism would predict sharing to be based solely on contingency – that there would be a strong correlation between value of resources given by A to B and resources given from B to A. Tolerated theft would predict a distribution of food based on both value asymmetries (i.e. *need*) and differences in resource holding potential and, under conditions of random variation in need and equal holding potential, would result in relatively equal distribution of food. Costly signalling does not actually make predictions about patterns of food sharing *per se,* but in-so-far as it is an explanation for why individuals would forage where there is a lack of producer control, it is consistent with the predictions of tolerated theft. There is, therefore, some overlap in the predictions made by the four hypotheses. For example, both tolerated theft and kin selection can produce patterns of contingency, costly signalling as co-operative intent to share is conceptually indistinguishable from reciprocal altruism, and, in so far as tolerated theft is about sharing based on asymmetries in marginal value of a resource, it is arguably already a component part of both reciprocal altruism and kin selection.

In recognition of the overlap between hypotheses, both conceptually and in the predictions they make about patterns of food sharing, researchers have moved on from piecemeal hypothesis testing to attempts to compare the relative explanatory power of each hypothesis. The various methods used include multiple linear regression (Gurven et al. 2002; Patton 2005), path analysis (Gurven 2004b; Gurven et al. 2000), quadratic assignment procedure (Schnegg et al. 2005), and multilevel regression modelling (Allen-Arave et al. 2008). Most recently, Koster and Leckie (2014) used a social relations model (SRM) to analyse data on food sharing among Nicaraguan horticulturalists. The SRM model calculates estimates of giver, receiver, and relationship effects, allowing the identification of relationships that are stronger than expected given the amount of giving and receiving done by the parties more generally (Kenny 1994). An even more recent paper by Koster and colleagues (2015) explores a multilevel extension of the SRM model. Nolin (2010a, 2012) uses random graph modelling approaches developed in social network analysis to explore the relative power of kinship, reciprocity, and distance. This kind of analysis requires conceptualising food sharing as a network with nodes (*individuals or households*), and edges (*food transfers between these units*).

Other aspects of production

As outlined in section 2.4 above, food sharing occurs after a long chain of decisions have been made about foraging and food production. If food is being shared in particular ways, this may have influence on the decisions made by individuals about foraging and production as well as fitness outcomes. Figure 6-4 plots the benefits and correlations with fitness that we may expect to see when food is shared for status as compared to when food is shared as kin nepotism. Although correlating patterns of food production or sharing with reproductive success, as has been popular with models of costly signalling (Kaplan & Hill, 1985; Smith et al., 2003), is problematic in so far as all hypotheses ultimately predict that sharing is fitness enhancing in some circumstances. That said, quantifying mid-range fitness outcomes, such as fertility, child survivorship, own survivorship, and spouses survivorship as well as indices of foraging and social reputation are useful in teasing apart these complex motivations (Gurven & Hill 2009) (Figure 6-4).

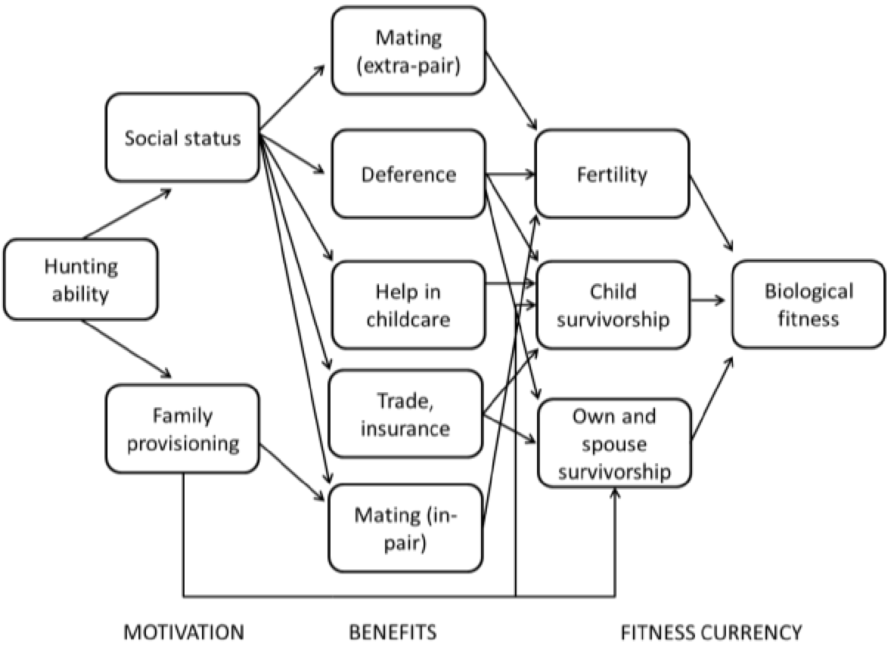

Figure 6-4: Outcomes of foraging and sharing decisions. Redrawn from Kelly (2013:151), itself redrawn from Gurven and Hill (2009:61)

6.3.5 Future directions in food sharing

To my mind, a fair summary of the existing food sharing literature would be that there is considerable overlap between the hypotheses relating to food sharing both conceptually and in terms of the predictions that can be derived from them, and that across multiple populations, multiple mechanisms appear to account for sharing. As Jaeggi and Gurven (2015) say, “one conclusion from multivariate analyses is that sharing is overdetermined; no single explanation accounts for all food transfers, and certain characteristics may work in concert” (p3-4). Getty (2005) suggests that “for now, the hypotheses seem like the proverbial blind men examining the elephant: each was partly in the right, and all were in the wrong!” (p563).

Future advances in understanding food sharing from an evolutionary point of view will almost certainly benefit from a (re)engagement with proximate mechanisms and cultural norms around sharing and stopping free-riders (Jaeggi and Guvren 2015, Kaplan & Gurven, 2005). I would also suggest that our understanding of hunter-gatherer food sharing would benefit greatly from situating the sharing we see more explicitly within the wider social organisation of our study populations. For example, the Agta, as we have seen in chapter four, live in households of relatively fixed composition, within camps that contain both a small number of closely related individuals (perhaps representing an *extended family*) and a large proportion of distantly or unrelated people. How is food sharing structured across these social layers? Perhaps the different sharing motivations described above apply to different social layers. The relationship between cooperation and social organisation is explored by Hooper et al. (2015a) who argue that “The size and composition of cooperative groups can be understood as a self-organized outcome of… choices… made under local ecological and social constraints” and describe a “framework for explaining the size and composition of foraging groups based on three principles: (*i*) the sexual division of labour; (*ii)* the intergenerational division of labour; and (*iii*) economies of scale in production” (p1).

I hypothesise that food is shared with different social layers for different reasons. For clarity, I will make predictions based on the four dimensions of food sharing identified by Gurven (2004). These are: *depth* (the proportion of a procured resource that is shared), *breadth* (the number of households a resource is shared with), *equity* (the difference in size of shares given to different individuals), and *balance* (the long term net gain or loss in resources given between two individuals). Within the household, relatedness is high, and ability to procure resources differs. Thus we might expect sharing to be motivated by kin nepotism, with high depth and breadth of sharing, and with tolerated long-term imbalances. If a unit of social organisation larger than the household but smaller than the camp exists (we could describe this as a residential cluster), sharing within this unit may be more moderate, although households in energetic deficit might be provisioned by related households with a surplus, as was the case for the Ache (Kaplan et al., 2000). Within the wider camp, relatedness may be low, and sharing conducted on the condition of reciprocation. The predictions are stated in Table 6-3 below.

Table 6-3: Predictions of patterns of food sharing in different social units. Depth refers to the proportion of food produced that is shared. Equality refers to how equal the shares received by different individuals are.

	Household	**Cluster**	**Camp**
Motivation	Kin Selection	Reciprocal altruism, kin selection to a lesser extent.	Reciprocal altruism, costly signalling
Relatedness	High	Moderate	Low
Depth	High	Moderate	Low
Equality	According to need (day to day energetic requirements)	According to need (inter-household provisioning)	According to need (risk reduction and 'health insurance')
Balance	Low (because they are closely related, imbalance is tolerated)	Moderate (some imbalance is tolerated as households are related).	High (lack of reciprocation is 'cheating')

6.3.6 Summary

In summary, we have a convergence between two bodies of literature within evolutionary anthropology. On one hand (as reviewed in section 6.1) we have some understanding of the *form* of multilevel social organisation but little insight into its *function* and how it structures cooperation in domains such as food sharing. On the other hand, we have much literature on why food is shared but little understanding of how this sharing sits within the wider social structure. By exploring the relationship between social organisation and food sharing in this chapter I hope to make an important contribution to both fields.

6.4 Methods

6.4.1 Behavioural data

The main data set analysed in this chapter is that collected on inter-household food sharing among six Agta camps. These data were collected according to the protocol set out in chapter 2.4.4. This protocol involved observational data collection on inter-household food sharing supplemented by daily interviews with each household. In total, I collected data on food sharing on 129 days across six camps and 61 households with a total of 760 household days (Table 6-4). Over these 760 household days I recorded 432 between-household transfers. Across the sample of 61 households, the mean household gave 0.61 food packages per day (SD = .41) (Figure 6-5).

Table 6-4: Summary of food sharing data across six Agta camps.

	Number of households	Days	Household days	Food packages given
Diago	13	26	264	146
Dipaguiden	7	21	76	61
Kanaipang	18	14	198	120
Dipagsangan	7	11	53	38
Magtaracay	8	9	52	42
Didikeg	8	22	117	25
TOTAL	**61**	**129**	**760**	**432**

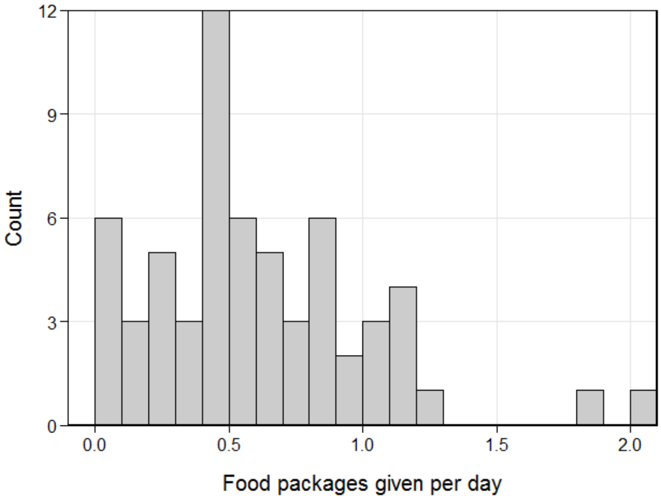

Figure 6-5: Histograms of the mean number of food packages given per day by each household ($n = 61$).

In order to better understand the function of food sharing among the Agta, in this chapter I also present data on foraging productivity, foraging group composition, and relatedness. In all cases, the data were collected according to the protocols set out in section 2.3. My sample of foraging productivity includes data on the 143 individuals in my six food sharing camps for whom I collected data on foraging returns on more than five days. In total, this represents a sample of 1,297 person days. The relatedness between the 19,949 dyads included in my food sharing sample was calculated using the scripts described in section 4.3.

6.4.2 Statistical methods

Identifying clusters in food sharing networks

As discussed at length in the literature review above, food is rarely shared with complete equity within hunter-gatherer camps. Instead, preferential food sharing relationships are often found between particular individuals or households. Do these preferential relationships represent consistent clusters? In many populations, clusters in food sharing have been described (e.g. Ziker & Schnegg 2005; Schnegg et al. 2005) and, theoretically, may be related to the variability in foraging returns, with larger clusters where foraging returns are more variable (Winterhalder, 1986). In order to determine whether food sharing clusters exist within Agta camps, I converted the inter-household food sharing data described above into a network, and used algorithms designed to detect 'clusters' or 'community structure' in networks.

A network can be said to have clusters when groups of nodes can be identified that have dense connections within them, and more sparse connections between them. Generally, in defining clusters within social networks, researchers are looking for non-overlapping clusters where each node is defined as belonging to only one cluster. The detection of clusters within a network requires the use of a community detection algorithm, of which there are several main classes. The most basic class employs the 'minimum cut' method which splits a network into a predetermined number of clusters in a way that minimises the number of edges between clusters (Karger 1993) (see example in panel B, Figure 6-6). With a predetermined cluster number, however, you simply 'get out what you put in'- not ideal for hypothesis testing.

Algorithms that do not rely on a predetermined number of clusters include the Girvan-Newman algorithm (Girvan-Newman, 2002). This algorithm is based on the assumption that the edge in the network with the greatest betweenness centrality (i.e. that lies on the largest number of shortest paths between nodes) is the most likely to lie *between*, rather than *within* clusters. The algorithm first calculates the betweenness of all edges in the network, and then removes the edge with the highest betweenness (see example in panel A, Figure 6-6). It will carry out these two steps until there are no edges left, producing a network dendrogram from which we can find the division that maximises modularity. Modularity is the proportion of edges that fall within the given groups minus the number which would be expected to fall within those groups if the network edges were distributed at random.

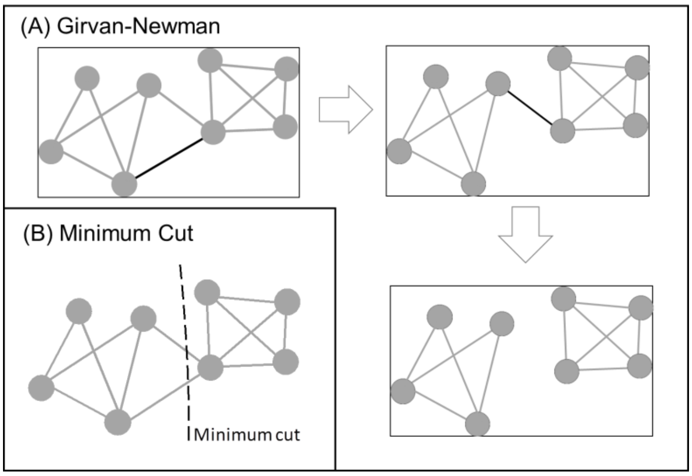

Figure 6-6: Community detection algorithms. Panel A shows the division of a graph according to the Girvan-Newman algorithm. For simplicity, multiple edges are deleted in each step in which they have the same betweenness values. Black edges represent those with the highest betweenness. Panel B demonstrates a simple example of the minimum cut method for graph division where the number of predetermined clusters is two.

The Girvan-Newman algorithm, then, is simply a means by which graph partitions that are likely to have high modularity can be identified. In a large network, this kind of algorithm is useful because it provides a (relatively) computationally inexpensive way to explore graph partitions which may have high modularity (other algorithms such as the 'fast-greedy' algorithm have also been suggested (Clauset et al. 2004)). In small networks, however, it is possible to divide the network up into all conceivable divisions, test the modulatory of each division, and return the division that maximises modulatory (Brandes et al. 2008). This is, of course, computationally expensive since the number of possible network divisions soon becomes huge. However, since the networks of between household food sharing analysed in this chapter are relatively small (ranging from seven to eighteen nodes), this method is feasible and is what I use to detect the presence of 'clusters' within camps. To run the algorithm, I use the 'cluster_optimal' function available in the 'igraph' package for R 3.1.1. (Csardi & Nepusz 2006; R Core Team 2014).

Once the optimal division of a network into clusters has been identified, how can the effect size or goodness-of-fit of the division? And how can statistical inferences be made?

The application of statistical inference to node, edge, or network level characteristics is often neglected, even within the traditional null-hypothesis-testing behavioural sciences. That said, a body of statistical tools using permutations-style tests have been developed in which node and edge identities are shuffled in order to generate an null-hypothesis distribution of values or test statistics (Anderson et al. 1999; Handcock et al. 2003). For the purposes of this chapter, modulatory (Brandes et al. 2008) will serve as an indication of how strongly clustered the food sharing networks are. As discussed above, modularity is the proportion of edges that fall within the given groups minus the number which would be expected to fall within those groups if the network edges were distributed at random.

Statistical tests

In all cases, statistical analyses were conducted in R 3.1.1 and employ and α level of 5%. For tests relating to sex or age differences in mean daily calorific productivity, I used independent 2-group Mann-Whitney U tests. To compare the proportion of kin of various kinds in various social layers, I used Chi-squared tests. For comparisons of the relatedness of individuals to their relative social layers, I used the Wilcoxon sign-rank test, a non-parametric alternative to the paired t-test.

6.5 Results

6.5.1 Relatedness and food sharing

Given the discussion of relatedness in food sharing in section 6.3, it is worth considering the relationship between the relatedness of households and the amount food sharing between them. In order to do this, I regressed, for each of the six study camps, the number of food packages exchanged between each dyad of households against the mean relatedness of the household members (see Table 6-5). Since these observations are not independent, I used a QAP (Quadratic Assignment Procedure) to evaluate the statistical significance of my results (Anderson et al. 1999). The QAP test is performed by running a series of permutations in which the rows and columns of matrix containing, in this case, dyadic relatedness, and recalculating the test statistic such that an expected distribution of values can be generated and against which the observed test statistic can be compared. From this, a p-value can be calculated. Conceptually, this method can be thought of as a permutations test. I ran this test in each camp twice (see Table 6-5) – once where household relatedness was calculated using standard coefficients of relatedness and once using the coefficient of shared reproductive success outlined in chapter five. Analyses were conducted in R using the 'qaptest' function in the 'sna' package (Handcock et al. 2003).

Table 6-5: Regression the amount of food sharing between households against their relatedness evaluated using standard coefficients of relatedness (left) and coefficient of common reproductive interest (right). P-values are produced using a Quadratic Assignment Procedure

	Coefficient of relatedness (*r*)			Coefficient of common reproductive interest (*s*)		
Camp	β	P	R^2	β	P	R^2
Diago	1.07	<.001	.34	1.69	<.001	.39
Dipaguiden	-.28	.280	.02	-.48	.27	.03
Kanaipang	.67	.001	.12	.98	<.001	.14
Dipagsangan	.92	.081	.08	1.5	.036	.20
Magtaracay	.34	.190	.27	.55	.160	.05
Didikeg	.60	.009	.25	.80	.008	.25

6.5.2 Households

Households, like camps, are easily identifiable on the ground. Across my sample, of 61 households, 49 consisted of simple nuclear families living in their own dwelling (See Table 6-6). The mean household size was 6.36 (SD = 2.49) individuals. As well as the core social unit (as described section 3.5 above), households are the primary unit of food sharing, with Agta consuming food produced by members of their own household on an average of 73.1% (±20.4) of days. What is the function of food sharing within the household? As outlined above, my food sharing data are derived from observations and interviews about inter-household food sharing. Insights into sharing within the household must therefore come from data on food production.

Women (*n* = 55, mean = 623kcal ± 713) had a significantly lower daily caloric productivity than men (*n* = 47, mean = 1,556kcal ± 997, *W* = 2047; *p* <.001, Figure 6-7). This gender difference in productivity may be a reflection of the time demands of young children on mothers, since mothers whose youngest child was under the age of two years (n = 16) had a lower daily productivity than mothers with a youngest child between the ages of two and sixteen (n = 26) (420kcal ± 680 vs. 1,052kcal ± 809, W = 101, *p* = .005). Fathers with children under the age of two years (n = 11) had a greater mean daily calorific productivity than those with a youngest child between the ages of two and sixteen, though not significantly so (n = 20; 1,796kcal ± 900 vs. 1,442kcal ± 591, *W* = 137, *p* = 0.28). This sex difference in couples with young children is similar to that reported for the Hadza (Marlowe 2003). Although this sex difference in productivity only lasts until the youngest child reaches 3-4 years of age (Figure 6-7, panel b), since 84% of women between 18 and 45 have children under this age, this can account for the overall sex differences seen in Figure 6-7a. Intra-household sharing, then, appears to facilitate the long-term energetic provisioning required to meet the high energetic costs of offspring.

Table 6-6: Frequency and proportion of households of various compositions among the Agta

Household type	Freq.	%
Adult couple and their children	44	72.1
Adult couple, their children, and one elderly parent	3	4.9
Young couple, no dependents	3	4.9
Single adult	2	3.3
Elderly couple, no dependents	2	3.3
Single adult and their children	2	3.3
Single adult, their children, and one elderly parent	1	1.6
Single parent, their children, and younger siblings	1	1.6
Elderly man and adult daughter	1	1.6
Adult couple with child of one	1	1.6
Adult couple, their children, and children of one adult	1	1.6
Total	61	100

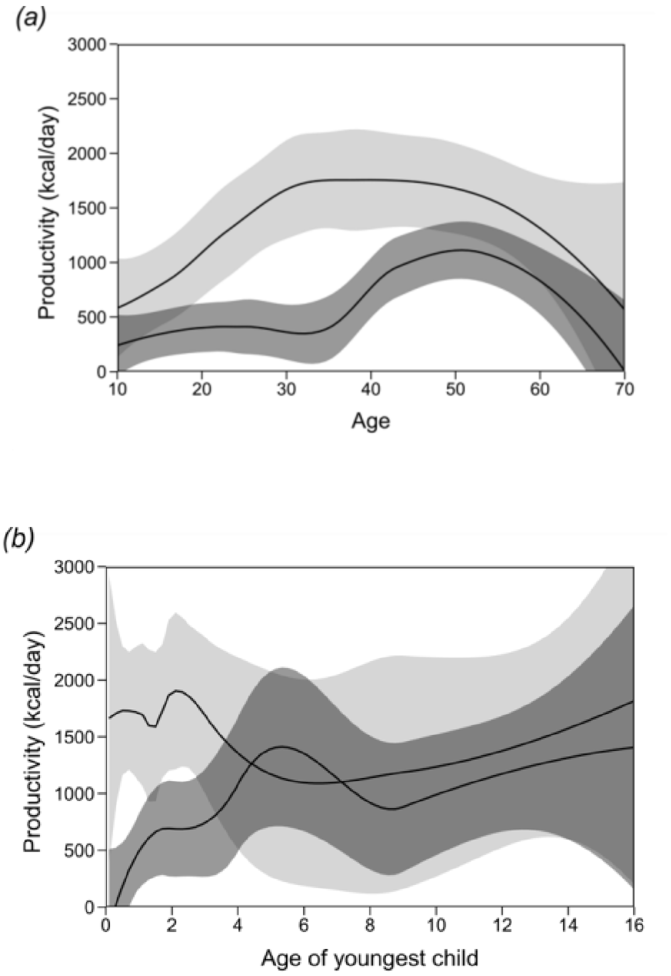

Figure 6-7: Calorific productivity of Agta men (grey) and women (black) by (*a*) age and (*b*) age of youngest child.

6.5.3 Clusters

Food sharing was highly concentrated between households (Figure 6-8), with 88.3% (SD = 16.3%) of the average Agta household sharing occurring with just three other households. In order to determine whether these concentrated sharing relationships represented consistent clusters, I constructed weighted networks of inter-household food sharing, where nodes represent households and edges represent the extent of food sharing between each household dyad. The weights of the edges in the network represent the proportion of days on which both households in the dyad were present in camp and exchanged food. Across the six study camps, clustering coefficients were high, ranging from 0.39 to 0.82 (see Table 6-7) suggestive of the existence of communities within camps. For each camp network, I used the community-detection algorithm discussed above (section 5.4) to explore all possible graph partitions and identify the partition that maximized modularity (Brandes et al. 2008) (Figure 6-9). Clusters defined in this way encompassed the majority of food sharing, with Agta households (n = 61) giving food to households in their cluster on 37.1% (SD = 27.0) of days, as compared to 10.3% (SD = 12.5) of days to households outside of their cluster (W = 1770, $p < 0.001$) (Figure 6-9). Five of the six study camps contained two clusters, while the largest camp contained six. The mean size of clusters among the Agta was 3.81 households (SD = 1.38).

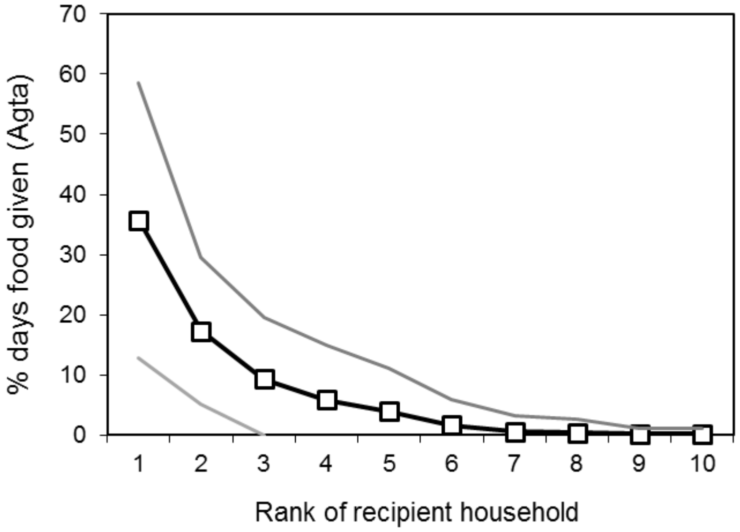

Figure 6-8: Mean proportion of days on which food was given to other households, ranked by household preference. Grey lines represent +/- 1 SD.

Table 6-7: Summary of the six Agta camps included in my study. Numerals in brackets refer to panels in Figure 6-9.

Community	*Camp members*	*Adult camp members*	*Number of households*	*Clusters detected*	*Transitivity*
(i) Diago	68	25	13	2	.65
(ii) Dipaguiden	42	13	7	2	.45
(iii) Didikeg	45	15	8	2	.40
(iv) Magtaracay	36	15	8	2	.80
(v) Kanaipang	96	36	18	6	.39
(vi) Dipagsangan	16	32	7	2	.82
Total	303	136	61	16	-

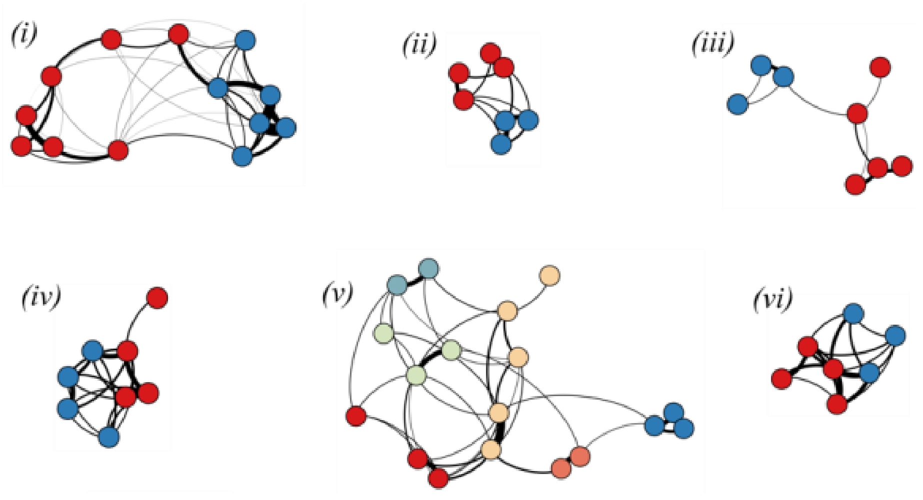

Figure 6-9: Inter-household food sharing networks for six Agta camps. Node colours reflect cluster membership. Networks were produced in Gephi using Force Atlas (Bastian et al. 2009).

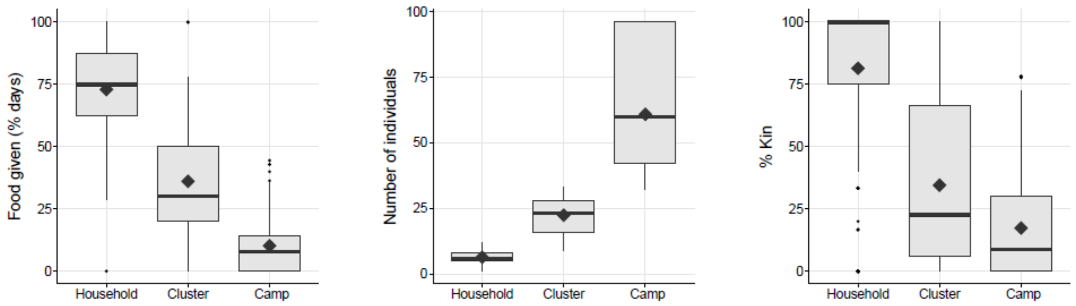

Figure 6-10: Box plots of (A) sharing, (B) group size and (C) relatedness across the household, cluster, and band for the Agta. Group size represents experienced group size. For all panels, n = 303 individuals. Diamonds represent the mean values.

6.5.4 The wider camp

If the majority of food sharing occurs within the household or cluster, what benefits do individuals derive from living in camps in terms of food sharing and production? I suggest that the wider camp may serve two purposes in this respect. First, although Agta households only consumed food produced by individuals from outside of the cluster on an average of 10.3% days (± 12.5), sharing outside clusters may still represent an important form of risk-reduction food sharing, particularly in the case of high value but difficult to acquire resources such as meat and honey. For example, compared to fish (a more predictable resource), meat and honey produced by the Agta came in larger package sizes (6,719kcal ± 8,504 vs. 2,496kcal ± 3,679, t = -2.61, P =.015), were obtained on a lower proportion of attempts (46.7% vs 83.6% $\chi^2 = 39.4$, P <.001) and, were shared with a larger proportion of available households (62% ±30% vs. 23% ± 24%, t = 4.16, P <.01).

Living in a camp increases the pool of available foraging partners. Of the 348 co-foraging dyads in our sample, 29.3% occurred between individuals in the same household, 29.6% between individuals in the same cluster, and 41.1% between individuals in the wider camp. The majority (60.1%) of these foraging trips were with unrelated individuals (see Table 6-8 for a full breakdown). Thus, while individuals preferentially share with related campmates, they forage mostly with unrelated ones.

Table 6-8: Relatedness of co-foraging dyads. *all are aunt/uncle-niece/nephew dyads, † all are cousin dyads.

Coefficient of relatedness	**Count**	**Percentage**
0.5	71	20.4
of which parent-child	(34)	(9.8)
of which siblings	(37)	(10.6)
0.25*	9	2.6
0.125†	29	8.3
0.0625	8	2.3
<0.0625	231	66.4
of which spouses	(22)	(6.3)
of which unrelated	(209)	(60.1)
TOTAL	**348**	**100**

6.5.5 Relatedness of layers

Individuals (n = 319) were more closely related to members of their household (mean *r* = 0.39, SD = 0.14) than their cluster (mean = 0.10, SD = 0.09, W = 48174, p <.001) and more closely related to individuals in their cluster than the wider camp (mean = 0.04, SD = 0.04, W = 33897, p <.001). Clusters also contained a larger proportion of ties between children (<13 years of age) and their grandparents and uncles/aunts than would be expected by chance, with 69% of child-grandparent ties ($\chi^2 = 33.1$, p <.001) and 64% of child-uncle/aunt ties ($\chi^2 = 142.1$, p <.001) falling within clusters.

6.5.6 Comparison with Mbendjele communities

In appendix C I provide a short format 'paper' version of this chapter. In this paper I compare the analysis of community structure, food sharing, and foraging among the Agta with similar data on food sharing among Mbendjele hunter-gatherers in the Republic of Congo collected by James Thompson. For purposes of the paper, I analysed the Mbendjele food sharing data in the same way as I analysed the Agta data described above. The Mbendjele sample consisted of three camps (Longa, Masia, and Ibamba) which contained 11, 8, and 13 households and 42, 31, and 47 individuals respectively. In these three camps, we identified 3, 3, and 4 clusters. The mean experienced cluster size was 3.10 households (SD = 1.10), similar to that found among the Agta (3.81 households, SD = 1.38). As among the Agta, individuals (n = 120) were significantly more closely related to their household than their cluster (household mean = 0.33, SD = 0.18; cluster mean = 0.08, SD = 0.10, W = 5381, p <.001), to whom they were more closely related than their camp (Mbendjele: mean = 0.04, SD = 0.04, W = 3717, p = .005) (Figure 6-11).

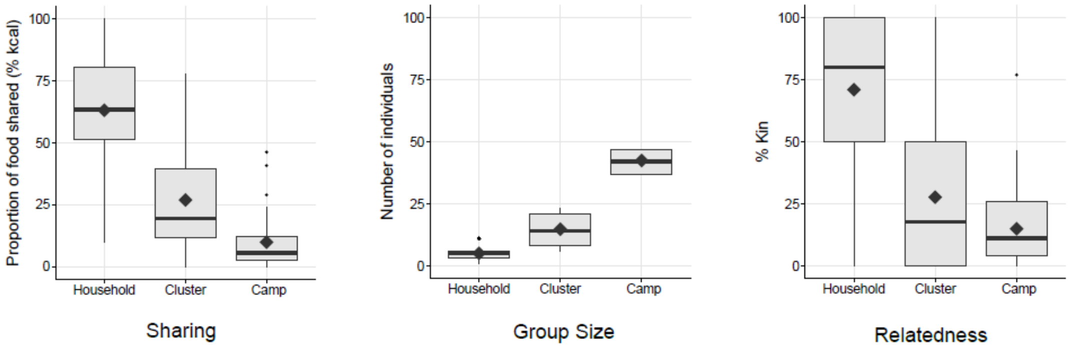

Figure 6-11: Box plots of (*left to right*) sharing, group size and relatedness across the household, cluster, and band for the Mbendjele. Group size represents experienced group size. For all panels, n = 120 individuals. Diamonds represent the mean values.

6.6 Discussion

In this chapter, I sought to examine the relationship between food sharing and multilevel social organisation among the Agta. Multilevel social organisation has been argued to be a universal feature of human sociality (Chapais 2011), and humans are said to have undergone a transition from an *atomistic* and top-down social organisation whereby individuals are found in fluid sub-groups of a bounded supra-group to a *molecular* and bottom-up social organisation where individuals are found in bounded sub-groups within a fluid supra-group (Lehmann et al. 2014; Grueter et al. 2012; Chapais 2008). Among the Agta, this molecular social organisation is clearly apparent – upon marrying, a husband and wife set up a new household which (as discussed in chapter four) can move regularly between camps of fluid composition.

In addition to the household and camp – units of social organisation clearly identifiable *on the ground*, in this chapter I have argued that an intermediate level of social organisation exists. By applying community detection algorithms to networks of inter-household food sharing, I was able to define a level of social organisation larger than the household but smaller than the camp. I describe this unit of social organisation as the 'cluster'. Thus, we can define a three tiered social organisation with individuals situated in households, within clusters, within the wider camp (as in Figure 6-12).

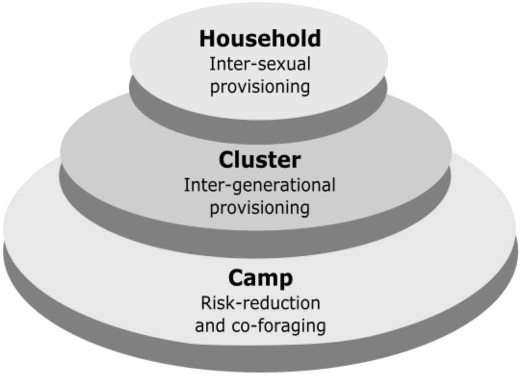

Figure 6-12: Schematic representation of multilevel social organisation and hypothesised function.

What is the function of these three layers? I hypothesise that each of these social layers serves a distinct function in food sharing, with the household facilitating inter-sexual provisioning, the cluster facilitating long-term provisioning by extended kin, and the wider camp representing a pool of foraging partners and individuals with whom foods of more variable return rate can be shared. As a whole, I would argue that multilevel social organisation allows individuals access to the range of social relationships required to mitigate against day-to-day variability in foraging success inherent in the human foraging economy (McElreath & Koster 2014; Winterhalder 1986), as well the long-term inter-personal dependency to which humans are committed due to our costly life-history niche (Kaplan et al. 2000; Mace 2000).

While previous studies have demonstrated that human groups often have a multilevel social organisation (Hamilton et al. 2007; Zhou et al. 2005), this work is the first to explore how this distinctive social organisation relates to cooperation among hunter-gatherers. The three levels of social organisation I identify may correspond to the three kinds of cooperative relationships that Hooper and colleagues argue were important in human evolutionary history (Hooper et al. 2014; Hooper et al. 2015), and which are evident in hunter-gatherer food sharing (Hawkes & O'Connell 1998; Allen-Arave et al. 2008; Wood & Marlowe 2013; Hooper, Gurven, et al. 2015; Jaeggi & Michael Gurven 2013; Ziker & Schnegg 2005). These are (*a*) male-female complementarity, as evident in within-household provisioning, (*b*) assistance from kin, which we observed within sharing clusters, and (*c*) cooperation with both related and unrelated individuals, as observed in the selection of foraging partners.

Previous work on food sharing in hunter-gatherers has often contrasted the relative contributions made by fathers (Marlowe 2003; Wood & Marlowe 2013; Gurven & Hill 2009), grandmothers (Hooper, Gurven, et al. 2015; Hawkes et al. 1989), and others (Hill & Hurtado 2009). By looking at the relationship between food sharing and multilevel social organisation, we are able to reconcile the importance of these previously contrasting social relationships.

Much previous literature on multilevel social organisation has explained its emergence as the result of optimizing processes that underlie other complex systems in nature (Oltvai & Barabási 2002; Vinicius 2010), as well as reflecting time and cognitive constraints (Dunbar 1992). Several studies have suggested that such processes result in the scaling ratios of around three found between social layers in both human and non-human societies (Hill et al. 2008; Hamilton et al. 2007; Zhou et al. 2005). My results provided mixed support for this hypothesis, with Agta and Mbendjele clusters containing an average of 3.81 (SD = 1.38) and 3.10 (SD = 1.10) households respectively. Camps, however, ranged between two and six clusters depending on size.

In addition to its implications relating to multilevel sociality, the data presented in this chapter also represent a valuable contribution to the cross-cultural data on food sharing in small-scale societies. In particular, it offers an insight into food sharing among people who rely heavily on fishing which, relative to hunting, tends to have more predictable returns and comes in smaller package sizes (Bliege Bird et al. 2002). Although conceptions of hunter-gatherer foraging and food sharing often focus on big-game hunting in open environments, the fisher-forager niche may have been of great importance in human evolutionary (O'Connor et al. 2011; Crellen et al. 2016).

6.7 Summary

Food sharing may have been one of the most important cooperative activities during human evolutionary history. How and why contemporary hunter-gatherers share food has therefore been a subject of intense interest. The relative importance of kin selection and reciprocity in explaining food sharing and the relative importance of contributions from fathers and grandmothers have previously been contrasted. In this chapter I explored how the unique social organisation of hunter-gatherers that includes several derived features such as pair-bonding, sexual division of labour, inter-generational transfers, and multilevel structure has to be taken into account to understand how food sharing operates. My results suggest that multilevel social organisation in hunter-gatherers facilitates multilevel food sharing among individuals in a camp, allowing them to meet long-term costs of the expensive human life-history strategy and to overcome short-term energetic shortfalls often encountered in foraging economies. These findings demonstrate the importance of spouses, kin, and unrelated individuals in food production and exchange, suggesting that multilevel sociality is a unique and necessary adaptation to the human foraging and life-history niche, promoting efficient food transfer within communities.

Chapter 7: Conclusions and general discussion

In this thesis I have examined the social organisation of hunting and gathering societies, with particular reference to Agta hunter-gatherers of northern Luzon, Philippines. Specifically, I explored the relationships between group relatedness and multi-local residence (*chapter 4*), between pair-bonding and the emergence of affinal kinship (*chapter 5*), and between household food sharing and community structure (*chapter 6*). In this concluding chapter, I provide an overview of my findings (section 7.1) before making some suggestions of future directions in this field (section 7.2) and closing remarks (section 7.3).

7.1 Overview of findings

Humans demonstrate remarkable success as a biological species and, as hunter-gatherers, have been able to adapt to ecological niches from the tropics to the arctic. This success is due, in large part, to our social intelligence – our *social brains* and ability to understand the intensions of others, cooperate, communicate using language, and to exchange cultural and technological ideas. What was it about the social organisation of humans in evolutionary history that required such advanced social cognition? In this thesis, I have argued that small-scale hunter-gatherers live in complex and multilevel societies in which individuals have long-term pair-bonds, recognise extended kin, and have extensive networks of relationships with unrelated individuals.

As I argue in chapter 1, there are no 'magic bullet' explanations in human evolution. Rather, we have a mosaic of derived traits. In this thesis, I have examined just one part of this mosaic – that relating to social organisation (Figure 7-1). My work has cast light on the relationship between multi-local residence and the frequency of interaction between distantly related individuals (*chapter 4*), between pair-bonding and affinal kinship (*chapter 5*), and how these traits combine to create a multilevel social organisation (*chapter 6*).

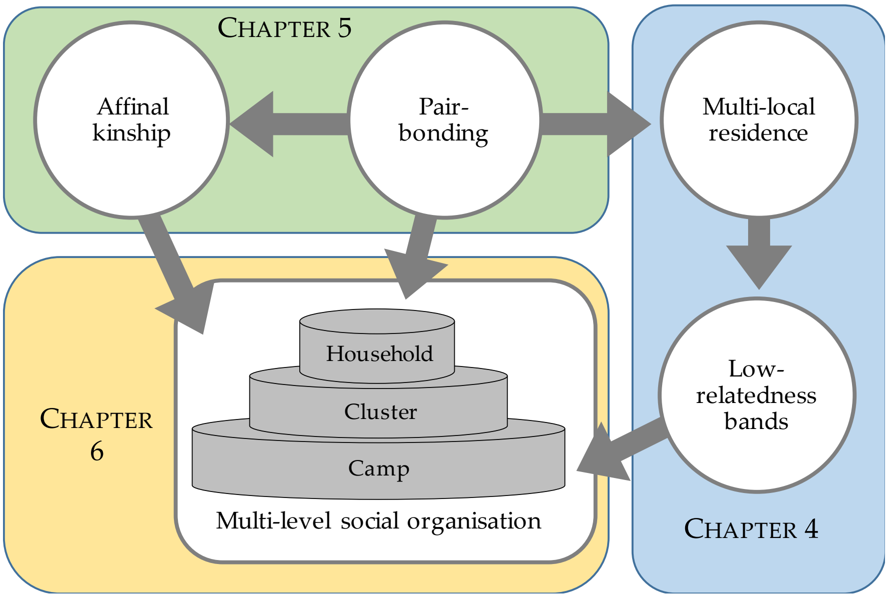

Figure 7-1: Scope of my thesis and relationships between the main findings of chapters four, five, and six.

7.2 Major implications and future directions

I believe that the research presented in this thesis makes an important contribution to something of a paradigm shift in how we understand the social organisation of 'simple' hunter-gatherer societies. The dominant paradigm in anthropology and the social sciences and humanities more generally was, for much of the twentieth century, of forager societies consisting of small, patrilocal, and closely related kin groups (Ember & Ember 1971; Radcliffe-Brown 1931; Service 1962; Steward 1955). Although anthropologists have long been presenting ethnographic evidence to the contrary (Lee 1979; Lee & DeVore 1969; Hill et al. 2011; Marlowe 2004) this paradigm has, implicitly or explicitly, continued to inform models of human social and behavioural evolution and of human behaviour more generally, for example informing understanding of the so-called 'environment of evolutionary adaptedness' (EEA) in evolutionary psychology (Panksepp & Panksepp 2000; Cosmides et al. 1992).

The work on hunter-gatherer social organisation presented in this thesis describes a social organisation which is multi-local, multi-layered, and in which kinship extends beyond consanguineal kin, allowing individuals to maintain an expansive network of social ties. This kind of social organisation is one that, if also characteristic of hunter-gatherers in human evolutionary history, could have co-evolved with (or facilitated the evolution of) many distinctive human traits such as extensive cooperation among both kin and non-kin (Burkart et al. 2014; Apicella et al. 2012), the cumulative transmission of technology and culture (Pradhan et al. 2012; Tennie et al. 2009; Boyd et al. 2011), and the ability to recognise and categorise distant kinship (Chapais 2014; Chapais 2009).

I should make clear that in my discussions of hunter-gatherer social organisation throughout this thesis, I have had in mind those hunter-gatherers like the Agta who are highly mobile, small-scale groups who generally have egalitarian social relations and an immediate-return economy. This is not to say that all hunter-gatherers in human evolutionary had this kind of system – as discussed in chapter one, we know that hunting-and-gathering can also support more complex social and political organisation (Ames & Maschner 1999; Kelly 2013) and that there is considerable variation even among 'simple' hunter-gatherers, especially when we consider the Australian groups (Lourandos 1997). That said, while the theoretical work in this thesis is informed by data on 'simple' hunter-gatherer societies, most of the elements of interest - pair-bonding, recognition of affinal kin, and multilevel sociality – are not specific to simple hunter-gatherers but are common characteristics of human sociality more generally (Chapais 2011). The only phenomenon of primary importance to my model of human social evolution that may be specific to simple hunter-gatherers is multi-local residence.

Sociality beyond the camp

The focus of this thesis has largely been social life *within* hunter-gatherer camps. What about sociality *beyond* the camp? How are larger groups structured, and what benefits do individuals derive from being part of them? To my mind, exploration of these questions represents an important avenue for future research. The first important question to be asked in this regard is to what extent groups beyond the camp actually exist among small-scale hunter-gatherer societies. The residential mobility seen among hunter-gatherers clearly demonstrates that individuals have social lives beyond the camp. But do these social networks overlap enough for bounded social groups to emerge? Or do social relationships simply cascade through space? The answer to this question has several important implications, discussed below.

Firstly, the structure of meta-groups has implications for the potential for biological and cultural group selection, and the emergence of ethnolinguistic diversity (Currie & Mace 2012; Boyd & Richerson 2009; Smaldino 2014). In recent years there has been renewed interested in group selection models, both in evolutionary biology generally (Nowak et al. 2010; Traulsen & Nowak 2006; Simon et al. 2013) and with specific reference to the role of group selection and between-group warfare in human evolutionary history (Henrich 2004; Gintis 2000; Bowles 2009; Bowles & Gintis 2011; Fry & Söderberg 2013; Kelly 2005; Wrangham & Glowacki 2012; Turchin et al. 2013). An assumption of the cultural and biological group selection models is that humans in evolutionary history lived in groups of bounded enough membership for (*a*) warfare to be a possibility, and (*b*) provide a strong group-level selective pressure. While inter-group lethal conflict may be rare in contemporary 'simple' hunter-gatherers (Fry & Söderberg 2013), among more complex hunter-gatherers there is both archaeological and ethnographic evidence of conflict (Kelly 2005; Kelly 2013), and theoretical reasons to suppose that it could occur (Smith 1988; Dyson-Hudson et al. 1978). Indeed, recent archaeological evidence from

Turkana provides clear evidence of lethal violence in late Pleistocene hunter-gatherers (Lahr et al. 2016).

A related issue is the importance of territoriality and resource defence among hunter-gatherers. As modelled by Dyson-Hudson and Smith (1978) in their 'economic defensibility model', the large home ranges typical of hunter-gatherers are not possible to defend by exclusion. Soft territoriality may develop, however, where permission is sought before use (Smith 1988; Layton & O'Hara 2009; Lowen & Dunbar 1994). A well-documented example is the system of reciprocal access to land among the Ju/'hoansi where social ties established through relatedness, fictive kin, and trading partnerships are required in order for an individual to be granted permission to forage in the land of another groups (Lee 1979; Wiessner 2014). By allowing neighbouring communities reciprocal access to land, such a system may, theoretically, serve to buffer risk in a way conceptually similar to food sharing within the camp (Smith 1988; Kelly 2013). Thus, the risks in the foraging economy which I argue to shape food sharing at the level of the house, cluster, and camp in chapter six may also shape wider social groups.

The structure of hunter-gatherer meta-groups also has implications for the exchange of information and ideas required for cumulative cultural evolution (Dean et al. 2012; Tennie et al. 2009; Hill et al. 2014; Vegvari & Foley 2014). Certainly, contemporary hunter-gatherers have extensive social networks, as well exemplified by the *Hxaro* exchange system of the Ju/'hoansi described above (Wiessner 2002; Wiessner 2014) and also evidenced in the archaeological record of Upper Palaeolithic Europe (Whallon 2006). An understanding of the pattern, process, and functional significance of knowledge transmission among a wider range of hunter-gatherer societies would represent an important contribution to the existing understanding of the relationship between social structure, demography and culture both in the present, and in human evolutionary history (Vegvari & Foley 2014; Powell et al. 2009).

Relatedness beyond descent

One of the central questions of evolutionary biology has been why organisms behave in ways that are detrimental to their own direct fitness, yet advantageous to the fitness of others. One of the most powerful explanations for such 'altruistic' acts has been kin selection theory (Smith 1964; Hamilton 1964) which holds that individuals can derive indirect fitness benefits through aiding individuals who are related by common ancestry and therefore share genes. The relatedness of individuals has strong predictive power for explaining behaviours across the natural world, including among humans (see section 6.3.3 for a full review). There is a gulf, however, between biological conceptions of relatedness and human conceptions of kinship that include not only consanguineal ties but also ties through marriage (affinal ties). In chapter five of this thesis, I presented the results of a model which demonstrates that individuals can, in fact, derive fitness benefits through aiding affinal kin since they share a common reproductive interest in the next generation. I believe that this shift from thinking of relatedness as shared ancestry to thinking of relatedness as common reproductive interest has many important implications.

Groups and human cooperation

Explaining how humans solve the "problem" of cooperation has become one of the central occupations of evolutionary anthropology (Boyd & Richerson 2009; Rand & Nowak 2013). Within human behavioural ecology, a body of theory has been developed in which individuals are assumed to be strategic agents whose behaviour represents a flexible response to their social, ecological, and economic context. Research on hunter-gatherer societies has made an important contribution to this field by providing examples of how cooperation in social domains such as childcare, foraging, and food sharing can be maintained in small populations without much in the way of third party punishment or social hierarchy. For all the discussion of cooperation within social groups, however, there has been relatively little in the way of discussion of how these groups form to begin with. In this thesis I have tried to shed light on this issue. Just as humans construct our ecological and environmental niches, so to do we construct our social groups. Just like the cooperation which occurs within them, the size, composition, and internal structure of human groups is a product of the socio-strategic decision making of individuals.

7.3 Closing remarks

In this thesis I hope to have made some important theoretical, methodological, and empirical contributions to evolutionary anthropology and to hunter-gatherer studies. I advocate the importance of thinking about groups not only as the arena for conflict and cooperation in social life but also as a product of these forces. I also advocate an alternative way to calculate the relatedness of individuals that may have important consequences for theory in both evolutionary anthropology and beyond, and argue that an understanding of cooperation in domains such as food sharing benefits from an understanding of the social structure of the groups in which it takes place. Although the ethnographic data I collected among the Agta may not have taken centre stage in all chapters of this thesis, I hope I have also made a valuable contribution to our understanding of the Agta and their way of life. In a field that is increasingly theory rich but data poor, this is perhaps the most important contribution.

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Appendix A

Nutritional data used to estimate calorific value of foraging returns

All data from the USDA National Nutrient Database for Standard Reference

English	***Agta***	***Binomial***	***USDA Ref.***	***kcal per 100g***	***Protein per 100g***
Giant mottled eel	Iget	*Anguilla marmorata*	15025	184	18.44
Mozambique tilapia	Tilapya	*Oreochromis mossambicus*	15261	96	20.08
Acute-jawed mullet	Banog	*Neomyxus leuciscus*	15055	117	19
Mullet	Banug	*Mugilidae sp.*	15055	117	19
N/A	Burasi	*Terapontidae sp.*	15055	117	19
Blackbarred halfbeak	Burik	*Hemiramphus far*	15055	117	19
Celebes goby	Burokkus	*Glossogobius celebius*	15055	117	19
Mud fish	Dalag	*Channa striata*	15055	117	19
Largesnout goby	Mori	*Awaous melanocephalus*	15055	117	19
N/A	Mudi	*Awaous melanocephalus*	15055	117	19
N/A	Usos	*Sillago sp.*	15055	117	19
Moray eel	Igat	*Gymnothorax eurostus*	15025	184	18.44
Lined bristletooth	Mahagta	*Ctenochaetus striatus*	15008	127	19
Surgeonfishes	Malalbad	*Acanthuridae*	15008	127	19
Squirrelfishes	Masaget	*Holocentridae*	15008	127	19
Wrasses	Mulmul	*Labridae sp.*	15008	127	19
Bluespine unicornfish	Sahunguan	*Naso unicornis*	15008	127	19
Chubs	Omipus	*Kyphosidae*	15008	127	19
Philippine warty pig	Laman	*Sus philippinensis*	17158	122	21
Pigeon	Laguiden		05160	294	18.47
Philippine Brown Deer	Ugsa	*Cervus mariannus*	17164	120	23
Gray's monitor lizard	Banag	*Varanus olivaceus*	05160	294	18.47
Rufus Hornbill	Kalaw	*Buceros hydrocorax*	05160	294	18.47
Tarictic Hornbill		*Penelopides panini*	05160	294	18.47
Water monitor lizard	Banag	*Varanus salvator*	05160	294	18.47
Python	Biklat	*Python reticulates*	05160	294	18.47
Honey	Pulat		19296	304	0.3
Spiny lobsters	Binigen	*Palinuridae sp.*	15147	77	16.52
Fresh water shrimp	Udang	*Macrobrachium lar*	15149	71	13
Common reef octopus	Kugita	*Octopus cyanae*	15166	82	14.91

Green Turtle	Pawikan	*Chelonia mydas*	93600	89	19.8
White nerite	Kararing	*Nerita plicata*	15171	81	9.5
Cowries	Puti/Sigay	*Cypraeidae*	15171	81	9.5
Top shells	Samung	*Trochidae sp.*	15171	81	9.5
Round Crabs		*Xanthidae*	15139	87	18
Shore Crabs		*Grapsidae*	15139	87	18
Banana	Musa sp.		09040	89	1.09
Papaya	Apaya		09226	43	0.47
Pineapple	Pinya		09266	50	0.54
Casava	Casava		11134	160	1.36
Sweet potato	Kamote	*Ipomoea sp.*	11507	86	1.57
Gabi	Taro	*Colocasia esculenta*	11518	112	1.5
Gabi (leaves)	Taro leaves	*Colocasia esculenta*	11520	42	5
Rambutan	Bulala	*Nepehelium sp.*		118	
N/A	Ilos	*Dioscorea filiformis*	11601	304	0.3

Appendix B

Sex equality can explain the unique social structure of hunter-gatherer bands

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Appendix C

Networks of food sharing reveal the functional significance of multilevel sociality in two hunter-gatherer groups