

The Role of Social Capital in Human Evolution: lessons from BaYaka Hunter-Gatherers

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I, Nikhil Chaudhary, 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.

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P0.1: Our friends. From left to right—Daniel, Semoi, Kamba, Bwaka, Deniz, Eteni, Tokidya, Ekbay, Nikhil (credit: James Thompson).



P0.2: Bakima and I during my initiation into *Ejengi* (credit: Deniz Salali).

Abstract

Many of *Homo sapiens*' defining characteristics relate to our sociality—our advanced mind reading abilities; sophisticated languages; diverse cultural norms and practices that manifest as highly differentiated rituals and religions; and 'hyper-cooperative' tendencies. Thus, understanding the evolution of human sociality is indispensable for a complete understanding of humanity. One question that remains unanswered is how individual differences in social integration within the group affect biological fitness.

I explore this question by studying BaYaka hunter-gatherers living in the rainforests of Northern Congo. For the vast majority of our species' history we lived as hunter-gatherers, hence such populations offer a valuable insight into human evolution. The overarching hypothesis presented is that cooperation is a fundamental means by which hunter-gatherers surmount the ecological challenges they face. Therefore, if certain individuals have superior access to cooperation from other group members, which I refer to as social capital, they are likely to achieve higher fitness.

I use childcare practices as a case study to demonstrate how essential cooperation is for the BaYaka. Employing a novel method, using wireless sensing devices to track proximate interactions, I find mothers only account for ~25% of the proximate interactions of 0–4 year olds. The analyses also show that this form of cooperation in childcare is preferentially directed towards kin and reciprocal partners.

I use economic gift games to measure social capital and confirm that it varies considerably between group members. Moreover, I find that it is associated with larger food sharing networks and higher body-mass index, indicating it enhances one's ability to buffer the food risk inherent with hunter-gatherer subsistence. Additionally, I show that social capital positively predicts polygynous marriage in men (whereas physical attributes do not), as well

as age-specific fertility in women. Finally, I find some evidence for a heritable component of social capital, suggesting that the evolutionary advantages it confers may accrue over multiple generations.

These results have important implications for our understanding of the processes underlying human social evolution. Additionally, they help to explain how fitness variance emerges in egalitarian hunter-gatherers, and why social integration is consistently linked with mental and physical health.

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1. Human Behavioural Ecology

“Nothing in Biology Makes Sense Except in the Light of Evolution” (Dobzhansky 1973).

1.1 Theoretical framework

Human Behavioural Ecology (HBE) is a field that represents a bridge between the social and natural sciences, and seeks to explain human behavioural diversity using the fundamental principles of evolutionary biology. Behavioural diversity is used here in the broadest sense, representing differences in behavioural patterns between populations, between individuals within the same population, and within the same individual at different points in time (Brown et al. 2011).

In contrast to other social sciences, evolutionary approaches to behaviour acknowledge and emphasise the fact that humans are members of the animal kingdom and products of evolutionary processes: genetic drift, gene flow, and central to the HBE approach, natural selection. Darwin’s theory of natural selection is elegantly simple—any trait that demonstrates variability, heritability and affects survival/reproductive outcomes will be subject to natural selection. This includes sexual selection—the enhanced replication of traits that improve mating access by increasing either one’s attractiveness to the opposite sex (intersexual selection) or one’s ability in same-sex competitions for mates (intrasexual selection). Over evolutionary time variants of traits that increase the reproductive output of their bearers will increase in frequency relative to less successful variants (Darwin 1859). Thus, organisms in the natural world appear well adapted for life in the environments they inhabit, almost as if they had been designed—the giraffe’s long neck, the chameleon’s colour changing camouflage, the polar bears thick coat etc. However, a slow blind process of trial and error, rather than intentional design, correctly characterises the process by which such adaptations came to be. The applicability of this process to morphology is widely recognised,

however, the principles of natural selection also drive the evolution of behavioural traits. Hence, whilst economics asserts humans behave to maximise their wealth, and psychology often emphasises well-being, the currency HBE is concerned with is evolutionary fitness i.e. the representation of copies of one's genes in future generations. Zoologists and behavioural ecologists have been applying such logic to understanding the behaviour of non-human animals for over a century, and HBE recognises that human behaviour can be understood in much the same way. Indeed, throughout this thesis I begin each chapter by situating the behaviour of interest in a broader evolutionary context, explaining where else in the animal kingdom similar behaviours can be found, and what explanations have been provided for the selection of such behaviours in species other than our own.

When studying behaviour from an evolutionary perspective, Tinbergen 1963 notes there are four relevant questions to ask:

1. What is the evolutionary history of the behaviour?
2. What is the development of the behaviour i.e. what factors during development brought the behaviour about?
3. What are the proximate causes of the behaviour (e.g. the physiological underpinnings of a behavioural response)?
4. What is the function of the behaviour i.e. how does it increase an individual's evolutionary fitness?

HBE is primarily concerned with the last of these questions and adopts an adaptationist stance. That is to say, it assumes behaviour is shaped by natural selection to maximise an individual's fitness under the ecological conditions that individual faces (Nettle et al. 2013). Ecological conditions refer to both physical (e.g. climate) and social (e.g. group size) aspects of the environment; and since these vary across populations, individuals, and the life-course they generate behavioural diversity. Inherent to this approach is the concept of behavioural

plasticity, whereby decision rules facilitate flexible responses to the environment. Thus, behaviour is not considered as rigid but as context dependent i.e. under conditions x do A, and under conditions y do B (Borgerhoff Mulder & Schacht 2012). HBE remains agnostic about the proximate mechanisms that underlie these plastic responses—*the phenotypic gambit*; and assume that genetic, phylogenetic and cognitive mechanisms do not significantly constrain the ability of individual behaviour to adapt to the local environment—*the behavioural gambit* (Nettle et al. 2013).

It is noteworthy that an individual's fitness comprises of their direct fitness (the replication of their genes in future generations via their own survival and reproduction), and indirect fitness (the replication of their genes in future generations via the survival and reproduction of genetic relatives who share their genes). Together these components are referred to as 'inclusive fitness' (Hamilton 1964).

I would like to clarify something here which commonly leads to misunderstandings and misinterpretations of HBE research among those unfamiliar with evolutionary approaches. Whilst in HBE we expect human behaviour to be adaptive and to serve genetic interests, such 'motivations' are not conscious. In fact, they are not unconscious/subconscious either. To use the human enjoyment of sex an example, during intercourse humans do not experience a narrative of 'I am enjoying this sex because it may result in conception of an offspring who shares my genes, and thus higher fitness i.e. greater representation of my genes in the next generation'. Nor is there a subconscious mind with such explicit motivations that conceals them from our conscious awareness in a manner resembling Freudian interpretations of dreams and behaviour. More simply, humans enjoy sex because individuals with gene variants which resulted in a phenotypic aversion to sexual intercourse would have not procreated and thus such variants became extinct. Conversely, those individuals with gene variants that equipped them with a sex drive, actively pursued sexual opportunities,

procreated and left descendants who inherited such drives. Of course, sexual behaviour is a far more complex phenomenon than described here, but I have trivialised it for the purpose of my example. Thus, while we expect human behaviour to be fitness maximising, we do not expect humans to have any conscious or subconscious interests in their evolutionary fitness, or to use the sentiments of Steven Pinker: “my genes...can go jump in a lake” (Pinker 1997).

1.2 Applications

Given its emphasis on behavioural diversity, human behavioural ecologists attempt to understand and predict behavioural practices across the spectrum of human populations, conducting research with hunter-gatherer, horticulturalist, agricultural, pastoralist and industrialised societies. The behaviours of interest can be subdivided into three principal categories—acquisition/production, distribution/cooperation, and reproduction/life-history—all of which are intrinsically interlinked.

Production research analyses the subsistence strategies of different societies. One of the first theoretical frameworks within HBE was Optimal Foraging Theory (OFT), which assumes that foragers’ production decisions should maximise the rate of nutrient acquisition (Emlen 1966; MacArthur & Pianka 1966). These decisions include prey choice—what resources are pursued, as well as patch choice—where to live and how long to stay there. Production research may also explore why individuals of different sex, age or skill within a society may adopt different production strategies. For instance, among hunter-gatherer groups men usually hunt for unpredictable and difficult to acquire game, whereas women specialise in gathering more reliable foods such as plants and yams. There is a long-standing debate amongst researchers as to whether or not this sex specialisation in production reflects a cooperative division of labour within the nuclear family (Lovejoy 1981; Lancaster et al. 2000).

Some argue that men's focus on resources which are difficult to acquire and widely shared among the group (rather than staying within the producer's family) is more likely a strategy to signal their skill and physical prowess in order to attract mates and allies (e.g. Hawkes et al. 2001; Bliege Bird et al. 2001).

Research into distribution and cooperation attempts to understand how resource transfers and other cooperative acts can be understood evolutionarily. The essential question is how cooperative behaviours that are seemingly costly to the actor but beneficial to the recipient could have been favoured by natural selection. For such behaviours to evolve, they must offer some ultimate (fitness enhancing) benefit to the donor preventing them from being outcompeted by selfish individuals (Axelrod 1981). In the case of food sharing—perhaps the most well studied form of cooperation—numerous models have been formulated postulating different benefits to cooperators, each of which have varying degrees of ethnographic empirical support (Gurven 2004a). These include classical kin selection—sharing with genetic relatives who share one's genes (Hamilton 1964); reciprocal altruism—sharing now in order to be repaid in future times of need (Trivers 1971; Gurven 2004b); costly signalling—share difficult to acquire food in order to signal one's quality and attract mates (Bliege Bird et al. 2001); tolerated theft—share to avoid the costs of defending the food from those in greater need (Blurton Jones 1984).

Reproduction/Life-history studies focus on two fundamental energy allocation trade-offs faced by an individual. Firstly, the trade-off between investing energy into growth versus reproduction (Migliano et al. 2007), and secondly between the quantity of offspring produced and the amount invested in each offspring (Lawson & Mace 2011; Quinlan 2007). The optimal solution to these trade-offs is dependent on local ecological conditions, such as the extrinsic mortality rate, and has consequences for parenting behaviour, fertility rates and life-history (the scheduling of key events over the life-course). These events include growth

rates, age at first birth, inter-birth intervals, menopause, longevity etc. Other key areas of study include why different mating systems emerge in different populations (Borgerhoff Mulder 1988; Marlowe 2000), as well as which attributes men and women value when selecting a mate (Sear & Marlowe 2009).

1.3 Other approaches

HBE differs from other social sciences due its evolutionary focus—while economics stresses profit and wealth maximisation and psychology highlights maximisation of well-being—HBE asserts it is fitness maximisation which drives individual behaviour. Whilst maintaining a focus on ethnographic fieldwork, HBE differs from sociocultural forms of anthropology in its employment of the hypothetico-deductive method and emphasis on quantitative analysis (Winterhalder & Smith 2000). Statistical techniques employed by the field are increasingly advanced and now include multi-level modelling, phylogenetic analyses and Bayesian methods. Since fitness is difficult to measure, studies examining fitness consequences of behavioural variation use proxies such as number of surviving offspring, mating access or longevity (Nettle et al. 2013). There are other fields also employing an evolutionary approach to human behaviour with different emphases and assumptions, namely Evolutionary Psychology (Barkow et al. 1992) and Cultural Evolution (Boyd & Richerson 1985). Unlike Behavioural Ecology, which studies adaptations of all animals, these two fields are solely focused on understanding human behaviour.

Evolutionary Psychology traditionally views human behaviour as being driven by a set of domain-specific modules, such as mate choice or cheat detection modules. Together these modules are assumed to constitute a genetically determined universal human nature. They are thought to have evolved in the 'Environment of Evolutionary Adaptedness' (EEA). Thus,

behaviour is considered to be adapted to a hunting and gathering lifestyle (Kanazawa 2003). Therefore, in contrast to the adaptationist approach of HBE, evolutionary psychologists expect behaviour is often 'mismatched' to modern environments and suboptimal or even maladaptive. A classic example is the common preference for foods high in sugars and fats, which were rare and valuable in the EEA, but are readily available in industrialised contexts and in turn lead to the high prevalence of obesity (Cordain et al. 2005). Another key difference between Evolutionary Psychology and Human Behavioural Ecology lies in its methodology, as ethnographic fieldwork is rare and Evolutionary Psychology studies typically use laboratory experiments and questionnaires with university students or other local participants.

The premise of Cultural Evolution is that cultural traits or memes (socially learned information that is expressed behaviourally) are analogous to genes in so far as they exhibit variation and are subject to selective forces (Dawkins 1976). Cultural traits are often adaptive since those which promote survival and reproduction will increase in frequency over time via typical selective processes and vertical inheritance from parent-child. However, unlike genes, cultural traits can also be transmitted horizontally within generations and change multiple times within an individual's lifetime. Social learning mechanisms such as prestige bias (do whatever high status individuals do) or conformity bias (do what most others do) drive horizontal transmission (Henrich & McElreath 2003). This field focuses primarily on generating mathematical models and simulations analysing cultural change; or conducting laboratory experiments to study social learning mechanisms.

Although these fields have meaningful differences between each other, such as their emphasis on genetics versus culture and universality versus variation, research is not always clearly or exclusively aligned to one of them. I have discussed HBE in the most detail here, since this is the field with which I most closely associate. Whilst the research presented in

this thesis is indeed derived from ethnographic fieldwork and often seeks to measure fitness consequences of behaviour, I also use experimental games, make references to cultural norms and inferences about human psychology.

2. Introduction—Evolution and Sociality

2.1 Why I chose to study sociality

Currently, when evolutionary scientists consider what it means to be human, there are a few themes that seem to reoccur in this discourse: language, theory of mind, cooperation and culture (Pinker 2010; Tomasello et al. 2005; Boyd & Richerson 2009). Whether these facets of humanity distinguish our species from the rest of the animal kingdom qualitatively or quantitatively is an area of contention. However, all these characteristics are hyper-developed in humans regardless of whether they may exist to some degree in other species. Furthermore, all these features of *Homo sapiens* are essentially social, which is why the study of human social evolution is fundamental to a complete understanding of humanity.

Humans are very adept at deciphering the beliefs, intentions and perspectives of other conspecifics—we understand that we and others have minds, and we are able to adopt the perspective of others' minds relatively accurately (Tomasello et al. 2005). This 'theory of mind' is inherently social, and evolved to help individuals navigate complex social landscapes, and reap the rewards of collaboration and cooperation with fellow group members, without being exploited by deceptive and manipulative conspecifics (Byrne & Whiten 1988).

Culture is a tool that allowed humans to maximise the returns on the potential benefits of sociality, and thrive across the world. Cultural rules and social norms maintain cohesiveness and facilitate effective cooperation within social groups (Henrich 2004). Additionally, our capacity for social learning and culture enables the transmission of information and innovations within and between social groups. This cultural transmission allows humans to surmount ecological pressures and adapt to changing environments with remarkable

efficiency since these cultural adaptations can evolve substantially faster than genetic ones (Boyd & Richrson 2009).

Communication is ubiquitous in the animal kingdom; however, human language is particularly sophisticated, whereby the use of an “open-ended combinatorial system” permits the production of an infinite set of messages (Pinker 2010). Language is inherently social, and has been posited to play an important role in the maintenance of social relationships, social coordination and social learning processes (Dunbar 1993; Origgi & Sperber 2000).

The key message here is that the defining characteristics of our species are components of social behaviour, this is why I chose to focus on sociality in the current thesis. In this introduction I will begin by explaining how sociality can evolve in the animal kingdom, and why some species are social whereas others are not. Following this, I will discuss the origins of sociality in the primate order, in which humans reside, and why primate sociality is particularly interesting. Finally, I will discuss the different levels at which sociality can be studied—species (why some species are social and others are solitary), group (how group composition affects the fitness of an average member), and individual (how differences in social positioning within the group affect individual fitness). I highlight that research at this lowest level, which investigates the evolutionary implications of individual differences in sociality within the group, is the most scant and therefore a chosen focus of this thesis.

2.2 Sociality and evolution—why live in groups?

Throughout the animal kingdom, a vast spectrum of sociality can be observed. Organisms such as armadillos and red pandas spend virtually their whole lives in isolation from adult conspecifics, interacting only occasionally for mating purposes (Reser 2014). At the other

extreme, within the orders Hymenoptera and Blattodea, some insects, such as bees and termites, form huge colonies with conspecifics and have highly sophisticated social structures and division of labour (Wilson & Hölldobler 2005). The sociality and interdependency of these organisms is so pronounced that their colonies are sometimes referred to as one large superorganism (Johnson & Linksvayer 2010). Other animals, such as some species of bats, dolphins, elephants and chimpanzees, do not have stable social groups, but form fission-fusion groups which aggregate and split at different times of day or year dependent on what activities they are carrying out and how resources are distributed (Aureli et al. 2008).

Given the diversity of social behaviour in the animal kingdom, various classification standards have been developed in an attempt to categorise species based on their social behaviour.

The following are the predominant groupings adapted from Wcislo & Danforth 1997:

1. Solitary—females are solely responsible for their brood, and adult members of the species do not interact, e.g. red squirrels (Digweed & Rendall 2009).
2. Subsocial—parents care for and guard offspring until the latter are adults, but do not interact with other adults, e.g. desert spiders (Schneider 1995).
3. Social—group-living by more than one adult, e.g. bottlenose dolphins (Lusseau 2003).
4. Eusocial—group-living of multiple generations, with division of labour and some members of the group do not reproduce, e.g. termites (Thorne 1997).

Previously, there had been some application by biologists of ‘Dollo’s law’ of irreversible evolution (Gould 1970), to sociality i.e. the contention that a species can only evolve to become more social, and that selection for reversals towards more solitary behaviour cannot occur. However, there is evidence from numerous invertebrates and birds that shifts in sociality over time are not always unidirectional (Wcislo & Danforth 1997; Grandcolas 1997;

Edwards & Naeem 1993). Instead, to understand social behaviour, or its absence, it is necessary to discern the relative costs and benefits that group-living has on the survival and reproduction of members of a species at a given point in space and time.

There are a few common advantages to sociality observed repeatedly in the animal kingdom, which underpin the evolution and maintenance of group-living. Predation defense is one of the most common pressures leading to the selection of sociality. Virtually all food eaten by animals is another organism of some sort (except in the case of fruit), therefore it is unsurprising that predation avoidance plays a major role in driving behaviour, and indeed social behaviour (Pinker 2011). The benefit of group-living for animals which are potential prey is two-fold. Firstly, there is an 'encounter effect' such that encounters between predators and prey are reduced when prey group together; this is because the likelihood of an encounter is not proportional to group size i.e. a group of 100 zebras does not encounter lions 100 times more frequently than a solitary zebra would (Inman & Krebs 1987). Additionally, there is a 'dilution effect'—the mere existence of other group members results in a decreased probability of a given individual being preyed upon during an encounter with a predator (Hamilton 1971). Provided, the encounter and dilution effects occur simultaneously, a given individual has a survival advantage from group-living (Turner & Pitcher 1986). The second advantage is that group-living facilitates increased vigilance, and reduces a predator's ability to surprise prey since individual prey can warn their fellow group members when a predator is spotted. For instance, vervet monkeys give different alarm calls depending on whether an eagle, leopard or snake has been spotted, and thus elicit appropriate defense behaviours by group members (Seyfarth et al. 1980).

Another hypothesised driver of sociality is cooperative foraging (Whitehouse & Lubin 2005). In contrast to the protection sociality offers to prey, it can also provide benefits to predators. This is particularly true when the probability of catching prey for an individual predator is

low, and the average payoff from predation improves via collaboration, which depends primarily on the average size and number of prey killed during an encounter (Packer & Ruttan 1988). Cooperative hunting is observed in numerous gregarious animals such as canids, herons, and some spiders. However, research suggests cooperative hunting is likely to be a secondarily advantageous behaviour which is a consequence rather than cause of gregariousness (Packer & Ruttan 1988).

Enhanced reproduction is another evolutionary benefit that can be derived from sociality, particularly eusociality. Cooperative breeding refers to a system in which there are non-reproductive helpers who do not reproduce themselves, but engage in activities such as foraging, nest building and brood care in order to aid the reproduction of other reproducing group members (Clutton-Brock 2002). The most pronounced examples of such a system can be found in the eusocial insects, where workers undertake different roles/castes to increase the reproductive output of the queen. The evolution of such a system may be related to the haploid-diploid genetics of these organisms, whereby females are more genetically related with their sisters than their own offspring; and therefore can achieve higher inclusive fitness by helping their mother reproduce than by reproducing themselves (Hamilton 1964). These societies of ants, bees, termites etc. offer a truly astounding example of sociality in the animal kingdom, where reproduction itself—the most fundamental tenant of life—is a group activity. In chapter 6 I discuss cooperative breeding in more detail, additionally I outline past research and present an analysis demonstrating the cooperative nature of human reproduction, which has led many scholars to label humans as cooperative breeders (Burkart et al. 2009; Hrdy 2005).

Thus, group living can provide evolutionary advantages in the form of predation defense, cooperative foraging and cooperative breeding. However, sociality is not a uniform trait across the animal kingdom because sociality also confers substantial costs to group

members, which can only be compensated for in some socio-ecological contexts. One considerable disadvantage that is concomitant with group-living is increased disease and parasite transmission caused by increased contact and proximity (Altizer et al. 2003). For instance, Nunn et al. 2003 found significant positive associations between measures of sociality in carnivores and white blood cell counts. Other disadvantages include emergent resource competition between group members, which is largely determined by the distribution of food resources, and extent to which they can be monopolised; this cost of sociality is discussed in more detail in the next section on primate sociality.

2.3 Primate sociality

In order to understand human sociality from an evolutionary perspective, which broadly speaking is the subject of this thesis, it is necessary to narrow the lens and examine sociality within our order—the primates. In this section I discuss the evolutionary origins of primate sociality; as well as the strong relationships formed in primate groups, which provide the foundation for the highly social behaviour of our species.

It is helpful here to define the terms social relationships/ties/connections, which I use interchangeably in the following sections. Whilst a relationship has been defined simply as a series of interactions in time between two individuals (Hinde 1976), I attach an assumption that such interactions are generally positive in nature. Thus, when I use these terms I am not referring to repeated interactions that are predominantly negative, such as aggression, or neutral in nature. I employ them in a manner similar to much of the literature cited, which focuses on positive interactions such as allogrooming (e.g. Schülke et al. 2010). References to the strength of such relationships/ties/connections should be considered to reflect the magnitude of such positive interactions, either in terms of frequency or quality.

2.3.1 Origins

Previously, the socio-ecological model provided the dominant explanation for primate social behaviour. This model asserts that primate groups evolved due to competition for high quality food patches, where cooperating groups are better able to defend and monopolise clumped resources than an individual acting alone (Wrangham 1980). On the other hand, increases in group size are also concomitant with reductions in individual foraging efficiency, since larger groups must travel further to sufficiently meet their nutritional demands and due to within-group competition for food (Janson 1988; Isbell 1991). In a comprehensive meta-analysis including most primate groups from prosimians to great apes (Janson & Goldsmith 1995), ~80% of studies were found to identify a significant association between day path length and group size. Thus, the socio-ecological model asserts that primate sociality and group size are determined by the relative effects of within and between-group competition for resources, which are a function of the spatio-temporal distribution and quality variation of food (Wrangham 1980; Isbell 1991).

The predominant competing hypothesis regarding the evolution of primate groups, places far more emphasis on predation defense as the primary selection pressure for sociality, as opposed to feeding competition (Alexander 1974; van Schaik 1983). Food competition is consequently relegated to being considered a constraint on grouping, rather than a fundamental driver of it. Recent phylogenetic research provides support for this alternative hypothesis, and suggests that primate sociality originated ~52 million years ago, coevolving with a shift from nocturnal to diurnal living (Shultz et al. 2011). For nocturnal primates, predation defense strategies are based on being inconspicuous, whereas for diurnal primates, group-living provides the safety in numbers described in the previous section (Silk 2011). This work undermines the socio-ecological model on two accounts suggesting: 1. Predation risk rather than food distribution and competition selected for group-living; 2. The

structure of primate groups has a strong phylogenetic signal (Pagels $\lambda = 0.983$), indicating group structure cannot react with perfect flexibility to ecological conditions but is in fact restricted phylogenetically (Shultz et al. 2011).

2.3.2 Deeper ties

There is an extensive body of research into primate sociality because it has a number of interesting characteristics. Sociality is truly at the core of primate behaviour, and although reversals from a social to solitary state have been found in other organisms, they are extremely rare in primate evolutionary history (Wcislo & Danforth 1997; Dunbar 2009). Within groups, primates form particularly strong social ties. An enlarged neocortex is found in taxa where pair-bonding (long lasting relationships) occur between reproductive partners, as is the case in many bird and mammal species (Dunbar & Shultz 2007). This specific encephalization is thought to aid individuals of these species in correctly choosing reproductive mates, and/or co-ordinating their behaviours with partners once a pair is established (Dunbar & Shultz 2007). However, amongst anthropoid primates, this association is no longer simply qualitative (enlarged neocortex with pair-bonds/non-enlarged without pair-bonds), but in fact becomes quantitative—neocortex size increases as a function of group size (Dunbar 1992). The implication of this result is that amongst primates, the intense bonding observed only between long-term reproductive partners in other taxa, is also present in non-reproductive relationships between fellow group members (Dunbar 2009).

Some scholars have criticised this work since group size is a relatively crude measure of social complexity and does not account for the topology of social networks within the group. Similarly, this work focuses primarily on the neocortex, and does not adequately attend to other cerebral structures involved in social cognition (Acedo-Carmona & Gomila 2016). There

are numerous other criticisms, however these are principally directed at inferences that social complexity is sufficient to fully account for the evolution of human intelligence and encephalisation, which is not of specific relevance here (see Acedo-Carmona & Gomila 2016 for review).

2.4 Social integration within the group

2.4.1 Investigating sociality at different levels

In section 2.1 it is outlined that sociality and group living emerge within a species when the benefits to an individual of that species (e.g. decreased predation risk, increased foraging success and help with reproduction), outweigh the costs (e.g. increased disease and parasite transmission and resource competition) in terms of biological fitness. Once group living is established, sociality becomes a central feature of a species' evolutionary landscape, and there are more complex emergent relationships between sociality and fitness. Two of these relationships, which have been examined in detail, are the effects of group size and composition. Group size has been found to have different effects across taxa. For instance, larger groups have been found to have both positive (e.g. leaf monkeys, Steinbeck & van Schaik 2001) and negative (e.g. long-tailed macaques, van Noordwijk & van Schaik 1999) effects on primate fitness. More macro trends across different taxonomic orders have been identified, such as the direction and magnitude of the effect of group size on fitness being dependent on the extent of cooperative breeding in a species (Clutton-Brock 2001). With respect to group composition, researchers have explored the impact of different characteristics of groups, such as sex-ratio and genetic relatedness, on fitness within different species (e.g. Griffin et al. 2005).

This research into whether a species is solitary/social and how group size/composition affects fitness in social species focuses on trends for an average individual of a particular species or group. To obtain a more complete understanding of the interaction between sociality and fitness, it is necessary to narrow the lens one step further—to analyse the impact of differences in sociality between individuals of the same group. Social relationships and interaction are not necessarily unbiased within the group, and are often structured by kinship, or in some species friendship. Brent et al. 2014 (p2) highlight that within many primate and human groups some dyads “engage in bi-directional affiliative (non-aggressive, non-reproductive) interactions with such a frequency and consistency so as to differentiate them from non-friends”. Thus, it is necessary to assess whether inter-individual differences in sociality within the group have evolutionary implications. Specifically, it is possible that those individuals with higher quality/quantity of social relationships may obtain advantages related to survival or reproduction over fellow group-members. It is at this lowest level—differences in individual social integration within the group—that evolutionary research is scant. The next section reviews the limited research investigating the fitness implications of sociality at this level.

2.4.2 Social integration within the group and primate fitness

The first studies investigating the evolutionary advantages of individual social integration were conducted on female baboons and macaques. In these taxa, relationships between female kin and gaining coalitionary support are crucial in securing a high rank in the dominance hierarchy (Silk 2007). This in turn translates to increased reproductive success since higher ranking individuals mature earlier, have higher infant survival and shorter inter-birth intervals (Silk 2007; see section 7.1.2 for more detail). However, social integration has been found to positively affect components of female fitness independently of rank. In

species of baboon, sociality indices (calculated based on approach and grooming behaviour) have been associated with increased longevity and higher offspring survival (Silk 2003; Silk et al. 2010). These studies represent a large step forward in our evolutionary understanding of sociality; however, they only focused on the effect of female-female ties, on female fitness in female philopatric species. Moreover, they study social integration in a broad sense, identifying which individuals take part in more affiliative interactions, but do not isolate the quantity or quality of an individual's social ties. Since then, a handful of studies have extended our knowledge on this topic to include opposite-sex social relationships, the role of social integration on male fitness, and differing effects of the quantity versus quality of relationships.

Another study on wild baboons from Kenya differentiated between female-female social connectedness and female-male connectedness, and actually found that whilst females in the top tertile of female-female connectedness had a 34% reduced mortality risk compared to those in the bottom tertile, female-male relationships were even more influential, reducing risk by 45% (Archie 2014). Studies on male reproductive outcomes have also been conducted. More socially integrated Assamese macaques (calculated based on grooming and association) benefit from cooperation in conflicts and achieve higher dominance rank, and in turn were found to sire more offspring in the subsequent mating season (Schülke et al. 2010). Unlike the other aforementioned studies, which measure general social integration based on the total frequency of various affiliative interactions and do not distinguish between quality and quantity of social relationships, Schülke focused on quality or 'bondedness' of male social ties; he calculated this based on the combined grooming and association frequencies of an individual's top three social partners. Conversely, a study on Barbary macaques examined the effects of both quality and quantity of social relationships independently, and found only the latter to have important survival benefits during a harsh

winter, which may be a result of better thermoregulation via huddling (MacFarland & Majolo 2013).

In summary, research thus far seems to consistently find positive effects of social relationships (both same-sex and opposite-sex relationships) and integration on components of primate fitness for both males and females. These advantages include increased longevity, offspring survival and mating access. Some of these effects are mediated by dominance rank and its associated fitness benefits; however, some studies find social integration provides advantages independent of rank. When sociality is dissected further into quantity and quality of relationships, the relative importance of these varies by species. The data are scant, and only cover a minority of primate species, leaving much work to be done to make more broad inferences about the importance of within-group social differentiation across species and ecological conditions.

This section has focussed on the non-human primate literature; there are only a handful of studies in other taxa—such as bottlenose dolphins and forked fungus beetles (Stanton & Mann 2012; Formica et al. 2012)—relating social integration to fitness, and none in humans. It is at this level of within-group social differentiation that evolutionary research is lacking. Therefore, a primary focus of this thesis is to offer some preliminary insight into the fitness implications of within-group differences in human social integration and social network position. In the next section I highlight that there is strong evidence for the existence of proximate mechanisms that motivate humans to form relationships within their groups, yet as noted here, research into the ultimate function (fitness benefits) of this social integration is lacking.

2.4.3 Proximate mechanisms for social integration in humans, but no ultimate functions

Human social groups can take a variety of forms, hunter-gatherer bands, farming villages, religious communities, neighbourhoods etc. Such groups are not unstructured aggregations, but consist of individuals with differentiated social relationships and levels of integration. Within any group we belong to, whilst some members may remain mere acquaintances or even strangers, with others (both kin and unrelated individuals) we form enduring social relationships. In fact, social integration is such a fundamental aspect of being human, that a lack of motivation to form social ties is either considered a pathology in itself (e.g. autism) or a consequence of some other pathology (e.g. depression) (DSM-5 2013; Brent et al. 2014). There is a wealth of research indicating that we have a host of psychological and physiological mechanisms designed to encourage us to foster and maintain social relationships, and to aid in our decisions regarding which group members to form such relationships with.

Neuropeptides, in particular oxytocin, facilitate the generation of cooperative relationships in humans. For instance, research using economic games has found that intranasal administration of oxytocin prior to experiments results in participants behaving with more trust and generosity towards other unknown players (Kosfeld et al. 2005; Zak et al. 2007). Additionally, social information has been found to activate many reward centres in the brain such as the orbitofrontal cortex and anterior cingulate cortex (Brent et al. 2014). Taken together, these findings highlight that our neuro-endocrine system has numerous components designed to aid in the formation of social relationships as well as the selection of social ties.

Forming such social relationships is important for well-being and has been consistently demonstrated to affect both self-reported and physiological proxies for stress. Social support is associated with lower levels of stress hormones such as cortisol and norepinephrine, as well as lower systolic blood pressure (see Seeman 1996 for review). Moreover, stress

responses resulting from conflict with group members are attenuated following reconciliation (Butovskaya 2008). Social isolation is also a major predictor for the development of major depression (Kendler et al. 2005). Given these links between social integration, stress and mental health, numerous researchers have suggested a key function of social relationships may be avoidance of these negative outcomes (e.g. Massen et al. 2010); however, this is a confusion of mechanism and function. Neuro-endocrine systems are mechanisms designed by natural selection to moderate our behaviour, desires and motivations. Thus, one purpose of stress is to motivate socially isolated individuals to foster positive relationships—the function of social integration is not to reduce stress, rather a function of stress is to encourage social integration.

Such interactions between the endocrine system and social behaviour are complex. Indeed, stress also plays a role in social *avoidance* of overcrowding or dominant/violent behaviour in hierarchical contexts (Beery & Kaufer 2015). However, since this thesis is concerned with the evolutionary benefits of social relationships within the group, I predominantly refer to the role of stress in motivating social integration, and the accompanying health consequences of this mechanism.

The research outlined in this section demonstrates that humans have a series of psychological and physiological mechanisms designed to facilitate social integration; specifically, the formation, maintenance and selection of social ties. For these systems to have evolved in humans, social integration must have had important ultimate effects on individual fitness, similar to those outlined for non-human primates in section 2.4.2. However, as alluded to earlier, there has been virtually no investigation into the effect of differences in social integration on individual fitness; which is a major aim of this thesis.

Given that our species lived as hunter-gatherers for most our evolutionary history, extant hunter-gatherer societies are particularly useful for inferring the evolutionary origins of

human traits. Therefore, I examine the possible effects of within-group differences in social integration on individual survival and reproduction among BaYaka hunter-gatherers.

Cooperation is the fundamental means by which our species buffered the ecological pressures we were exposed to as hunter-gatherers (Hill & Hurtado 2009). Following this, the principal hypothesis of this thesis is that if certain individuals are better able to foster social relationships, they would have superior access to cooperation, and in turn would likely experience advantageous survival and reproductive prospects under the harsh conditions of hunter-gatherer subsistence. Thus herein, based on this hypothesis and the premise that social relationships have a cooperative function, rather than refer to social integration, I use the term social capital. I define social capital as “*an individual’s access to cooperation from other group members*”. This cooperation may take numerous forms, including help with childcare; the sharing of food or knowledge; and aid with foraging. Thus, an individual’s social capital can be considered to represent how much help s/he receives in these activities from other members of the group. I operationalise social capital using an economic gift game (see chapter 5 for details).

Before providing more detailed information about the BaYaka hunter-gatherers (chapter 4), it is appropriate to briefly outline evolutionary theories of cooperation since this is a recurrent theme and central to the proposed thesis.

2.5 The evolution of cooperation

Cooperation is widespread in the living world, and occurs at numerous levels of organisation—between cells, individuals, groups, and species. Although there are some facets of human cooperation that *may* be exceptional, cooperation per se is certainly not limited to humans. Even bacteria have genetic systems specialised to carry out collective

behaviours such as the formation of protective biofilms and expression of virulence factors to attack hosts (Wingreen & Levin 2006). Among our species, we consider charity a virtue, and create organisations with the sole purpose of effectively providing aid to those in need.

To approach such behaviours scientifically, it is necessary to clearly define what is meant by the term cooperation. Traditionally, biologists used the term altruism to refer to behaviours in which an actor incurs a cost in order to provide a benefit to the recipient; where costs and benefits are measured in terms of individual direct fitness (West et al. 2006). Such acts, initially appear to create an evolutionary paradox—how is it possible that natural selection has not eliminated altruists and favoured purely selfish individuals who do not engage in these behaviours that reduce individual fitness (Axelrod & Hamilton 1981).

Over the last fifty years, scientists with a variety of expertise ranging from genetics and zoology through to game-theory and mathematics have contributed vastly to our understanding of this paradox. Given that experts from many different fields have been researching this subject, the terminology used in such work is variable. Some scholars also use the term cooperation to refer to these behaviours in which a cost is incurred by the actor and a benefit experienced by the recipient (e.g. Nowak 2006; Clutton-Brock 2009). I use the term cooperation in the same way; however, one must always be cautious to define these terms since their use is not uniform in the literature (West et al. 2006).

Numerous conditions and mechanisms which are conducive for the evolution of cooperative behaviour have been established. In this section I introduce the two most well-established explanations, namely kin selection and reciprocal altruism (Hamilton 1964; Trivers 1971). Additionally, I will discuss why some scholars assert that human cooperation cannot be explained by these mechanisms and requires an alternative explanation known as cultural group selection (e.g. Henrich 2004; Richerson et al. 2016). These are the three mechanisms that are referred back to later in the thesis; therefore, it is necessary to outline them here. I

do not discuss other mechanisms, such as costly signalling and indirect reciprocity (for explanations of these see Zahavi 1975; Nowak 2006), since they are not of central importance to the proposed thesis.

2.5.1 Kin selection

Hamilton developed the concept of *inclusive fitness*, highlighting that natural selection ultimately acts at the level of the gene rather than the individual. An organism's inclusive fitness is constituted of both their direct fitness i.e. replication of one's genes via one's own reproduction, and indirect fitness i.e. replication of one's genes via reproduction of others with whom one shares genes (Hamilton 1964). Provided a cooperative action satisfies Hamilton's rule: $Br > C$, it may increase an organism's inclusive fitness, even if it is at a cost to their direct fitness (Hamilton 1964). Here 'B' refers to the fitness benefit to the recipient of the altruistic act, 'C' is the fitness cost for the actor, and 'r' is the coefficient of relatedness between the actor and recipient i.e. the proportion of genes they share.

Hence the concept of inclusive fitness can explain cooperative actions between genetic kin, which is why this mechanism is referred to as kin selection (Maynard-Smith 1964). The theory elegantly explains the behaviour of eusocial insects in which workers forgo their own reproduction to aid the queen's reproduction. Due to the haploid-diploid genetic structure of taxa within the Hymenoptera order, such as bees and ants, females are more genetically related to their sisters (75%) than their own offspring (50%). Therefore, their inclusive fitness is maximised by helping their mother produce more sisters rather than by producing their own offspring i.e. workers have been selected to behave purely to increase their indirect fitness and completely neglect their direct fitness (Hamilton 1964).

Kin selection in nature is usually not so extreme, and most animals do not follow a pure strategy of indirect reproduction. Instead, most organisms capable of kin recognition behave to enhance their own reproduction, and cooperate to enhance the fitness of their relatives in certain situations under which Hamilton's rule is satisfied. A famous example comes from the alarm calls of squirrel monkeys. These calls satisfy the conditions of cooperation since they provide a benefit to conspecifics that hear them and are warned of an approaching predator; additionally the caller incurs a fitness cost by directing the attention of the predator towards him/herself. The frequency with which squirrel monkeys produce alarm calls is a positive function of the number of genetic relatives in spatial proximity, as would be predicted by kin selection (Sherman 1977).

2.5.2 Reciprocal altruism

Kin selection can only explain cooperation between genetically related individuals, however cooperation also occurs between unrelated individuals and even members of different species; hence Trivers developed the concept of reciprocal altruism (Trivers 1971). In certain circumstances one may be able to provide a large benefit to another individual at a small cost to oneself. If the situation is likely to be reversed in the future, an individual will enhance their long-term fitness by incurring a small cost and cooperating now in order to receive a large benefit in the future. Thus, repeated interactions between individuals are required for cooperation to enhance fitness via reciprocity; and cooperation can only evolve if the probability of another encounter between the two individuals is greater than the cost to benefit ratio of the act (Nowak 2006). The likelihood of repeated interactions in a species is determined by a host of factors such as lifespan and dispersal rates (Trivers 1971).

Additionally, for cooperation to evolve under this system, individuals must direct their cooperation towards others who will return the favour. Indiscriminate cooperators would be outcompeted by non-cooperative conspecifics that enjoy the benefits of receiving cooperation without incurring the costs of providing it. Axelrod (1984) formally demonstrated that the most effective strategy of cooperation is '*tit-for-tat*'. Under this rule an individual A cooperates with another B in their first dyadic interaction, and then subsequently only cooperates with B if B cooperated with A in their previous interaction. This strategy allows one to reap the long-term rewards of cooperation without being exploited by non-cooperators.

Vampire bats that rely on blood for food, and share blood via regurgitation provide an example of cooperation via reciprocal altruism. These bats die of starvation after just 70 hours of fasting; and their weight and time until starvation decreases exponentially with time since last feed (Carter & Wilkinson 2013; Wilkinson 1984). This exponential relationship is conducive to a scenario in which a donor can provide a large benefit at a relatively small cost; since a donor, who has fed more recently than a recipient, loses less time until starvation than the recipient gains (Wilkinson 1984). Although the exact mechanism behind this cooperative regurgitation has been subject to controversy, a recent controlled experiment found reciprocity was 8.5 times more important than relatedness in explaining blood sharing, and 64% of sharing dyads were unrelated (Carter & Wilkinson 2013).

2.5.3 Human 'hypercooperation' and cultural group selection

Despite the widespread utility of kin selection and reciprocal altruism in explaining cooperation, some scholars argue that these mechanisms are insufficient to explain human cooperation (Gintis et al. 2003). Specifically, they assert that unlike other social species, in

which cooperation tends to be limited to kin, or in some cases small sets of unrelated reciprocators, humans regularly cooperate with unrelated individuals on a large scale and are 'hyper-cooperators' or 'ultrasocial' (Wilson & Gowdy 2014; Burkart 2014). People often appear to be behaving for the benefit of the group, at a cost to themselves, e.g. in warfare (Matthew & Boyd 2011). Additionally, some humans engage in seemingly altruistic behaviours towards individuals who are unlikely to have the opportunity to reciprocate—we give money to charity and donate blood to strangers (but see Zahavi 1975 for alternative explanation).

In the past, some scholars explained the evolution of cooperation using the concept of '*group selection*', whereby individuals were thought to act for the benefit of the group/species, for example by regulating their family size to avoid overpopulation (Wynne-Edwards 1962). This concept is invalidated because selfish free-riders would outcompete those acting for the good of the group since they could reap the benefits of their cooperative conspecifics' behaviour without incurring the costs of cooperation themselves (Dawkins 1976). Thus, those acting for the good of the species would go extinct.

More recently the concept of cultural group selection has become popular, specifically with reference to large-scale human cooperation. It differs from the rejected notion of traditional group selection in that it does not assume individuals ultimately act for the benefit of the group. Rather, it claims that social institutions and between-group competition realign individual interests with group beneficial behaviour. The argument is as follows: due to rapidly varying climates during the Middle and Upper Pleistocene, humans evolved the capacity for social learning and culture since there was strong selection for the ability to adapt quickly to changing environments, and cultural adaptation is substantially faster than genetic adaptation. Culture facilitated stable behavioural variation between groups and suppressed individual variation within groups, since cultural norms regulated the behaviour

of group members and individuals violating such norms were punished. In turn, groups with social norms that promoted group beneficial behaviours and punished selfish free-riders functioned more effectively and were successful in inter-group competition; whereas non-cooperative groups went extinct. Simultaneously, genetic selection favoured individuals who could function well within these cooperative groups and avoid punishment. Thus, natural selection equipped individual psychology with other and group regarding preferences, an ability to internalise group norms and punish violators, and emotions such as guilt and shame to regulate selfish motivations (Boyd & Richerson 2009; Boyd et al. 2010).

I refer to cultural group selection since it currently receives much attention within Human Behavioural Ecology. However, it is noteworthy that the concept is in essence a form of '*multilevel selection*'. Multilevel selection asserts that social groups can be 'vehicles' of selection for genes in the same way as individuals can be (Wilson et al. 2007). Depending on the relative strength of within-group versus between-group competition, group-beneficial behaviours can be favoured by natural selection. This is particularly likely under circumstances in which the force of selection within the group is attenuated via social institutions (Wilson & Sober 1994).

2.6 Summary and thesis

Across the animal kingdom there is a plethora of different social structures, and whilst individuals of some species spend virtually their whole life in isolation, in other species social lives are critical for survival (Wcislo & Danforth 1997). This diversity is a result of varying benefits and costs of sociality across taxa, where group living can offer advantages related to predation defense, foraging and reproduction (Turner & Pitcher 1986; Whitehouse & Lubin 2005; Clutton-Brock 2002), and handicaps in terms of disease transmission and food

competition (Altizer et al. 2003; Wrangham 1980). In the case of the primate order to which *Homo sapiens* belong, following a shift to a diurnal lifestyle ~50 million years ago, the benefits of reduced predation risk in groups resulted in the evolution of group living and group size was only constrained by within-group food competition (Alexander 1974; Shultz et al. 2011; Janson 1988). This was the beginning of the human trajectory towards the complex social animals we are now, and the development of our defining features such as language, theory of mind and culture. Whilst there is a wealth of research into the effects of sociality on fitness between species, and different groups of the same species, there is relatively little exploration into how individual differences in social integration within the group affect evolutionary outcomes. Indeed, primates form differentiated social relationships within the group, which has been a primary selective pressure for encephalization that facilitates the effective navigation of complex social landscapes (Dunbar 1992). Social differentiation is extremely pronounced in our own species—our relationships vary from strangers to best friends, some of us are loners whilst others are social butterflies, and the introvert/extrovert continuum is acknowledged as one of the two foundations of human personality. It is for this reason that studying the effects of individual social differentiation within human groups is especially important.

Hunter-gatherers offer a useful avenue for understanding human sociality, its origins and evolutionary history, since this subsistence mode occupies more than 90% of human history (Lee 1999). The thesis proposed here is that hunter-gatherers rely profoundly on cooperation to mitigate risks inherent to their lifestyle (demonstrated in an analysis of hunter-gatherer reproductive and childcare practices in chapter 6). Consequently, within-group differences in social capital (cooperative social relationships with other group members) have important implications for individual fitness (demonstrated in chapters 7 and 8). Therefore, over human evolutionary history there has been strong selection on social capital, and those individuals with more social capital within hunter-gatherer groups experienced evolutionary

advantages. Thus, humans are equipped with a suite of physiological and psychological proximate mechanisms encouraging the formation and maintenance of social relationships, which explains the repeated observations of a strong association between social integration and mental/physical health (Seeman 1996).

3. Overview of Thesis Structure

This thesis attempts to gain insight in to the evolution of human sociality by investigating an extant hunter-gatherer society—the Mbendjele BaYaka, a Pygmy population from the Congo rainforest. I will begin by providing an ethnographic and demographic description of the study population (chapter 4). In the following chapter (5), I outline the data collection and fieldwork process, and the details of the methods used. The three chapters that follow constitute the analysis and research section of the thesis.

Section 2.2 highlighted that one major benefits of sociality can be more efficient reproduction via cooperative breeding where group members forego their own reproduction to help rear the offspring of others. Many researchers argue that humans are also cooperative breeders, and in chapter 6 of this thesis I address this question. I implement a new method using remote sensing wireless technology to construct childcare networks, and analyse the extent to which these networks conform to a cooperative breeding model. Specifically, I examine who helps mothers with childcare, and why such helping behaviours may have evolved i.e. how they benefit the helper. I then discuss how the answers to these questions resemble and differ from the species of birds and mammals who are traditionally referred to as cooperative breeders. The results also demonstrate that cooperation is vital to hunter-gatherers and is preferentially directed towards kin and reciprocal partners.

In section 2.4 I noted that research into social evolution can occur at several levels—species (why are some species social whereas others are not); group (how does social group size/structure affect the fitness of average group members); and individual (how do individual-level within-group differences in sociality affect fitness). I highlighted that research at this lowest level is scarce, limited to a handful of taxa and absent in humans. Having established the importance and directed nature of cooperation in the first analysis

chapter, in the subsequent two chapters (7 and 8), I investigate how within-group differences in sociality affect evolutionary outcomes.

In chapter 7, I examine whether individual differences in social capital (access to cooperation from other group members) may provide a mechanism for the emergence of inequality and fitness variance in hunter-gatherers despite their politically egalitarian organisation. Chapter 8 continues with this theme and tests whether individual differences in male social capital (alongside physical attributes) may explain the prevalence of polygyny (albeit low) in hunter-gatherer societies, which is not readily explicable using existing models of marriage systems.

Following these three analysis chapters, in chapter 9 I end with a summary and discussion of the overall findings and how they contribute to our knowledge of human social evolution. Key areas of discussion include the evolution of cooperation between unrelated individuals; the role of social capital in generating inequality and fitness variance in egalitarian contexts; the ultimate explanation for associations between social integration and health; and the scope of remote wireless sensing technology in future research.

4. Ethnography and Study Population

4.1 Hunter-gatherers as a model

Hunter-gatherer populations are the best extant approximation of the conditions of human evolutionary history, since prior to the Neolithic revolution ~10,000 years ago, our species lived under this subsistence mode (Lee 1999). However, there is variation between extant hunter-gatherer groups (Kelly 1995), and such variation was likely even more pronounced in the past when such groups were more numerous and widely distributed in terms of the number of environments they occupied. Therefore, there has been some debate regarding the utility of extant hunter-gatherers as a model of ancestral societies.

Extant hunter-gatherer societies are sometimes referred to as 'marginal remnants' of ancestral societies, and are considered to have been pushed into remote low productivity environments by agricultural populations after the Neolithic expansion. Thus, their current way of life may not resemble that of hunter-gatherers prior to this period, who occupied a larger array of less harsh environments (Barker 1999). Additionally, given that extant hunter-gatherers have two distinct forms of social organisation—mobile/egalitarian (referred to as simple hunter-gatherers; includes the BaYaka) versus semi-sedentary/hierarchical (referred to as complex hunter-gatherers)—there is debate regarding which of these systems better reflect ancestral groups (Ames 1994). Some scholars also argue that some contemporary hunter-gatherer groups may actually be descendants from farming ancestors who have readopted this mode of subsistence, rather than representing a lineage that have practiced hunting and gathering without interruption (e.g. Oota et al. 2005).

Nevertheless, there is also substantial evidence supporting the use of extant hunter-gatherers as a model for human evolutionary history, and rebuttals to the aforementioned criticisms of such use. An analysis of habitat productivity of foragers and agriculturalists from

the Standard Cross-Cultural Survey, found that the 'marginal remnants' contention is poorly supported. Extant warm-climate foragers actually live in slightly higher quality habitats than agriculturalists; and in environments of similar productivity levels to those in Eastern Africa where modern humans likely evolved (Porter & Marlowe 2007). Moreover, climatic data indicate that ancestral groups are surely well approximated by simple (e.g. the BaYaka), rather than complex, hunter-gatherer groups since the ecological conditions of the Last Glacial period would have enforced a mobile lifestyle dictated by the availability of food supplies (Richerson et al. 2001). Similarly, archaeological sites do not suggest our ancestors maintained permanent settlements, rather they appear to be temporary camps (Shultziner et al. 2010). Further evidence comes from the fossil record, which shows a trend of reductions in body-size sexual dimorphism and canine size during hominid evolution. Such changes are indicative of a reduction in intra-sex competition and a flattening of dominance hierarchies (Shultziner et al. 2010).

Thus, although it would be fallacious to consider the BaYaka as 'living fossils', there are some general social and economic patterns that both extant simple hunter-gatherers and our ancestors appear to share. These include some level of food acquisition risk, mobility, egalitarianism and multiple family residency. Therefore, the Mbendjele BaYaka still provide the opportunity to make valuable inferences about human evolutionary history.

4.2 The Mbendjele and African Pygmies

The Mbendjele are a Pygmy population living as *simple* hunter-gatherers (this term refers to hunter-gatherer societies that are mobile, and do not accumulate/store material resources or have a social hierarchy) in the rainforests of the Congo Basin, with an estimated population of 15–20,000 (Lewis 2014). The specific groups we spent time with were situated

in the Sangha and Likoula regions of Northern Congo-Brazzaville, residing in a part of the forest known as the Ndoki forest. The term Pygmy is used by numerous groups, sometimes in a derogatory manner, thus in Congo the alternative term *autochthones* i.e. indigenous peoples is promoted. However, biologists simply use the term Pygmies to refer to populations with an average male height < 155cm (Cavalli-Sforza 1986; Migliano et al. 2007). There are numerous other Pygmy populations inhabiting the forests of West and Central Africa, and within Congo-Brazzaville itself other groups include the Mikaya, Luma, Aka, Koba, Tua, Ngombe and Baka Pygmies (Lewis 2002; Fig.4.1). The Ngombe and Baka speak Ubangian languages, whereas the other Pygmy populations in the Congo speak Bantu languages (Lewis 2002). However, all these populations share similar fables, rituals and ethnic markers such as teeth sharpening (P4.1) and scar tattoos (P4.2) (Cavalli-Sforza 1986). Indeed, the Mbendjele refer to themselves and all such groups as *Yaka* or *BaYaka* (plural), and consider all BaYaka as *bisi ndima*—people of the forest (Lewis 2002). Accordingly, in this thesis I use the terms BaYaka and Mbendjele interchangeably; since most previous research on BaYaka Pygmies has been conducted on Aka societies from Central African Republic, I specify this when making reference to such works. In total there are estimated to be 920,000 Pygmies in the Central African forests (Olivero et al. 2016). These Pygmies have a shared genetic history, and split from non-Pygmy groups between 50–90,000 years ago (Olivero et al. 2016).

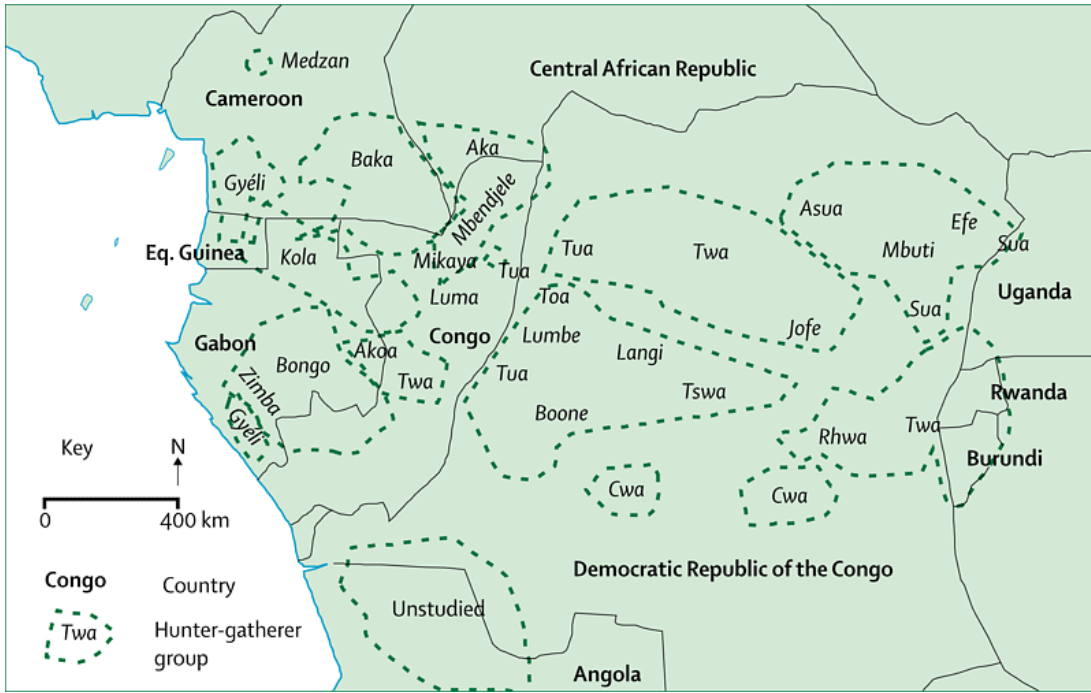


Figure 4.1: Distribution of Pygmy groups in Central and West Africa (Lewis 2002).



P4.1: Onge, a young man with sharpened teeth, the Mbendjele say sharpened teeth make them more attractive. Interestingly the same practice occurs in other hunter-gatherer groups such as the Agta from Philippines, indicative of convergent evolution (credit: Nikhil Chaudhary).



P4.2: Semoi with traditional BaYaka scarring tattoos (credit: Nikhil Chaudhary).

4.3 Social organisation

The Mbendjele are mobile hunter-gatherers, and do not accumulate material resources, other than a couple of pots and machetes (Lewis 2002). They live in multi-family camps or *langos*, which vary in size from as small 10 to as large as 90 (P4.3). *Langos* consist of numerous small huts (*fumas*) organised together in a clearing away from dangerous unstable trees that pose a risk during storms. *Fumas* tend to be occupied by nuclear families, but regularly also include grandparents or foster children, and can also be inhabited by a group of single men. They are simple structures made from a lattice of lianas covered in large leaves, and only take a few hours to make, facilitating the Mbendjele's mobile lifestyle (P4.4). Family units regularly move around and camp membership is fluid. Reasons for moving are often subsistence based and motivated by gaining access to resources hotspots or trade opportunities. However, the Mbendjele may also move based on more specific needs, such

as aid with childcare from relatives following the arrival of a new born, or in response to a conflict with another individual/family. In contrast to previous misconceptions emphasising virilocality, like many hunter-gatherers the Mbendjele are multi-local and will usually live with members of both the husband and wife's natal family at different point during their married life (Hill et al. 2012). This multi-local residence results in low levels of genetic relatedness in Mbendjele camps, and only ~25% of dyads in the camps we visited were genetically related at the 0.25 level (Dyble et al. 2015).

The Mbendjele are predominantly serially monogamous, and tend to have long lasting offspring bearing relationships with 1–2 individuals over their lifetime. There is no official marriage institution, but a partnership is marked by the establishment of a new *fuma* for a couple. Additionally, men are expected to engage in a few years of brideservice for their parent-in-laws (Meehan 2005); and they also pay a brideprice, which was traditionally in honey and forest products and now takes a monetary form (Lewis 2002). Polygyny does occur at low levels among the Mbendjele, and is the principal subject of chapter 8. It is estimated that between 10–15% of men in the Central African Republic Aka are married polygynously (Hewlett 1988), this figure resembles the average polygyny rate among hunter-gatherers of 15% (Marlowe 2005). When a man has multiple wives, they usually reside in different camps, and he divides his time between them.

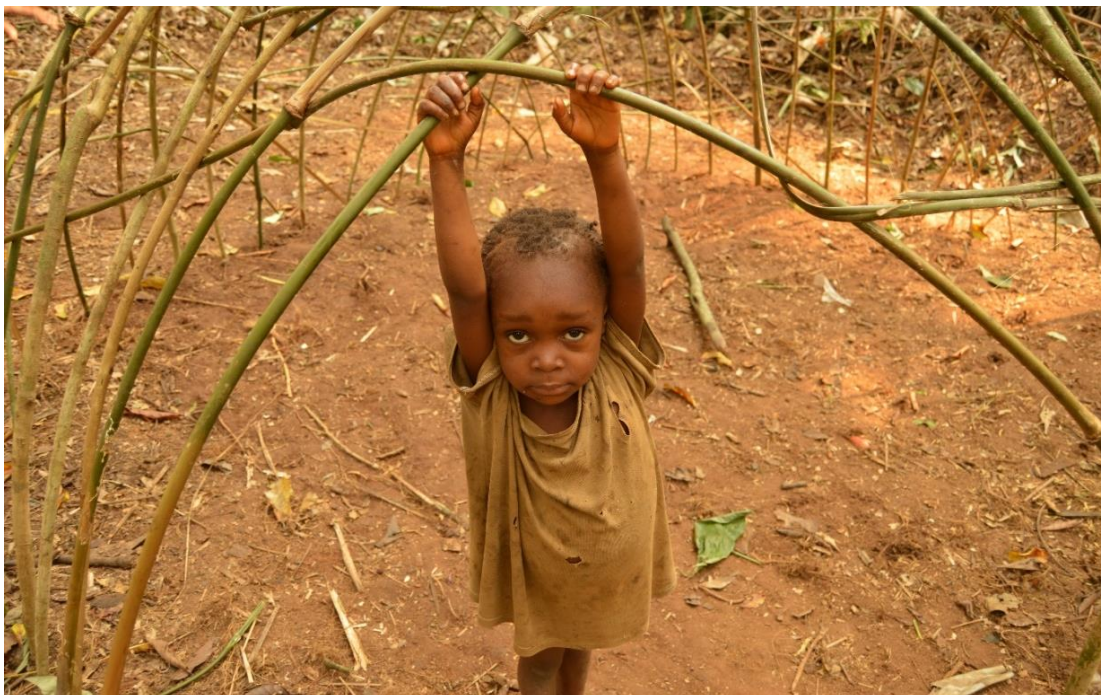
Another key feature of Mbendjele social organisation is the importance of egalitarianism. The concept of autonomy is fundamental in Mbendjele society, and no individual has the right to force another to do something. This is reflected in the absence of formal hierarchy. There are three recognised positions in Mbendjele society—*kombeti*, *tuma*, and *nganga* (Hewlett 1991). *Kombetis*, are appointed spokespersons for the camp and principally manage interactions with non-BaYaka groups such as farmers, researchers, and tourists; they also have influence on camp decisions related to movement and subsistence (Hewlett 1988).

Tuma refers to skilled elephant hunters, however this is not reserved for a select few, in fact in some camps almost half the households will contain a *tuma* (Lewis 2002). Given the decline in elephant hunting due to conservation efforts, I did not encounter this term during our fieldwork trips. The final title—*nganga* refers to specialist healers who have demonstrated their mastery of *bwanga* (forest medicines) by successfully healing the ailments of those who have sought their aid. It is noteworthy that none of these labels impart any authority on their bearers, the influence that accompanies these positions depends on the individual's level of social support, charisma, skill and generosity (Hewlett 1991; Lewis 2002).

The egalitarian ethic extends both across ages and genders (Lewis 2002; Dyble et al. 2015). Even young children enjoy large amounts of autonomy, they are rarely scolded and not subjected to the strict rules that we are familiar with in industrialised societies. Instead, they are granted freedom to explore their environment, which is an essential means by which they learn about forest life. It is common for infants to experiment freely with machetes and embers before they are even competent walkers (P4.5), and adult intervention will only occur if an accident is about to occur. By the time a child is weaned they spend most of the day in mixed age/sex playgroups, spending many hours of the day away from adults. With respect to gender, neither sex is submissive to the other (Dyble 2015), and the 'struggle' for dominance is play-acted through gender specific rituals in which groups of one sex sing and dance whilst insulting the other. For instance, women may come together and sing lyrics such as "*lenga dika ma dongi*" (penis stop sleeping) (Lewis 2002); uniting in this manner shows men that they cannot dominate or oppress a woman as doing so would entail picking a battle with all her same-sex peers. Men and women both contribute to subsistence, which leaves little scope for exploitation by either sex.



P4.3: Masia—a small Mbendjele *lango* (credit: Nikhil Chaudhary).



P4.4: The lattice structure of a partially built *fuma*, which will soon be covered by leaves (credit: Nikhil Chaudhary).



P4.5: Dili and his younger brother musua (still breastfeeding) experiment with machetes (credit: Deniz Salali).

4.4 Subsistence, division of labour and trade

The Mbendjele are predominantly hunter-gatherers, and none of the groups included in this thesis engaged in wage labour. Men's primary activity is hunting, using snares (P4.6) or shotguns, which are borrowed from farmers. Other BaYaka groups are recorded to engage in net hunting (Hewlett 1991), which is an activity conducted by men and women in concert, but we did not observe any net hunting during our fieldwork trips. Traditionally the BaYaka also used crossbows and spears for hunting, however this is rare now given the higher efficiency of shotguns when they are available; spears are still used to kill prey caught in their traps. Common prey include *mbongo* (antelope; P4.7), *kema* (monkey), *ngwia* (forest hog) and *mukwake* (crocodile). These are *banyama* (meat) in contrast to *banyodi* (birds). Other foraging activities of men include climbing trees as high as 40 metres using vine harnesses to collect *bwoi* (honey; P4.8) or *mbila* (palm nuts). Honey collecting is usually conducted in (extended) family units, whilst the men climb the trees and collect the honey, women are

constructing baskets to store the honey and preparing smoking branches wrapped in leaves that are used to pacify the bees. Women principally forage for wild yams such as *mea* and *ekule*, and wild leaves such as *koko*. Additionally, women conduct fishing trips in which they use a particular fruit to poison and immobilise *baswi* (fish), then they construct small dams and finally use baskets/buckets to empty water out of the dams and seize the fish. Additionally, women are responsible for collecting firewood and water, food processing and cooking, building *fumas* and weaving mats and baskets. Children also contribute to production by engaging in foraging tasks that do not require much skill or strength such as collecting fruits or wild mushrooms. Girls will begin accompanying older women on fishing and gathering trips around the age of five or six (P4.9), and boys will begin to join their fathers on hunting trips by age ten. Subsistence activities vary by season—the dry season is usually from December–February, and fishing is much more common; similarly, during certain months in the late rainy season caterpillars constitute an important part of the diet (Bahuchet 1988).

Hunting patterns are also affected by local politics. CIB (Congolaise Industrielle des Bois), the domestic logging company, a subsidiary of Olam, is in charge of allocating zones where the BaYaka can reside in the forest (P4.10). Additionally, in order to gain their conservation certificate, they must limit the hunting of certain species, a directive they attempt by employing ‘ecoguards’. Unfortunately, these ecoguards persecute the Mbendjele, often without just cause. The CIB headquarters are situated in Pokola, a logging town bordering the areas of forest we worked in. The inhabitants of Pokola largely rely on game for food, which has increased demands on Mbendjele hunting and the bushmeat trade. The forces of ecoguards, conservationists, the bushmeat trade, and the availability of shotguns all have substantial influence on BaYaka subsistence. Thus, the effect on Mbendjele hunting practices, diet, acquisition risk and food sharing all require further study as all these factors

influence evolutionary interpretation of data and observation (see section 9.7 for future research suggestions).

In addition to consuming their own production, the Mbendjele also trade forest products with farmers for cigarettes, alcohol, and cultivated foods such as manioc. It is not uncommon for one or two farmers to stay in Mbendjele camps for long periods of time in order to engage in frequent trade. However, the relations between BaYaka and neighbouring farmer groups are complex and often unfriendly. Thus, such exchanges are not free from conflict, which we witnessed on numerous occasions. Whilst the farmers discriminate against the Mbendjele and consider them uncivilised lesser beings, the Mbendjele often refer to Bantu farmers as *bebobo* (gorillas) due to their large stature and aggressive nature.

There is disagreement about the history of the relations between Pygmy and farmer groups. Some researchers assert that there are not sufficient carbohydrates in the forest for Pygmies to have ever lived independently from farmers (Bailey et al. 1989; Blench 1999; Headland 1987). However, more recent research indicates the biomass of wild tubers exceed 5kg/ha and thus Pygmies could have subsisted in the absence of farmers (Sato 2001). Regardless of this debate, it is generally agreed that the BaYaka have had long-standing exchange relationships with farmers for over a thousand years, which initially began with the trade of forest products for iron, salt and cultivated foods (Lewis 2002). Currently, many categorise the farmer-Pygmy relationship as one of ownership in which each Pygmy has a *konja* (owner) from birth to death (Grinker 1994). However, my experience resembles contradictory arguments that if a BaYaka is unhappy with their relationship with a farmer, they can move to other parts of the forest and forge relationships with other farmers (Kohler & Lewis 2002).



P4.6: Kamo sets a *motambo* (trap) in the forest (credit: Nikhil Chaudhary).



P4.8: Ndolo uses a leaf package of smoking embers to pacify the bees as he climbs for honey (credit: Nikhil Chaudhary).



4.7: Iboko and his son return from checking their traps with antelope and honey badger (credit: Nikhil Chaudhary).



P4.9: Mbuange, nine years old, returns from a fishing trip. with an (credit: Nikhil Chaudhary).



P4.10: Two logging vehicles parked up in the camp Longa (credit: Nikhil Chaudhary).

4.5 Religion and ritual

Religion plays a central role in organising Mbendjele social life (Lewis 2002). Their concept of *ekila* may be of particular interest to human behavioural ecologists, as numerous evolutionary predictions appear to be integrated in this concept. *Ekila* can refer to many things including blood, menstruation, food, health etc. (Lewis 2008). Its use is complex, however it can generally be considered a term to denote forbidden/taboo practices—everyone has their own *ekila*, which they do not want to ruin by engaging in *ekila* activities since this will result in adverse foraging and reproductive outcomes (Lewis 2002; 2008). It is *ekila* to eat certain foods, and different foods are *ekila* for different people depending on their family, age, sex, life-stage (e.g. certain foods are only *ekila* for pregnant women or widows), and who acquired the food (e.g. certain parts of game must not be eaten by the hunter) (Lewis 2008). Similar food restrictions based on life-stage and sex, particularly those directed at pregnant and lactating women, have been observed in other small-scale societies in Africa such as the Lese horticulturalists (Bentley et al. 1999). Such food taboos may be important in structuring sharing relationships, or avoiding foods that may be dangerous for vulnerable individuals. It is also *ekila* for a couple to have sex until their baby has finished breastfeeding. This rule may be important for the avoidance of overly short inter-birth intervals which may compromise infant survival. The evolutionary interpretations offered here are mere speculation, and have no empirical evidence available yet to support them. It is noteworthy that there is some contradictory evidence suggesting following food taboos may be maladaptive and reduce female health and reproductive success (Bentley et al. 1999; Aunger 1994).

Another fundamental aspect of Mbendjele religious life are *mokondi massana* (spirit dances/plays) and clubs. The Mbendjele have numerous single-sex religious clubs, each of which is associated with a particular *mokondi* (spirit of the forest); men have more religious

clubs than women. This aspect of Mbendjele religious life is very secretive, thus the description provided here is limited since I do not wish to break the promises of secrecy I have made. Additionally I use the narrative a Mbendjele would use which may seem rather peculiar and confusing to read. Indeed, the reason it is relevant to discuss these clubs is because they play an important role in bonding and generating solidarity among their members, which I discuss further in chapters 7 and 8. Such solidarity is evident in my choice to not disclose unpermitted details here. In fact, rare violations of religious secrets have been met with serious violence in the past according to our guides. Additionally, the *nganja* (secret area for initiates) provides a space to discuss hunting trips and transmit foraging advice.

In many *mokondi massana*, the whole community gets together to sing and dance in order to entice the *mokondi* which feed off the music and dance. During the *massana*, the *bangonja* (initiated) and the *konja wa mokondi* (spirit controller) will bring out the forest spirit if the singing and dancing is of sufficient quality. These *massanas* vary by region, in terms of the songs involved and the specific spirits that are beckoned. They can be traded or sold with different subgroups who wish to adopt a *massana* they may have seen when visiting another subgroup. During our fieldwork trips, I have been initiated into four of the male religious clubs—*Bobe*, *Ejengi*, *Monano* and *Sho*. The initiation process tends to follow a particular structure. I will use a brief summary of *Ejengi* as an example since it the most important and extensive male initiation. Initially the *mboni* (uninitiated candidate) has to do some public activity. For *Ejengi* this entails not leaving a *fuma* for numerous days and having no contact with their family (P4.11). Then on the final day he sits in the open clearing in the centre of the camp for a few hours while the sun is at its peak, and will have numerous encounters with the forest spirit (P4.12; P4.13). This public part of the ceremony is not so torturous for all the religious clubs, and sometimes simply involves dancing with the forest spirit in front of the rest of the camp (P4.14). Next, the *mboni* (uninitiated) is taken by all the *bangonja* (initiated) to the hidden *njanja* path (sacred path). What happens here is secret,

but in the case of *Ejengi* and *Sho* involves the *mboni* undergoing some more suffering. Finally, one learns the secrets of the club, which are usually related to the specific *mokondi*. Now initiated, one is permitted to dance with the specific *mokondi* in future *massanas*, enter the *njanga* path with other *bangonja* whenever one pleases, help in the initiation of future *mboni*, and receive a share of initiation fees. The process of undertaking these initiations is one of my fondest memories during my time with the Mbendjele. I felt honoured to be accepted by them for initiation, and I am sure that they appreciated my participation. Whenever I met a new group of Mbendjele, they always smiled when I explained I was initiated into certain clubs, and I feel this had a significantly positive influence on my friendships with other men.



P4.11: From left to right: Bakima (guardian), James, Mebo, Nikhil (*mboni*-initiates). We have finished the period of isolation in a *fuma* and now prepare for the public part of the *Ejengi* initiation process (credit: Deniz Salali)



P4.12: We, the *mboni*, sit directly in the heat of the sun, supervised by Bakima our guardian. Other *bangonja* (initiated) and women temporarily take some of our pain for us by staring into the sun (credit: Deniz Salali).



P4.13: *Ejengi* the forest spirit appears in response to the singing and dancing of the camp (credit: Deniz Salali).



P4.14: *Monano*, a forest spirit, comes to dance with the *bangonja* (initiated men) during a young man's initiation (credit: Aude Rey).

4.6 Demography and study population

The data from this thesis are derived from visits to six forest camps—Longa, Enoko and Mbaya (fieldwork trip 1, April–June 2013); and Longa, Ibamba and Masia (fieldwork trip 2, March–July 2014). Their geographic location can be seen in Fig. 4.2. Longa was visited on both trips, but due to the flexible residence patterns and the high mobility of the BaYaka, the composition of this camp had changed substantially between the two visits. Table 4.1 indicates the social structure of each of the six camps. Certain individuals were present in multiple camps due to movement patterns. Figure 4.3 is a population pyramid of the whole study population (individuals who appear in multiple camps are not double counted). There is a marked absence of individuals in the 15–20 age-group, particularly males. This is largely because many teenagers now live out of the forest in villages, where there are schooling and employment opportunities.

Table 4.1: Camp size by sex and number of households, as well as time spent in each camp.

Camp	Group Size (males)	No. Households	Study Period
Longa1	99 (45)	23	Apr–May 2013
Enoko	12 (9)	6	May-13
Mbaya	69 (30)	15	Jun-13
Longa2	108 (49)	23	Mar–Apr 2014
Ibamba	61 (33)	10	May-14
Masia	43 (20)	10	June–July 2014
Study Population	368 (173)	-	-

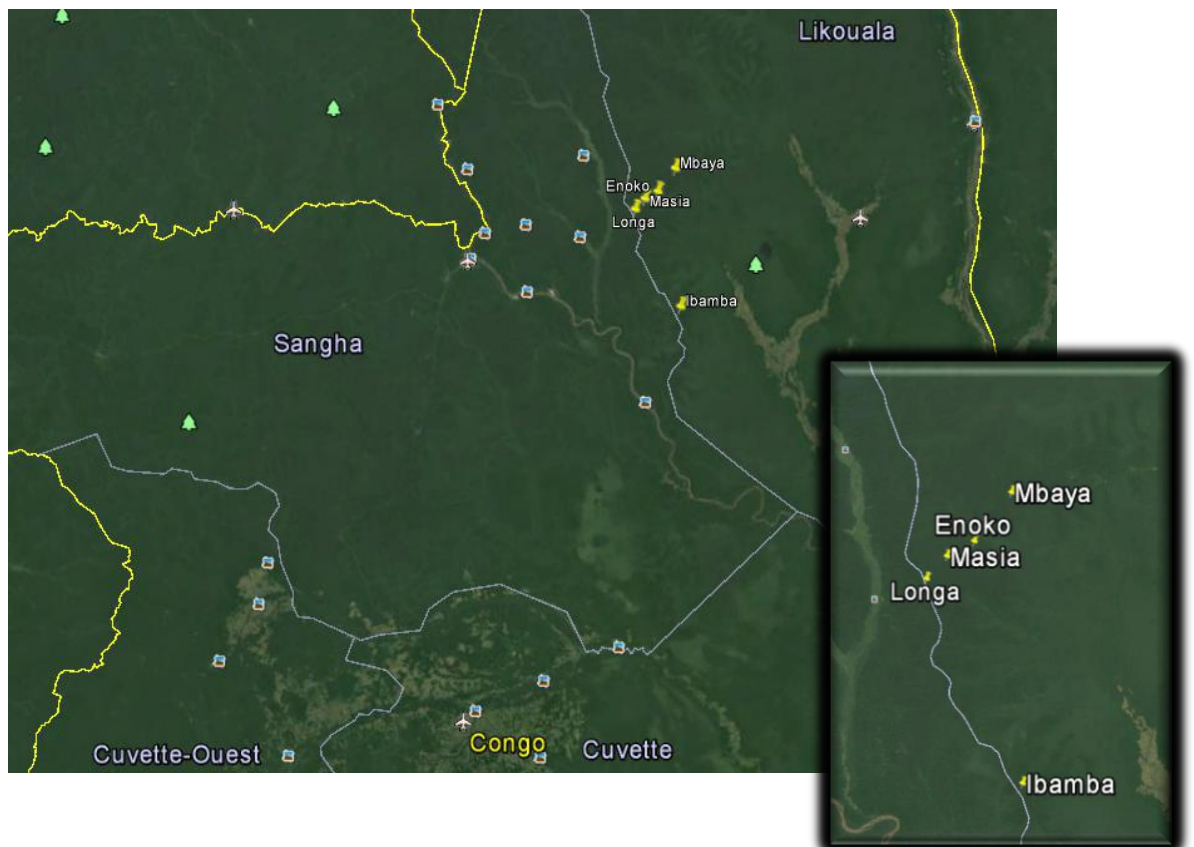


Figure 4.2: Geographic location of study camps. Produced using Google Earth.

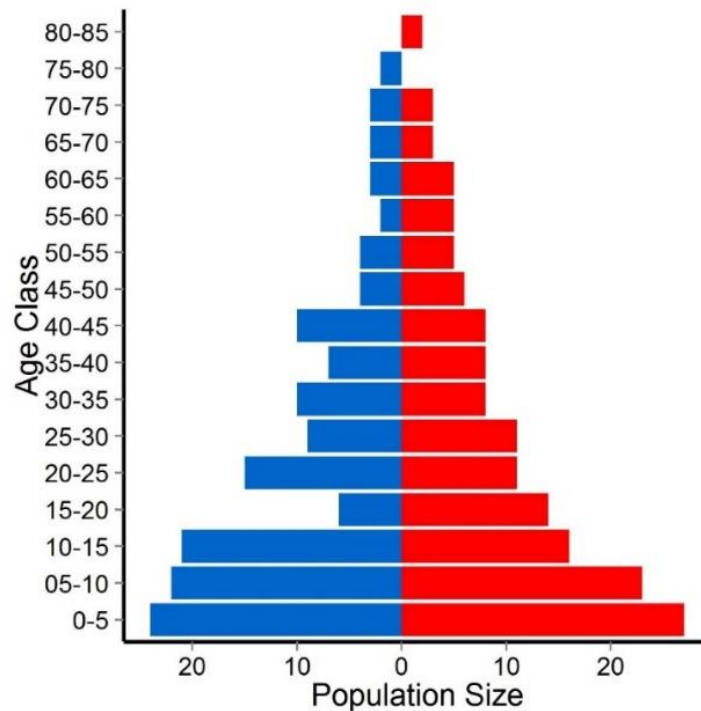


Figure 4.3: Population pyramid of the study population. Blue = men, red = women.

Given that our sample included less than 100 reproductively aged women, to calculate fertility rates of the Mbendjele I analysed the completed fertility of post-reproductive women, rather than calculate 'total fertility rate' using conventional demographic methods. Post-menopausal Mbendjele women had had on average 6.1 live births S.D. +/- 2.6. Additionally, to calculate inter-birth intervals I only used data using individuals who are currently still dependents (under 16). The highest level of resolution for our age estimates is likely with this group rather than older individuals since we have access to more ageing cues such as height and dental development. I calculated the average inter-birth interval as 3.4 years S.D. +/- 1.6. Given the high fertility and relatively short inter-birth intervals of the Mbendjele, mothers have the challenge of raising multiple dependent offspring simultaneously, and thus require a lot of help from other camp members in this task. Understanding the nature of this cooperative reproduction is the focal point of the analyses and discussion in chapter 6.

5. Methods

5.1 Fieldwork overview and our team

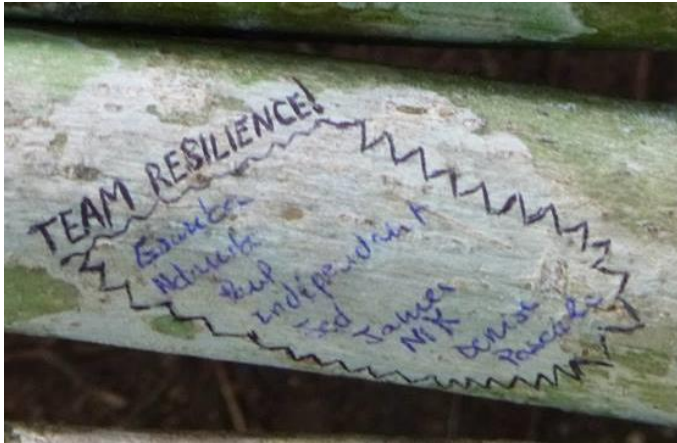
In total I spent just under seven months in the field spread over two trips—the first from April–June 2013, and the second from March–July 2014. We visited eight Mbendjele camps—six in the forest and two in a logging town named Pokola; these camps are situated in the Sangha and Likoula regions of Northern Congo. Reaching these areas involved a flight from London to Brazzaville, the country’s capital, followed by another domestic flight or coach trip to Ouessou in the North of the country, and finally a piroque across the Sangha River to Pokola. We resided in a hotel in Pokola whilst resting between trips to forest camps, which provided us with the comforts of a bed, shower and pizza. We usually travelled from Pokola to forest camps in taxis, gaining access via the logging roads. Reaching one camp, Ibamba, was particularly difficult since the logging road was not being used frequently, and so was littered with fallen trees, and renowned by taxi drivers as a hotspot for elephants and gorillas. Thus, this trip involved a high fee, regular stops to shift tree blockages, two instances of the taxi overheating, and two encounters with gorillas; but we got there in the end.

James Thompson and Gul-Deniz Salali—two other PhD students from UCL Anthropology—were with me for the entirety of the fieldwork; Pascale Gerbault (post-doctoral researcher, UCL Genetics), Jed Stevenson (post-doctoral researcher, UCL Anthropology) and Aude Rey (MSc student, UCL Anthropology) were also part of our team for periods of the fieldwork. Their companionship was a great help in overcoming any temporary stints of cultural shock, which are an inevitable feature of such work. During our first trip, our team also included Paul Mekounu, our translator fluent in French and Mbendjele; Esimba, who acted as a general helper to us since he had grown up in the forest; and Dambo, our chef (P5.1; P5.2). These additions to our team were introduced to us by Jerome Lewis, who has worked with

the Mbendjele for over two decades, and provided invaluable support in settling us into our fieldwork. On our second trip, after numerous French competency interviews with Mbendjele students in Pokola, we added two more translators to our team—Gifanho and Nicolas Yupi. Thus James, Deniz and I had a translator each, greatly improving our efficiency relative to our first trip when we were all reliant on Paul. Over the course of our trips we built up a small network of working relationships so that we had various ‘go to guys’ for routine tasks such as buying and delivering supplies, and drivers who knew what dates we needed transport to and from particular camps.



P5.1: From left to right—James, Pascale, Jerome, Esimba, Jed (standing); Independent, Nikhil, Deniz, Paul, Dambo (sitting) (credit: Ingrid Lewis).



P5.2: Team Resilience (trip 1) (credit: Nikhil Chaudhary).

5.2 Living and working with the community

We were always greeted with smiles and excitement upon arrival at each Mbendjele camp. Having finished introductions, the first task was always to set up our tented base camp before nightfall (P5.3). We would usually choose a location a short walk from the Mbendjele camp to provide some level of privacy for both the Mbendjele and ourselves, whilst retaining quick access to the camp. Another crucial consideration was finding a location that was safe from unsteady trees, which were serious hazards during storms and undoubtedly the most terrifying aspect of the fieldwork.

Building relationships is an important part of fieldwork when simultaneously living and working with a community. First and foremost, it makes the experience far more enriching for both parties, and I certainly have countless happy memories of my time in the forest. Additionally, the data collection process itself is far more pleasant when working with people who are receptive and fond of you, than those who consider it a chore. Although my



P5.3: Our camp in Masia (credit: Nikhil Chaudhary).

Mbendjele language skills slowly developed over the fieldwork, they never reached a stage where I was capable of having a long flowing conversation with the Mbendjele in the absence of my translator. However, we found other ways to bond. Some of my closest bonds were formed playing games with the children, who never tired of receiving piggy-backs and being spun around upside down (P5.4). Each week we would organise a *massana*, where the whole community comes together and sings to beckon the spirits of the forest. Additionally, over the two trips, I underwent four initiation rites, as described in chapter 4, which are an integral part of Mbendjele religious life (P5.5; P5.6). All these activities showed the Mbendjele our genuine enjoyment of their company and appreciation of their culture, allowing us to build trust and friendship with communities who are, unfortunately, accustomed to discrimination and exploitation.

Although rare, the fieldwork was not completely devoid of social tension. The Mbendjele understandably perceived us as extremely wealthy, and given the regularity of sharing in their culture it is not surprising that we were continuously asked for food, money, cigarettes etc. This is something one soon adjusts to, and the key to overcoming this issue was sticking to a sustainable protocol. We had calculated what we could afford to give in advance of the fieldtrips, and thus for each section of the work we had pre-planned gifts of food, which was given to a participant upon completion of a specific interview/observation etc. Additionally, a monetary gift was given to the community once all work in a given camp was completed. There were instances of tension when we sometimes had to refuse requests for food/money. These were usually resolved by calling a camp meeting and explaining we are students, and detailing exactly what gifts we are able to give for particular tasks.



P5.4: Children (Bokosa, Abudalay, Mapumba, Gidel, Motuma, Pamela) excited to see the photos I have taken of them (credit: Deniz Salali).



P5.5: Ready for *Ejengi* initiation with Bakima (middle) who acted as a guardian during the ceremony (credit: Deniz Salali).



P5.6: My scar from my encounter with the *mokonodi Sho* during my initiation into this cult (credit: Nikhil Chaudhary).

5.3 Daily routine

Our routine was relatively consistent throughout the fieldwork, and developed organically in a manner to match that of the Mbendjele. We would wake up between 05:00 and 05:30 to have a cup of tea and some oats before starting work at 06:00, by which time most of the Mbendjele have risen. This first session of work continued until around midday when we would stop for lunch, it was also usually the most productive period of the day. This is because the intense afternoon sun resulted in a few hours of lethargy and lack of enthusiasm to work, both on the part of our team and the Mbendjele. Moreover, working at this time of day was made extremely difficult by the *mbongo mbongo* stingless bees that repeatedly stick to your body and fly into your eyes. A shorter productive period of data collection would then occur between 15:00–17:30 as it cooled down and remained light. Working hours were sometimes more stringently defined when conducting observations which require that specific times of the day are covered in a systematic manner. Having finished work, I would enjoy a bath in a nearby lake or in our camp using a bucket with water collected earlier in the day. Then in the evening the whole team would sit down together for dinner. Lunch and dinner meals consisted of supplies bought from Pokola such as spaghetti, corned beef and sardines. During periods when none of the team were collecting data about foraging or food sharing behaviour we would exchange/buy forest foods from the Mbendjele, which were much tastier than the supplies we had brought. None better than antelope covered in a gravy made from koko leaves mixed with supplies of peanut butter, although I tended to avoid *piko* (the internal organs of game; P5.7).



P5.7: *Piko* kebabs—preparing the internal organs of an antelope (credit: Nikhil Chaudhary).

5.4 Data collection

Prior to collecting any data, soon after arrival in a camp we would gather the whole camp together and outline the main work we wished to conduct. We also gave a mock demonstration, for example we conducted reproductive histories and anthropometric measurements on each other. Before taking part, the work was re-explained to all participants and then they signed/gave a thumb print to provide informed consent (see appendix 5.1 for consent form).

5.4.1 Genealogies and reproductive histories

Genealogical interviews were conducted with all adults in each camp (P5.8; P5.9). In these interviews participants were asked to list/answer the following for themselves, each of their parents and grandparents:

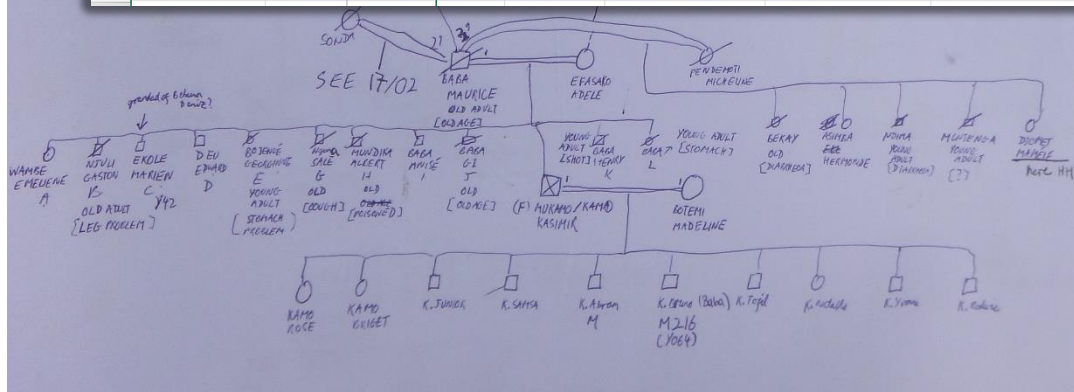
- All spouses
- In the scenario where a man had multiple spouses, whether 'when x married the second woman had he already finished his relationship with the first woman or did he continue with both women at the same time'
- All offspring, their sex, and with which spouse each offspring was conceived
- Whether a listed individual was alive or deceased
- The cause of death for deceased individuals
- The stage of life at which an individual passed away: breastfeeding baby/child/teenager/adult/old adult

These data allowed us to define the relationship type (spouse/sibling/cousin/affine etc.) and assumed genetic relatedness for all dyads in our study sample. One key difficulty in this process is the fact that the Mbendjele often have many names/nicknames, therefore it can be difficult to identify when two participants are referring to the same individual but using a different name. We would ask the participants to list all names of a given individuals, and would try to identify any cases where the same individual was named differently by different participants by cross checking the names of other relatives. Initially the information was recorded by hand to create family trees, before being processed on computer (P5.8).



P5.8: Jed and Pascale conducting our first reproductive history interview with the help of Independent (credit: Nikhil Chaudhary).

	A	I	J	M	N	O	P	Q	
1	FullID	Name1	Name2	Gender	BirthOrder	Mother	Father	Partner1	Partner2
1662	CMA01701M650	kamo	casimir	M	E	CML01203U072	CML01203U071	CML01203U075	NA
1664	CMA01708M651	kamo	abram	M	E	CML01203U75	CMA01701M650	CMA01708M682	NA
1666	CMA01702M652	mamele	jomette	F	NA	CMA01701U2006	X095	CMA01702U2037	M653
1668	CMA01702M653	bepika	edmond	M	C	CMM00708X182	CMM00708X183	CMA01707U2081	M652
2205	CMA01702M654	bepika	lalice	F	A	CMA01702M652	CMA01702M653	NA	NA
2218	CMA01702M655	mukango	raisa	F	C	CMA01702M652	CMA01702U2037	NA	NA
2243	CMA01702M656	indango	frederique	M	C	CMM00706NY109	CMA01701U2001	NA	NA
2244	CMA01702M657	baba	maurice	M	A	CMA01702U2046	CMA01702U2044	NA	NA
2245	CMA01702M658	noel	mukiyo	M	A	CMM00702NX061	CMA01702U2053	NA	NA
2246	CMA01702M659	ekoli	serafin	M	E	CML00304X104	CML00304Y042	CMA01702U2062	NA
2248	CMA01704M660	ekoli	sophie	F	G	CML00304X104	CML00304Y042	CMA01704M661	NA



P5.9: Top: An example of the final format the data are transformed to before using *R* code to determine the genetic relatedness between all dyads in the study population. Bottom: A pre-electronic version of a genealogy of Kamo Kasimir (node with an X). Circular nodes refer to females, square nodes to males. Diagonal lines represent deceased individuals. Letters below nodes indicate birth order. Double lines attaching nodes indicate spousal relationships; numbers above these double lines indicate marriage order. Single horizontal lines attaching nodes indicate sibling relationships; vertical single lines indicate parent-offspring relationships. Life-stage and (ailment) below birth order letters represent age and cause of death (credit: Nikhil Chaudhary).

5.4.2 Anthropometrics

We took anthropometric measurements from all willing adults and children in the forest camps, and a sample of the large town camps in Pokola. Since we were using equipment which the Mbendjele were unfamiliar with, we would always demonstrate taking each measurement on ourselves to reassure participants of its safety. Additionally, we would measure older siblings before young children in order to attenuate any fear of young participants. The following measurements were taken (see appendix 5.3 for anthropometric data collection sheet):

- Height (adults and children) using a Harpenden anthropometer (P5.10). To ensure accuracy, two researchers would take the measurements; with one ensuring that the anthropometer was perpendicular to the ground and that the participant was standing straight, whilst the other noted the reading.
- Length (babies) using measuring tape. This process was more difficult, and required two researchers to keep the baby laid down in a flat position on a mat, whilst one researcher used measuring tape to note the baby's height.
- Weight (adults and children) using a Philipps/Salter weighing scale. It was necessary to find hard ground and place a flat wooden plank underneath the weighing scale to ensure it would provide an accurate reading. The researchers weighed themselves to confirm the scale was working correctly in a given area.
- Weight (babies). The weight of a baby's parent was taken and then another measurement was taken immediately after with the same parent holding the baby in order to determine the baby's weight.
- Hand-grip strength (adults only) using a manual dynamometer. Participants had three attempts with each hand, and were instructed to keep their arm straight and perpendicular to the ground.
- Dental development (all individuals who were not adults).



5.10: I am measuring the height of Musua (credit: Nikhil Chaudhary).

5.4.3 Honey stick gift game

The purpose of collecting these data was to map out an adult-adult social network, and to discern individuals' levels of social capital i.e. how willing other camp members were to cooperate with them. We used the Gift Game procedure described in Apicella et al. 2012. This game was played with all adults in three forest camps, i.e. with all willing members of a camp, and was completed as quickly as possible, usually within 2–3 days. All instructions were spoken in French by the researcher, and then immediately repeated in Mbendjele by the translator. The key features of the protocol for the game were:

1. Participants were asked to accompany the researcher and translator to a private area. The choice to play the game in private was not due to a concern that participants' choices would be influenced by social pressure/expectations—the Mbendjele are egalitarian and place a lot of emphasis on individual autonomy.

Instead, the aim of playing in private was to avoid group members, who happened to be physically present during the protocol, from being more prominent in a participant's mind, and in turn more likely to receive a nomination from the participant.

2. Participants were shown three honey sticks, and told that real honey was within them.
3. Participants were told they must decide to whom they would like us (the researchers) to give the honey sticks.
4. Participants were told they could give freely i.e. all three sticks to one individual or one stick to three different individuals etc.
5. Participants were told they could nominate any adult in their camp other than themselves.
6. After the games had been completed with all adults in camp, the honey sticks were distributed according to the results, but recipients were not told who nominated them.

5.4.4 Food transfer observations (conducted by James Thompson)

Households were observed over two to four hour time blocks, each observed for a total of 24 or 36 hours depending on the camp. Observations were evenly distributed between 06:00 and 18:00 and spread over several days. During observation periods, a record was made of all food produced by a focal household. If division of resource packages occurred, all recipient households were identified. For all food cooked and consumed by the household, the type and amount of food were recorded and all those who ate the food were identified. Therefore, for each individual it was possible to calculate the number of other camp members from whom s/he received food. Additionally, it was possible to calculate a rate of

meals and calories received. James Thompson calculated calories by estimating the weight of food eaten by multiplying the number of units of a food item consumed by an individual (e.g. yams) by the average weight of a single unit of that food; in cases where the food was not observed being cooked, the weight of the food was estimated based on the number of plates of food. These weight estimates were then transformed to calories using published nutritional values.

5.4.5 Ageing

Most of the analyses in this thesis include data on participants' age. However, since the BaYaka are unfamiliar with our calendar and do not keep track of their age, we were required to estimate their age. This was a large part of the project and a new method for ageing individuals in small-scale societies was developed which involved three stages—constructing relative age lists, assigning initial age estimates and obtaining final estimates; these are outlined below.

Constructing relative age lists

To construct a relative age list, photographs of all camp members were taken in each camp we visited. These were then divided into rough age cohorts (<1; 1-2; 2-5; 5-10; 10-15; 15-20; 20-25; 25-30; 30-40; 40-60; 60+) based on visual estimations of the research team and our local translators/guides. Following this, we called all members of a camp to sit down around a mat upon which we laid out all the photographs of a given cohort (starting from the youngest cohort). Firstly, we asked the participants to identify the oldest member of the cohort, and then we picked up the remaining photographs. Then one by one we displayed the photographs of the other cohort members to the participants. After each photograph was displayed, we asked the participants the name of the individual on the photograph to

verify they recognised who it was. The Mbendjele BaYaka are very mobile, therefore all participants were very familiar with all members of our study population, including those from other camps. Next, we asked where the photo should be placed on the mat—to the right of an already placed photo if the current individual was older, and to the left if s/he was younger. After each placement, we confirmed that the newly placed individual was older than the photograph on its left and younger than that on its right; in some instances where individuals were considered equal in age, their photographs were placed above/below each other. If there was any disagreement among the participants, they were instructed to discuss amongst themselves and arrive at one answer together. After ranking within a cohort had finished, using the same process we checked whether individuals judged to be the youngest of that cohort were older/younger than the oldest individuals of the previous cohort. This process was repeated for all cohorts (P5.11).

Our research was conducted over two fieldwork trips, and we obtained three relative age lists for participants in the Minganga region (all camps we visited except Ibamba). At the end of the first trip, having obtained photographs of all individuals from this trip, we conducted the above process in two camps. This provided two distinct relative age lists, which both included all members from Minganga that we had met in this first fieldwork session—180 individuals. Then at the end of the second trip we obtained one more relative age list including all members from Minganga in the entire study population—240 individuals. The camp Ibamba is in a different region called Ikelmeba, far from Minganga, thus participants from this camp were not familiar with those from the other camps in the study population. Therefore, we constructed a separate relative age list for the camp Ibamba—60 individuals.

Assigning initial age estimates

Unfortunately, no one in our study population knew their own ages or ages of their offspring. We were able to assign absolute ages to a handful of participants. These individuals were

either born during the study period, or confirmed by their parents to have been born at the same time as the logging road by the camps was constructed, which we know occurred in 1997. For all other participants, the three field researchers who visited all the BaYaka camps estimated a lower and upper bound of their age. These age ranges were informed by dental development, reproductive histories, birth order and visual appearance.

Obtaining final age estimates

Alongside Mark Thomas and Yoan Diekman, a new method was developed to obtain the final age estimates. We derived a probability density distribution for ages by integrating the information from the initial age brackets and all the relative age lists using a Gibbs sampling framework. We then collapsed the full distributions and generated point estimates, namely the mean age for each individual. Full details of this process and the evidence for its superior accuracy compared to previous techniques, such as steady-state population models (Howell 1979) and fifth order polynomial regressions (Hill & Hurtado 1996), are described in the prepared manuscript (see appendix 5.4).



P5.11: I am creating a relative age list with based on consensus answers from members of the camp Mbaya (credit: Deniz Salali).

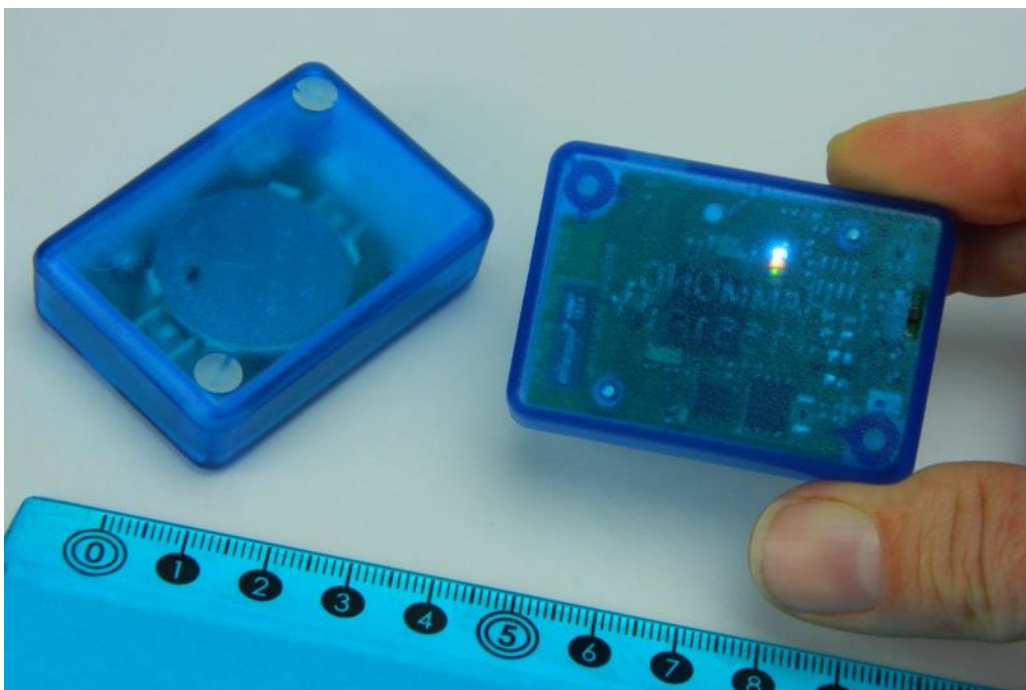
5.4.6 Motes

5.4.6.1 Protocol

We implemented the motes in three camps—Longa, Ibamba and Masia. Motes are portable remote wireless sensing devices (P5.12; P5.13). The specific mote we used was the UCMote Mini with a TinyOS operating system, which was then custom engineered to our needs by a software engineer on our project—Wallace Hobbes. This was by no means a small feat and required months of development and testing prior to the fieldwork to optimise the battery life and memory of the devices. Additionally, Wallace had to train us in using the TinyOS system so that we could programme the motes in the field. The programme we developed resulted in each mote emitting a beacon (radio signal) every two minutes, which was then received by any other mote within a defined proximity to that sender mote. Upon receiving a beacon from another mote, the recipient mote stored the following information within its internal memory—the sender’s unique ID and a time stamp indicating the number of milliseconds that had elapsed between the time the mote was turned on and the time the beacon was received. After the end of the motes sub-study, by downloading all the information from each mote’s internal memory, we were able to construct proximity networks that indicated the amount of time any dyad of individuals included in the sub-study spent in proximity to each other.



P5.12: Nguna-Midi Daniel wearing his mote in its sack (credit: Nikhil Chaudhary)



P5.13: The UCMote Mini against a ruler (credit: Wallace Hobbes)

The main features of the protocol were as follows:

1. Each mote was fully charged and the software programme was uploaded on to each mote.
2. Each mote was turned on, and the exact time (to the second) at which a given mote was turned on was noted.
3. Each mote was wrapped in cling film to avoid water damage, and then put into an elastic belt pocket, which could be worn by participants (P5.12).
4. All motes were distributed to all camp members, household by household. The unique mote ID given to each participant was noted. We explained to each household that each mote has a unique id number. Thus, it is very important that everyone wears the mote they were given for the entirety of the sub-study, and that parents should ensure their children do not exchange motes. We also wore motes ourselves for the duration of the sub-study to put the participants at ease that the motes were in no way dangerous.
5. We noted the time at which all camp members had received their mote—this is the official start of the sub-study.
6. We repeated steps 1–4 for any new camp members that arrived over the course of the sub-study, and noted the exact time at which they were given a mote.
7. Motes were taken back off any individual leaving the camp before the end of sub-study, and we noted the time they left.
8. Anytime an individual was observed not wearing a mote, we noted the individual and the time, and then requested the individual to put their mote back on.
9. We collected motes back seven days (or nine days in Ibamba) after the official start of the sub-study, and confirmed that each individual was still wearing the same mote they were given.

The main stages in processing the data to construct proximity networks were the following:

1. We downloaded the data from each mote's internal memory onto the computer; and then checked through each mote's data to confirm the data were stored correctly, and the mote was not damaged/ did not malfunction during the sub-study.
2. We then provided Wallace (our software engineer) with these data, and information regarding the time each mote was turned on, the time the sub-study started, the time any individuals joined/left, any periods of time an individual was observed not wearing their mote, any faulty motes and the time the sub-study ended.
3. Using this information, Wallace provided us with a matrix for each camp, which specified the number of beacons shared between each dyad during daylight hours (05:00–20:00), since we did not want our data to simply represent the BaYaka's sleeping patterns. Since the data were used to study childcare practices, dyads of interest were those between *egos* (infants/children four years old and under) and *alters* (potential carers—any individuals over four years of age in the camp).
4. We then calculated the maximum number of possible beacons a dyad could have shared i.e. the number of two minute intervals during daylight hours that both ego and alter were recorded as participating in the motes sub-study. By dividing the number of beacons ego received from alter by the maximum possible number of beacons, we calculated the **proportion of time** ego and alter spent in proximity to each other.
5. Additionally, we calculated the total number of beacons received by each ego. By dividing the number of beacons ego received from alter by the total number of beacons received by ego, I calculated the **proportion of ego's interactions** that were with alter.

5.4.6.2 Proof of concept

In this thesis, the motes data were used to examine BaYaka childcare practices; specifically, to examine proximate interactions between egos (infants/young children < 4 y.o.) and alters (potential carers). Proximity (<3m distance) is frequently used as a measure of low investment care in studies of childcare practices among hunter-gatherers (e.g. Meehan 2009; Marlowe 1999), since it is the minimum requirement for carers to supervise, and when necessary intervene or attend to young. In chapter 6, I examine non-maternal (alloparental) proximate interactions with BaYaka children; such interactions may be an important way in which camp members help mothers rear their offspring. Proximate care may play an important role in freeing up mothers to engage in other tasks. Trade-offs between childcare and subsistence tasks are one of the principal challenges faced by hunter-gatherer women who have to raise multiple dependent offspring simultaneously (Hurtado et al. 1992; Kramer 2005; 2010). Alloparental supervision of young provides mothers with an opportunity to reallocate time to other tasks such as foraging, collecting water, caring for other offspring and domestic jobs.

The implementation of remote wireless sensing technology in studies of proximity is relatively new, and has not previously been attempted in the field of human behavioural ecology. Traditionally, such data are collected using focal sampling techniques (Altmann 1974). To validate the data from the motes, and as a proof of concept, I compared data from the motes with data obtained from focal follows of eight infants using traditional techniques outlined below:

Adults were told in advance not to alter their behaviour towards a child just because I was conducting an observation. Each focal child was observed for nine hours, split in to three sessions. Early sessions took place from 06:00–10:00; middle sessions were from 10:00–14:00; and late sessions were from 14:00–18:00. In each session, a fifteen minute break was

taken after every 45 minutes of observation, resulting in three hours of observation per four hour session. Each child was observed for one early, one middle and one late session, each occurring on different days to minimise biases resulting from the time of day/activities of one specific day. Observation sessions were split into a series of 30 second intervals, in which I would observe the child for 20 seconds then record my observations for 10 seconds as instructed by an audio device. In each interval, I would record the names of all individuals within a distance of three metres to the focal child, and any individuals who were touching the focal child (see appendix 5.5 for data collection sheet).

Comparison of data from motes and focal follows

For the analyses in chapter 6 I use two statistics derived from the motes data: 1. The **proportion of ego's (child) proximate interactions** that are with alter (non-maternal carer); and 2. **The proportion of time** ego and alter spend in proximity to each other. To validate that the motes provided meaningful data, and that these derived statistics are useful measures of low investment care, I compare these specific statistics with data derived from my focal follows. I present data for the eight infants that I conducted focal follows on, and focus on five principal categories of non-maternal carers: fathers, siblings, grandmothers, grandfathers, and aunts/uncles. Firstly, I compare the proportion of an infant's alloparental interactions that are with each of these categories of caregiver according to the motes versus the proportion of alloparental interactions i. closer than three metres and ii. touching according to my focal follows (Table 5.1). For instance, I compare 1. of all of ego's beacons what proportion were from ego's father's mote, with 2. from my observations of all interactions ego has closer than 3m, what proportion were with ego's father, and 3. from my observations of all touching interactions ego has, what proportion were with ego's father. Secondly, I conduct the same comparison, but rather than calculating proximate (motes)/<3m (observations)/touching (observations) alloparental interactions as a

proportion of ego's **interactions**, I calculate them as a proportion of **time** i.e. what proportion of time is ego's father's beacons picked up by ego's mote/ is ego's father observed (during focal follows) closer than 3m/ touching ego (Table 5.2). Additionally, this second analysis is conducted per capita rather than cumulatively. Hence if an infant spends 10% of time with one sibling and 20% of time with another, the statistic presented would be 15% rather than 30%. The summary results from these comparisons are presented in Tables 5.1 and 5.2; in Appendix 5.6 and 5.7 individual tables for each of the eight infants can be found.

Table 5.1: Proportion of infant's (n=8) interactions that are with six categories of caregivers. Percentages are means derived from data on eight infants. The first two columns represent data from focal follow observations specifying the proportion of interactions closer than three metres/touching which occurred with each category of caregiver. The final column represents data from the motes.

Relationship	< 3m (obs)	touching (obs)	motes
Father	34.8	6.2	18.0
Siblings	37.8	6.0	23.3
Grandmothers	27.6	5.1	11.3
Grandfathers	4.4	0.4	2.4
Aunts/Uncles	19.8	3.5	7.0

Table 5.2: Proportion of time an infant (n=8) spends within three metres (column 1) or touching (column 2) an average individual from each category of caregiver based on focal follow observations. The final column represents the time spent in proximity to each category of caregivers based on the motes sub-study. The results here differ from table 5.1 as they show the percentage of *time* an infant is in proximity to x; conversely table 5.1 shows the percentage of an infant's *interactions* that are with x.

Relationship	< 3m (obs)	touching (obs)	motes
Father	13.4	17.0	11.4
Siblings	19.8	18.0	22.0
Grandmothers	12.4	18.8	10.9
Grandfathers	1.5	0.5	3.0
Aunts/Uncles	8.8	12.5	7.3

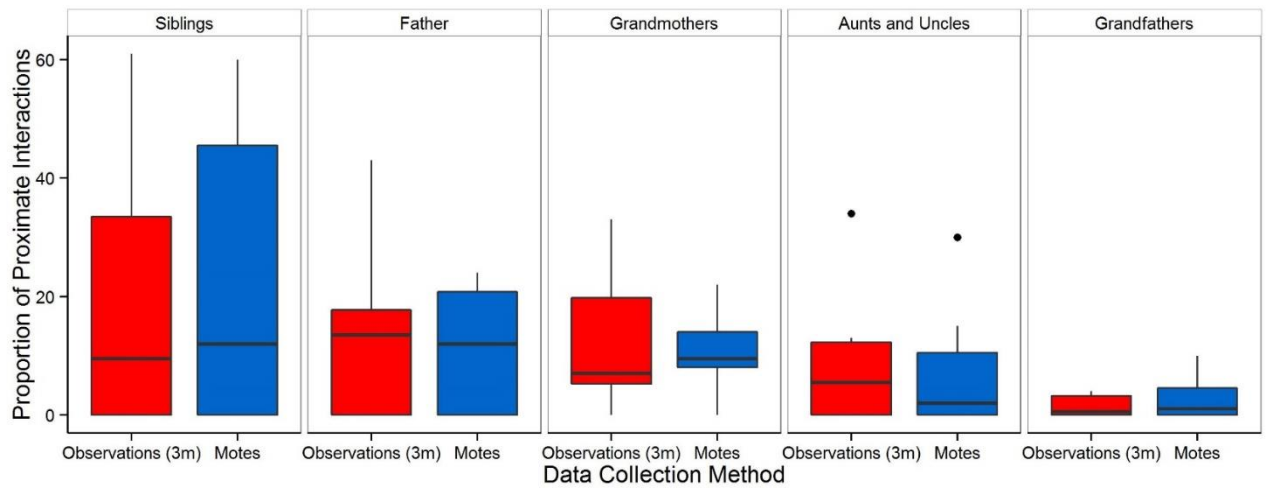


Figure 5.1: Proportion of an infant’s (n=8) proximate interactions coming from different categories of non-maternal caregivers based on observational focal follows (red) and motes sub-study (blue). Circles indicate outliers. There is strong correspondence between the motes and observational data.

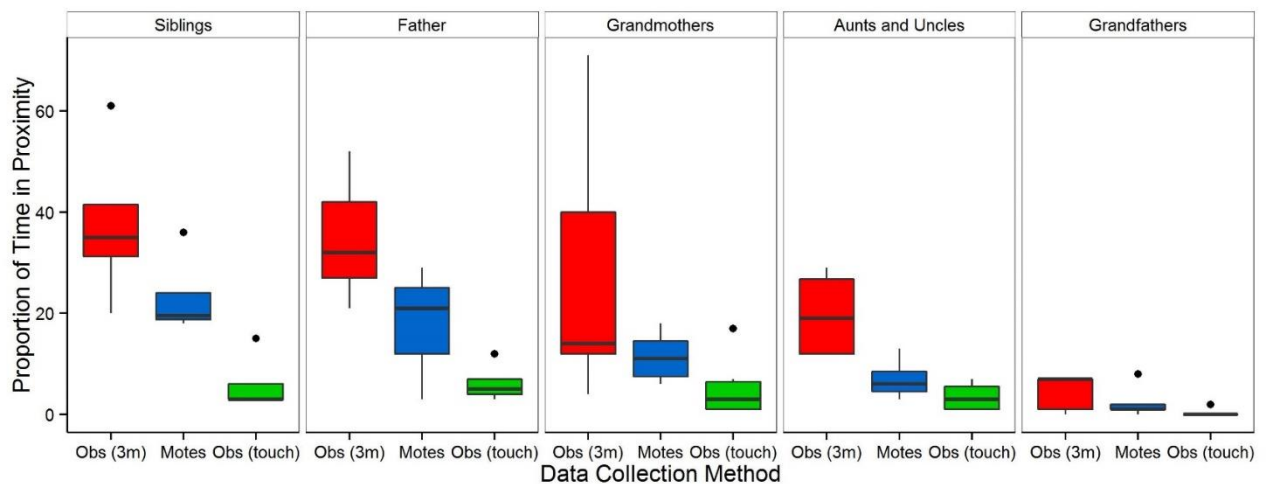


Figure 5.2: Proportion of time an infant (n=8) spends in proximity to different categories of non-maternal caregivers based on observational focal follows where proximity is defined as <3m distance (red), touching distance (green) and motes (blue). Circles indicate outliers. The results indicate that the motes recorded interactions at proximity between 3m and touching distance i.e. approximately arm’s length.

Table/Figure 5.1 indicate a striking similarity between the proportion of ego’s interactions closer than three metres with each category of alter according to my focal follows, and the proportion of ego’s motes interactions with each category. Perfect correspondence was not expected since the motes sub-study and focal follows did not perfectly overlap—the motes

were worn for at least seven days, whereas a focal follow was conducted for nine hours split over three days. Additionally, because conducting focal follows is so time intensive it was not possible for all follows to be conducted during the period of the motes sub-study. Nevertheless, the general trends are very similar, indicating the motes data provide a valid measure of the relative amount of proximate interactions provided by different alloparents.

The results from Table/Figure 5.2 demonstrate that the motes appear to be recording interactions somewhere between touching distance and three metres. Although perfect correspondence is not expected for the reasons outlined above, the motes data are consistently between the proportion of time ego and alter were observed closer than three metres and the time they were observed touching. Therefore, motes data on time ego spent with alter are probably more comparable to studies which use 'arm's length' as a measure of proximity (e.g. Hewlett 1991), rather than those that use three metres. However, the analyses in chapter 6 are focussed on the *relative* importance of different helpers; and I do not make cross-cultural comparisons of the absolute proportion of time helpers spend in proximity to young. Therefore, all analyses and subsequent discussion remain valid.

Measuring proximity between alloparents and infants/young children is an important part of studies on cooperation in child rearing, which is a central topic of research in human behavioural ecology. Whilst hunter-gatherers are known for their relaxed parenting style in which even infants are permitted to explore their environment freely (Lewis 2002), the presence of machetes, fires, and dangerous insects/animals means infants and young children still require constant supervision by someone. Thus, low investment help in the form of physical proximity and supervision by alloparents frees up mothers to concentrate on other subsistence related tasks, or to attend to other offspring.

In this section I have demonstrated that the use of motes offers a promising avenue for future research on childcare and provides meaningful data on the relative importance of

different helpers. I implement the motes data in chapter 6 to examine numerous questions relating to BaYaka childcare practices such as the role of unrelated helpers, the sex/life-stage characteristics of alloparents and the possible adaptive benefits of providing allocare.

Traditional methods of focal follows using focal sampling techniques are very time intensive since researchers can only physically observe and make recordings on one child at a time. Conversely the motes can simultaneously record interactions of all camp members without the researcher even being present. Hence the motes provide opportunity for much larger sample sizes and can record data for much longer periods. Focal follows only provide nine hours' worth of observation data per child. Although observations occur over three different days, and cover different times of day, nine hours is a very short period of time and subject to large biases. For instance, if a child's father is on a hunting trip or if it rains during these nine hours (and in turn individuals remain in very close proximity in their household), the dataset obtained differs substantially to one in which such events do not occur. Motes data are derived from a period that lasts at least a week, and thus provide a much more accurate representation of proximate interactions, and are substantially less affected by such biases. Of course focal follows have the benefit of being higher resolution since one can collect more detailed information such as the specific activity occurring between carer and child e.g. holding, soothing, affection etc. Therefore, in future research, a combination of motes and a small sample of focal follows offers the opportunity for large, long term and high resolution data on childcare interactions.

6. Allocare among the BaYaka

6.1 Introduction

6.1.1 Context

In numerous species of birds, mammals and insects reproduction is a cooperative activity and non-maternal individuals aid with rearing offspring—such species are categorised as ‘cooperative breeders’. Human mothers also receive substantial help in raising offspring and in turn are often also termed cooperative breeders. In this chapter I will begin by outlining the theory and evidence regarding how cooperative breeding evolves in non-human species. I will then go on to explain why human reproduction is also a cooperative activity, and summarise the literature regarding two principal questions—who helps human mothers with rearing offspring and why? I then present an analysis of the BaYaka childcare system, addressing aspects of these questions that remain unanswered or lack empirical evidence. Finally, I discuss the results and their implications for the classification of humans as cooperative breeders. In the broader perspective of this thesis, this chapter provides a case study of the importance of cooperation in hunter-gatherers, and demonstrates that this cooperation is not unbiased within the group, and thus differences in social capital, i.e. access to cooperation, are likely to be important for individual fitness.

6.1.2 Cooperative breeding and eusociality

In the introduction to this thesis various benefits of sociality were outlined, including enhanced reproduction (section 2.2). Cooperative breeding refers to a social system, which among vertebrates predominantly occurs in species of birds (3–9% of species) and mammals (2–10% of species), in which group living and reproduction are inextricably linked (Hatchwell

& Komdeur 2000; Hatchwell 2009; Lukas & Clutton-Brock 2012). Under such systems, the majority if not all breeding within the group is restricted to a dominant pair, who are supported in the rearing of their offspring by non-reproductive helpers who remain in their natal group for part/all of their life following reproductive maturity (Griffin & West 2003; Lukas & Clutton-Brock 2012). Helpers' reproduction is suppressed by dominants in a number of ways including the use of pheromones, destruction of subordinate eggs and infanticide (Young et al. 2006; Koenig et al. 1995). Subordinate helping behaviours, also called alloparenting, include incubation, feeding, defense, grooming and nursing of the dominant pair's young (Jennions & Macdonald 1994; Hatchwell & Komdeur 2000).

A particularly extreme form of cooperative breeding occurs among 'eusocial insects', found within the order Hymenoptera and Isoptera. Here workers are organised into different castes with morphological and behavioural adaptations for specialised helping tasks whilst the queen of the colony reproduces (Robinson 1992). Cooperative breeding and eusocial systems have been key subjects of research for evolutionary scientists for decades as they pose an evolutionary dilemma—how could the strategy of forgoing one's own reproduction to help the reproductive and parenting efforts of another ever have been favoured by natural selection? Indeed, Darwin noted they pose "one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory...from being sterile they cannot propagate their kind" (Darwin 1859, p236).

Numerous explanatory hypotheses have been set forward, the majority of which are variants of each other founded on the principle of inclusive fitness (Hamilton 1964). Under conditions in which personal reproduction is sufficiently restricted, maximisation of inclusive fitness may be best achieved via a strategy focussing on increasing indirect fitness by helping related breeders. The Ecological Constraints Hypothesis (ECH) asserts this may occur due to high risks of dispersal (e.g. predation); lack of suitable territories resulting from high population

density or low territory turnover; lack of mating opportunities (e.g. due to the operational sex ratio); and low probability of successful reproduction (e.g. low food availability) (Emlen 1982). Other scholars argue that it is slow life-history traits such as a long lifespan that result in overcrowding within a population, and in turn a low availability of breeding territories—The Life History Hypothesis (LHH) (Brown 1987; Russell 1989). The ECH and LHH each have differing levels of support from intraspecific, interspecific and experimental research, and neither can explain the evolution of cooperative breeding in every species that displays it (Hatchwell & Komdeur 2000; Arnold & Owens 1998).

The advantages of pursuing indirect benefits may be particularly pronounced among the eusocial Hymenoptera due to their haploid-diploid sex determination system, which results in females being more related to their sisters (0.75) than their own offspring (0.5) (Hamilton 1964; but see Andersson 1984). The foundational importance of kinship in stimulating helping behaviour is well supported. An analysis of 15 bird and three mammal cooperatively breeding species found a strong and consistent relationship between probability/amount of help given and relatedness between a potential helper and young (Griffin & West 2003). Additionally, monogamy and low promiscuity of dominant breeders has been demonstrated to be fundamental to cooperative breeding and eusocial evolution in birds, mammals and insects, since this maintains a high degree of relatedness between breeders' offspring (Lukas & Clutton-Brock 2012; Hughes et al. 2008; Cornwallis et al. 2010).

The human mode of reproduction is also frequently labelled as cooperative breeding since females do not raise their young independently, but receive assistance from others. This help is considered of central importance to the demographic success of our species and supporting our unique life-history (Kaplan et al. 2000; Kramer 2010). Moreover, it has been suggested to have set the stage for the evolution of human cognitive evolution and in turn the defining features of our species such as language and cumulative culture (Burkart et al.

2009; 2014). In the rest of this introduction I will outline the theory behind why there is a need for help in human reproduction, who provides help, and possible evolutionary mechanisms driving helping behaviours. These questions are then addressed in an analysis of cooperative childcare in the BaYaka. One key area of discussion is the extent to which the results support the labelling of humans as cooperative breeders and how similar they are to the systems outlined above.

6.1.3 Human life history and help with reproduction

The human mode of reproduction is remarkably successful, and is largely responsible for the demographic success of our species (Kramer 2010). Compared to the other great apes, humans reproduce substantially faster with inter-birth intervals of ~3 years, approximately two years less than chimpanzees and six years less than orangutans (Kramer 2010; Kramer & Otarola-Castillo 2015). Moreover, human offspring experience a higher probability of survival to maturity compared to our ape cousins, attributed to their extended period of being provisioned (Kramer 2005). Our ability to simultaneously reproduce faster and experience higher offspring survival initially appears contradictory to the fundamental quantity-quality reproductive trade-off (Becker & Lewis 1973; MacArthur & Wilson 1967). Indeed, the combination of short inter-birth intervals, high offspring survival prospects and an extended period of dependence results in human mothers having to raise multiple dependent offspring simultaneously (Kramer 2010; 2014). However, women have a limited amount of time and energy to invest into somatic maintenance, childcare, reproduction, lactation and foraging, and attending to the needs of all offspring alone is not feasible for mothers (Meehan et al. 2013). The solution to this time/energy allocation problem lies in a unique stage of human life-history, which allows mothers to receive help with reproduction.

Unlike other mammals in which breastfeeding (infancy) is followed by nutritional independence (juvencity), human offspring are weaned early and then enter childhood—an intermediate stage in human ontogeny (Bogin 1997; Fig. 6.1). Following weaning, offspring still require substantial provisioning to support their development, in particular their metabolically expensive brain growth, and dependence continues long beyond other apes (Bogin 1997). However, the insertion of childhood in lieu of an extension of infancy is very significant to mothers since offspring no longer require breastmilk, thus women can reallocate the energy that would be needed for lactation towards another pregnancy (Kramer 2005). Meanwhile the nutritional and childcare needs of their weaned offspring can be subsidised by group members other than the mother. Thus, via the insertion of childhood into human life-history, female reproductive output is no longer solely a function of maternal time an energy but also alloparental effort, facilitating the concomitant shortening of inter-birth intervals and enhancement offspring survival.

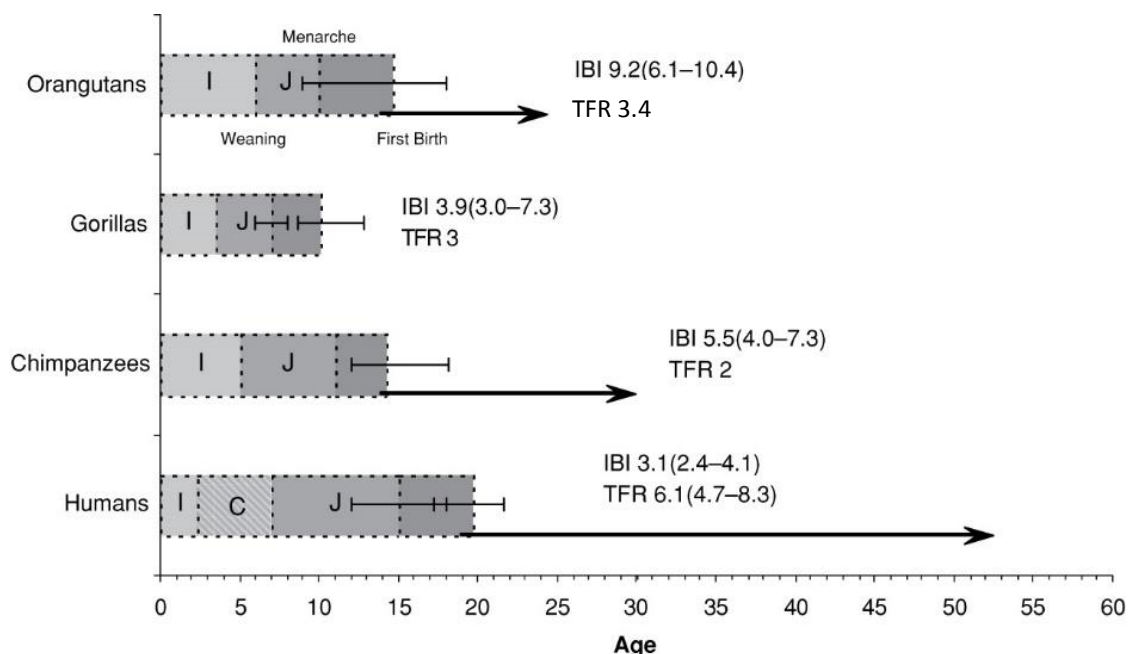


Figure 6.1: Adapted from Kramer 2010. A comparison of great ape life-history schedules. 'I' = infancy, 'J' = juvenile period, and 'C' = childhood. 'IBI' = inter-birth interval and 'TFR' = total fertility rate. Errors bars show ranges for age at menarche and first birth. Arrows show life expectancy given survival to reproductive age.

There is now strong empirical evidence for alloparenting in human societies. In a review of 45 natural fertility populations, in almost every study at least one non-maternal individual (alloparent) was found to have a positive impact on child survival (Sear & Mace 2008). Likewise, helpers have been demonstrated to significantly increase female reproductive success in numerous human societies (Kruger & Konner 2010). Alloparenting can take the form of direct care i.e. behaviours which occur in physical proximity to the infant/child including supervising, carrying, bathing etc.; or indirect care which are other forms of investment such as food provisioning and territory defense. An extreme example of help with direct care comes from Efe Pygmy infants who are in physical contact with an alloparent 60% of the time, have on average 14 different allocarers in a day, and are nursed by multiple women (Tronick et al. 1987; Ivey 2000). The importance of indirect care is comparable, for instance an average reproductive Ache couple produces a net deficit of their nuclear family's caloric requirements for approximately 30 years—the majority of their reproductive career (Hill & Hurtado 2009). Clearly alloparenting is essential in human reproduction, begging the questions of who provides help to mothers, and why they do so. For the rest of this introduction I will review research exploring these questions, focussing largely on hunter-gatherer studies since my analyses are conducted on data from BaYaka hunter-gatherers.

6.1.4 Who helps?

The question of who the key alloparents are in human societies has been the source of much debate among human behavioural ecologists. Specifically, the relative importance of fathers and grandmothers has divided opinion. Traditional models emphasise pair-bonding in human relationships, asserting that the male strategy is to assist their spouse in rearing mutual offspring (Lovejoy 1981). Couples engage in division of labour, in which male hunting specialisation returns protein and lipids from game that complement the carbohydrate

production from their wife's gathering. Similarly, when a mother's production is compromised by pregnancy or lactation, fathers compensate; for instance among the Hadza, men increase their production of honey when their wives are nursing (Marlowe 2003). Advocates of this 'male-provisioning' model highlight that since males produce the majority of calories in most societies e.g. 87% among the Ache, fathers are indispensable to their offspring (Lancaster 2000; Hill & Hurtado 1996).

Others argue that male subsistence effort among hunter-gatherers is not indicative of paternal investment. Meat has high sharing breadth—it is widely shared and a lower proportion is consumed by the acquirer's family than for other foods. Among the Hadza only ~10% of large game and 5% of medium and small game is eaten by the hunter's household, and men who acquire more game do not receive more via contingent sharing (Hawkes et al. 2001). Moreover, men forage for unpredictable and difficult to acquire game often with low return rates, suggesting their motivation may be signalling of phenotypic quality to potential mates rather than parenting effort (Hawkes et al. 2001; Bleige Bird et al. 2001). Finally, in a review on natural fertility populations, 68% of studies found no association between father presence and child survival (Sear & Mace 2008).

For the reasons above, numerous researchers have suggested that grandmothers may have a more vital role in alloparenting than fathers; and grandmaternal help has been proposed to provide an explanation for the evolution of menopause (Hawkes et al. 1998). Menopause at first appears an evolutionary paradox since women are no longer able to directly increase representation of their genes in future generations, hence it is unclear how a post-reproductive lifespan could be favoured by natural selection. Hawkes argues that as the climate dried in Plio-Pleistocene Africa, there was an increased dietary reliance on geophytes, such as roots and tubers, which children are unable to dig and process themselves (Hawkes & Coxworth 2013). Therefore, unlike other apes where fecundity and

physiological systems deteriorate simultaneously and terminate before age 50, in our lineage there was selection for an extended lifespan during which women could contribute to provisioning their grandchildren and increase their own fitness indirectly (Hawkes et al. 1998). In support of the grandmaternal alloparenting role, elderly women have been found to be efficient and hardworking foragers, as well as net producers (Hawkes et al. 1989). Similarly, studies of direct childcare frequently find grandmothers to be essential caregivers, for example among Martu aborigines, they provide almost as much high investment care to infants as mothers do, and substantially more than any other type of allocarer (Scelza 2009). Furthermore, in the same review in which father presence increased child survival in only ~30% of studies, grandmaternal presence had a positive impact in 60% (Sear & Mace 2008; but see Strassmann & Kurapati 2010 for alternative interpretation). It appears that post-menopausal women do expend substantial time and energy in rearing grandchildren. However, some argue that the importance of grandmothers is limited since many children do not have access to grandmaternal care owing to residence patterns or mortality (Hill & Hurtado 2009; Ivey 2000).

Thus far, the evidence outlined has been mixed and this likely reflects the true state of affairs. Given the vast range of demographic, subsistence, residence and mating patterns that characterise human social systems, it is unlikely that the relative importance of fathers and grandmothers is consistent across populations. Indeed, numerous researchers have emphasised the flexibility of alloparenting systems and the facultative nature of caregiving from different individuals (Meehan 2005; 2014). Focussing on direct care, which is the principal subject of this chapter, fathers from the Alyawara provide less than 1% of an infant's childcare (Denham 1974), whereas Aka fathers provide 16% (Hewlett 1988). Similar levels of inter-cultural variation are found for grandmothers who provide ~1% of childcare among the Maya (Kramer 2005), and up to 15% among the Martu (Scelza 2009). Clearly there is no uniform answer regarding who helps mothers most with reproduction. In fact, even within a

given society the alloparenting roles of fathers and grandmothers interact in complex ways. Hadza grandmothers spend more time with grandchildren when their genetic fathers are absent due to death or divorce (Crittenden & Marlowe 2008; Marlowe 2005). Likewise, Aka fathers provide more care to their offspring when living in patrilocal camps where offspring do not have access to care from maternal grandmothers and other kin (Meehan 2005).

Other categories of caregivers have received substantially less attention than fathers and grandmothers. Nevertheless, the contribution of siblings to childcare, particularly older sisters, tends to be high fairly consistently, exceeding 30% of total care in numerous societies (Kramer 2010). Additionally, although juveniles may be poor foragers of resources that require significant skill or strength to produce, they often collect easily acquired foods such as fruits and shellfish in excess of their own needs, which can then be used to provision younger siblings (Kramer 2005). However, siblings' role as caregivers is particularly complex and while they may contribute to economic production and direct care, depending on their age they may also be competitors to young children. Whilst siblings who are more than a few years older tend to have positive effects on child survival in the majority of cases (Sear & Mace 2008); those who are closer in age have been found to be detrimental to child health (e.g. Magvanjav et al. 2012). Outside of the categories discussed thus far, other potential helpers are relatively understudied, and their alloparenting contribution is often lumped together as 'other helpers' rather than analysed individually. In the studies which have been conducted, grandfathers often contribute very little to direct or indirect care and have little effect on child outcomes; and a variety of positive, negative and neutral effects have been found for aunts and uncles (Scelza 2009; Sear & Mace 2008).

There is virtually no research examining the role of unrelated individuals in providing direct care among hunter-gatherers. The ubiquity of cooperation between genetically unrelated people has been stressed as a defining feature of humans (Burkhart 2014; Boyd & Richerson

2009), and given that childcare is a fundamental cooperative activity in foraging societies, this question deserves more attention. The little empirical data which are available hints at the possible importance of unrelated adults as caregivers. Among the Efe Pygmies and the Hadza, unrelated individuals cumulatively provide 35% and 31% of allocare respectively, which in both cases is a higher proportion than any other category of non-maternal caregiver (Ivey 2000; Marlowe 2005). Despite this, little else is known about direct care from unrelated individuals and there is a lack of more detailed analyses, hence this is one of the main areas of analytical focus in this chapter. Having outlined the main sources of alloparenting, I will now introduce the hypotheses for how human alloparenting behaviour could have been favoured by natural selection.

6.1.5 Why care?

Providing allocare comes at a cost in terms of time and energy, and thus requires an explanation of how such behaviour can increase the donor's fitness; there are three primary hypotheses. Firstly, caregiving in humans may be motivated by indirect fitness benefits as is the case in other cooperatively breeding species (Hamilton 1964). This explanation is the most thoroughly tested by anthropological research and has strong support—the time spent holding Hadza infants has a significant positive association with the coefficient of relatedness between allomothers and the infant (Crittenden & Marlowe 2008). Similar patterns have been observed in the Efe where related individuals are more than twice as likely to provide allocare as non-kin, and relatives with a coefficient of relatedness of 0.5 are 17 times more likely (Ivey 2000).

Another possibility is that caregiving relationships are motivated by reciprocity. This may be in-kind (you care for my infant today while I go foraging, and I will care for yours tomorrow);

or not-in-kind (you care for my infant and I will give you some other resource in exchange). These hypotheses have been tested in non-human primates. For instance, capped langur monkeys with dependent offspring develop reciprocal allocaring partnerships (Stanford 1992). Other species have been found to exchange allocare with mating access to the mother or social support in conflicts (Ross & MacLarnon 2000). However, despite the thorough examination of reciprocity in human food sharing, the role of childcare in cooperative reciprocal relationships is poorly tested in our species. The one examination of childcare reciprocity in a hunter-gatherer population found no association between the amount of allocare an individual provides to an infant, and the amount of help with childcare or food provisioning they receive from the infant's parents (Ivey 2000). Nevertheless, given the scarcity of such analyses, both in-kind and not-in-kind reciprocity are tested in this chapter.

The final adaptive explanation I wish to discuss here is that alloparenting may be a process of 'learning to mother' in which female subadults gain experience in caregiving such that they are more effective mothers when they have their own offspring (Lancaster 1971). Indeed, in an analysis of 186 human societies, pre-reproductive females were found to provide a substantial amount of childcare, more than any other age-sex category except adult females since the latter includes mothers (Weissner & Gallimore 1977). In non-human primates, there is some evidence that more experienced allocarers grow up to be more effective mothers. For instance, the offspring of vervet monkeys have higher survival rates if their mother spent more time engaged in allomothering as a juvenile (Fairbanks 1990). Comparable tests of the relationship between alloparenting experience and maternal proficiency are not present in humans.

Other hypotheses have been put forward such as group augmentation, whereby helping to raise others' young provides direct benefits associated with group size e.g. enhanced predation protection or superior performance in inter-group conflict (Kokko et al. 2000).

Additionally, it has been suggested that helping behaviour may be a result of coercion by breeders which subordinates comply with to avoid punishment, harassment or expulsion from the group (Clutton-Brock 2002). However, I do not discuss these in detail as they are not possible to test with the data I have collected.

6.2 Aims and rationale

1. Identify the different sources of alloparent and the importance of unrelated caregivers.

To ascertain the general childcare system of the Mbendjele it is necessary to quantify the amount of care provided by different categories of alloparent. In addition to simply analysing how care varies with the relationship type between carers and recipients (father, grandmothers, siblings, nonkin etc.), I also aim to discern the relative proportion of care provided by different age-sex categories and reproductive status categories. Investigating caregiving through these different demographic dimensions facilitates comparison with species that are traditionally classed as cooperative breeders and an evaluation of the usefulness of labelling humans as such.

I also aim to elucidate in more detail the role of unrelated individuals in providing direct care. As alluded to above, some studies of hunter-gatherer childcare find that cumulatively unrelated camp members provide more care than any other category of helper (Crittenden & Marlowe 2008; Ivey 2000; Marlowe 2005). Despite this, further analysis regarding their role as alloparents is lacking and there are numerous questions to answer, some of which I attempt to address in this chapter: Is their large cumulative proportion of care simply a result of there being many unrelated camp members who may each contribute a small quantity of care at a low cost, or are there a few important 'best friends' who individually offer considerable aid to mothers with dependent offspring? What are the age, sex and

reproductive status of unrelated helpers? Finally, what are the possible motivations behind their caregiving since no inclusive fitness benefits are available? This final question relates to the second main aim of this chapter.

2. Test the different hypothesis of why caregiving may be adaptive.

Section 6.1.5 outlines the three primary hypotheses as to how individuals may increase their fitness via caregiving—kin selection, reciprocity and learning to mother. The first of these has received the most testing, and genetic relatedness has been found to be positively associated with frequency of care in numerous foraging populations (Crittenden & Marlowe 2008; Ivey 2000). However, it is possible that multiple mechanisms drive caregiving simultaneously to different extents, and there is a lack of research into the role of in/not-in-kind reciprocity and learning to mother as motivators of allocare. Moreover, there are examples of hunter-gatherer food sharing where transfers initially appeared to be driven by kin selection, but further analysis revealed sharing was better explained by reciprocal relationships that are preferentially formed with kin (Allen-Arave et al. 2008); a similar scenario may characterise childcare and call into question the evidence for inclusive fitness. Therefore, in this chapter I aim to test both the kin selection and reciprocity hypotheses and assess their relative importance in Mbendjele childcare.

6.3 Methods and analyses

The analyses presented in this chapter are based on data from the motes (remote wireless-sensing device); which were used to create proximity networks. The motes emit a remote signal (beacon) every two minutes, which is then received and recorded with a time stamp into the memory of any other mote within 'arm's length' of the sender mote. By analysing all signals received by each mote, we were able to construct daylight hours (05:00–20:00)

proximity networks. Proximate interactions are used as a proxy for care. In these analyses egos refer to recipients of care (infants and young children $\leq 4y.o.$) and alters refer to donors of care (individuals older than four years old); I chose this threshold of four years old for the following reasons. Among the BaYaka there is an extremely narrow window of time in which a child makes the transition from receiving care to providing it. By age four children will participate in caring for infants or younger children in a meaningful way, conducting activities such as feeding, soothing and carrying infants. With respect to receiving care, many other studies focus only on the first few months or years of infancy (e.g. Ivey 2000; Meehan 2005). However, caring behaviours continue well beyond the first year. Additionally, one could argue that allocare actually becomes more important when infants/young children are slightly older and become less dependent on breastfeeding, since there are increased opportunities for non-maternal caregiving. Whilst there is of course variation between different families, this age categorisation of recipients/donors of care provides the most accurate representation of caregiving relationships based on my experience.

The data come from three camps. In Ibamba there are 7 egos and 40 alters; in Longa there are 8 egos and 58 alters; and in Masia there are 4 egos and 15 alters. All egos are four years old or younger; of the 19 egos 7 were already weaned during the study period. Not all relevant data were present for all individuals for each analysis, thus sample sizes are indicated with results. For more information on the motes sub-study and a full justification for motes proximity data as a meaningful measure of childcare see section 5.4.6. It is necessary to keep in mind that the data provided by the motes reflect proximate interactions, which is being used as a proxy for care. The clear shortcoming with this proxy is that it does not directly measure the quality of care being given. For more discussion on this limitation see sections 5.4.6.2 and 6.5.

6.3.1 Key variables

a) *Proportion of Allocare*—the fraction of all non-maternal care provided to ego by alter. This is calculated as the number of beacons received by ego's mote from alter's mote divided by the total number of beacons received by ego's mote from all non-maternal motes.

b) *Care*—the proportion of total time that ego and alter are in proximity (arm's length) to one another. This is calculated as the total number of beacons received by ego's mote from alter's mote as a fraction of the maximum number of beacons that could have possibly been received over the course of the sub-study. The maximum number of beacons is calculated as the total number of two minute intervals that both ego and alter are recorded as participating in the sub-study. Thus, while 'Proportion of Allocare' measures proximate interactions as a proportion of all non-maternal proximate interactions, 'Care' measures proximate interactions as a proportion of time.

c) *Alter's Life-Stage*—a categorical variable defining alter's life stage as either: subadult; reproductive; or post-reproductive. Subadults are individuals who are both under 18 years old and not in a long-term relationship i.e. not residing in a *fuma* with their spouse. Post-reproductive individuals are those who are both older than 50 years old and have not had any offspring for more than five years. All other individuals are categorised as being in the reproductive life-stage.

d) *Weaned*—a binary variable indicating whether ego is weaned or not.

e) *Kin*—a binary variable indicating whether ego and alter have a coefficient of relatedness ≥ 0.125 .

f) *Relatedness*—a categorical variable quantifying the coefficient of relatedness between ego and alter calculated from genealogies constructed using data from reproductive histories. This can take the value of 0.5, 0.25, 0.125, 0.0625 and 0. In cases where the estimated

coefficient of relatedness does not fit into one of these categories due to multiple paths of relatedness, the coefficient is rounded down to the nearest category. For instance, if ego's parents are first cousins, then the coefficient of relatedness between ego and ego's father is rounded down from 0.5625 ($0.5 + 0.0625$) to 0.5.

g) Breeder—a binary variable indicating whether alter is in the reproductive life-stage or not.

h) Alter's Dependents—a discrete variable indicating the number of offspring (or foster children) under 16 years old living with alter at the time of the motes sub-study.

i) Ego's Dependent Siblings—a discrete variable indicating the number of siblings or adopted siblings under 16 years old living with ego's parents.

j) Sex Homophily—a binary variable indicating whether ego and alter are the same sex.

k) Care Reciprocity—the sum of 'Care' provided by ego's parents to children and infants less than four years old in alter's household. Hence values for this variable are only calculated for alters with offspring under four years old.

l) Food Reciprocity—the number of thousand calories transferred from ego's household to alter's household over 24 hours of observation (data collected by James Thompson). Hence values for this variable are only calculated for alters living outside of ego's household.

For full details on the motes sub-study, reproductive history interviews, food transfer observations and aging participants see methods (chapter 5).

6.3.2 Analyses

1. To provide an overall picture of sources of allocare:

i. I identify the 'Proportion of Allocare' provided by different categories of carer: fathers, grandmothers, grandfathers, siblings, uncles/aunts, other kin and non-kin. This analysis is cumulative i.e. it does not control for the number of potential carers in a particular category, but represents the combined importance of *all members* of a given category.

ii. I identify the 'Proportion of Allocare' provided by different life-stage/sex groups. This analysis is cumulative i.e. it does not control for the number of potential carers in a particular category, but represents the combined importance of *all members* of a given category.

iii. I identify the amount of 'Care' (proportion of time spent in proximity to ego) provided by an average individual from each category of carer: mother, father, grandmothers, grandfathers, siblings, uncles/aunts, other kin and non-kin. This analysis is 'per capita' i.e. it *does* control for the number of potential carers in each category, and it represents the importance of an *average member* of a given category.

2. To determine the importance of breeding status and kinship on allocare I conduct Wilcoxon signed rank tests of:

i. Whether 'Breeders' cumulatively provide a higher 'Proportion of Allocare' than non-breeders.

ii. Whether 'Kin' cumulatively provide a higher 'Proportion of Allocare' than non-kin.

3. To further examine the role of unrelated individuals in the allocare system I compute:

i. The mean 'Proportion of Allocare' individually provided by the most, 2nd most...7th most caring unrelated alter. These data provide insight into whether all unrelated individuals equally contribute a low amount of allocare, which cumulatively constitute a significant amount or whether a few particular unrelated individuals act as important sources of allocare.

ii. The life-stage/sex characteristics of all alters who individually provide more than 5% of any unrelated ego's allocare.

4. To test the role of kin selection in allocare provided to ego by a given alter, I use a linear mixed effects model. The response variable is 'Care'. The key predictors are 'Relatedness' (representing the r in Hamilton's equation); 'Alter's Dependents' (representing the C —since it is likely to be more costly for individuals with more of their own offspring to expend time and energy into allocare for others); and 'Ego's Dependent Siblings' (representing the B —since mothers with more dependents may benefit more from help from alloparents as they are in greater need). Other fixed effects include 'Alter's Life-Stage', 'Alter's Sex', 'Ego's Sex', 'Ego Weaned' and 'Sex Homophily'. Ego ID and Alter ID are fitted as crossed-random effects since multiple carers can care for each child, and multiple children can be cared for by each carer. The full model was then reduced via backward stepwise removal of variables to minimise AIC scores until only significant variables remained in the model. AIC refers to 'akaike information criterion' and is a measure of model quality. Models with lower AIC scores are estimated to lose less information i.e. be less 'distant' from reality (Burnham et al. 2011).

5. To test whether reciprocity could explain allocare, I use the same linear mixed effect model as (4), but only include any predictors/controls that were in the final reduced model. I conduct two models to test both for in-kind and not-in-kind reciprocity:

i. in-kind: I include 'Care Reciprocity' as an additional predictor. This model includes all non-parental camp members with offspring under the age of four as potential alters. 'Alter's Life-Stage' is excluded as a predictor since only reproductive stage individuals are included in this model.

ii. not-in-kind: I include 'Food Reciprocity' as an additional predictor. This model includes all camp members from outside the household for which food transfer data are available.

6.4 Results

6.4.1 Who provides care?

Our results demonstrate that allocare is fundamental to child rearing among the BaYaka, as on average $\sim 77\%$ $SD \pm 9\%$ of proximate interactions with infant/young children (under 4 y.o.) come from non-maternal individuals. This is substantially higher than estimates of approximately 50%, which tend to be reported for other small-scale societies (Kramer 2010), partially owing to the fact that in addition to infants, our sample also included young weaned children who do not require as much time in proximity to their mothers since they are no longer breastfeeding. For instance, proximate maternal interactions constituted under 10% of care received for one of the weaned boys who was just under four years old. The effect of age on proportion of interactions which are non-maternal is indeed positive, but this result does not reach significance likely due to the small sample size (linear regression: $\beta=0.01$; $p=0.490$). Similarly, as expected, the proportion of interactions that come from non-maternal carers is higher for weaned versus breastfeeding dependents; however, again this result does

not reach significance (randomisation test with 9999 Monte Carlo resamplings: $Z=1.20$; $p=0.243$). I outline the benefit of including both breastfeeding and weaned young children in the discussion.

From the child's point of view, cumulatively siblings provide a higher proportion of allocare (32%) than any other category of alloparent, closely followed by nonkin who provide 30% (Fig. 6.2a). A similar picture emerges when analysing the relative amount of time alloparents spend in proximity to the child per capita i.e. controlling for the number and presence of individuals in each category (Fig. 6.3). Again, siblings are the most important category of alloparent, followed by fathers who spend 16% of their time in proximity to their young offspring compared to 11% by grandmothers. The striking difference from the per capita results is the contribution of nonkin, whilst cumulatively they are more or less the equally most important category alongside siblings, per capita they spend the least amount of their time in close proximity to young at ~1%.

Analysing the sources of allocare from a different dimension (Fig. 6.2b), non-breeding individuals (subadults and post-reproductives) cumulatively provide a significantly higher proportion of allocare than reproductive camp members (Wilcoxon signed-rank: $V=21$; $p=0.007$). Consistent with the central role of siblings outlined above, subadults provide 54% of allocare, followed by reproductive individuals who provide 35%, and finally post-reproductive individuals provide only 11%. Whilst in both categories of non-breeding alloparents more care comes from females; interestingly among reproductive age individuals, males provide more allocare (21% vs 14%). However, this is likely due to the fact that the category of male reproductive alloparents includes fathers. On average fathers provide 10% of allocare, if they are excluded from this analysis, then again female reproductive alloparents provide more allocare than their male counter-parts (15% vs 12%).

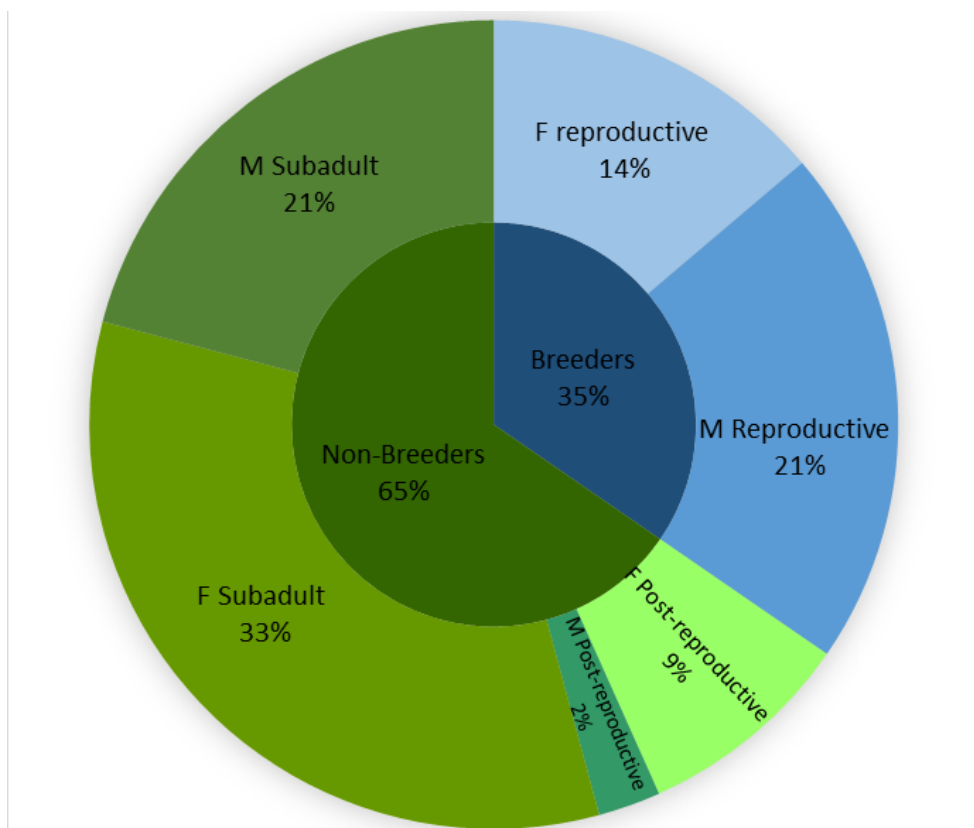
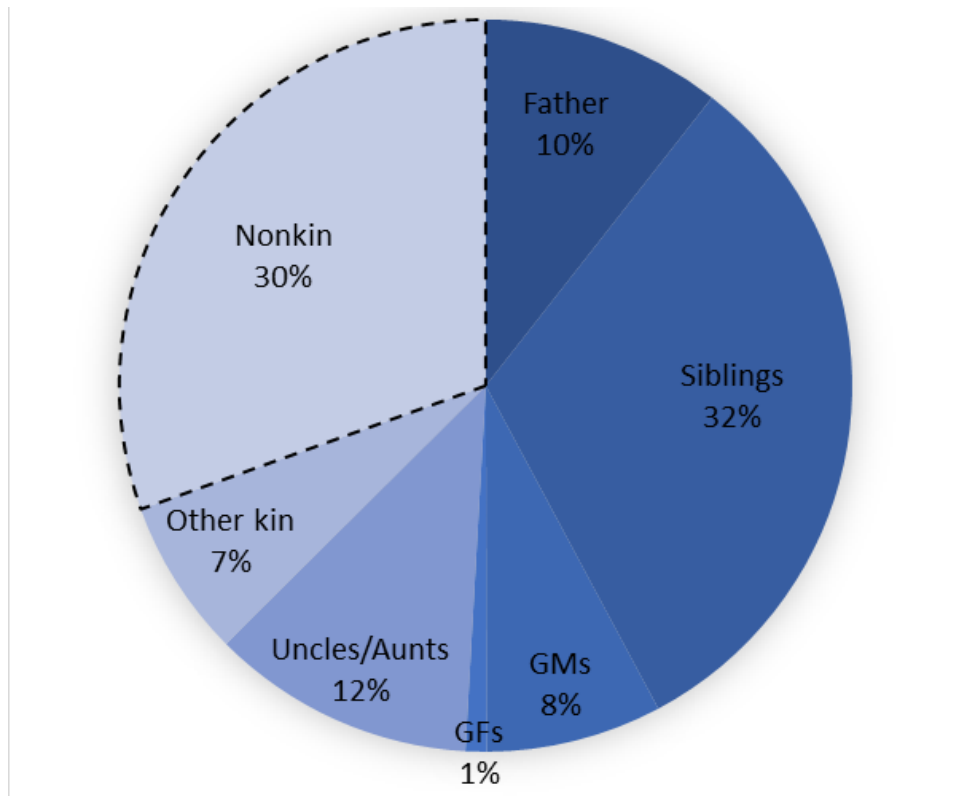


Figure 6.2: a) Top—pie chart showing cumulative proportion of ego's (infant/child; n=17) proximate interactions derived from each category of non-maternal alters (allocarers). b) Bottom—inner pie chart represents the cumulative proportion of ego's (n=17) proximate interactions from breeding vs. non-breeding non-maternal alters; outer pie chart shows cumulative proportion of ego's interactions from each sex/life-stage category of non-maternal alters. These proportions are cumulative i.e. they *do not* control for the number of potential carers in a particular category. For instance, if an ego has two siblings who provide 10% and 20% of ego's allocare respectively, the cumulative proportion of allocare provided by siblings is 30%. For 'per capita' calculations, which control for the number of potential carers in each category of carer see Fig. 6.3.

With respect to the role of unrelated camp members, although cumulatively kin do provide a significantly higher proportion of allocare than nonkin (Wilcoxon signed rank: $V=27$; $p=0.005$), as a category unrelated alloparents appear to be one of the most important, providing 30% of allocare. Figure 6.4 shows the average proportion of allocare provided individually by the seven ‘most caring’ unrelated helpers contrasted against related individuals. Whilst the proportion of allocare provided by each unrelated alloparent rapidly declines, on average infants and young children have a handful of particularly caring nonkin in camp (see Fig. 6.4). The three most caring unrelated helpers individually each provide more care to ego than an average relative with coefficient of relatedness 0.125; and together these three helpers constitute approximately 20% of a child’s total allocare. Thus, the substantial cumulative contribution of nonkin to allocare is not simply a product of children having a large number of unrelated camp members who individually provide a small amount of allocare. Instead children tend to have 2–3 particularly helpful unrelated alloparents. If we define an unrelated helper as any individual that provides more than 5% of allocare to any unrelated child, then 19 out of a possible 113 individuals in the study are considered unrelated helpers. Their sex/life-stage characteristics are shown in Table 6.1.

Table 6.1: Sex/life-stage of the 19 important unrelated allocarers; where important unrelated allocarers are defined as individuals providing more than 5% of any unrelated ego’s total proximate interactions.

	Subadult	Reproductive	Post-Reproductive
Male	4	5	1
Female	4	4	1

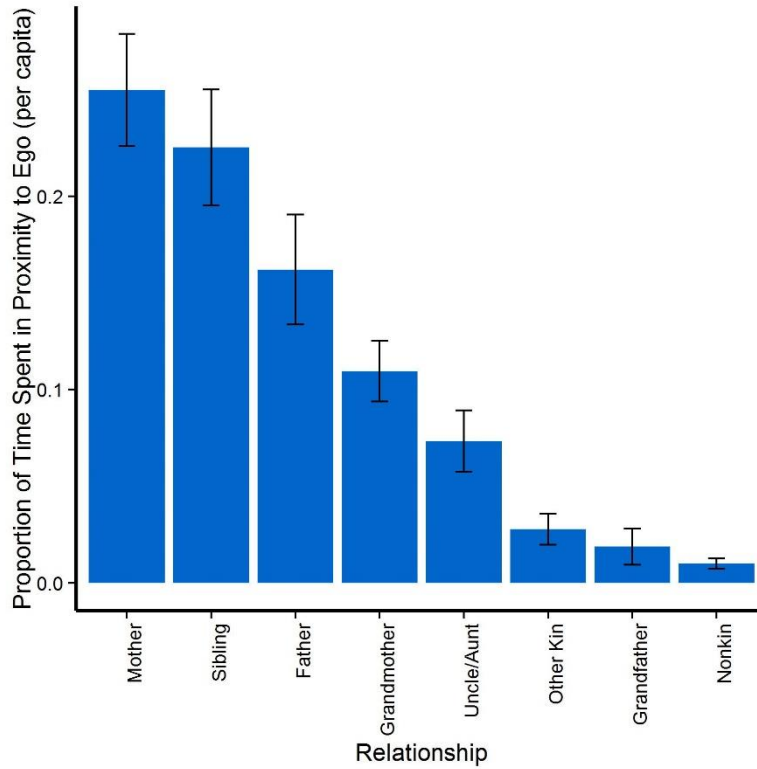


Figure 6.3: Proportion of time an average individual from each category of alter spends in proximity to ego. Black bars indicate standard errors. These calculations are ‘per capita’ i.e. they *do* account for the number of potential carers in a particular category. This differs from Fig. 6.2 in that if an ego has two siblings who provide 10% and 20% of ego’s allocare respectively, the per capita proportion of time spent in proximity to ego for the sibling category is 15% $([10+20]/2)$ rather than 30%.

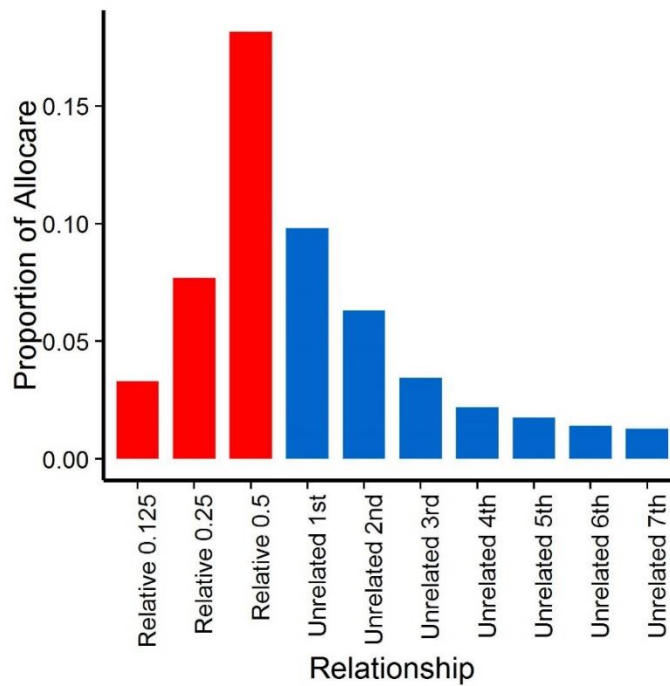


Figure 6.4: Red bars represent the proportion of ego’s proximate interactions derived from an average alter related to ego at the 12.5%, 25% and 50% level. Blue bars represent the average proportion of ego’s proximate interactions derived from the most–7th most caring unrelated alters.

6.4.2 Why care?

I used a linear mixed effect model to analyse the different variables that could possibly affect the amount of time alters (carers) spend in proximity to egos (infants/young children), and to test the kin selection hypothesis for allocare (Table 6.2). There was no effect of ego's sex or sex homophily between ego and alter, indicating that carers do not preferentially provide care to young of either sex or their own sex. As expected, and consistent with the results from the previous section, female alloparents provide significantly more care than their male counterparts; and subadults provide the most allocare followed by reproductive individuals and finally post-reproductive individuals, but the difference is only significant with the latter.

The results largely conform to the kin selection hypothesis; the amount of time spent in close proximity to ego increases incrementally and significantly with the coefficient of relatedness between ego and alter. The effect of genetic relatedness is even significant at a coefficient of relatedness of 0.0625. At its maximum, alters with a coefficient of relatedness of 0.5 to ego spend 16% more of their time in close proximity to ego than unrelated alters (see Table 6.2; Fig. 6.5). Additionally, alter's number of dependent offspring has a significant negative effect on allocare. This is consistent with predictions since providing allocare is likely to be more costly to individuals who have to invest time and energy caring for their own offspring. Finally the effect of ego's number of dependent siblings, on the amount of allocare received by ego is negative and close to significance. This is contrary to predictions, I address potential explanations for this result in the discussion. The results from the final two models indicate that in addition to kin selection, both in-kind and not-in-kind reciprocity motivate allocare (Fig. 6.6). Whilst controlling for genetic relatedness, there is a significant association between amount of care provided from alter to ego and both care provided from ego's household to alter's offspring ($\beta=0.16$, $p=0.001$; $n=111$; see appendix 6.2 for full results), and calories transferred from ego's household to alter's ($\beta=0.01$, $p=0.000$; $n=373$; see appendix 6.3). Thus, in addition to indirect benefits, it appears allocare is also motivated by direct benefits in

terms of reciprocated care and food transfers. I tested for any interaction effects between genetic relatedness and reciprocity, but no significant effect were observed.

Table 6.2: Effect of genetic relatedness on the proportion of time any alter (carer) spends in proximity to ego (infant/child). Reference levels for categorical variables are indicated in the second column. Significant results are presented in bold. Both the full model including all variables and the final reduced model are shown. Model selection occurred via backward stepwise removal of variables in order to minimise AIC scores, all intermediate models are presented in appendix 6.1

Predictor (n=790 dyads)	Reference factor	Full Model		Reduced Model	
		β (S.E.)	P	β (S.E.)	p
ego and alter $r=0.0625$	unrelated	0.016 (0.01)	0.001	0.016 (0.01)	0.001
ego and alter $r=0.125$	unrelated	0.038 (0.01)	0.000	0.037 (0.01)	0.000
ego and alter $r=0.25$	unrelated	0.061 (0.01)	0.000	0.061 (0.01)	0.000
ego and alter $r=0.5$	unrelated	0.162 (0.01)	0.000	0.162 (0.01)	0.000
alter's no. of dependents	not factor	-0.003 (0.00)	0.048	-0.003 (0.00)	0.049
alter's life stage (reproductive)	pre-reproductive	-0.005 (0.00)	0.229	-0.005 (0.00)	0.217
alter's life stage (post-rep)	pre-reproductive	-0.012 (0.01)	0.012	-0.012 (0.01)	0.013
alter's sex (male)	female	-0.010 (0.00)	0.002	-0.010 (0.00)	0.002
ego's sex (male)	female	0.013 (0.01)	0.125	-	-
ego and alter same sex	different sex	0.000 (0.00)	0.881	-	-
ego's dependent siblings	not factor	-0.004 (0.00)	0.093	-	-
ego weaned	breastfeeding	0.001 (0.01)	0.919	-	-
AIC		-2832.887		-2871.474	

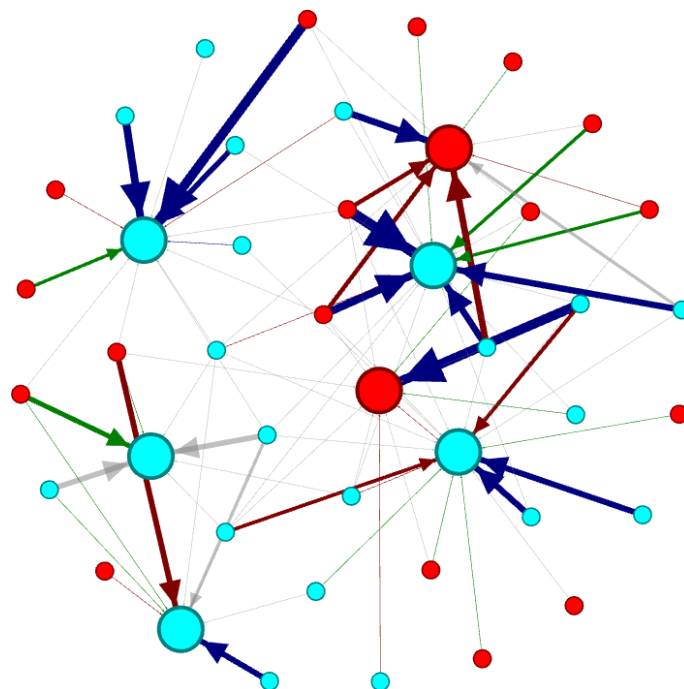


Figure 6.5: Relatedness and allocare in camp Ibamba. Large nodes are egos (infants/children), small nodes are alters (carers). Blue nodes are male, red nodes are female. Arrow colour reflects coefficient of relatedness between ego and alter (blue=0.5; green=0.25; red=0.125; grey=unrelated [<0.125]). Arrow width reflects the proportion of time alter spends in proximity to ego. Graph created using *Gephi 0.8.2*.

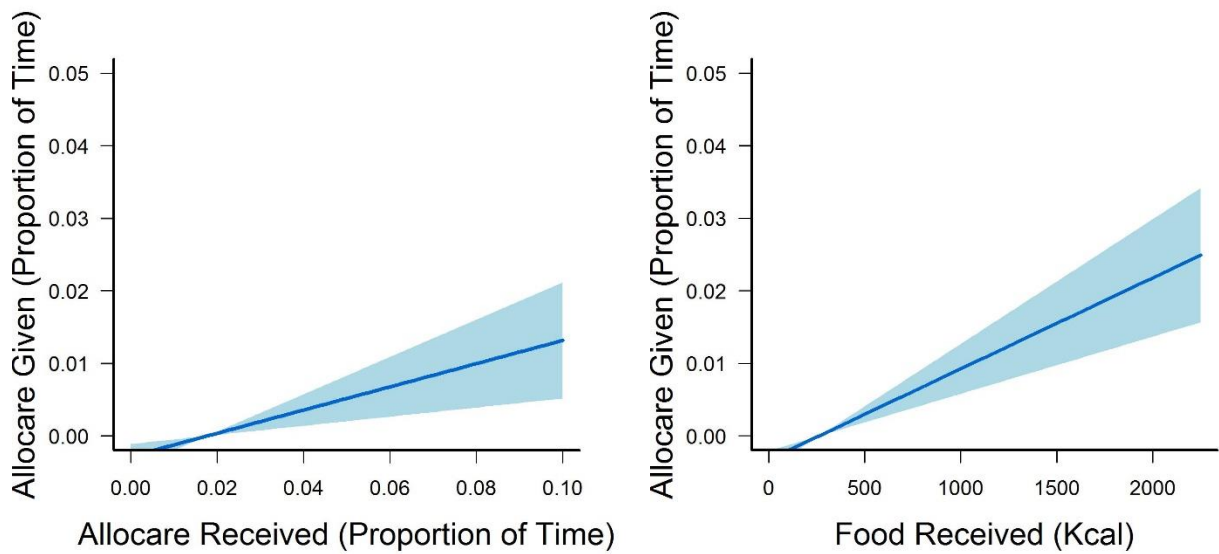


Figure 6.6: Allocare provided to ego by alter and a) Left—the amount of allocare provided to alter’s offspring by ego’s parents [in-kind reciprocity]; and b) Right—the average number of calories transferred from ego’s household to alter’s over 24 hours [not-in-kind reciprocity]. These graphs were plotted using the ‘vreg’ package in R, which allows graphical representation of the effect of a single predictor based on the results of a regression with multiple predictors.

6.5 Discussion

In this chapter I have used data from remote wireless sensing devices (motes), rather than traditional focal sampling techniques (Altmann 1974), to study childcare practices among the Mbendjele. The results here demonstrate that this technology can be effectively employed to provide large high resolution data that answer research questions relating to the human mode of reproduction, in this case—who provides allocare and why allocare may be adaptive for caregivers.

As expected, the results confirm the fundamental importance of allocare (and cooperation) in hunter-gatherers, as only about a quarter of young dependents proximate interactions are with their mothers. This estimate is substantially lower than the 50% of care, which is reported relatively consistently for mothers in small-scale societies (Kramer 2010). One primary reason for this is that childcare studies tend to focus on young infants typically under

18 months old (e.g. Hewlett 1988; Meehan 2005; Ivey 2000), whereas this study included young from 0–4 years of age, and young children spend considerably less time with their mother at the latter end of this age range. I extended the age range beyond early infancy because prior to the age of four, children are still often recipients of caring behaviours such as being carried, soothed, fed, taught etc. and require some level of supervision to avoid potential accidents with fires or dangerous animals. Moreover, one could argue that the importance of allocare actually increases after early infancy. As outlined in section 6.1.3, it is early weaning in human life-history that facilitates opportunities for others to help mothers in childcare since weaned children no longer require their mother's breastmilk, and therefore are more flexible in terms of who cares for them. For instance, among Aka foragers paternal allocare is lowest in the first year of an infant's life, but fathers spend more time with their offspring from ages 1–4 (Fouts 2008). In fact, the lower proportion of maternal care found here may also be in part explained by the practice of allonursing among the Mbendjele, which further exaggerates opportunities for non-maternal caregiving. I observed instances of non-maternal breastfeeding in five of the 11 infants in the current sample, which almost always occurred while mothers were out foraging. Nursing Hiwi and Ache women spend significantly less time foraging and have significantly lower food acquisition rates than non-nursing women (Hurtado et al. 1992). The practice of allonursing may be an effective solution to similar maternal trade-offs between foraging effort and childcare for the Mbendjele, allowing women to leave their infants with allomothers while they go on longer foraging trips.

Additionally, as expected we find no significant sex bias in allocare received by boys and girls (Table 6.2). In other subsistence modes labour patterns and marriage systems can drive sex biased investment/neglect in the form of infanticide, provisioning, childcare and inheritance (Cronk 1991; Hartung et al. 1982; Diamond-Smith et al. 2008). For instance, in pastoralist cattle keeping populations, inheritance patterns are heavily male biased since transferring

cattle resources increases the number of wives that sons can marry and in turn maximises reproductive success (Holden & Mace 2003). However, among hunter-gatherers, resources aren't accumulated, males and females contribute to subsistence and labour tasks, and polygyny is limited; hence I did not expect any sex bias in investment. There was also no significant bias in allocare towards young who are the same-sex as an alloparent. However, from my experience such patterns do not emerge until later in life when children begin to participate in sex-specific subsistence tasks. For instance, young girls may begin to accompany older females on fishing or gathering trips around the age of six; and for boys, by about age 12 they will accompany their fathers and other men on hunts or to set traps.

Who cares?

Turning attention to who provides allocare, specifically the controversial relative importance of grandmothers and fathers, the data here provide a balanced picture. In the introduction I explained that there is no consistent pattern across societies or even within subsistence modes, and the relative contributions of these caregivers is determined by local ecology and demography. Often within a given population there is a clear 'winner' in this debate. For instance, in the review of Sear & Mace (2008) of kin effects on child survival, in only 3 of the 11 populations in which both fathers and grandmothers were studied, did both have a positive effect on survival. Among South American hunter-gatherers the importance of male provisioning has been emphasised and the contribution of post-reproductive female help is negligible (Hill & Hurtado 2009). Conversely, among Martu Aborigines while grandmothers provide more than 20% of allocare, paternal care constitutes only 3% (Scelza 2009). However, here it appears both categories are relatively important in BaYaka childcare. Fathers provide on average 10% of a child's proximate interactions and grandmothers 8%

(Fig. 6.2a); in terms of the proportion of their time they are in proximity to the child, these figures are 16% and 11% respectively (Fig. 6.3).

These findings are somewhat inconsistent with Hewlett's notable research depicting another BaYaka group (Aka) as having 'the best dads in the world'. Fathers were recorded as being within an arm's length of their infants for more 50% of time and held infants for 22% of daylight hours (Hewlett 1991). However, those estimates were only derived from data when males were in camp, if this control is removed then fathers were in arms reach only 20% of daylight hours (adapted from Fouts 2008), resembling the 16% found in the present study. Additionally, Hewlett attributes the high levels of paternal care largely to the fact that the Aka engage in net hunting, which both men and women participate in; hence the sex division of labour is less specific and men play a more active role in childcare (Hewlett 1991). In contrast, at least currently, hunting is a male only activity for the Mbendjele; hence according to Hewlett's explanation, comparably high levels of paternal care would not be expected. Moreover, different alloparenting patterns have been found among different Aka groups, demonstrating that even within the same ethnolinguistic group alloparenting systems may vary across time and space. For instance, another study investigating the importance of different kin on child anthropometric outcomes found grandmaternal presence was positively associated with height, weight and weight for height at different stages of infancy/early childhood, whereas paternal presence had no effect (Meehan et al. 2014). In the Mbendjele case here, both fathers and grandmothers seem to play a similar role in allocare, with fathers contributing marginally more.

Despite the attention payed to fathers and grandmothers in hunter-gatherer research, here I find siblings as the most important category of alloparents, constituting 32% of non-maternal proximate interactions. Per capita, an average sibling spends 23% of their time in proximity to younger siblings under four years of age, which is almost as much as mothers'

26%. Such findings are not an anomaly and data from other populations also implicate siblings as the most important allocarers providing 54% of allocare among the Efe and 23% among the Agta (Kramer 2010; adapted from Goodman et al. 1985). Although the role of elder siblings has primarily been noted for agricultural populations (Draper & Harpending 1987), these results demonstrate that they deserve more attention in hunter-gatherer populations. Their neglect in discussions of hunter-gatherer alloparenting may be due to more research attending to provisioning than direct care, and usually within foraging societies either grandmothers or fathers will provide more provisioning than siblings. However, direct allocare is important in freeing up mothers to forage, and still reduces energetic burdens on mothers. Additionally, because siblings are often still nutritionally dependent and require provisioning themselves, they are categorised as dependents requiring care rather than providing it. However, this form of discrete categorisation is over simplistic—whilst not being net producers in terms of foraging, they still contribute actively and substantially to childcare. One of the most striking differences in hunter-gatherers compared to industrialised societies is the extremely narrow window of time in which a child makes the transition from being cared for to becoming a carer. By the age of four, children can be seen to carry, soothe, feed, supervise and provide medical/hygiene related behaviours towards younger siblings.

As infants begin the weaning process and spend less and less time in proximity to their mothers, a large part of their day is spent in mixed age-sex playgroups, including children from age three to those well into their teenage years. This is why siblings are found to be the most important category of alloparents and subadults generally contribute 54% of allocare (Fig. 6.2b). Again, this seems to be a consistent pattern in hunter-gatherer groups—subadults provide 56% of allocare among Efe Pygmies, and constitute 62% of Hadza allomothers (Ivey 2000; Crittenden & Marlowe 2008). These playgroups are a very important stage in childhood, not only do they free up mothers to reinvest energy in foraging and reproduction,

they also provide a learning environment for young children. In these playgroups, I have observed children fishing, climbing trees using vine harnesses (a technique adult men use for honey collecting), building *fumas* (huts), cooking and sharing yams, mock hunting, and conducting children's versions of *massana* (song and dance religious rituals involving forest spirits). Hence in these playgroups, younger children are exposed to and learn about subsistence tasks, sharing norms and aspects of religious life, which are all vital to a successful BaYaka forest life.

The final category of caregiver I wish to discuss here is nonkin. Human cooperation between genetically unrelated individuals has been emphasised as a defining characteristic of our species (Boyd & Richerson 2009). Yet, the role of nonkin in allocare has received little attention; thus, elucidating this role was one of the primary aims of this chapter. Whilst unrelated camp members are often lumped together with 'other helpers' in numerous studies of allocare, the little available data suggest that cumulatively they provide more than any other kin category of carer—35% and 31% in the Efe and Hadza respectively (Ivey 2000; Marlowe 2005). Very similar findings are obtained here for the BaYaka, as 30% of non-maternal proximate interactions occur with unrelated individuals, which is effectively the joint most important category alongside siblings, who make up 32% (Fig. 6.2a). Although the per capita data indicate most nonkin spend very little time with unrelated young ~1% (Fig. 6.3), the trend is not uniform. Figure 6.4 demonstrates that on average a child has three carers who each provide more allocare than an average camp member related at the 0.125 level, and together these three unrelated alloparents constitute approximately 20% of allocare. In fact, the most caring unrelated alloparent on average provides ~10% of non-maternal proximate interactions, so is of similar importance as fathers and more importance than grandmothers. Important unrelated alloparents are split fairly equally between the sexes and subadult and reproductive life-stages, whereas post-reproductive individuals are usually not important unrelated alloparents (Table 1). Thus, the subadults likely represent

unrelated helpers in playgroups, and the reproductive age unrelated helpers are likely mothers' 'best friends'.

Why care?

With respect to the hypotheses invoked to explain how providing allocare could be adaptive for caregivers, we find some level of support for all three hypotheses; indeed, there is no reason why these explanations should be mutually exclusive and cannot work in tandem. The kin selection hypothesis predicts that allocare should be directed towards genetically related young who share genes with the alloparent, thus increasing their indirect fitness. This is the only explanation which has been well tested for human societies, and results confirm a positive association between the coefficient of relatedness and amount of allocare provided. For instance, among the Hadza the proportion of time alloparents spend holding an infant increases to ~1% if the coefficient of relatedness is 0.125, 8% for 0.25 and 9% for 0.5 (Crittenden & Marlowe 2008). Similar findings are reported in the present study, and the coefficient of relatedness between child and caregiver is positively associated with time spent in proximity. The effects are incremental strength, and I find evidence for an effect of relatedness even at the low coefficient of 0.0625, which has not been tested in previous research (Table 2).

Although other studies have examined the effect of relatedness—the 'r' in Hamilton's inequality (Hamilton 1964), this is not a complete test of the kin selection hypothesis. The 'B' and 'C' terms of the inequality are often neglected. Thus, it is necessary to discern whether helpful behaviours are directed to those where the benefits to the recipient's fitness is greatest, and the cost to the donor's is minimal. Hence, I predicted that the more dependent offspring alloparents had themselves, the less allocare they would provide, since the time and energy involved are more costly and diverting resources away from their own progeny. Indeed, the model confirmed a significant negative association between alter's number of

dependent offspring and allocaring effort (Table 2). Additionally, I predicted that allocare would be directed towards mothers with the greatest dependency loads, optimising the 'B' term of the inequality since these women are the most in need of assistance. However, contrary to predictions the direction of the effect was opposite and verging on statistical significance ($p=0.09$)—I found a negative association between ego's number of dependent siblings (i.e. the dependency load of ego's mother) and the amount of allocare directed towards ego. Nevertheless, there is a complex relationship between these variables since egos with more siblings may receive less care because alloparental help has to be shared among a larger sibling set. Thus, it is possible that mothers with higher dependency loads do in fact receive more help with childcare overall. However, since the model only examines allocare received by one of her offspring rather than the sum of all her offspring, a negative association is observed.

Despite the support for the kin selection hypothesis, these results are not sufficient to explain all BaYaka alloparenting—as discussed above unrelated individuals also play an important role in childcare. The role of reciprocity in providing direct benefits to allocarers who receive some form of help in exchange for their efforts has been poorly tested in human populations. The one test in hunter-gatherers found no relationship between alloparental effort towards a child and resources received by that child's mother or father among Efe Pygmies (Ivey 2000). Conversely, here I find evidence for both in-kind (childcare in exchange for childcare) and not-in-kind (childcare in exchange for food) reciprocity, even after controlling for kinship (Figure 6.6; appendix tables 6.2/6.3). Thus, it appears alloparents can increase their fitness via both indirect and direct mechanisms. Reciprocal altruism is commonly reported in food sharing studies, and in fact a meta-analysis of human and non-human primate food sharing found the effect of reciprocity to be strongest in the BaYaka (Jaeggi & Gurven 2013). Given that reciprocity seems to be fundamental in cooperative relationships for the BaYaka, the results found here are hardly surprising; nevertheless, this

confirmation is a valuable contribution to the field given the lack of empirical evidence for reciprocity effects involving childcare in the existing literature.

The final adaptive explanation for allocare is the learning to mother hypothesis, which suggests that allocare provided by female subadults improves their ability to effectively mother their own offspring later in life, since they gain an opportunity to learn how to care for infants and young children (Lancaster 1971). I did not test this hypothesis explicitly. However, the results do offer some support as female subadults constitute a third of a child's allocare, considerably more than any other sex/life-stage category (Fig. 6.2b). To conclusively confirm this hypothesis, it is necessary to demonstrate that alloparental experience in early life is actually associated with mothering skill, as has been found in some primate species (e.g. Fairbanks 1990; Ross & MacLarnon 2000).

The important role of kin selection and reciprocity in determining BaYaka allocare patterns, provide further evidence for the importance of individual differences in social capital; those individuals with more kin or reciprocal relationships are likely to benefit from increased access to this important form of cooperation. This attends to a primary aim of this thesis since the evolutionary implications of within-group differences in sociality are understudied (see section 2.4), and likely to be especially important in humans since we form highly differentiated social relationships within our social groups.

Are the BaYaka cooperative breeders?

Given the fact that numerous non-maternal individuals are involved in rearing young, humans are frequently characterised as cooperative breeders (e.g. Hrdy 2005; Burkhardt 2009) —a term traditionally reserved for some species of birds and mammals and the eusocial insects (see section 6.1.2). There are a range of different criteria that have been

proposed as classification conditions for cooperative breeding systems such as—whether help with reproduction is obligate or facultative; the level of reproductive skew in a social group; the proportion of nests in which non-maternal individuals help young etc. (Hatchwell 2009; Sherman et al. 1995). However, more generally the point of cross-species classification systems is to examine the socio-ecological drivers and consequences of evolutionary systems that emerge via convergent evolution across taxa. In the case of eusocial insects and cooperative breeding mammals and birds, the system that is of specific interest is the combination of delaying/foregoing personal reproduction (direct fitness) and helping genetically related others with their reproduction (indirect fitness). Note that direct benefits to helpers have previously been hypothesised for cooperative breeders (e.g. see group augmentation hypothesis Kokko et al. 2001), but recent work indicates it is indirect benefits that are necessary for the system (Lukas & Clutton-Brock 2012).

Here we do find similar patterns in alloparenting—a significant majority (65%) of allocare comes from non-breeding BaYaka and genetically related individuals (70%). However, 35% of allocare is from breeding individuals, suggestive of some communal breeding (Lukas & Clutton-Brock 2012), and the non-breeding helpers are not necessarily foregoing their own reproduction, e.g. subadults are not physiologically able to reproduce. Moreover, two principal findings of this study are that unrelated individuals are important helpers, and mechanisms other than kin selection, such as reciprocity, motivate allocare. Therefore, at least some of the help BaYaka mothers receive in childcare does not share the fundamental tenets of bird and mammalian cooperative breeding systems—foregoing personal reproduction, and alloparenting genetically related young. The only form of help which does potentially satisfy these conditions is grandmaternal care. Hawkes suggests that the trade-off involved in the selection of female post-reproductive longevity was delaying age at reproductive maturity in order to invest in the soma and extend life-expectancy (Hawkes et al. 1998). Therefore, a grandmother's ability to care for her related grandchildren does come

at a cost to her personal reproduction (in early life). However, I find grandmothers are responsible for only 8% of allocare. Therefore, I do not believe the classification of the BaYaka as cooperative breeders is a useful one since they do not share the fundamental aspects of reproductive modes in bird and mammalian species that are classified as such. It is the sacrifice of personal reproduction that accompanies helping behaviour which made bird/mammalian cooperative breeding systems so fascinating to behavioural ecologists; thus the observation that human mothers receive help in their reproductive career is not sufficient to catalogue humans as cooperative breeders. An important caveat to this conclusion is that the data presented here do not account for the quality of care provided, which I discuss more in the next section. Thus, one cannot rule out the possibility that, due to differences in quality of care, grandmothers are the most important category of carer despite providing only 8% of non-maternal proximate interactions.

Conclusion, limitations and future research

In this chapter I have demonstrated the utility of remote wireless sensing devices (motes) in evolutionary research into childcare. Conducting motes observations in three BaYaka camps on a total of 19 infants/young children and 113 carers, I gathered information on the amount of care provided by different categories of helper, and tested hypothesis regarding how alloparenting effort can be adaptive. Findings of particular note are the importance of siblings as carers, here they constitute 32% of proximate interactions with young, more than any other category. Additionally, the results provide some preliminary data regarding the role of unrelated individuals in hunter-gatherer childcare systems—cumulatively unrelated camp members provide 30% of allocare, the majority of which is provided by 2–3 particularly close nonkin. Finally, we find support for both in-kind and not-in-kind reciprocity, as well as kin selection, as drivers of allocare. The process of exchanging care for care/food had

previously received little testing, and the results here highlight the supplementary role of direct fitness benefits in the evolution of alloparenting. In the border scope of this thesis, these results have demonstrated both the importance of cooperation for hunter-gatherers, and the fact that this cooperation is directed preferentially towards kin and reciprocal partners. Given that cooperation is biased within the camp, it is likely that certain individuals with access to more cooperation, i.e. with more social capital, achieve evolutionary advantages—the next two chapters attempt to confirm this empirically.

In contrast to traditional focal sampling techniques (Altmann 1974), motes are less time-intensive for researchers; thus, they can provide proximity data for large sample sizes and over long-periods of time, in turn minimising biases in datasets. However, a limitation of this approach and the analyses presented here is that proximity is not a perfect proxy for allocare. Research has identified that childcare can vary from different carers in terms of the ratio of high investment (carrying, playing, hygiene etc.) to low investment (watching, proximity etc.), and the amount of multi-tasking that occurs during proximate interactions (Kruger & Konner 2010). A combination of motes research and focal follows in future research would provide large, long-term and high-resolution data on childcare practices. Moreover, the present study only investigates direct care, while food provisioning is a major form of alloparenting in hunter-gatherers (Hill & Hurtado 2009). Thus, it is necessary to examine direct and indirect alloparenting to gain a complete picture of help with reproduction. For instance, it may be the case that one category of alloparent does not provide much childcare because they spend the most time foraging in order to help with provisioning; such patterns will only be discernible in studies that simultaneously examine direct and indirect helping.

Other questions that remain unanswered are whether alloparental experience gained as a subadult improves females' mothering abilities in later life, as suggested by the learning to mother hypothesis. This is a particularly difficult relationship to test since all subadult

females gain substantial experience in allomothering, perhaps because the selective pressure of learning to mother has now already equipped females with allomothering tendencies. Thus, there is little variation in whether female subadults practice childcare before rearing their own offspring. Additionally, it is difficult to measure mothering ability since child health and survival outcomes are influenced by many variables, therefore such a study would require large well controlled datasets. Finally, I have offered some preliminary insight in to the role of unrelated alloparents, more detailed examination into the quality of their care offers a promising avenue for future research.

7. Social Capital in Hunter Gatherers: Does egalitarianism translate to equality in resource access and fitness?

The publication based on this chapter can be found in appendix (publications).

7.1 Introduction

7.1.1 Context

In contrast to many non-human primate species and non-foraging human societies, which have clear pathways to inequality such as dominance hierarchies and resource storage/inheritance (Ellis 1995; Borgerhoff Mulder et al. 2009), simple hunter-gatherer groups do not accumulate resources and are also politically egalitarian (Woodburn 1982; Cashdan 1980). Thus, it is unclear how social structure can lead to inequality and fitness variance in this context, if at all.

As specified in the introduction, social capital refers to access to cooperation from other group members; where cooperative behaviours are those in which the actor incurs a cost and confers a benefit to the recipient (Nowak 2006). In hunter-gatherer groups, cooperation frequently occurs in the context of food sharing and childcare (Gurven 2004a; Crittenden & Marlowe 2008). In this chapter I examine whether differences in social capital may facilitate the emergence of inequality and fitness variance among hunter-gatherers. Thus, this analysis represents a large step in addressing a gap in the literature outlined in section 2.4—how do within-group differences in sociality affect fitness? It is necessary to specify that the term inequality is used purely in an economic sense pertaining to differences in material resource access. It is not referring to differences in social capital i.e. differences in the number of cooperative partners one has within the group. The aim of this chapter could in fact be

reframed as an investigation as to whether for the BaYaka social resources (social capital) can be converted into material resources and in turn create material inequality.

I begin by introducing the theory and evidence that explain why the social organisation of egalitarian hunter-gatherers differs from non-human primates and non-foraging human societies, and why inequality is less predictable in the former. Next I highlight the importance of cooperation in hunter-gatherer societies, paying particular attention to how contrasting models of food sharing practices are/are not conducive to inequality. I then present an analysis indicating that differences in social capital provide a mechanism for inequality and fitness variance to emerge and accrue. I finish by discussing the broader implications of these results for human social evolution, and highlighting promising avenues for future research.

In the broader scope of this thesis, having seen the importance and kin/reciprocity based nature of cooperation for the BaYaka, the logical question is whether certain individuals with better access to cooperation, i.e. more social capital, experience evolutionary advantages; this question is addressed in the present chapter.

7.1.2 Hunter-gatherers and the evolution of egalitarianism

In great ape and most non-foraging human societies there is clear resource inequality and social hierarchy, which have meaningful consequences for evolutionary fitness (Ellis 1995; Borgerhoff Mulder et al. 2009). In primates organised by dominance hierarchies, high ranking individuals can exploit subordinates and benefit from superior access to mates and food resources (see Ellis 1995 for review), and in turn achieve higher fitness. Broadly, in males, dominance has been associated with fitness via increased mating access, offspring survival, longevity, reproductive career length and harassment of others during copulation (Ellis 1995). Similarly, high ranking females benefit from increased fertility, offspring survival,

longevity, as well as earlier age at first reproduction and shorter inter-birth intervals (Ellis 1995). The pathways and extent to which high rank translates to increased reproductive success varies by species and socio-ecological context. Due to increased socio-cognitive complexity (see section 2.3.2), in many primate species the achievement of high rank is not simply dependent on physical superiority but also the availability of social support in competition for rank (Silk 2007). In fact, in some species of omnivorous cercopithecids ranks are heritable to some degree. For instance, among female baboons, macaques and vervets, mothers and close kin provide young females with coalitionary support to ensure their position in the hierarchy; thus the fitness benefits associated with dominance can accrue down matrilineal lines over multiple generations (Silk 2007).

Inequality and fitness variance are also rife in non-foraging human societies, where material resources and wealth can be stored, accumulated and inherited; thus, inequalities accrue and inflate over generations (Mulder et al. 2010; Betzig 2012). Similarly, social positions are often transmitted inter-generationally, further perpetuating the persistence of differences in resource access. From chiefdoms consisting of a few thousand people to nation states of millions, throughout history those individuals who inherited positions in the top strata have experienced disproportionate access to wealth. Subsequently they achieve higher fitness via a combination of increased access to mates, and a superior ability to successfully provide for larger families (Nettle & Pollet 2008). An extreme example comes from the Asian empires—Y-chromosome research estimates that ~40% of living Asian men may be descendants of just eleven powerful rulers from the last few thousand years (Balaesque et al. 2015).

Although social hierarchy and inequality were likely present in the *Pan-Homo* last common ancestor (PHLCA), and are evident in post-Neolithic human populations, one cannot assume this trend was uninterrupted in the millions of years between these two eras (Knauff et al. 1991). It has been proposed that the prevalence of hierarchy in fact follows a U-shape—

present in PHLCA and the last 10,000 years since the emergence of agriculture, but absent for the majority of *Homo sapiens*' history when our species lived as simple hunter-gatherers (Knauff et al. 1991). Simple hunter-gatherers have been characterised by the 'egalitarian syndrome', which refers to a political system where there is no tolerance of individual attempts to exert dominance or authority over others i.e. no social hierarchy (Boehm 1997; Erdal & Whiten 1994). Ethnographies of many extant African and Asian hunter-gatherers emphasise that any such attempts are rebottled with 'levelling mechanisms' by the rest of the band. These include ridicule, ostracism and can even escalate to execution (Whiten & Erdal 2012; Boehm et al. 1993). Such cultural innovations facilitate 'reverse hierarchy', where the majority act together to suppress the power of any one individual (Boehm et al. 1993); the ability to form these group-wide coalitions requires very sophisticated social cognition and may be unique to humans (Gavrilets et al. 2008).

Smaller coalition formation occurs in both chimpanzee males and bonobo females (Sommer et al. 2011), indicating that the cognitive antecedents required for egalitarian enforcement via levelling mechanisms and reverse hierarchy were likely present in the PHLCA (Whiten & Erdal 2012). This begs the questions as to why egalitarianism evolved in human evolutionary history, and is in stark contrast to the pronounced dominance hierarchies present in our closest relatives. The answer likely lies in the foraging niche occupied by our ancestors. Ellis (1995) asserts that there is an 'inverted U' association between resource availability and the payoffs to dominance. When resource availability is moderate, high ranked individuals can monopolise them; however, if resources are very easy to obtain and cannot be monopolised, then the benefit of high rank is reduced. At the other extreme, if resources are very difficult to acquire such that cooperation between multiple individuals is necessary, this reduces an individual's ability to exert dominance on fellow group members whom s/he is dependent upon. This latter scenario likely reflects the hunter-gatherer foraging niche, and explains why egalitarianism evolved in our species. As humans began to rely on large food packages of

game which were unpredictable to obtain, there was an increased dependence on food sharing between individuals to reduce acquisition risk (see section 7.1.3 for more detail). This mutual dependence resulted in an inability for any individuals to express dominance because it became too costly to exploit conspecifics who may retaliate via rejection/withholding cooperation (Boehm 1997; Whiten & Erdal 2012). Hence dominance hierarchies were eroded, and exploitation and resource monopolisation were no longer viable mechanisms for generating inequalities among hunter-gatherers.

Dominance hierarchies facilitate resource monopolisation by high ranking individuals over subordinates; and agricultural societies have the opportunity for resource storage and accumulation. Given that hunter-gatherer societies lack both of these features—they are egalitarian (lack resource monopolisation) and do not have storage systems (lack resource accumulation)—this raises the question of whether inequality can exist under these conditions. To answer this question, it is necessary to examine the nature of resource transfers amongst foragers.

7.1.3 Risk and food sharing in hunter-gatherers

As mentioned above, the foraging niche occupied by hunter-gatherers is characterised by uncertainty and acquisition risk. Kaplan et al. (2000) categorise food resources into three groups: collected (readily available from the environment e.g. fruit, grass); extracted (non-mobile nutrients embedded/hidden within the environment e.g. roots, nuts); and hunted (mobile organisms). Collected foods are substantially easier to acquire than extracted or hunted nutrients. However, the hunter-gatherer diet is primarily focussed on these latter two categories of rare but nutrient dense resources—only 8% of the diet is comprised of collected foods compared to 95% in chimpanzees (Kaplan et al. 2000). Hunted foods

constitute ~60% of calories in the average forager diet, yet are particularly hard to obtain (Kaplan et al. 2000). For example, Hiwi men from Venezuela only successfully acquire meat on 24% of days they forage, this proportion is 27% for the Kalahari Desert !Kung, and 21% for the Agta from the Philippines (Hill & Hurtado 2009; Hill & Kintigh 2009; Headland 1986). Therefore, these populations rely extensively on resource transfers to insure against the acquisition risk that is inherent with their diet. The Ache provide a striking illustration of the necessity of food sharing—it is estimated that without sharing, an average family would have access to less than 1000 calories per individual on 27% of days, whereas after accounting for food transfers this frequency is reduced to 3% (Kaplan et al. 1990).

Hunter-gatherer ethnographies frequently refer to the practise of 'demand-sharing' of food (e.g. Lewis 2002). This describes a system of transfer where producers of food do not selectively choose how much and with whom to share; instead, other camp members actively demand a share of the kill and force the hunter to redistribute it. Marlowe recounts that Hadza men requested to hide meat in his Land Rover in anticipation of the inevitable demands and harassment they would face if they were to bring it to camp (Marlowe 2004). The theory behind why this demand sharing is accepted by the hunter is known as the 'Tolerated Theft' model. It asserts that the effort any individual employs to contest for a portion of the kill will be a function of the marginal value that portion holds to them (Blurton Jones 1984; 1987). Given that there are diminishing marginal returns on food, after consuming a portion of the meat, the cost of defending resource for the hunter exceeds the marginal benefit of keeping the rest. This is because other individuals who have not yet had a share will value the meat highly and invest considerably in a contest for it. Therefore, producers are better off succumbing to the demands of their hungry campmates and sharing out the food. These norms of demand-sharing and an obligation to share when asked are embedded in the culture of foraging groups. Researchers note that in hunter-gatherer

societies such as the !Kung and Ache, accusations of being stingy or a non-giver are the most grave insults one can receive (Lee 1979; Gurven 2004a).

Gurven notes that in reality “cultural rules or expectations need not mesh with daily transactions” (Gurven 2004a, p550). Despite, a lot of ethnographic support and some quantitative evidence for the occurrence of demand sharing/tolerated theft (Lewis 2002; Peterson 1993), systematic analyses of food sharing practices suggests this model does not provide a full account of what is going on. In numerous hunter-gatherer societies individuals have been found to preferentially share with kin (e.g. Agta and Batek) or reciprocal partners (e.g. Aka and Hiwi) (Griffin 1982; Endicott 1988; Gurven 2004a; Gurven 2004b). An extreme case in point is the Lamelera whale hunters who are 122 times more likely to share food with related siblings than an unrelated individual; and 192 times more likely to share food with an individual who has previously shared food with them compared to someone who has not (Nolin 2010). This is what one would expect if there was some level of producer control, as sharing food with kin can indirectly increase the donor’s inclusive fitness since the recipient is genetically related (Hamilton 1964). Similarly, sharing with individuals whom one has long-standing reciprocal relationships with provides the donor with a future benefit when s/he is repaid by the recipient (Trivers 1971). This matches the practice of directed cooperative childcare found in the previous chapter.

The fundamental difference between the potential modes of resource transfer outlined here is the existence of absence of producer control. Under a demand sharing system, producers of food do not control who that food is transferred to but are deferent to the requests of other camp members. Conversely, under systems of kin selection and reciprocity, food producers actively choose to transfer resources to selected recipients. The reality of whether hunter-gatherer resource transfers are characterised by producer control has important implications for whether inequality can emerge, as I explain below.

7.1.4 The importance of social capital

Simple hunter-gatherers are egalitarian and lack the social hierarchy present in many non-human primate species and in post-Neolithic human societies; thus, there is no opportunity for resource monopolisation (Section 7.1.2). Additionally, they lack storage mechanisms found in other subsistence modes and industrialised populations, and so cannot accumulate resources. However, resource transfers are a fundamental practice in hunter-gatherer groups due to the risk inherent with a foraging niche focused on rare nutrient dense resources; and various different mechanisms are proposed to underlie food sharing, outlined in the previous section. These alternative mechanics have important implications for understanding whether inequality can exist in politically egalitarian hunter-gatherers. If there is no producer control and food is shared entirely based on demand sharing/tolerated theft, a relatively equal distribution of food is predicted. Conversely, provided there is some producer control, as indicated by most quantitative analyses which find food transfers are biased by reciprocity and kinship, inequality can emerge.

Certain individuals may have more access to cooperation from other group members (social capital), by either being more related to or forming more reciprocal cooperative alliances with fellow camp members; and subsequently may have better resource access as preferential recipients of food transfers. Cooperative relationships extend to other activities beyond food sharing, and cooperative childcare is a particularly prominent feature of hunter-gatherer populations (see chapter 6). Children spend a considerable proportion of their time being cared for and supervised by adults outside the household e.g. almost 25% of the time Hadza children are held is comprised of carers outside the nuclear family (Crittenden & Marlowe 2008). This cooperative childcare provides an extra avenue by which social capital can increase resource access, as it allows mothers to expend more time and energy foraging (Hurtado et al. 1992; Meehan et al. 2012). Thus, social capital may be extremely valuable to

foragers, increasing the likelihood that they are the recipient of resource transfers and also increasing their ability to produce resources themselves. Indeed, anthropologists have asserted that in a hunter-gatherer context widening one's social network may be particularly important (Bailey et al. 2014). However, no research has actually examined the extent of within-group differences in social capital, nor whether it may facilitate inequality or have meaningful implications for individual fitness. In section 2.4 I outline that evolutionary research into sociality at this lowest level, the effects of within-group differences in sociality, is scant; and thus a primary goal of this thesis is to examine such effects and their implications for our understanding of human social evolution.

7.2 Aims & rationale

1. Identify whether there is within-group variation in social capital

Despite considerable research highlighting the importance of cooperative activities such as food sharing and childcare in hunter-gatherer groups, there has been little attempt to quantify the extent to which inter-individual differences in access to these cooperative activities exist. Therefore, the first aim of this chapter is to discern for both sexes the presence/magnitude of inter-individual differences in social capital. I also assess whether any such differences can be explained by differences in genetic relatedness to the rest of the camp.

2. Examine whether differences in social capital translate to differences in resource access and the ability to buffer risk

If there is any element of producer control, one expects that resource transfers are likely to be biased by factors such as kinship and reciprocity, rather than more or less equally distributed as predicted by the tolerated theft model. Here I aim to discern whether those

individuals with more social capital actually have greater/more stable resource access in terms of the amount of food received and number of individuals from whom food is received. Additionally, I will examine whether this potential inequality in resource access is reflected in an association between social capital and body mass index (BMI), which is used as a proxy for nutritional status. It is worth acknowledging that whilst BMI data is a useful tool and easy to collect, it has some limitations as a proxy for nutritional status/health. For instance, BMI does not account for the composition of weight, i.e. fat versus muscle mass/visceral versus non-visceral fat, or differences in body shape (Ahima & Lazar 2013). Moreover, it has been found to be an unreliable indicator of cardiometabolic health (Tomiya et al. 2016).

3. Examine whether social capital increases fertility

Section 2.4.2 identifies associations between social relationships and components of individual fitness in non-human primates, however such analyses have not been conducted in human populations. Nutritional status has a large influence on fecundity (Roberto et al. 2008), therefore if social capital does indeed aid in buffering food risk and improving nutritional status, women may be able to reproduce at a faster rate and shorten inter-birth intervals. Therefore, I hypothesise that women with more social capital will have higher age-specific fertility.

4. Determine whether social capital is heritable

Positions in social hierarchies are partially or entirely heritable in some non-human primates and non-foraging societies. This heritability enables the inequalities and evolutionary advantages associated with rank to accrue and persist over multiple generations. The final aim of this chapter is to identify whether there is a heritable component to social capital, which may act in a similar way to rank positions in this egalitarian context.

Together the answers to these questions will help to determine whether individual level competition has been important in the evolution of human sociality i.e. whether those individuals with more social relationships in our evolutionary history had superior resource access and in turn higher reproductive success despite the likely egalitarian nature of ancestral societies.

7.3 Methods and analysis

7.3.1 Key variables

a) Social Capital—calculated by standardising the number of honey stick nominations ego received in the honey stick gift game by camp and sex.

b) Relatedness Score—Ego's total relatedness to camp is calculated by adding up genetic relatedness between ego and all other camp members. For instance, if ego has one sibling and one cousin in camp and is unrelated to all other camp members, his/her total relatedness would be $0.5 + 0.125 = 0.625$. Relatedness scores are attributed by standardising ego's total relatedness by camp and sex to match how social capital is calculated.

c) Rate of Food Received—the total number of meals ego receives from outside the household during the food transfer observations divided by the number of hours that ego was observed.

d) Number of Food Donors—the number of different households from which ego received food.

e) Body Mass Index (BMI)—calculated using the following formula: $\text{weight (kg)} / \text{height (m)}^2$.

f) Fertility—the total number of offspring ego has sired based on their reproductive history interview.

For full details on the honey stick gift game procedure, food transfer observations, height/weight measurements and reproductive history interviews see methods (chapter 5).

7.3.2 Analyses

1i. To determine the presence and extent of inter-individual variation in social capital, Kernel-Density distributions of the raw number of honey stick nominations received by an individual in the gift game are plotted. A separate distribution is constructed for each of the three camps in which the game was played, and for each camp distinct distributions are plotted for each sex.

ii. To discern whether there is any significant difference between the extent of male variation and female variation in social capital, Levene's tests are used to identify if there is more variance in the number of honey stick nominations received by either sex.

iii. To identify whether variation in social capital is purely a result of variation in genetic relatedness to the rest of the camp, linear regression is used. The response variable is social capital, and the predictor is relatedness score.

2. Multiple regression is used to analyse the effect of social capital on:

i. The amount of food ego receives. The response variable is 'Rate of food received', and the predictor is social capital; age, sex and camp are controlled for.

ii. The number of food donors ego receives food from (response). The predictor is social capital; age and sex are controlled for. Some individuals' food transfers were observed for 36 hours and others only for 24 hours, a dummy variable is used to control for this. Camp membership is not controlled for since it is strongly correlated with observation length, and therefore meaningful inferences about variation between camps is not possible.

iii. To test whether nutritional status is affected by social capital, I have regressed BMI over social capital. Separate regressions are run for each sex. Both regressions control for age-class. For women age classes are reproductive/post-reproductive, since there is a significant decline in BMI for the latter. For men, age classes are under/over 45 since there is a significant decline in BMI for the latter. Regressions also control for camp membership, since the data were collected from each camp at different points in time; thus, controlling for camp membership avoids any biases that may result from seasonal changes in BMI.

3. Multiple regression is used to identify if there is an association between social capital and age-specific fertility. The response variable is fertility i.e. number of live births, and the predictor is social capital; age and age² are used as controls since the majority of our sample have not yet completed their reproductive careers and fertility has a quadratic relationship with age.

4. To examine whether social capital is heritable, gamma correlations between ego's social capital and i. ego's father's/ ii. ego's mother's social capital are conducted using the *rococo* package in R. These correlations could only be conducted on a limited subset of the sample since most participants did not have a parent participating in the gift game. Gamma correlations were chosen since they are appropriate for small sample sizes and data with many ties.

7.4 Results

7.4.1 Social capital exhibits individual-level variation

Figure 7.1 shows the distributions of total number of honey sticks received by an individual in the honey stick gift game. It is clear that there is individual-level variation in number of gifts received for both sexes. The extent of male variation is particularly striking, producing

multi-modal distributions in all three camps, where certain men receive substantially more honey sticks than their peers. For instance, the most ‘popular’ man in Ibamba received 17 honey sticks compared to the male mean of 4.5; in Longa these figures were 9 and 2.6 respectively; and in Masia 8 and 2.8 respectively. Levene’s tests confirm a significantly larger variance in male compared to female social capital in two of the three camps (Table 7.1). The lack of significance in camp Masia is likely a result of the small sample that is concomitant with the camp size. Nevertheless, both sexes exhibit notable variation in social capital; therefore, if these relationships translate into differences in resource access, there is the potential for social capital to impact fitness.

It is noteworthy that the effect of individual differences in genetic relatedness to members of one’s camp is not a major predictor of number of gifts received ($\beta=0.19$, $p=0.067$). Although the result verges on statistical significance, it only explains a very small proportion of the variance in social capital ($R^2=0.036$). Therefore, individuals who are more genetically related to other camp members do not have significantly more social capital than their counterparts who have less kin in camp.

Table 7.1: For each camp the following are indicated: Number of men and women; the range in number of honey stick nominations for each sex; the test statistic (T) and p-value from Levene’s tests examining whether there are significant differences between the sexes in variance in number of nominations.

Camp	n	Range	T	p
Longa				
Men	22	0–9	5.55	0.023
Women	25	0–5		
Masia				
Men	11	0–8	2.62	0.123
Women	9	0–5		
Ibamba				
Men	11	0–17	7.41	0.011
Women	18	0–5		

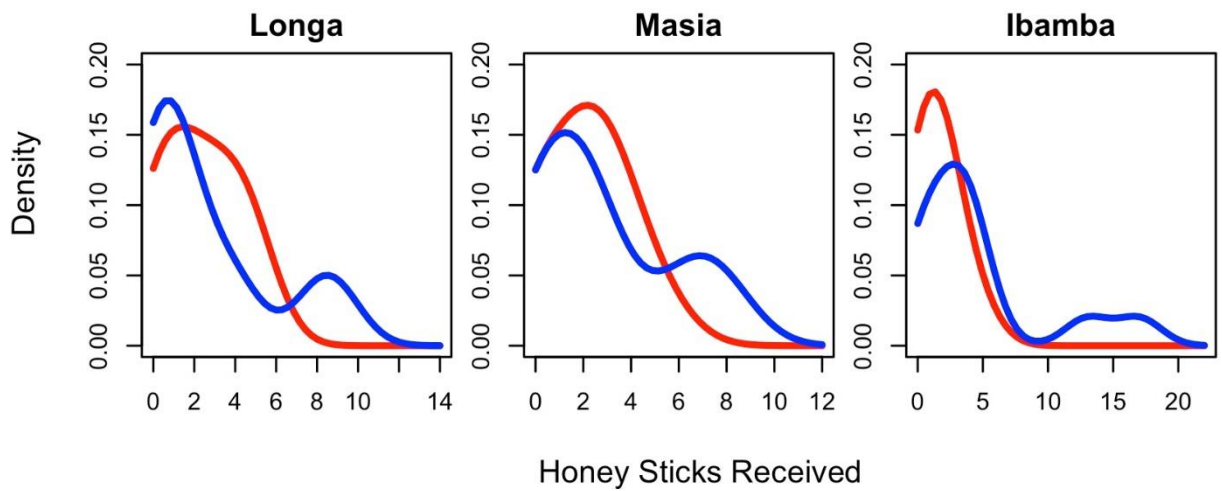


Figure 7.1: Kernel-Density distributions of the number of honey-stick nominations received per individual for men (blue) and women (red) in three Mbendjele camps.

7.4.2 Social capital provides advantages in buffering food risk

The average number of meals received by ego each hour from outside the household were 0.13, 0.17 and 0.21 in camps Ibamba, Longa and Masia respectively. This camp-level variation likely reflects slight differences in foraging strategy. In particular, meat constituted a significantly higher proportion of Masia’s production compared to the other camps. Given that meat has considerably larger sharing depth than other foods i.e. is shared more often (Gurven 2004a), it is unsurprising that Masia is the only camp with a ‘Rate of food received’ significantly different from the others.

Although there are significant differences between camps, social capital was not found to have a significant association with ‘Rate of food received’ ($\beta=0.02$, $p=0.511$, $n=69$; Table 7.2). However, there was a significant positive relationship between social capital and the number of different households from which an individual received food over the course of the food transfer observations ($\beta=0.24$, $p=0.005$, $n=53$; Table 7.3). Therefore, although individuals with more social capital may not always receive more food, they do receive food from a

larger pool of donors, which may be particularly important in times of scarcity. This advantage is indicated by the final set of results in this section—a significant positive association between social capital and BMI for both men ($\beta=0.53$; $p=0.032$; $n=39$), and women ($\beta=0.90$; $p=0.003$; $n=34$); with a larger effect for the latter (Figure 7.2). Table 7.4 presents the full results of these regressions.

Table 7.2: Effect of social capital on ‘Rate of Food Received’ (average number of meals received from outside the household each hour); $n=69$. A dummy variable is used to control for ego’s sex, where the reference category is female; and a continuous variable to control for age. Camp membership is also controlled for, and the reference camp is Ibamba.

Predictor	β	S.E.	p
Social Capital	0.010	0.016	0.511
Age	-0.001	0.001	0.187
Sex (Male)	-0.054	0.033	0.106
Camp (Longa)	0.044	0.038	0.254
Camp (Masia)	0.081	0.041	0.049

Table 7.3: Effect of social capital on number of food sharing donors from outside the household; $n=53$. Some individuals’ food transfers were observed for 36 hours and others only for 24 hours; therefore, the variable ‘36h Observation’ is a dummy variable used to control for whether ego’s food transfers were observed for 36 hours rather than the reference category of 24 hours. A dummy variable is also used to control for ego’s sex, where the reference category is female; and a continuous variable to control for age.

Predictor	β	S.E.	p
Social Capital	0.244	0.088	0.005
Age	-0.003	0.006	0.657
Sex (Male)	-0.189	0.182	0.297
Observation(36h)	0.894	0.223	0.000

Table 7.4: Effect of social capital on female ($n=39$)/male ($n=34$) BMI. Models control for whether an individual is post-reproductive (female)/over 45 (male) since there is a significant decline in BMI for these age-groups in our sample. Individuals over these age thresholds are denoted as part of ‘Age-Group 2’, compared to a reference category which includes individuals under these age thresholds. Both regressions also include camp membership as a control; the reference camp is Masia.

Predictor	Female BMI			Male BMI		
	β	S.E.	p	β	S.E.	p
Social Capital	0.90	0.28	0.003	0.53	0.24	0.032
Age-Group 2	-1.73	0.60	0.007	-1.45	0.54	0.011
Camp—Ibamba	0.78	0.73	0.292	1.60	0.66	0.021
Camp—Longa	1.07	0.75	0.162	-0.77	0.60	0.211

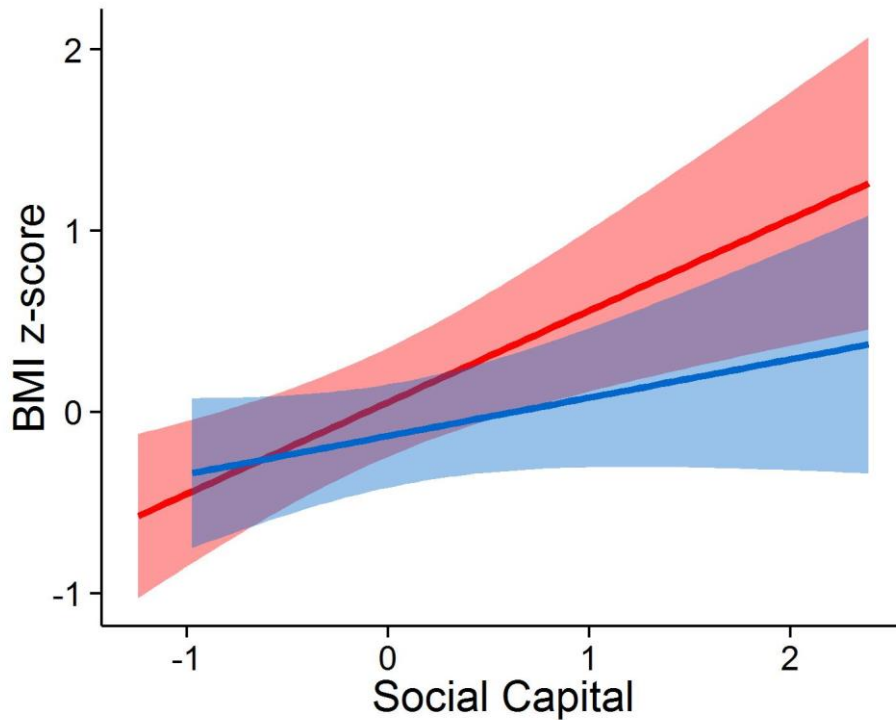


Figure 7.2: Social capital and BMI z-score (standardised by sex and age category—pre/post reproductive age for women and over/under 45 for men). Shaded bands indicate 95% confidence intervals. Males=blue, females=red.

7.4.3 Social capital is associated with higher fertility in women

Social capital is associated with significantly higher age-specific fertility in women ($\beta=0.19$; $p=0.010$; $n=49$) (Figure 7.3); the result is also positive for men, but not significant ($\beta =0.07$; $p=0.32$; $n=43$, full results in Table 7.5). The former significant association cannot be explained by reverse causality, whereby women with higher fertility had more offspring participating in the game and therefore higher social capital. Only a third (16/49) of the women included in the analysis actually had offspring playing the gift game; and of the 22 mother-offspring pairs in the game there was only one instance of an individual selecting their mother as the recipient of one of their honey stick nominations. An alternative reverse causality explanation may argue that participants preferably distribute their honey sticks to women who have more offspring since they may be in greater need. In this scenario, it is higher

female fertility which drives the number of honey sticks received. However, female participants were at different stages of their reproductive career and offspring of older participants may have already reached adulthood, thus a participant’s total fertility does not necessarily match their current number of dependent (under 16) offspring. We find no significant correlation between a woman’s current number of dependent offspring living in the household and social capital ($G=0.14$, $p=0.280$, $n=51$). This suggests in the initial association between social capital and age-specific fertility, social capital is affecting fertility rather than vice-versa.

Table 7.5: Effect of social capital on age-specific fertility for females ($n=49$) and males ($n=43$).

Predictor	Female Fertility			Male Fertility		
	β	S.E.	p	β	S.E.	p
Social Capital	0.187	0.073	0.010	0.069	0.070	0.321
Age	0.146	0.028	0.000	0.150	0.036	0.000
Age ²	-0.001	0.000	0.000	-0.001	0.000	0.003

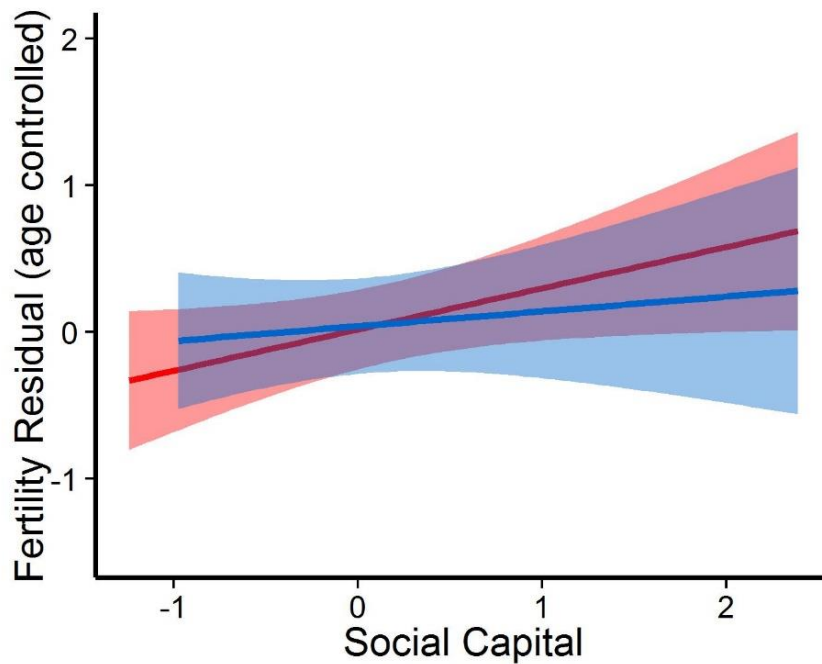


Figure 7.3: Social capital and age-specific fertility for men (blue), and women (red). Fertility Residual is calculated as the residual from the regression: $fertility \sim age + age^2$ i.e. a residual of -2 represents an individual who has had two fewer live births than would be predicted by their sex and age according to the specified regression. Shaded bands indicate 95% confidence intervals.

7.4.4 Social capital is partially heritable

The gamma correlations indicate that ego's (male or female) social capital as an adult is positively correlated with ego's father's ($G=0.65$, $p=0.002$; $n=14$), and ego's mother's ($G=0.17$, $p=0.294$; $n=26$) social capital (Figure 7.4); but these results are only significant for the former.

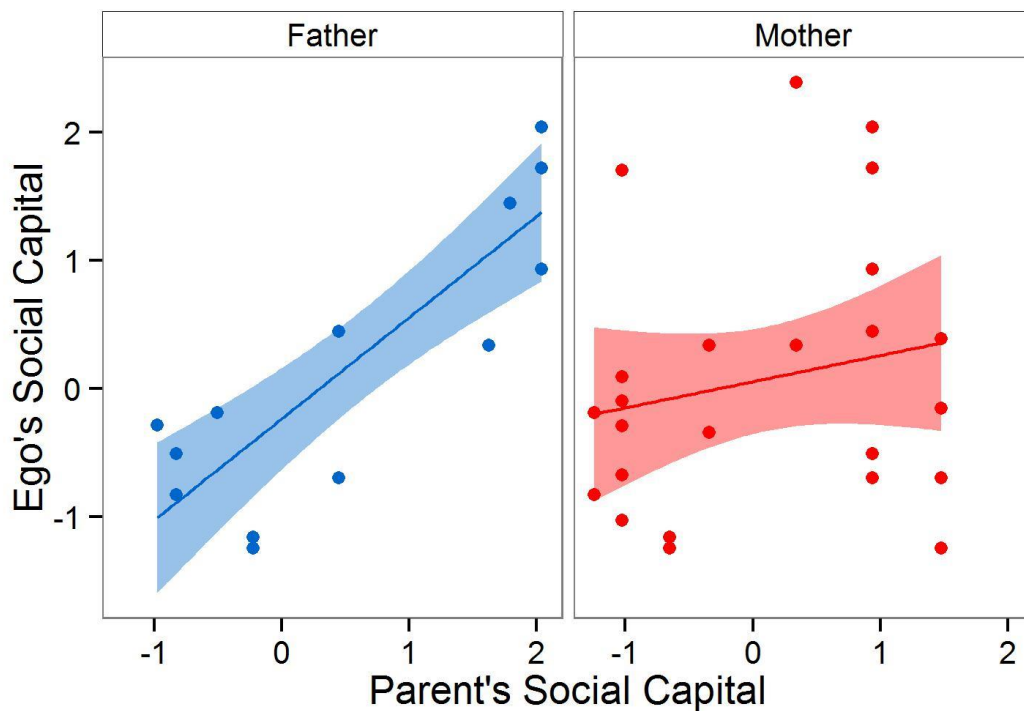


Figure 7.4: Relationship between ego's social capital and ego's father's (blue; $n=14$) and ego's mother's (red; $n=26$) social capital. Shaded bands indicate 95% confidence intervals.

7.5 Discussion

To review the results of this chapter, I find that social capital exhibits individual-level variation, and this variation appears to have meaningful implications for resource access and fitness. More specifically, those individuals with more social capital were not found to receive significantly more food, but did receive food from a greater number of households. I also find

that social capital is significantly associated with higher BMI for both sexes, and age-specific fertility in women. Finally, I find some evidence for the heritability of social capital—ego's social capital is significantly correlated with that of ego's father, but not ego's mother. Taken together, these findings have important implications for understanding whether inequality can emerge in an egalitarian hunter-gatherer context. Additionally, they offer a valuable contribution to our understanding of how within-group differences in social integration can affect fitness, a research question which has not received enough attention, particularly in our species. I will begin this section by attending to each result in more detail, and conclude by discussing the broader implications.

Individual variation in social capital

Like many African and Asian hunter-gatherers, the BaYaka are politically egalitarian and lack the social hierarchies found in many primates and non-foraging societies (Lewis 2002; Borgerhoff Mulder 2009). Attempts at authoritarian behaviour are rebottled with levelling mechanisms, and during my fieldwork the few such attempts I observed were simply made a joke of by other camp members. Although the absence of dominance relationships removes the ability for any individual to exploit another or monopolise resources, political egalitarianism does not necessarily prevent individuals from selectively choosing with whom to cooperate, nor does it impose an equitable distribution of resource transfers. Hunter-gatherers are notoriously cooperative, particularly when it comes to food sharing and childcare (Gurven 2004a; Crittenden & Marlowe 2008). Figure 7.1 provides a graphical demonstration of the fact that in all three BaYaka camps visited, certain individuals have more access to cooperation i.e. more social capital than others. This variation provides a necessary foundation for inequality; without dominance and the ability to exploit others, it is only through the voluntary cooperation of group members that one can improve resource access.

A trend which emerged consistently across all three camps, was larger variability in social capital among men compared to women; there are a few possible explanations for this. Firstly, because meat acquisition is much more unpredictable, it is shared more often and more widely than gathered foods (Gurven et al. 2002; 2004b). Therefore, since only men hunt, they may have more opportunity to form cooperative alliances via food sharing, explaining why those individuals at the tails of the social capital distributions are all men. Moreover, if food sharing is a primary means of developing alliances, the larger variation in male social capital is somewhat expected given that male hunting skill varies significantly more than female gathering efficiency (Gurven et al. 2002). Another possible explanation may lie in Mbendjele religion. A central aspect of Mbendjele life is the process of undergoing sex-specific initiation rites to gain membership to various religious cults. These cults have been highlighted to increase bonding and solidarity amongst their members (Lewis 2002). There are a greater number of male cults and more variation in membership to these among men, which in turn may lead to greater male variation in the ability to form same-sex alliances.

It is noteworthy that in camps Longa and Ibamba, the man who received the most/joint most number of honey sticks in the honey stick gift game was the *kombeti*, and in Masia there was no *kombeti* since the camp was recently established. *Kombeti* is a position of camp spokesperson, which in my experience is always held by a man. This position does not violate egalitarianism as it is appointed and does not hold any absolute authority, and definitions of egalitarianism often highlight that it does not preclude the presence of 'weak leaders'. Given that in two camps the *kombetis* contribute considerably to the extreme male variation in social capital, one may ascribe the greater male than female variation to the fact that this position is only held by men. However, *kombetis* are appointed based on social support (Lewis 2002); therefore, it is social capital that drives attainment of the position rather than vice versa.

Social capital, resource access and fertility

Having established that variation in social capital exists, the analyses indicate that this variation likely leads to differences in resource access and has implications for fitness. Although over the short observation periods systematic differences in 'Rate of food received' were not found, individuals with more social capital did receive food from a larger number of households. The primary benefit of food transfers is to provide insurance against nutritional shortfalls, which are concomitant with the risky foraging niche, and the principal ecological pressure faced by hunter-gatherers (Kaplan et al. 2000). Therefore, individuals with a larger pool of food donors are likely 'hedging their bets' more effectively, which is evidenced by their healthier BMI (Fig. 7.2). Thus, our results do not provide direct evidence for the presence of inequality and it appears that resource access may be fairly equal at times. However, the findings suggest that perhaps during periods of scarcity, those with more social capital may experience superior resource access and a more stable nutritional income.

To relate this to the discussion of food sharing, section 7.1.3 notes that different mechanisms are postulated to explain food transfers in hunter-gatherers. More specifically, if there is a demand sharing/tolerated theft system, inequality is unlikely to emerge. Conversely, under a system where some producer control exists and individuals can preferentially share food with kin or reciprocal partners, then those individuals with more social capital can actually gain an advantage in resource access. A meta-analysis of food sharing in 38 human and non-human primate groups highlights that reciprocal transfers are more prevalent in the BaYaka than any other group included in the study (Jaeggi & Gurven 2013). This finding corroborates the inferences made here that there is some level of producer control, and therefore social capital can result in inequality.

This potential inequality may have important implications for evolutionary fitness. Maintaining a healthy BMI is particularly important for women as low body weight disrupts ovulatory processes, and can cause secondary amenorrhea (Roberto et al. 2008). Thus, BMI may be the mediating factor explaining the observed positive association between social capital and age-specific fertility. The more social capital a woman has, the less likely she is to suffer nutritional deficits, low BMI and periods of anovulation; in turn she is able to effectively invest energy in reproduction and avoid excessively long inter-birth intervals. The same analysis did not find social capital to be a significant predictor of the number of offspring a man sires. I attend to this relationship in detail in the next chapter—it appears social capital may only benefit male fitness for those males with extremely high social capital since they have increased mating access (see chapter 8), whereas the result here indicates at moderate levels social capital provides no significant advantage for most men. If social capital has more consistent or larger effects on female than male fitness in hunter-gatherers, it follows that natural selection on social relationship formation/maintenance would have been more pronounced for women than men for most of our evolutionary history. Interestingly, in research on modern populations women are frequently reported to invest more in maintaining strong relationships with a larger number of individuals (Mysterud et al. 2006; Dyble et al. 2014).

These findings related to social capital and fertility must be treated with caution. The measure of social capital is a ‘snapshot’ collected at one particular point in time, whereas data on fertility reflect reproductive histories that span up to thirty years. Accepting any significant effects of the former on the latter relies on the assumption that the snapshot estimate of social capital is representative of an individual’s social capital throughout the course of their reproductive career. We do not find any significant correlation between social capital and age for either sex, which would certainly violate this assumption (men: $G=0.19$, $p=0.14$; women: $G=-0.02$, $p=0.85$). Nevertheless, it is still possible that an individual’s social

capital varies across time. Therefore, this result must be treated as preliminary until it is confirmed by research using methods such as risk ratio analysis which do not rely on the same assumption.

The inheritance of social capital

Finally, the results indicate that ego's social capital is significantly correlated with that of ego's father. The mechanism behind this partial heritability is not investigated here; however, there are a few possibilities. Firstly, one's ability to forge new alliances and maintain long term social ties may be a heritable trait in itself or mediated by heritable components of personality. An analysis of school friendship networks using a twin study design, found that 46% of the variation in frequency with which an individual is named as a friend can be accounted for by genetic factors (Fowler et al. 2009). Moreover, researchers have identified genetic polymorphisms mediating levels of social integration (Creswell et al. 2014). Alternatively, one's social capital may be determined by some independent skill such as foraging efficiency or traditional ecological knowledge; if these skills are inherited genetically or culturally by offspring then associations between parent and offspring social capital would arise. Finally, the inheritance may operate via the direct transmission of cooperative alliances from parents to offspring. This interpretation is most consistent with the results as it can explain the significant association with paternal but not maternal social capital. If relationships are transmitted inter-generationally, an individual's social capital would be more closely associated with the parent whose sex has higher variability in number of social relationships, in this case fathers.

Given the lack of formal hierarchy in politically egalitarian hunter-gatherers, there is no opportunity for the inheritance of social status observed in some non-human primate species and larger complex human societies (Silk 2007; Thomas & Mark 2013). However, in the same way that rank inheritance in these setting facilitates the accrual of fitness benefits within

family lineages over multiple generations, the partial heritability of social capital may act in a similar manner in an egalitarian setting. Rather than inheriting a rank that augments fitness via resource monopolisation, hunter-gatherers may inherit cooperative alliances which improve fitness by enhancing their ability to cope with their risky foraging niche.

Conclusion—broader implications and future directions

Taken together, the findings of this chapter indicate that certain individuals have more social capital than others, i.e. access to cooperation is not distributed equally within camps, and in turn are better able to buffer the food risk concomitant with hunting and gathering. For women, this even translates to higher fertility. Furthermore, due to the partial heritability of social capital these advantages in resource access and fertility can accrue over multiple generations. Thus, in egalitarian hunter-gatherers, which lack social hierarchy and resource accumulation, it is social capital that may explain documented patterns of fitness variance and fertility inheritance (Betzig 2012; Blum 2006).

As well as providing insight into the mechanisms behind inequality and fitness variance, the findings of this chapter offer a significant contribution to evolutionary research on sociality more generally. In Section 2.4 it is noted that research into the evolutionary implications of individual differences in sociality is scant and limited to a handful of taxa. Given that humans form very differentiated social relationships, relationships ranging from mere strangers to best friends, the effects of within-group differences in social integration are likely to be very pronounced. This is to my knowledge the first study examining these effects and providing empirical evidence for their importance.

Moreover, the results provide a valuable insight into the origins of human sociality. The widespread nature and extension of human sociality and cooperation beyond small kinship networks are considered defining characteristics of our species. Many researchers

emphasise the importance of inter-group competition in the evolution of these traits, whereby groups with cultural norms which were better able to promote widespread cooperation in largely unrelated groups outcompeted others (Boyd & Richerson 2009; see section 2.5.3). Our results do not undermine the possibility of selection between groups, but highlight that competition also occurs within groups, and individuals who were able to accumulate more social capital likely experienced evolutionary advantages. We find substantial inter-individual variability in social capital, which largely cannot be explained by kinship networks, and has meaningful consequences for health and fertility. Cooperation is an integral means by which hunter-gatherers deal with their unpredictable environment, and extends across many activities including childcare, foraging and food sharing (Meehan et al. 2013; Hill 2002; Gurven 2004a). In the same way that low-relatedness groups with a greater capability to harness cooperation performed well in warfare and resource competition, individuals within such groups who harnessed more cooperation may have had increased resilience against the unpredictable foraging niche typifying our species' origins. Thus, the extension of individuals' social networks may have been an important selection pressure and determinant of fitness in human evolutionary history, where those with more social capital had augmented survival and reproductive outcomes. Hence our results suggest competition within the group is a possible alternative mechanism that may have driven the extension of human sociality beyond small units of related individuals.

The work also offers insight into the ultimate reasons behind research findings from public health. Social isolation is consistently associated with a multitude of negative health outcomes such as increased risk of developing mental health illnesses, higher physiological stress and poorer recovery from a host of conditions, including myocardial infarction and stroke (Seeman 1996; House et al. 1988). Given that our findings suggest social capital may have been an important driver of individual fitness variance in human evolutionary history, one would expect natural selection to have equipped our species with physiological and

psychological mechanisms encouraging the formation and maintenance of social relationships. The listed health risks related to social isolation may be by-products of these reinforcement mechanisms, experienced by individuals who fail to socially integrate sufficiently. Interestingly, recent psychiatric research demonstrates that lack of social support has a greater impact on women's risk of developing clinical depression (Kendler & Gardner 2014); this is consistent with the finding that social capital has a larger effect of women than men's fitness.

Future directions

This chapter has also raised some important questions and avenues for future research. If social capital has been a fundamental force in human evolution, to further our understanding it is necessary to discern how it is attained in a hunter-gatherer context. Is alliance building a skill in its own right, and one that can be inherited; or is an individual's social capital related to some other capability such as foraging skill or traditional ecological knowledge? Additionally, future work with larger samples could offer a more definitive answer regarding the association between social capital and fertility. Rather than use age-specific fertility, a long-term variable which reflects the length of ego's reproductive career, risk-ratio methods could identify the effect of one's social capital on their current likelihood of reproducing. This analysis would be more appropriate since my measure of social capital reflects an individual's current social position, which may not necessarily match their social capital at previous times during their reproductive career.

8. Polygyny in Hunter-Gatherers—the role of social capital

The publication based on this chapter's analysis can be found in appendix (publications).

The publication based on this chapter's introduction can be found in appendix (publications).

8.1 Introduction

8.1.1 Context

Given the relative modernity of the Neolithic transition, deciphering the social structure and selective pressures experienced by hunter-gatherers is invaluable in understanding the suite of evolutionary adaptations possessed by humans today. One remaining question regarding human social structure is the evolution of marriage and mating systems, which have been demonstrated to have knock-on effects on parenting strategies and family dynamics, violence and crime rates, inheritance systems and marriage payments. This chapter is principally concerned with polygyny—where one man mates with/marries multiple women. Such a system is associated with decreased paternal care for offspring (Strassman 1981), increased male-male aggression (Schmitt and Rohde 2013), patrilineal inheritance systems (Hartung 1982), and brideprice marriage payments (Goody 1973). The socially imposed monogamy observed in many industrialised societies today is not representative of the majority of human populations. In fact, some form of polygamy is legal/generally accepted in over 70 countries worldwide (OECD 2010), and polygyny is estimated to be permitted in more than 80% of human societies (Murdock 1967). Therefore, it is still very relevant to our understanding of contemporary human behaviour.

Most research into the determinants and outcomes of polygyny has focused principally on non-foraging societies, which only reflect a short and recent stint of our species' evolutionary history. However, hunter-gatherer groups can offer additional insight into the

mating/marriage systems that characterise our past. In this chapter, I consider the case of the BaYaka who have a polygyny rate typical of extant foraging populations (Marlowe 2005), and examine how the determinants and outcomes of polygyny may vary in hunter-gatherer subsistence.

I will begin by providing some necessary theoretical background from evolutionary biology regarding the dynamics of sex differences in mating behaviour. Following this I will explain how these result in the emergence of different mating and marriage systems in particular ecological contexts, and under what conditions polygyny is likely to occur. I will then outline why hunter-gatherer polygyny poses a problem for current theoretical models. The analysis section of this chapter investigates the fitness outcomes and possible determinants of polygyny in a hunter-gatherer context, highlighting that it is still adaptive for men and may be achieved by those with high social capital. I finish by discussing the implications of these results for our understanding of human marriage practices.

In the broader perspective of this thesis, this chapter offers further insight into how within-group differences in sociality can affect access to mates and male fitness. Chapter 6 demonstrated that cooperation is important and directed towards kin and reciprocal partners in hunter-gatherers, using allocare as a case study. Following this, Chapter 7 demonstrated that given cooperation is directed, those individuals with more social capital actually benefit from improved health and fertility outcomes, and social capital is heritable. If social capital provides these important benefits, we might also expect it to play a fundamental role in marriage practices, the current chapter examines this proposition..

8.1.2 Sex differences in parental investment and female choice

Trivers defined parental investment as *'any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring'* (Trivers 1972, p. 139). These investments include energetic investments such as producing gametes, material investments such as provisioning an offspring with nutrients, and behavioural investments such as guarding offspring from predators. Males and females have different costs of reproduction, which begin with anisogamy—the fusion of two different gametes in sexual reproduction. The male sex cell is small and metabolically cheap to produce, whereas the female sex cell is larger and more costly. Usually the female is the sex, which invests more in the offspring given the initial sunk investment of the more costly sex cell (Trivers 1972). Conversely, the extent of male parental investment varies considerably between species, sometimes being limited to the contribution of sperm; e.g. in fish species with internal fertilization males do not participate in any brood care (Perrone & Zaret 1979); while in other cases male parental investment includes considerable provisioning and protection for extended periods of time, as observed in many bird species (Møller & Cuervo 2000).

Given that the male gamete is cheap and that it is usually females who invest more in offspring, males have a fast potential reproductive rate. Thus, the limiting factor of a male's reproductive success is access to opportunities to fertilise female sex cells. Hence, polygyny is advantageous to males since it increases these opportunities. On the contrary, female reproductive rates tend to be restricted by the production of costly sex cells and considerable investments in rearing offspring; hence, access to mates is not the primary limiting factor of female fitness (Clutton-Brock & Vincent 1991). Therefore, it is typically females who are the more choosy sex in terms of mate selection. This phenomenon is referred to as 'female choice' (Trivers 1972).

The traits valued by females of a particular species are largely determined by the necessity of male parental investment for the successful siring of offspring. Among species where this is low and unnecessary, females will predominantly select mates based on their genetic robustness (in terms of survival and reproduction prospects) and complementarity. Here, complementarity refers to the preference for genomes, which will produce healthy offspring when combined with one's own genome. For instance, among many species of *Drosophila*, females will favour males with more rare genotypes since this results in the production of offspring with more genetic diversity (Petit & Ehrman 1969). However, in other species where male parental investment is more pronounced and bi-parental investment is more crucial to offspring survival, alongside purely genetic characteristics, females consider the willingness and ability of a male to provide high quality investment (Trivers 1972). This preference explains the courting ritual where males offer females nuptial gifts as demonstrations of their willingness and ability to invest. Such behaviours are common in bird species (Lack 1940), and indeed in our own—the diamond engagement ring is an appropriate signal of a man's commitment to invest resources (Miller & Kanazawa 2007).

The preferences outlined here help to explain why different mating and marriage systems emerge across different species and socio-ecological conditions. This chapter is primarily concerned with the occurrence of polygynous marriage; therefore, in the following section I will describe how these tenants of female choice determine the contexts in which polygyny can or cannot evolve.

8.1.3 Explanations for polygyny

8.1.3.1 Polygyny with female choice

Male dominance and lek mating

In species where male parental investment is low or non-existent and female choice is based primarily on genetic quality, the occurrence of polygyny needs little explanation. In these cases, the majority of females are expected to mate with the few most genetically superior males, resulting in extreme biases in mating access and very skewed distributions of male reproductive success (Sherman 1999). Female mate selection in these contexts is usually guided by male-male interactions such as competitions for status or lek displays (Emlen & Oring 1977). Males aggregate and use costly signals, which cannot be faked, to display their quality and attract females (Zahavi 1975). The most well-known example of lekking comes from the plumage displays of peacocks, where males with more elaborate trains are preferentially selected as mates, since these trains are reliable indicators of the growth and survival prospects of a given male's offspring (Petrie 1994). Lek displays need not be visual, and can take numerous forms including chemical and vocal signals (Sherman 1999). For instance, male kakapo parrots from New Zealand engage in extravagant vocal rituals. They emit low-frequency 'booming' sounds that can be heard from a distance of up to 5km for 6–8 hours per night, this booming continues for up to three months at a time. Although, the males are not clustered in a lekking 'arena', since they are still in earshot of one another, the booming display is considered a form of 'exploded lek' (Morales et al. 2001). Females then approach and mate with selected males (Merton et al. 1984).

In lek systems, a very small minority of attractive males are responsible for the majority of copulations (Sherman 1999). Nevertheless, not all females will necessarily mate with the same one (genetically best) male, since their genomes may differentially compliment those

of available males. For instance, among house finches, although females generally prefer more ornamented males—those with more colourful breast patches—their preferences are not all identical as they also consider their specific genetic similarity with potential mates (Oh & Badyaev 2006).

The polygyny threshold model/resource-defense polygyny

It is outlined above that in numerous species, including our own, male parental investment exceeds the mere contribution of sperm. In many species fathers play an important role in provisioning their spouses and offspring with resources, or defending territories where resources can be acquired. Unlike lek systems, in these species females pay close attention to male provisioning ability when selecting a mate. This then begs the question, given the rule of female choice, why would a female ever choose to participate in a polygynous pairing where she would have to share the resources of her mate with other females he is paired with? For these taxa, an explanation for the occurrence of polygyny has been developed known as the '*polygyny threshold model*' (Orlans 1969). The central premise is that a female's evolutionary fitness is determined by the habitat quality/access to resources her mate can offer her. There is a level of inequality in males' resource holding such that a female will achieve higher biological fitness being paired as the second partner of a resource rich male than she would as the first partner of a resource poor male. This is because with sufficient inequality, a fraction of a rich male's resources, which are shared amongst multiple spouses, may be greater than the total sum of a poor male's resources. This level of inequality is the '*polygyny threshold*', and once it is surpassed polygyny is predicted to occur. Therefore, the polygyny threshold model predicts that the incidence of polygyny in a social group of any species where male parental investment is important, should be closely associated with the degree of stratification in male resource holding.

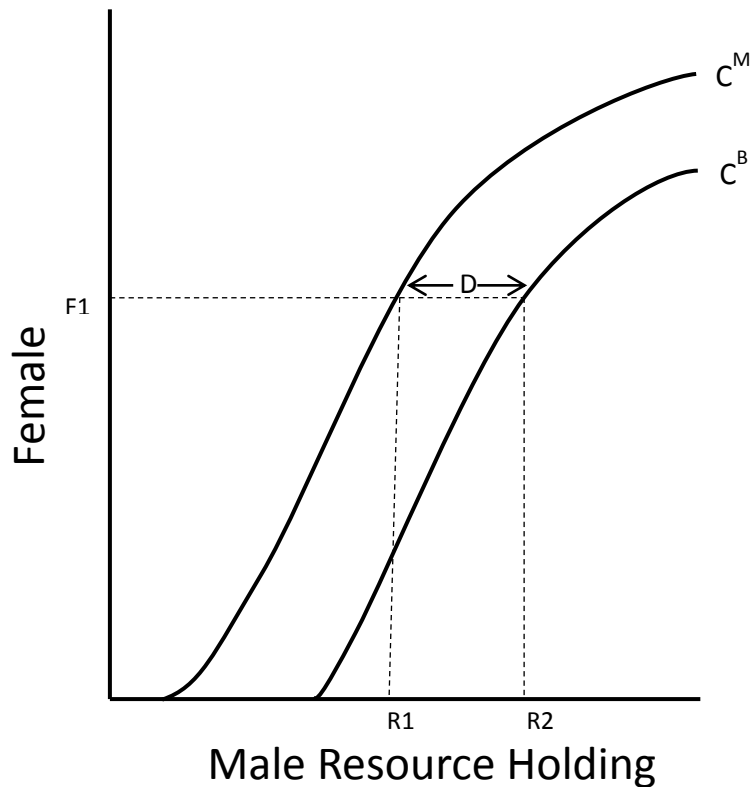


Figure 8.1: The polygyny threshold model, adapted from Orians 1969. C^M reflects the relationship between female fitness and resource holding of a male she is monogamously paired with, whereas C^B is the relationship between female fitness and the resource holding of a male she is bigamously mated with. D is the polygyny threshold. Full explanation, using $R1$, $R2$ and $F1$ is below in main text.

Figure 8.1 provides a graphical representation of the polygyny threshold model. The curves reflect the relationship between a male's resource holding and the fitness of a female pairing with him a) monogamously (C^M), or b) bigamously (C^B). For any given level of male resource holding, curve C^B is lower than curve C^M because resources must be shared if a female is paired to a male bigamously, and in turn her fitness is lower than if she was monogamously paired with him and had exclusive access to his resources. However, for any level of resources provided by an unpaired male, there is a corresponding higher level of resources provided by an already paired male which would result in a given female achieving the same fitness. For instance, a female would achieve the same fitness ($F1$) being paired monogamously to a male with resource holding $R1$ as she would being paired bigamously with a male with resource holding $R2$. D is the minimum level of inequality in male resource

holding necessary for females to achieve the same fitness via bigamous mating as monogamous mating—the polygyny threshold.

There are many examples in the animal kingdom where the polygyny threshold/resource-defense polygyny occurs. An extreme example comes from a bird—the orange-rumped honeyguide—for whom beeswax is a vital nutritional resource, and only a small minority of males control territories with scarce bee nests. Females are keen to gain access to these territories in order to feed on the bees wax. Thus, these males are able to copulate with many sexually receptive females within the valuable territories they control. Conversely, non-territorial males have negligible reproductive opportunities resulting in extreme skew in male mating access and reproductive success (Cronin & Sherman 1976).

8.1.3.2 Polygyny without female choice

Mate-defense polygyny

In contrast to the polygyny threshold model/resource-defense polygyny, '*mate-defense polygyny*' occurs when males defend females directly, rather than defending resources valued by them (Emlen & Oring 1977). This form of polygyny is most likely to occur when females are spatially clumped, and in turn more defensible. Dominant males are then able to aggressively exclude conspecifics from access to females, and form harem units in which they monopolise mating opportunities. For instance, female pinnipeds often form large aggregations due to a paucity of suitable parturition sites, enabling dominant bulls to monopolise copulations with large harems of cows (Bartholomew 1970). Harem formation can be a more active process and does not necessarily require females to form dense aggregations; in the case of Hamadryas baboons, males actually kidnap and herd females into defensible harem groupings (Maestriperi et al. 2007).

8.1.4 Homo sapiens, hunter-gatherers and polygyny

Narrowing the focus to humans, compared to the rest of the mammalian class our species are somewhat of an anomaly since in approximately 95% of mammalian species male parental investment is very limited (Geary 2000). In contrast, whether it is manifested in the form of hunting for the next meal or paying tuition fees, paternal investment is ubiquitous and extensive across much of the spectrum of human societies. This high male parental investment can be attributed to a combination of two factors—the restricted reproductive rate of women and the highly dependent nature of human children.

Due to the nine month internal gestation period and the subsequent phase of lactational amenorrhea, women are very limited in the quantity of offspring they can produce over the course of their reproductive career. Additionally, the narrow female pelvic canal designed for bipedalism combined with strong selection for encephalization has resulted in the '*obstetric dilemma*', where human children are being born altricial with a substantial proportion of brain growth having to occur post-partum (Rosenberg & Trevathan 2002). Thus children have an extended period of dependence, requiring extensive provisioning to support their metabolically expensive development (Kaplan et al. 2000). Therefore, women have been strongly selected to show mate preferences for men who demonstrate a capacity for high male parental investment, and who can provide resources to maximise the quality of the limited quantity of (highly dependent) offspring they can produce. In a study of 37 cultures across six continents, Buss (1989) showed that women consistently place high value on cues of male resource holding potential. Given this preference for resources in mate choice, and provided the norm of female choice is not violated, theoretically the polygyny threshold model should be applicable to predict when polygyny will emerge in human populations. Specifically, the prevalence of polygyny should increase with male resource inequality.

The polygyny threshold model predictions have been applied successfully both between and within human populations. As predicted, societies with substantial stratification of male wealth have higher rates of polygyny. For example, a study of Native American societies demonstrated a positive association between polygyny prevalence and the extent to which males within that society could control and monopolise resources (Sellen & Hruschka 2004). This trend has also applied at the macro level of nation states. Schmitt and Rohde (2013) calculated a '*Human Polygyny Index*' (HPI) for 38 nation states based on the number of sexual partners reported by men and women, and find a strong positive association between a nation's HPI and their index of income inequality (GINI index). Additionally, within societies with sufficient inequality, as predicted by the polygyny threshold model, it is the resource rich males who achieve polygyny. For instance, in Uganda, which is highly dependent on agriculture, ownership of land is a strong predictor of a man's likelihood of having more than one wife (Pollett & Nettle 2009). Nettle and Pollett (2008) also analysed selection gradients of wealth in 11 societies, and found strikingly high positive selection on male wealth in the two polygynous societies from their sample; providing further evidence that it is indeed resource rich males who experience the fitness benefits of polygyny.

The polygyny threshold model has been the most widely applied model of polygyny to our species because of the importance women place on resources when choosing a mate; however, in certain socio-ecological contexts this preference is attenuated and so other models are more applicable. A case in point is horticulturalist societies, which actually have the highest polygyny rates of any subsistence mode despite the fact that there is little variation in male wealth (Marlowe 2000). Clearly, these observations cannot be explained using the polygyny threshold model. Instead, Marlowe suggests this form of polygyny more closely approximates the 'mate-defense' model, and in these societies men compete amongst themselves for status and monopolisation of women (Marlowe 2000).

Despite the successful application of existing theoretical models of polygyny, these models are based on assumptions that may not be valid in the hunter-gatherer context that represents the majority human evolutionary history. Given that simple hunter-gatherers do not accumulate resources, the occurrence of polygyny cannot be directly explained by the polygyny threshold model. Nor can it be explained by the mate-defense model since these groups are egalitarian and lack hierarchy; therefore there are no dominant males who can monopolise groups of women and use aggression to exclude other men from mating access. Yet according to cross-cultural research polygyny is prevalent at a low–moderate rate of approximately 14% in extant hunter-gatherer groups (Marlowe 2005); this estimate refers to the percentage of married males who are polygynously paired. This level of polygyny is modest, nevertheless it still has meaningful evolutionary implications and cannot be readily explained by existing models.

Although differences in male reproductive success have already been explored in some foraging populations, these studies have focused on the relationship between hunting skill and variation in frequency of extra-marital affairs i.e. polygynous mating (see Gurven & von Rueden 2006 for review). However, the occurrence of contemporaneous legitimate partnerships between multiple women and one man, i.e. polygynous marriage, within a hunter–gatherer context, remains largely unexplored. In contrast to extra-marital affairs, women engaging in polygynous marriages are incurring the substantial cost of sharing a provider for themselves and their offspring. It is for this reason that polygynous marriage is a particularly interesting phenomenon. This chapter seeks to provide some preliminary insight into the determinants and outcomes of polygynous marriage in a hunter-gatherer context. Herein, the use of the term polygyny refers specifically to marriage practices, and excludes the practices of extra-marital affairs unless explicitly stated.

8.2 Aims & rationale

1. Investigate whether polygynous marriage increases male fitness in a hunter-gatherer context.

Although previous anthropological research consistently finds that polygynously married men achieve higher reproductive success, these findings are derived from societies that accumulate wealth, and thus some wealthy men are able to afford multiple families (e.g. Betzig 1992). Given the lack of material resource storage in hunter-gatherer subsistence, polygynous men may be inadequately equipped to support multiple families. Therefore, here polygynous marriage could instead represent a maladaptive behaviour resulting in increased offspring mortality and lower fitness. To address this, we test how marital status affects a man's age-specific fertility and more importantly, number of living offspring.

It is worth clarifying here that polygynous marriage differs from serial marriages in two major ways, both of which are likely to interact with the consequences for fitness of all parties involved. Firstly, men married polygynously have a higher reproductive rate since they are regularly mating with more than one woman. This is not the case for men who engage in serial non-simultaneous marriages, whose reproductive rate will be more or less the same as purely monogamous men. Secondly, polygynous men are acting as a parent for children from multiple spouses. Conversely, BaYaka men who have switched spouses often withdraw all investment from children born to their previous spouse, and redirect such investment to those being raised with their current spouse. This is likely because paternal investment requires paternal presence since hunter-gatherer men do not accumulate resources over time which can then be transferred in space. Therefore, once a man has left a spouse and no longer lives with her, he also no longer spends time in the physical presence of offspring sired with her; hence his paternal investment is limited to offspring sired with his new spouse.

2. Identify alternative mechanisms that may explain the occurrence of polygyny via female choice in hunter-gatherers.

We explore mechanisms that could facilitate the achievement of polygyny by a few hunter-gatherer men. Women may engage in polygynous marriages because certain men are of a sufficiently high quality that the fitness benefits outweigh the costs of marrying an already married man. Here quality refers to any attributes possessed by a man that ultimately result in increased fitness for a woman marrying him. We investigate whether polygynous BaYaka men differ in quality from their non-polygynous counterparts across two dimensions—phenotypic quality measured by physical attributes of height and hand-grip strength, and social capital quality determined by economic gift games. Phenotypic quality may increase a man's mate value as it reflects genetic quality, which will be inherited by his offspring, thus increasing their viability in a strenuous environment with high mortality risk (Gangestad & Buss 1993). Previous studies have mixed results; however, researchers have found positive associations between number of marriages (including serial marriages) and height in Baka Pygmies from Cameroon (Becker et al. 2012), and strength in the Hadza (Apicella 2014). Alternatively, in the absence of material wealth, social capital may be the resource that enables certain men to afford multiple families. Anthropologists have highlighted the importance of wide social networks to buffer risk associated with hunter-gatherer subsistence (Bailey et al. 2014); and the previous chapter presents empirical evidence for this. Therefore, men with high social capital may be preferred marriage partners for women and the only individuals who can effectively support multiple families.

3. Identify whether females whose husbands are married polygynously achieve lower fitness than those who are monogamously married to their husbands.

A woman's evolutionary fitness is determined by both her fertility and offspring survival. There is some research indicating that polygyny can be detrimental to both of these

components of female fitness, and thus cannot be explained as an adaptive female choice. The polygyny-fertility hypothesis refers to the occurrence of lower fertility among polygynously married women compared to their monogamous counterparts, which is most likely caused by reduced coital frequency (Bean & Mineau 1986). In a review of 86 studies, 64 found evidence for the polygyny-fertility hypothesis (Josephson 2000). Moreover, the offspring of women married polygynously may also incur increased mortality risk since they have access to a smaller proportion of their father's parental investment. The results concerning offspring mortality are inconsistent and vary cross-culturally. For instance a study using demographic and health surveys from Ghana found that children whose fathers are married polygynously experience higher childhood mortality (Gyimah 2009); conversely, among the agro-pastoralist Kipsigis from Kenya, there is no significant effect of marital status on offspring survivorship (Borgerhoff Mulder 1989). Therefore, in this chapter I also aim to identify whether being married polygynously is adaptive for females, or whether these women achieve lower fitness than their monogamously married counter-parts.

8.3 Methods and analyses

8.3.1 Key variables

a) Marital status (polygynous vs monogamous) —during reproductive histories, participants were asked to list all their spouses. If a man listed more than one spouse, he was asked 'when you married the second woman had you already finished your relationship with the first woman or did you continue with both women at the same time?' If the answer to this question was yes, men were coded as polygynous. Information on whether men were polygynous at the time of data collection was not collected. Therefore, I do not distinguish between men who were previously (temporarily) polygynous and those who still are; I refer

back to this limitation in the discussion. An important distinction that is made, is between polygynous men and serially monogamous men—I have outlined the evolutionary significance of this distinction in the previous section (8.2).

b) Husband's marital status (polygynous vs monogamous) —this is a dummy variable representing female participants and refers to whether their husband has ever been married polygynously.

c) Social capital—this is calculated by standardising the number of honey stick nominations ego received in the honey stick gift game by camp and sex.

d) Hand-grip strength—participants squeezed a manual dynamometer three times with each hand, the top score of the six attempts are used in this analysis.

e) Height

f) Fertility—the total number of offspring ego has sired according to their reproductive history interview.

g) Living offspring—the number of ego's offspring who were alive at the time of data collection.

For full details on reproductive history interviews, the honey stick gift game procedure, height/hand-grip measurements see methods (chapter 5).

8.3.2 Analysis

1. To test the effect of marital status on male fertility and reproductive success I use multiple regression:

i. The response variable is fertility. Marital status (polygynous) is a dummy variable predictor and age and age² are used as controls since the majority of our sample have not yet completed their reproductive careers and fertility has a quadratic relationship with age.

ii. The response variable is living offspring. Marital status (polygynous) is a dummy variable predictor. Due to the more complex relationship between age and number of living offspring we modelled this relationship separately and found that a 3rd order polynomial regression provides the best fit. Therefore age, age² and age³ are used as controls.

2. To determine whether phenotypic quality/social capital explains why certain men are polygynous I conduct one-way randomisation tests with 9999 Monte Carlo re-samplings comparing polygynous and non-polygynous men across these dimensions. For phenotypic quality, I compare their height and hand-grip strength. Social capital is measured as stated above.

3. To identify whether women whose husbands have been married polygynously achieve lower fitness I use two multiple regressions:

i. The response variable is fertility. Husband's marital status (polygynous) is a dummy variable predictor and age and age² are used as controls since the majority of our sample have not yet completed their reproductive careers and fertility has a quadratic relationship with age.

ii. The response variable is living offspring. Husband's marital status (polygynous) is a dummy variable predictor. Due to the more complex relationship between age and number of living offspring we modelled this relationship separately and found that a 3rd order polynomial regression provides the best fit. Therefore age, age² and age³ are used as controls.

8.4 Results

8.4.1 Men in polygynous marriages have higher reproductive success

14% (10/70) of men in the sample are/have ever been married polygynously. This is a rate of men who achieve polygyny in their lifetime, which may overstate polygyny prevalence as compared to other ‘snapshot’ estimates. Conventional snapshot estimates calculate the proportion of men married polygynously at one specific point in time. However, comparably high levels have been found in other BaYaka Pygmy groups using the snapshot method e.g. Central African Republic Aka (Hewlett 1988). Such estimates are considerably higher than most well-studied hunter-gatherer groups e.g. 4% in Ache; 6% in Kung (Schmitt & Rohde 2013), but are probably more representative of foraging societies on the whole, which have a mean male polygyny rate of approximately 14% (Marlowe 2005).

From informal discussions with some men, I did receive the impression that polygynous marriages were more likely to break down. Nevertheless, even if some men coded as polygynous only had a period of overlapping reproduction with multiple women which did not persist throughout their reproductive career, our results demonstrate that our sample of polygynous men do sire significantly more offspring and reproduce at a faster rate. Additionally, polygynous men have more living offspring for their age indicating that polygyny is still adaptive to men in a hunter-gatherer context despite speculated increases in offspring mortality risk (see Table 8.1/ Fig. 8.2).

Table 8.1: Effect of male marital status on male i) fertility and ii) living offspring. Age and age² are used as controls in i, and age³ is also included in ii since these controls best model the relationship between age and fertility/living offspring. The predictor polygynous is a dummy variable, with reference category monogamous.

n=70 (10 polygynous)		Fertility			Living Offspring		
Predictor	β	S.E.	p	β	S.E.	p	
Polygynous	0.446	0.136	0.001	0.458	0.167	0.006	
Age	0.149	0.027	0.000	0.549	0.155	0.000	
Age ²	-0.001	0.000	0.000	-0.010	0.003	0.002	
Age ³	-	-	-	0.000	0.000	0.004	

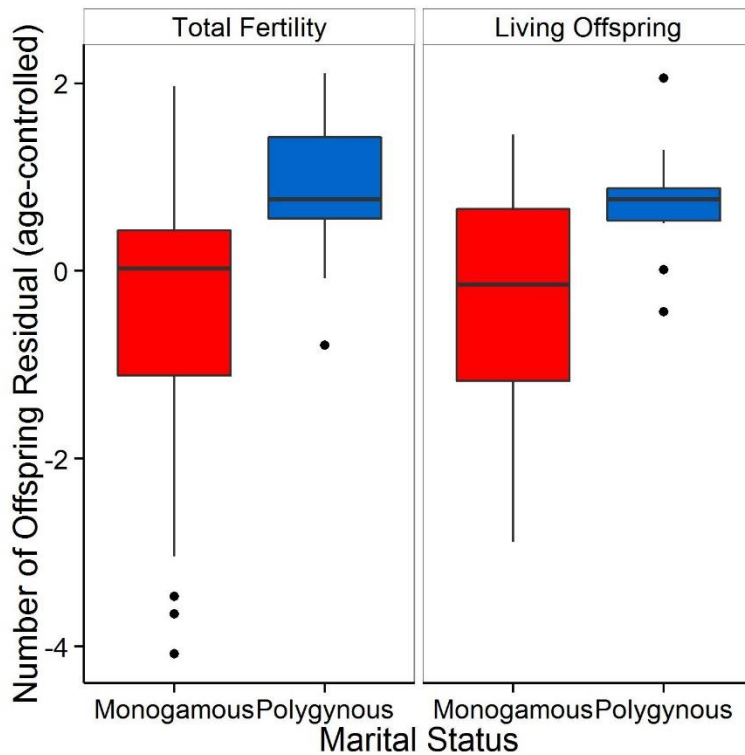


Figure 8.2: Marital status and fertility/number of living offspring (n=70, 10 polygynous). The y-axis variable (Fertility Residual) is calculated as the residual from the regressions in Table 7.1 i.e. a residual of -2 represents an individual who has had two fewer live births/living offspring than would be predicted by their age according to the specified regression. Circles represent outliers.

8.4.2 Social capital but not phenotypic quality is associated with polygyny

Our results do not provide support for the hypothesis that men who achieve polygyny are of higher phenotypic quality. Polygynous men in our sample are slightly taller and stronger than non-polygynous men but these results are marginal and do not approach statistical significance (see Table 8.2).

However, polygynous men do have significantly more social capital than non-polygynous men ($p=0.034$) (see Fig. 8.3/Table 8.2). In two of the three camps where the gift game was played, the individual with the highest number of gifts was polygynous. Both of these men were the *kombetis* (an appointed spokesperson for a camp) of their respective camps. In Longa, this individual received 9 honey sticks compared to a camp male average of 2.6;

similarly, in Ibamba these figures are 17 and 4.5 respectively. It is also noteworthy that in Ibamba there were three polygynous men, who ranked first, third and fourth in popularity out of the 12 men in that camp.

Table 8.2: Phenotypic quality and social capital of polygynous and non-polygynous men. Sample sizes are indicated, the first value is total sample size, and the value in parenthesis refers to the number of polygynous men in the sample.

Attribute	n	mean (polygynous)	mean (non-polygynous)	Z	p
Height (cm)	66 (10)	155.7	154.6	-0.500	0.616
Hand-Grip	62 (10)	46.6	45.7	-0.174	0.871
Social Capital	45 (5)	0.888	-0.105	-2.124	0.027

Table 8.3: Effect of husband's marital status on female i) fertility an ii) living offspring. Age an age² are used as controls in i, and age³ is also included in ii since these controls best model the relationship between age and fertility/living offspring. The predictor polygynous husband is a dummy variable, with reference category monogamous husband.

Predictor	Fertility			Living Offspring		
	β	S.E.	p	β	S.E.	p
Polygynous Husband	0.130	0.144	0.369	0.142	0.520	0.785
Age	0.134	0.021	0.000	1.020	0.214	0.000
Age ²	-0.001	0.000	0.000	-0.020	0.005	0.000
Age ³	-	-	-	0.0001	0.000	0.000

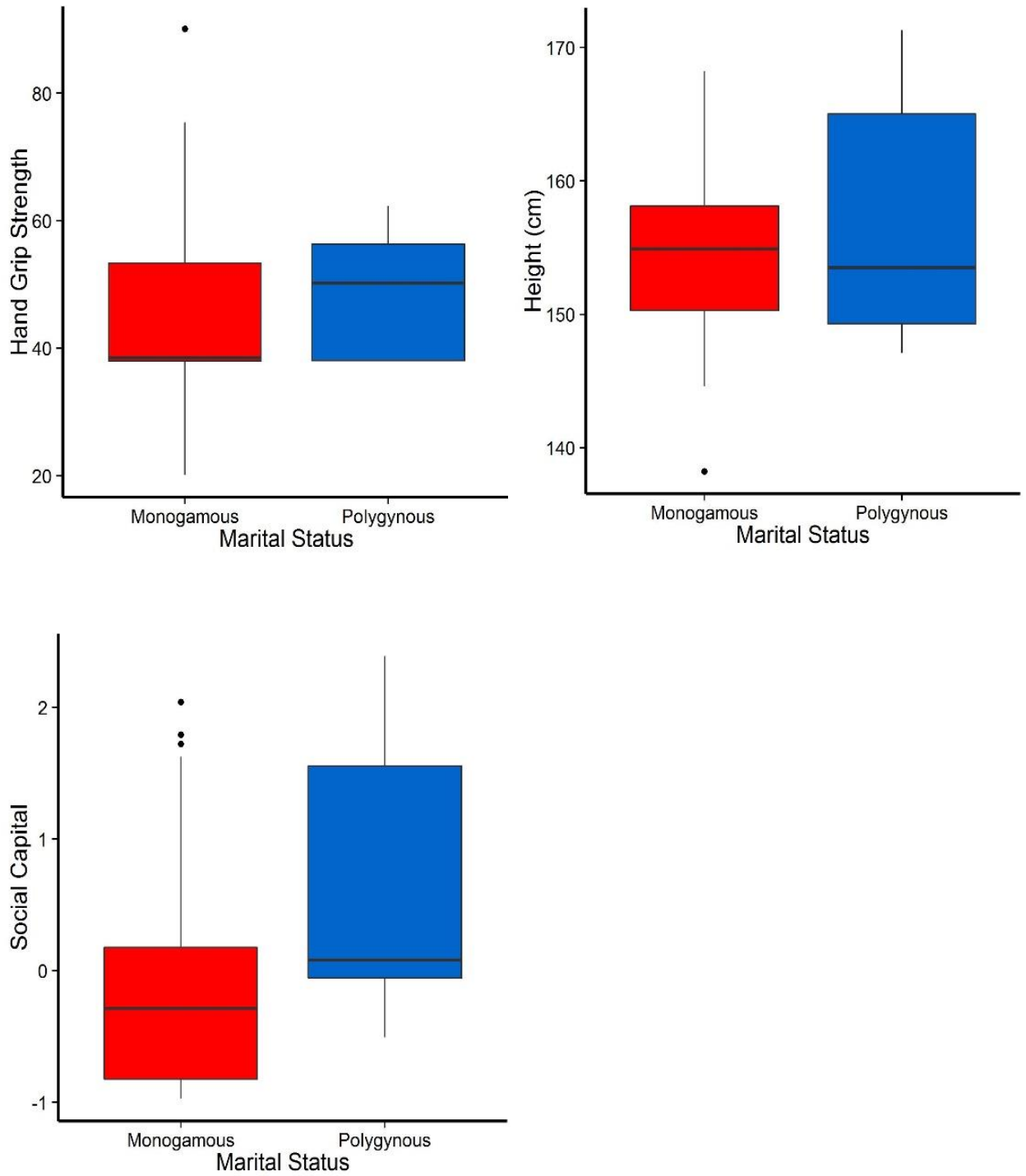


Figure 8.3: Social capital/height/hand-grip strength of polygynous and non-polygynous men. Circles represent outliers, horizontal lines represent medians. A significant difference is only present for social capital.

8.4.3 Polygyny is not detrimental to female fitness

The results from Table 8.3 indicate that there is no significant difference between the age-specific fertility or number of living offspring of women paired to polygynous versus monogamous men. These results are consistent with the idea that polygyny may be an adaptive female choice optimum for fitness, indeed the coefficients for polygynously married women are actually positive, but do not reach significance.

8.5 Discussion

Due to the restricted quantity of offspring a woman can produce over the course of her reproductive career, and the highly dependent nature of human children, a primary determinant of women's fitness is the access to resources their mates can provide for them and their offspring. For this reason, the polygyny threshold model successfully predicts the prevalence of polygyny in many human populations, and the incidence of polygyny within a society is strongly associated with the level of inequality in male resource holding (Schmitt & Rohde 2013; Sellen & Hruschka 2004). This raises the question of whether polygyny was even possible before the Neolithic transition prior to the accumulation of material resources, and whether human origins are strictly (serially) monogamous. Here we present a preliminary insight in to this question by exploring both whether polygynous marriage is actually beneficial to men/women in a hunter-gatherer context, and how certain men achieve polygyny without material wealth. I find polygynous men have greater reproductive success; my measures of social capital but not phenotypic quality explain which men achieve polygyny; and women married to polygynous men do not incur net fitness costs.

It is possible that polygynous marriage is a recent maladaptation amongst BaYaka men copying neighbouring Bantu farmer groups, in which polygyny is more frequent. Unlike

farmer groups, hunter-gatherers do not store and accumulate resources, hence polygynous men may not be equipped to effectively support larger families. However, even if higher rates of polygyny are new to the BaYaka Pygmies, they do not seem to be maladaptive for men. Polygynous men do not only sire more offspring, but also have more living offspring for their age. These results demonstrate that in spite of the lack of resource accumulation, polygyny enhances male reproductive success; and any potential costs to male fitness, such as increases in offspring mortality that result from the wider division of paternal investment, are offset by enhanced fertility.

With respect to the determinants of which men achieve polygyny, we assessed the importance of phenotypic quality and social capital since there are reasonable hypotheses for why these traits would be valued by hunter-gatherer women.

Strength and height have been frequently found to increase male attractiveness since they are signals of genetic quality (Lassek & Gaulin 2009; Lynn & Shurgot 1984; Dunbar et al. 2000). In environments of high pathogen stress, such as those experienced by the BaYaka, women may place particular value on genetic quality to increase the viability of their offspring (Gangestad & Buss 1993; Ember et al. 2007). Additionally, in contexts where male provisioning is less important, women shift mate selection strategies away from 'resource shopping' towards 'gene shopping' (Marlowe 2003); and male signalling of genetic quality becomes more fundamental in mating dynamics (Kokko 1998). In contrast to a more typical pattern amongst hunter-gatherer groups where the majority of provisioning comes from men's hunting production (Kaplan et al. 2000), amongst BaYaka Pygmies (Aka) from Central African Republic male and female contribution to subsistence is roughly equal in terms of calories (Hewlett 1993). Therefore, we might expect BaYaka women to place relatively more value on genetic quality since the relative importance of male provisioning is lower than in

other hunter-gatherer populations. In spite of this socio-ecological context, our results suggest that polygynous men do not differ significantly in strength or size.

These results should not be considered as conclusive evidence that male phenotypic quality is unimportant in the BaYaka marriage market, since only two physical attributes are examined. A recent study of the Hadza with numerous measures of physicality found effects on reproductive success that differed in direction and significance. For instance running speed and upper-body strength were negatively and positively correlated with reproductive success respectively (Apicella 2014). These findings highlight that operationalising phenotypic quality with just two variables may be over simplistic, and certainly does not provide an exhaustive analysis. Thus, one must be cautious when generalising these results. Additionally, the short stature of Pygmy groups has been hypothesised to be a positively selected trait (but see Migliano et al. 2007 for alternative by-product explanation), and to provide advantages to hunter-gatherers in thermoregulation (Cavalli-Sforza 1986); mobility in forest environments (Turnbull 1986); and starvation endurance in low-productivity environments (Diamond 1991). Therefore, individual variation in height may not be reflective of differences in genetic quality in this population.

We find polygynous men have significantly more social capital than their non-polygynous counterparts. This finding is unlikely to be due to reverse causality i.e. polygynous men having more affinal kin playing the game, since when a BaYaka man has multiple wives, they tend to reside in different camps among which he divides his time. Accordingly, none of the polygynous men in our sample had multiple wives living in the same camp. It is also noteworthy that my measure of social capital reflects a man's level of social capital during the study period. Due to limitations with the data collection process, it is possible that some of the men coded as polygynous were only polygynous in the past, and no longer are.

Therefore, it is possible that there is some temporal misalignment between the measure of social capital and polygynous status; hence the result must be treated with some caution.

Another potential confound of our result is that our measure of social capital covaries with some other trait which may mediate its effect on marital status. In particular, many researchers have highlighted that hunting prowess is a route to high social status in foraging groups (Gurven & von Rueden 2006). Moreover, good hunters are more attractive marital partners since spouses of these men may benefit from increased fertility and child survivorship (Gurven & von Rueden 2006). For example, in a sample of Ache men, 74% of children born to good hunters had survived until the study period compared to 57% of poor hunters' children (Kaplan & Hill 1985). Data on hunting success among BaYaka men were not collected, thus it was not possible to test possible correlations between hunting and social capital or polygyny. Nevertheless, there are numerous plausible explanations as to why social capital may increase a man's mate value in its own right.

The relative importance of social capital in the mating market is likely to be affected by BaYaka food sharing patterns. A variety of sharing systems have been identified within hunter-gatherer societies, these can be categorised into those with (kin selection/reciprocity) and without (demand sharing/tolerated theft) producer control (see section 7.1.3; Gurven 2004a). With respect to mate value, if producer control is absent, then food sharing is unbiased and widespread; in turn women are unlikely to place much importance on the strength of a man's social network since food can simply be demand-shared from other camp members. However, among the BaYaka, research consistently finds evidence for producer control and reciprocal biases in food sharing (Kitanshi 1998). In a meta-analysis of food sharing of 32 human and non-human primate groups, reciprocity in food transfers was found to be more prevalent in a Central African Republic BaYaka group than any other group in the study (Jaeggi & Gurven 2013). Hence establishing cooperative relationships is likely to be

crucial to securing a stable nutritional income for one's family. The previous chapter provides empirical evidence that our measure of social capital is indeed closely associated with the number of camp members from whom an individual receives food ($\beta=0.24$, $p=0.005$). Due to the absence of food storage in the dietary niche occupied by humans for the majority of our evolutionary history, risk reduction is considered to have been one of the most important adaptive problems faced by our species (Kaplan et al. 2000). This remains the case for modern day hunter-gatherers, and thus within these communities, men with an abundance of social support, who are in turn better equipped to buffer food risk, are likely to be more attractive marital partners.

When a polygynous man is staying in another camp with a different wife, his foraging contribution is completely absent. Thus, unless female production covers 100% of provisioning, women incur a cost by marrying polygynously. Moreover, in this group of BaYaka only men hunt, and the protein and fat content of meat they provide are necessary dietary compliments to female gathering. Additionally, fathers in BaYaka groups have been found to provide more direct care than any other society in the world (Hewlett 1993). It is this paternal care that facilitates female production, freeing up mothers to invest time in foraging. Thus, a polygynously married woman, in the absence of her husband, is also likely to encounter more difficulties balancing the time and energetic trade-offs between direct childcare and foraging (Hurtado et al. 1992; Meehan et al. 2012). Therefore, it is possible that the wives of polygynous men may rely on their husband's large social network for provisioning and allocare when he is residing in another camp with a different wife.

Another reason BaYaka women may value a potential mate with high social capital relates to the position of *kombeti*. This position can be described as an appointed spokesperson for the camp that has influence, but not absolute authority, over camp decisions regarding subsistence and movement, as well as interactions with farmer and other non-BaYaka groups

(Hewlett 1988). There are numerous reasons why these individuals may have higher mate value to women. Although the BaYaka generally do not accumulate resources, they occasionally receive storable materials such as money, clothes and machetes from interaction with tourists, researchers, and farmers. *Kombetis* may manipulate the distribution of these resources. When we have given gifts for a camp, the *kombeti* would direct their distribution and usually end up with a larger share (not overtly); they also receive more goods such as cigarettes from farmers (Hewlett 1993). Additionally, these men, through their prestige, may be more able to influence group decisions in their favour thus increasing their mate value further. Such an effect has been found in prestigious Tsimane men who in turn have favourable fitness outcomes (von Reuden et al. 2010). Finally, dental research also suggests *kombetis* may have access to a more nutritious diet; this may be a result of other camp members sharing more high quality foods with them (Walker & Hewlett 1990). This position of *kombeti* is appointed, thus attaining and maintaining it relies on social capital. When choosing a partner, BaYaka women may consider whether a man is a *kombeti*/ his prospects of becoming one, and thus preferentially marry men with high social capital. In our sample there are only two *kombetis*, both of whom are polygynous and had the most social capital in their respective camps, providing some support for this pathway.

Regardless of which pathway moderates the selection of female preference for men with more social capital, the translation of this preference to polygyny appears to be adaptive for women and fit the predictions of the female choice approach. I find that women married polygynously achieve the same fitness as their monogamously married counter-parts. Thus, the high social capital of their husbands must in some way compensate for the cost of having to share his time and resources.

The BaYaka are simple hunter-gatherers i.e. they do not store or accumulate resources. Given that applications of the polygyny threshold model to human societies are premised on

male wealth inequality, for which resource accumulation is a precondition, such explanations do not initially seem appropriate for simple hunter-gatherer contexts. However, the polygyny threshold model was first developed for bird and non-human mammalian populations (Orians 1969), in which male resource provisioning does not occur via wealth storage/accumulation but superior access to resource-rich territories. Similarly, BaYaka men with high social capital may be better able to provision their spouses either now or in the future via stronger food sharing networks or improved prospects of becoming *kombeti*, rather than resource accumulation.

Our findings that polygynous hunter-gatherer men experience advantageous fitness outcomes and have more social capital provide an important step in understanding hunter-gatherer marriage, and whether/how polygynous marriage was even possible before the Neolithic. Cross-cultural research indicates that on average ~14% of men are polygynous in foraging groups (Marlowe 2005). How such a system evolved is an important question for evolutionary anthropologists. Traditional models of polygyny such as the polygyny threshold model and the mate-defense model are often considered inapplicable to hunter-gatherer societies since these groups do not accumulate resources or establish dominance ranks. However, despite the lack of resource accumulation, the previous chapter described that inequalities in resource access may emerge via differences in social capital. Here I demonstrate a mechanism somewhat analogous to the polygyny threshold whereby stratification of male social capital, which has implications for resource access and the ability to buffer food risk, rather than material wealth provides a mechanism for the emergence of polygyny. The results here also provide another pathway by which within-group differences in sociality have meaningful implications for fitness—a primary goal of this thesis and a research area that previously lacked strong empirical support (see section 2.4).

Future directions

To enhance our understanding of this topic further it is necessary to decipher how men accrue social capital. A sensible starting point would be to collect data on hunting skill, which has been associated with increased mating access and prestige in foraging groups (Gurven & von Rueden 2006). Other potential routes to social capital may lie in the religious structure of the Mbendjele. Australian Aborigine men enhance their status via initiation rites and secret knowledge (Artemova 2003). Similarly, there are a vast number of initiation rites that occur at different stages of a Mbendjele man's life, some which all men participate in and others which only a fraction of men undergo. Status can be further augmented by becoming a *konja wa mokondi*, where one becomes an authoritative figure in the initiation of others. *Nganga* is another of the few recognized positions held by the BaYaka and refers to healers with advanced knowledge of *bwanga*—forest medicines (Lewis 2002). In BaYaka groups, knowledge is considered an especially valuable resource (Lewis 2015); thus individuals holding specific expertise may be particularly valued by camp members and more likely to accrue social capital. It is also possible that acquiring social capital is a skill in itself, and men vary in their ability to form and maintain alliances with camp members.

Additionally, I found that women whose husbands have been married polygynously achieve the same fitness as monogamously married women. In the current analysis I have not distinguished between first and second wives of polygynous men, and whether these wives have had previous marriages. A thorough analysis would require a larger dataset with enough women who have only ever been married polygynously (second wives who are still currently paired with their husband, and have no previous marriages) to avoid these confounding factors.

9. Discussion and Conclusions

In this thesis, I collected a range of data concerning social capital, health, reproductive outcomes, food sharing, marriage systems, and childcare practices of the Mbendjele BaYaka Pygmies—a population of simple mobile hunter-gatherers residing in the rainforest of Northern Congo Brazzaville. I have presented three analyses chapters in which I explore aspects of BaYaka cooperation and sociality, and discuss their implications for our understanding of human social evolution. In this final conclusion I wish to begin by reviewing the findings of this thesis. Following this I will highlight the major implications of the results, paying particular attention to three main ideas: 1. the notion that hunter-gatherers are egalitarian; 2. the contention that cultural group selection drove the evolution of cooperation between genetically unrelated humans; and 3. consistent findings in fields such as psychology, public health, epidemiology and medicine that demonstrate an association between social integration and health outcomes. Finally, I will explore future directions for study and research questions that have arisen. Specifically, I discuss avenues relating to: 1. identifying how social capital is acquired in hunter-gatherer societies; 2. the relationship between social network centrality and fitness; and 3. the scope of remote wireless sensing technologies in evolutionary research.

9.1 Summary of findings

In chapter 6 I investigated the childcare system of the BaYaka, and in line with previous research confirmed that allocare or non-maternal childcare is an essential component of hunter-gatherer childrearing—maternal care accounted for approximately one quarter of all childcare received by the 0–4 year olds in my sample. Using proximity measured by the motes devices as a proxy for allocare, I found that per capita, siblings are the most important

category of non-maternal caregiver, followed by fathers, grandmothers, uncles/aunts, cousins, grandfathers and finally unrelated individuals. Unlike in other research, both fathers and grandmothers played a central role and there was not a clear-cut winner in the debate regarding their relative importance. Similar to the per capita results, cumulatively siblings provide a higher proportion of allocare (32%) than any other category. Parallel results have been found in other hunter-gatherers—such as the Efe and Agta Pygmies, (Kramer 2010; Goodman et al. 1985)—suggesting that perhaps the role of siblings in allocare has been incorrectly overshadowed by investigations of paternal and grandmaternal care. Moreover, the results also indicated that cumulatively, unrelated individuals are almost of equal importance to siblings, providing 30% of allocare. Scouring the literature, similar estimates have been found in Efe and Hadza societies (Ivey 2000; Marlowe 2005), emphasising that unrelated allocare requires further study. The results suggested that generally young children have a handful of important unrelated alloparents, who are more important than distant kin, and occasionally more important than fathers and grandmothers. As well as investigating who provides care, I examined the hypotheses as to why allocaregiving may be adaptive. In addition to finding support for the kin selection hypothesis, which has been previously demonstrated in other hunter-gatherers (Ivey 2000; Crittenden & Marlowe 2008), I found evidence for in-kind (childcare for childcare) and not-in-kind (childcare for food) reciprocity. To my knowledge this is the first demonstration of reciprocal cooperative exchanges involving childcare, such exchanges must underpin the alloparenting from unrelated individuals mentioned above. This chapter uses BaYaka childcare as a case study to demonstrate that cooperation is fundamental to hunter-gatherer societies, this cooperation is not unbiased within groups but preferentially directed towards kin and reciprocal partners, and this cooperation extends to unrelated camp members. Chapters 7 and 8 largely build upon these key points, to examine the effects of within-group differences in access to cooperation i.e. social capital.

In chapter 7, using a honey stick gift game I demonstrated that social capital varied within camp, particularly among men, and this variation cannot simply be explained by differences in genetic relatedness to other participants. Due to the risky foraging niche occupied by hunter-gatherers, cooperation is at the heart of these societies—food transfers insure against nutritional shortfalls, and allocare facilitates the successful rearing of multiple dependent offspring and eases maternal childcare-subsistence trade-offs (Hill & Hurtado 2009; Hurtado et al. 1992; Meehan et al. 2009). Accordingly, my findings demonstrate that inter-individual variation in social capital has important implications for evolutionary fitness. The results show that those with more social capital have larger food sharing networks and in turn are better able to buffer food risk, indicated by their significantly healthier body-mass index (see section 7.2 for limitations of BMI). Moreover, women with more social capital were found to have higher age-specific fertility, confirming the evolutionary significance of cooperative ties. Although, a similar fertility association is not found for men, chapter 8 reveals that men with *very* high social capital are more likely to marry polygynously, which I find increases reproductive success even in a hunter-gatherer context where resources cannot be accumulated and used to provide for multiple families. Conversely, physical attributes of height and hand-grip strength were found to have no significant association with male marital status. The final result in chapter 7 established a significant positive correlation between an adult's social capital and that of their father, suggestive of some form of inheritance.

In summary, chapter 6 demonstrated that cooperation is extensive between related and unrelated camp members, and is directed towards family and 'friends'. Building upon this premise that cooperation is not uniformly distributed within camps, chapters 7 and 8 confirm that differences in access to cooperation have effects on evolutionary fitness in the form of health, fertility and marital outcomes. Furthermore, these differences are heritable allowing such benefits to accrue over generations, and for the natural selection of traits that increase

social capital. I now wish to discuss the implications of these findings for the concept of hunter-gatherer egalitarianism; theories of the evolution of cooperation between nonkin; and the relationship between social integration and health.

9.2 Are hunter-gatherers truly egalitarian?

Non-human primate societies and non-foraging human societies typically contain social hierarchies (Sapolsky et al. 2005; Ellis 1995). Additionally, in non-foraging human populations, such as agricultural, pastoralist, and industrialised societies, wealth in the form of money, land, cattle etc. is accumulated and inherited. In turn this leads to the emergence of inequality, as windfalls to a lineage can be accrued and reproduced in the next generation and thus their effects accumulate over time (Borgerhoff Mulder et al. 2010). Given that simple hunter-gatherers usually do not have social hierarchies, nor do they accumulate wealth, they are often described as being 'egalitarian' (Cashdan 1980; Woodburn 1982). The egalitarianism of hunter-gatherers is manifested in 'politically assertive' egalitarian behaviour such as the self-deprecation of good hunters and levelling mechanisms such as ostracism, mockery and even violence towards those attempting to exert dominance (Woodburn 1982). Similar patterns are present among the BaYaka, and other researchers have commented on their egalitarian ethos (Lewis 2002).

Perhaps implicit in these descriptions of egalitarianism is the notion that individuals experience equality of resource access. Ethnographies refer to demand and needs based food sharing and cultural norms emphasising redistribution, which attenuate any differences in access to food (Lewis 2002; Peterson 1993). However, the results of this thesis indicate that despite the lack of social hierarchy and accumulation of resources, cooperation in the form of childcare and food sharing is distributed unequally and tends to be directed towards

specific partners; in turn this results in inter-individual variability in resource access. Thus in the case of the BaYaka, egalitarianism is not synonymous with equality. This trend is likely applicable to all hunter-gatherer groups, since whenever examined quantitatively, cooperation is not unbiased but follows networks of kinship, reciprocity and reputation (see Gurven 2004a for review). The research here simply takes these findings a step further by demonstrating that directed and biased cooperation results in cooperation (social capital) being unequally distributed among camp members, and this in turn has implications for fitness.

Whether or not these findings violate the characterisation of simple hunter-gatherers as egalitarian is a semantic issue. The Oxford dictionary defines egalitarianism as “believing in or based on the principle that all people are equal and deserve equal rights and opportunities”. The Merriam-Webster definition is more specific and defines it as “a belief in human equality especially with respect to social, political and economic affairs”. While the former definition primarily focuses on an absence of oppression and discrimination, the latter invokes concepts of social and economic equality, which are violated according to this thesis. Without a clear definition for egalitarianism, it is difficult to conclude on this matter. However, previous conceptions of the term in an anthropological context have implied that egalitarianism is concomitant with a reduction in phenotypic variation and reduces the force of natural selection on within-group competition (Boehm 1997), this thesis shows this is not the case. Given that it is unclear as to whether egalitarianism is decoupled from equality, the terms dominance and prestige can provide a more useful political description of simple hunter-gatherers. Dominance can be defined as improved resource access, resulting from the perception of other group members that ego can inflict costs on them. Conversely prestige is improved access resulting from the perception that ego can confer benefits to them (von Rueden et al. 2010). Where dominance is a form of oppression and is imposed, prestige is voluntarily given. Given that this thesis demonstrated without formal hierarchies

resource access still varies due to variation in social capital, rather than describing simple hunter-gatherers as egalitarian it would be more accurate to assert that dominance relationships are absent (but prestige is not).

9.3 The evolution of cooperation between unrelated individuals

Within evolutionary perspectives on human behaviour, one school of thought asserts that the evolution of human cooperation cannot be explained using traditional mechanisms applied to other animals such as kin selection and reciprocal altruism. Specifically, these theorists state that the large scale at which humans cooperate e.g. in warfare, and the extent of cooperation between unrelated individuals defines cooperation within our species compared to the rest of the animal kingdom (Boyd & Richerson 1992; 2009). They argue that due to variable climates during the Middle and Upper Pleistocene, there was selection for social learning and culture which facilitated rapid adaptation to varying environment conditions. This led to differences in cultural norms between groups. Groups with cultural norms which encouraged group beneficial behaviours and punished violators were able to outcompete other groups in between-group competition for resource access and warfare. Simultaneously, human psychology evolved to include pro-social motives and norm internalisation in order to allow individuals to function and avoid punishment in these highly cooperative groups (Boyd & Richerson 2006).

Given that the evolution of cooperation via cultural group selection is theoretically possible, its actual role in human evolutionary history depends on the relative magnitude of within versus between-group competition (Price 1970). Whilst advocates of CGS state that culture dampens the former and magnifies the later, this thesis shows that within-group competition for cooperation is not trivial in this hunter-gatherer population. Indeed, the founders of CGS

acknowledge “*these new tribal social instincts were superimposed onto human psychology without eliminating ancient ones favouring self, kin, and friends*” (Boyd & Richerson 2006, pp. 17). As we see in the case of the BaYaka, regardless of any cultural norms encouraging group wide cooperation, cooperation is still directed to “self, kin, and friends”, facilitating within-group differences in social capital and in turn fitness. Thus the ubiquity of cooperation between unrelated individuals can be explained via traditional within-group competition mechanisms. In numerous non-human animals there is small-scale cooperation between unrelated group members (Clutton-Brock 2009). Given that in hunter-gatherers cooperation often served as a buffer to risky environments, there was likely pressure to expand cooperative networks, and due to the low relatedness of hunter-gatherer camps this involved forging more extensive alliances with nonkin. This thesis offers empirical evidence for this pathway, since variation in social capital cannot be explained by differences in genetic relatedness to the group, and has meaningful implications for an individual’s ability to buffer ecological pressures and their reproductive success.

I am not refuting that between-group competition was important in human evolutionary history, but asserting that one cannot discard the role of within-group competition in the evolution of extensive cooperation between unrelated individuals. In fact, it is over simplistic to assume all forms of human cooperation evolved in the same way. For instance, the case of cooperating in the context of warfare is distinct from activities such as childcare and food sharing, since it is a public good where the fruits of one’s cooperative effort cannot be directed to certain recipients, rather they are enjoyed by the whole group. Perhaps, it is necessary to invoke CGS arguments to explain such large scale undirected cooperation. However, the main point I wished to make here is that this thesis offers empirical validation for a pathway to the evolution of extensive cooperation between unrelated individuals that does not require cultural group selection.

9.4 Why is social integration linked with positive health outcomes?

For decades researchers from numerous fields have found an association between social integration/social support/social isolation and both mental and physical health outcomes (see Seeman 1996 and Cohen & Syme 1985 for reviews; also see section 2.4.3), the research outlined in this thesis offers an ultimate explanation for such associations. Higher social integration is associated with lower levels of self-reported and physiological proxies for stress, as is reconciliation after conflict (Seeman 1996; Butovskaya 2008). This relationship with stress may be responsible for other findings linking social support to reduced incidence, severity and improved recovery from conditions such as myocardial infarction and stroke, as well as lower mortality risk (Cohen & Willis 1985; Seeman 1996). Moreover, lack of social integration has been identified as a major risk factor for depression (Kendler et al. 2005; Kawachi & Berkman 2001). It is clear that the human neuro-endocrine system responds to social integration, the question which follows such findings is why?

In section 2.4.1 I explained that sociality can be studied at many levels—cross-taxa, species, group and finally within group. It is at this lowest level where research is scant, and thus discerning the extent and consequences of within-group variation in sociality was a primary goal of this thesis. This is particularly important in humans since we form highly differentiated social relationships within our group, ranging from mere strangers to best friends, and some individuals are isolated whereas others are popular.

The findings presented suggest that in the hunter-gatherer context that represents the majority of human evolutionary history, social integration was an important determinant of survival and reproductive prospects in a harsh risky environment. Individual differences in social capital within the group may have been a major driver of fitness; thus natural selection is likely to have equipped humans with physiological and psychological proximate mechanisms encouraging the formation and maintenance of social relationships and

avoidance of social isolation. Generally, stress responses may serve to motivate socially isolated individuals to change their situation, but in certain circumstances chronic isolation may result in the stress response having negative impacts on mental and physical health.

9.5 Future directions—how do hunter-gatherers accumulate social capital?

The most pressing question arising from this thesis is how can we explain the variation in social capital in the BaYaka, and hunter-gatherers generally? Less than 5% of the variance in social capital can be explained by differences in genetic relatedness to the camp, and thus requires further explanation. While this thesis has demonstrated reciprocity to also be important in cooperative relationships, the question still remains why some people may have more reciprocal partners than others. If social capital has important outcomes on evolutionary fitness, traits that enhance an individual's ability to accrue it should be under positive selection. This offers a promising avenue for future research, and here I offer some sensible starting points.

Despite levelling mechanisms that attempt to disassociate hunters from their yield, such as mockery of good hunters and invoking the involvement of luck (Woodburn 1982), many anthropologists suggest hunting success is the most important determinant of social status among foragers (see Gurven & von Rueden 2006 for review). In fact, some human behavioural ecologists argue that the reason men hunt is not primarily to provision their families but actually to gain social status. Thus, by hunting difficult to acquire prey and sharing these widely in the camp, men are able to demonstrate their phenotypic prowess to mates and allies and augment their status (Bleige Bird et al. 2001; Hawkes et al. 2001). In many studies, this association is implicit following the finding of a relationship between hunting ability and access to mates or reproductive success (see Smith 2004 for review).

Moreover, von Rueden et al. (2008) investigated the association more explicitly and indeed found that hunting ability predicted respect from the community among Tsimane foragers.

Nevertheless, some of the men with high social capital were not frequent hunters. Additionally, hunting ability cannot explain differences in BaYaka women's social capital. Another possibility is that special knowledge enhances an individual's social capital. Lewis (2015) explains that intellectual property in the form of particular dances, songs, religious and medicinal knowledge constitutes a special economy among the Mbendjele, and these goods can be traded and inherited. Indeed, the religious cults are perhaps one instance in which political egalitarianism is suspended, and informal hierarchy is introduced. The *mboni* (uninitiated) are forbidden from certain activities and instructed how to behave during *massanas* (spirit plays) and initiations by the *bangonja* (initiated), and ultimate power resides with the *konja wa mokondi* (spirit controller). It is possible that those with specialist knowledge such as *konja wa mokondi* with their religious knowledge, or *ngangas* (healers) with the knowledge of *bwanga* (forest medicine) gain social capital since other BaYaka wish to gain their favour in order to trade or inherit knowledge from them. Indeed, researchers of other foraging groups, including Australian Aborigines have commented on how religious institutions and initiations create social inequality (Artemova 2003).

Alternatively, rather than be associated with some other trait such as hunting or knowledge, the ability to accrue social capital may be a skill in itself. In section 2.1, I mentioned that the hyper-developed theory of mind is one of the defining characteristics of our species (Tomasello et al. 2005). Our advanced mind reading ability and understanding the motivations, desires and intentions of others is thought to have allowed individuals to reap the rewards of cooperation and collaboration without being exploited by selfish individuals (Byrne & Whiten 1988). In the same way, those with superior theory of mind may be more

capable of expanding and maintaining cooperative relationships, which I show here has important implications for fitness.

Hunting ability, special knowledge and theory of mind have all been demonstrated to be somewhat heritable (Smith et al. 2010; Lewis 2015; Xia et al. 2012), and thus could explain the partial heritability of social capital observed in this thesis. Future studies should attempt to independently quantify social capital using techniques such as the honey stick gift game used here, and then gather data on these possible predictors perhaps by conducting questionnaires to ascertain hunting and knowledge reputations. However, this may be a difficult feat since the egalitarian ethos of hunter-gatherers results in discomfort or refusal to respond to questions asking for the names of talented individuals.

9.6 Future directions—social network centrality and individual fitness

In this thesis I examined the impacts of individual differences in direct access to cooperation from the group. However, analysis of dyadic ties does not offer a complete picture of within-group differences in sociality, individuals are in fact part of a complex polyadic web of relationships (Krause et al. 2009; Brent 2015). Social network analysis (SNA) is a technique which has become increasingly popular over the last decade which facilitates quantification of an individual's direct and indirect (i.e. connections of connections) ties within their social context (Brent et al. 2011). SNA can provide measures of both direct and indirect 'centrality' for all members of a network, and these centrality positions may have effects on fitness. Here I will describe some of the principal measures of centrality and explain how they may possibly affect hunter-gatherer fitness:

- i. *Degree (direct)*—this is the number of ties an individual has. As I have demonstrated in this thesis, given that cooperation serves as insurance for

hunter-gatherers, those with more ties may benefit from a more effective insurance network gaining more stable access to food.

- ii. *Strength (direct)*—this is a measure that accounts for both the number and strength of connections an individual has. Some ties are stronger than others, and weak ties may have little effect on fitness if they do not confer benefits—for instance individuals who one is weakly tied to may not share food in desperate times.
- iii. *Betweenness (indirect)*—if all individuals are considered as nodes, and ties between them as edges or paths, ego's betweenness is calculated as the number of dyadic shortest path lengths that pass through ego. Thus it is a measure of ego's role as a broker, connecting disparate parts of the network. Individuals with high betweenness may have lower fitness as they are more exposed to infectious diseases.
- iv. *Clustering Coefficient (indirect)*—an individual's clustering coefficient measures whether their ties are tied to each other. Returning to the concept of social ties as a form of insurance, an individual may be better off having ties who are not tied to each other and reside in different parts of the social network. Different subgroups forage together in BaYaka camps. It may be that some of ego's ties are unsuccessful with their foraging efforts on a particular day, however, if ego has connections with other unconnected subgroups, these individuals may have been more successful and can share with ego. Thus, low clustering coefficient, or having friends who are not friends with each other may be seen as a form of hedging one's bets.
- v. *Eigenvector (indirect)*—this is a measure of how connected the individuals ego is connected to are. If secondary sharing occurs in hunter-gatherers, being

connected to an unpopular person may be far less advantageous than being connected with a popular member of the camp.

Studying how an individual's direct and indirect centralities affect fitness would provide a more complete understanding of the evolutionary implications of within-group differences in sociality. It has been suggested that natural selection may be less able to act on social network position since it may be difficult for an individual to affect their indirect ties and position (Lea et al. 2010). However, this is not the case for all indirect measures of centralities, for instance it is common place for individuals to try and befriend the 'popular kid', as a form of active maximisation of eigenvector centrality. The social brain hypothesis states that human encephalisation evolved with social complexity (Dunbar 1992). Perhaps one major pressure for neocortex expansion was to keep track of third party relationships in order to manipulate indirect social network centrality. Associations between network centralities and fitness have been identified in numerous non-human taxa such as chimpanzees, bottlenose dolphins and forked fungus beetles (Gilby et al. 2013; Stanton & Mann 2012; Formica et al. 2012). Additionally, social network positions have been found to be heritable and associated with specific serotonergic polymorphisms in humans and rhesus macaques (Fowler & et al. 2009; Brent et al. 2013). Therefore, similar investigations in humans are a promising avenue for future research.

9.7 Future directions—the effect of third party forces on hunter-gatherer subsistence

Throughout this thesis, the results presented have been assumed to shed light on human evolution based on the premise that they are derived from a hunter-gatherer population, which to a certain extent reflects ancestral human societies in terms of socio-ecology and selective pressures. However, extant hunter-gatherer groups are exposed to many outside forces which would not have existed in our species' evolutionary past. For the BaYaka and

many other extant hunter-gatherers, these include conservation laws and guards; shotguns; and an expansion of the bush meat trade. To assess the strengths and weaknesses of using hunter-gatherers as a model of human history, and the validity of findings such as those presented in this thesis, it is necessary to understand how these forces of modernity affect subsistence patterns. Relevant questions include: how shotguns/conservation efforts affect hunting return rates and prey choice; and how trade affects consumption patterns, food risk and sharing patterns.

9.8. Future directions—the scope of remote wireless sensing technology in evolutionary research

In this thesis I used motes (remote wireless sensing devices) to construct proximity networks and study BaYaka childcare practices. The implementation of motes has many advantageous over traditional focal sampling techniques, namely the generation of larger sample sizes; it is less time and effort intensive once the technology is prepared; it provides an objective measure of proximity which is not subject to inter-observer unreliability; and it facilitates data collection over a longer time frame. For all these reasons, the results are less subject to bias than observational methods.

In addition to their usefulness for future studies of childcare, motes offer an effective method for the study of numerous subject areas of interest to evolutionary research. The devices are flexible in terms of battery life, and the software installed on to them can be customised to the needs of a given study. It is possible to programme the motes to emit beacons at different time intervals, alter the number of beacons the mote can record at one time, and alter the distance at which the mote records beacons. In section 5.4.6.2 I provide a validation of these devices by comparing their results with those of my observations, the

remarkably similar results provide a proof of concept. The motes can be used in future research relating to long term mobility and residence patterns, the ontogeny of social networks, gender differences in sociality, the transmission of disease and cultural information, and seasonal changes in network properties etc. The potential of these devices in evolutionary research is truly vast, and their effective implementation in this study is likely the most valuable contribution of this thesis.

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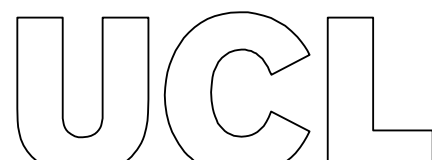
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Appendix

Appendix 5.1

Participant Consent Form

Hunter-gatherer resilience: A project with University College London



This project will be developed at **University College London**, by Dr Andrea Bamberg Migliano and participants of the “hunter-gatherer resilience” project including PhD students and post-doctoral researchers.

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

- **Measure and weigh people** to understand how people grow and change as they get older;
- **Understand how the food people eat affects how they grow;**
- **Take sample of saliva to get DNA.** DNA can tell us how you are related to other pygmies, why you are different from farmers, and why some people get sickness like malaria more often than others.
- **Ask about your family**, to understand how you are related to each other.

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

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

Appendix 5.2

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

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

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

Name of Participant (block letters):	
Signature:	Date:

*Name of Authorised Representative (block letters):	
Signature:	Date:
*Use this signature block only used in such cases where the participant is not capable of providing his/her own informed consent	

Name of Investigator (block letters):	
Signature:	Date:

Two copies of this form will be provided: one will be kept by the researcher, the other is for you to keep.

Thank you for your help

Appendix 5.3

ID: A/____/____ Sex: M F Est. Age:.....

How?.....

..... Actual Age:.....

Year _____ of _____ Birth:.....

Season:.....

Weaned? Y N Age at Weaning.....

Birth Order:..... Village:.....

Born in/from:.....

Other Information:.....

.....

.....

.....

Height	cm
Shoulder Width	cm
Hip Width	cm
Weight	kg
% Body Fat	%
% Body Water	%
Bone Mass	kg
Head Circ. (<18 y/o)	cm
Teeth Age	years
Skin Fold Thickness	<i>PTO</i>
Hand Grip Strength	<i>PTO</i>

Appendix 5.4

Title: Improved Age Estimation For Cross-Sectional Studies Of Small-Scale Societies

Abbreviated title: A Method For Improved Age Estimation

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Key words: Gibbs sampler, Agta, hunter-gatherers, aging method, fertility

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ABSTRACT

Objectives: Precise estimation of age is essential in evolutionary anthropology, especially to infer population age structures and understand the evolution of human phenotypic diversity. However, in small-scale societies (e.g. hunter-gatherer populations) where time is often not referred to in calendar years, accurate age estimation remains a challenge. We address this by proposing a Bayesian approach that accounts for age uncertainty inherent to fieldwork data.

Materials and Methods: We developed a Gibbs sampling Markov chain Monte Carlo algorithm that produces posterior distributions of ages for each individual. This procedure uses individuals ranked from youngest to oldest and age ranges or distributions per individual. We first validate our method on 65 Agta individuals whose ages are known, and compare it to previously published regression-based approaches. We then use data on 587 Agta collected during fieldwork in the Philippines to show how the posterior distributions generated by our method can be statistically integrated into classical anthropological analyses, here age-specific fertility patterns.

Results: We show that our method generates accurate age estimates superior to regression-based approaches. We demonstrate how to derive age-at-birth distributions from the posteriors of mother and child using convolution.

Discussion: The flexible Gibbs sampling approach presented here permits multiple partial ranks to be considered, and produces full posterior age distributions rather than point estimates. This approach will be especially useful to improve cross-cultural life history dataset for small-scale societies living in diverse environments.

Precise estimation of the age of individuals is essential in evolutionary anthropology. Central questions requiring age estimates include inferring timing of life-history events (e.g. menarche, marriage, first and last child, death), assessing infant growth and development trajectories, and estimating age structure properties of a population (e.g. the potential for population growth or decline, recovering signatures of epidemics, and assessing vulnerability to ecological perturbations). Population age structures are crucial for any adaptive study concerning the evolution of human phenotypic diversity. Humans have important life-history derived features which differ from non-human Hominids, such as shorter inter-birth intervals, longer lifespan, reproductive senescence, extended post reproductive longevity, and extended childhood dependence ¹. These life history traits vary within human populations, likely in response to differences in ecology such as differential rates of mortality leading to variations in the slow-fast continuum ² as well as in energetics and rates of growth ³. However, very few studies have highlighted variability in life history traits in traditional societies ⁴⁻⁶, as accurately estimating the age of individuals can be challenging. This is particularly true for populations where individuals do not relate their age to calendar years, such as the majority of hunter-gatherer populations and some other small-scale societies. While an ideal approach to address questions about life history traits in small-scale populations is longitudinal studies, these are rare (but see Hurtado and Hill, 1996; Early and Headland, 1998). There is consequently a need for methods to estimate ages based on cross-sectional data from these populations.

A few approaches have been proposed to estimate ages in small-scale populations (reviewed in Hurtado and Hill, 1996). The simplest one is visual inspection and approximate clustering into age cohorts (e.g., infant, child, teen, adult, old age). A clear disadvantage of this method is its lack of precision, which limits understanding life-history variables that themselves require a refined age structure, such as age at first birth, menarche or death. Furthermore, differences in physical appearance trajectories in forager populations in comparison to known western counterparts (e.g., children may appear younger than western counterparts, while middle/old age individuals

may appear older) are most likely to cause misattribution of ages. Howell (1979) proposed an alternative 'steady-state model' approach to overcome these difficulties and applied it to the Dobe !Kung. This method assumes a static population structure, ascertains a relative age list of all individuals, and estimates both the death and fertility rates of the population. This permits approximation of the population age structure by mapping these rates onto different life-tables (in which 80% for example live to age 1, 75% live to age 2, etc.) and selecting the one with the best correspondence. Caveats of this approach include potential lack of matching life tables, and growing populations for which the rates are unknown⁸. Furthermore, static population models fix the proportion of individuals that live up to a certain age, which may obscure differences in life-history adaptations.

Because of these shortcomings, Hurtado and Hill (1996) (also see Jones et al. (1992) for the Hadza) designed an alternative method to estimate the ages of Ache hunter-gatherers that does not assume a static population. It is based on a relative age list including all individuals and absolute ages for a subset of them. The relative age list is constructed by first dividing the population into age cohorts containing individuals of approximately the same age. Each individual ranks all others within his/her cohort, as well as those in the cohorts above and below his/her, as either older or younger than himself/herself. From this a single relative age list is produced per cohort by merging the individuals' lists and minimising the number of contradictions in rank, followed by a master relative age list of all cohorts combined. The absolute ages of some of the individuals are obtained from birth certificates, estimated from known events, or by an "age-difference chain" (individuals are questioned about their age at the time a younger individual was born by picking an individual of known age matching their age at the time of birth of the younger individual)⁸. Given these and the relative age list, a fifth-order polynomial curve is fitted with relative rank and age as the independent and dependent variables, respectively. Finally, the ages of the remaining individuals are estimated as the value of the polynomial curve at the corresponding rank.

Despite improving upon previous methods, this approach still presents several drawbacks. First, the choice of fifth-order polynomial is arbitrary and not further validated, previous authors (Jones et al., 1992) have for example used polynomials of third-order. Some ages may be fitted poorly by a polynomial, while overfitting may also be an issue, especially for data sets with few known absolute ages. In addition, the uncertainty associated with absolute age estimates is not taken into account. For example, in age-difference chains the error is cumulative, leading to high uncertainty, especially for older individuals. Also, birth certificates may occasionally be inaccurate.

Here, we present a new Bayesian method for age estimation improving upon previous approaches. We design a Gibbs sampling Markov chain Monte Carlo algorithm that integrates prior uncertainties inherent to any absolute age estimate. It generates full posterior distributions of ages for each individual rather than only point estimates. We show that our method generates more accurate age estimates than regression-based approaches. As an empirical validation, and to show the flexibility of our method in the context of actual fieldwork, we present a case study on Agta from the Philippines. Finally, we analyse age-specific fertility patterns in the Agta fully integrating the uncertainties in the estimated ages of mother and child. This demonstrates how the posterior distributions produced by our method can be statistically integrated into classical anthropological analyses.

MATERIALS AND METHODS

Estimating ages by Gibbs sampling

In contrast to previous approaches, we address age estimation using a fully probabilistic framework. This method requires two types of input data: (i) a ranking of all individuals by age (i.e. an ordering of the type *A* is younger than *B* is younger than *C* etc.); and (ii) a list of individuals, each with an associated *a priori* age distribution. For example, the distribution may be uniform, with simple hard bounds on the plausible age range of the individual (i.e. not younger than *l* and not older than *u*; all ages in between are equally probable). These are processed to generate a probability distribution of age

per individual. This allows downstream analyses to incorporate the full uncertainty associated with point estimates (e.g. by confidence intervals around the mean age), or in the best case to directly use the full age distribution of an individual (see below).

Formally, we consider a vector x with ages of n individuals, that is $x = (x_1, \dots, x_n)$. Each x_i , that is the age of each individual, is distributed according to an arbitrary distribution function $P_X(x)$ specified *a priori*. In addition, x must satisfy the constraint imposed by the specified age ranking, that is $x_i < x_j$ for all $i < j$ (i.e. here the ranking is from youngest to oldest), or equivalently, $P_X(x_1, \dots, x_n) = 0$ holds for the joint distribution of $X = (X_1, \dots, X_n)$ whenever $x_i \geq x_j$ for any $i < j$. A naïve approach to sample from the joint distribution is to randomly draw an age for each of the n individuals independently, and then test if the resulting sample satisfies the ranking constraint. If not, the value is discarded. However, in all but very simple cases this turns out to be inefficient or even computationally intractable, as most of the samples generated by this approach need to be discarded.

To solve this more efficiently, we implement a Gibbs sampling approach, which samples from the joint distribution directly without having to discard any age-vector. The key to do this is to only consider univariate conditional distributions, i.e. the age distribution of one individual when all other individuals are assigned a fixed value from their respective range (Walsh (2004), p. 16), i.e. $P_X(x_i | x_1, \dots, x_{i-1}, x_{i+1}, \dots, x_n)$. How an initial set of values x satisfying the age ranking can be found is described below (point 1). Iterating over all individuals i in this manner generates a sample x , and it can be shown that the sequence of samples x thereby generated converges to the desired target joint distribution (Walsh (2004), p. 17).

In our case, a Gibbs sampler can be constructed in the following manner. Denote the k^{th} sample of x by $x^{(k)} = (x_1^{(k)}, \dots, x_n^{(k)})$. Assume for example that $P_X(x) \sim \text{Unif}(l, u)$, i.e. the age of any individual is distributed uniformly within an interval bounded by values l and u . We note that alternative distributions for $P_X(x)$ are easily accommodated in a way analogous to the one

described below. Setting $x_0 := -\infty$ and $x_{n+1} := \infty$ for the sake of simplicity, our Gibbs sampler proceeds as follows:

1) Initialise the first sample $k = 0$:

$$x_i^{(0)} = \max(x_{i-1}^{(0)}, l_i), \text{ for } i \in \{1, \dots, n\}$$

2) Iterate K times to generate $K + 1$ samples, i.e. $k \in \{1, \dots, K\}$:

$$x_i^{(k)} \sim \text{Unif}(\max(l_i, x_{i-1}^{(k-1)}), \min(u_i, x_{i+1}^{(k-1)})), \text{ for } i \in \{1, \dots, n\}$$

This procedure generates as many samples as desired. As always with empirical distributions, the general tradeoff is that more samples occupy more memory space and require longer computation time, but reduce the stochastic sampling error and therefore better approximate the underlying distribution. Figure 1 illustrates for 5 fictitious individuals the type of input required and output generated by our method.

Validation and benchmarking

We validate our approach on 65 Agta hunter-gatherers from Casiguran (the Philippines), whose exact dates of birth are known ¹³, and can be directly compared to the estimates generated by our Gibbs sampler. As input data, we derived a relative ranking from the known dates of birth, and three of the authors (DS, AP & MD) assigned upper and lower age bounds to these individuals based solely on visual inspection of the accompanying pictures (done prior to knowing the actual dates of birth). In order to make the results comparable, we summarized each full posterior distribution produced by the Gibbs sampler by its mean, which can then be easily compared to the known age of the individual by calculating the difference between the two.

Besides validating our results against the known true ages, we also compare the quality of our inference against two alternative methods: the regression approach, fitting a fifth-order polynomial ⁸, and a non-parametric alternative based on local regression with LOESS (local regression).

We implement a five-fold cross validation strategy, i.e. we randomly split the data into five groups of 13 individuals and consider each group in turn.

For each group, we estimate the regression equation and use it to deduce the ages of the remaining individuals. For the Gibbs sampler, known ages are taken into account by choosing point masses as priors for the age of an individual rather than uniform densities over the age interval. Figure 2 sums up our setup: the random partitioning of the individuals in five groups (top row), the known ages and the lower and upper limits (i.e. age brackets) derived from the individuals' picture, and the regression curves. Note that the regression approaches do not include the information on uncertainty provided by the age brackets in their inference, whereas our Gibbs sampler approach does. To ensure a fair comparison, we also test a fifth-order polynomial regression fitted on known ages of 13 individuals for a given partition additionally including the midpoints of the age brackets for all other individuals. Lastly, we also run our Gibbs sampling approach entirely without known ages, i.e. solely relying on the information from the age brackets and the ranking of individuals.

Case study: Palanan Agta

We apply our age estimation method based on Gibbs sampling to data we collected on the Palanan Agta, a hunter-gatherer population from north-east Luzon, north of the Casiguran Agta mentioned above, in order to showcase the application and flexibility of our method. We describe the collection of the two types of data required as input: the relative age rankings and prior age ranges for all individuals.

In order to construct relative age rankings, we took and printed photographs of all individuals in every camp. Individuals were then assigned to approximate age cohorts (0-4, 4-8, 8-12, 13-19, 20-45, and 45+). Those not easily assigned to one cohort were included in the two nearest cohorts (e.g., an individual aged ~45 would be included in both the 20-45 and 45+ cohorts). Either individually or in small groups, we presented these photographs to individuals from a target cohort, one at a time. The target cohort was the cohort the individual ('ego') was included in, as well as all cohorts younger than ego. Cohorts, especially for children, were often presented together, so that some rankings included, for instance, all individuals aged 0 to 12. Individuals from a

specific camp were shown pictures of others from their camp and neighbouring camps. More distant camps were not included due to a lack of familiarity, unless ego knew individuals from more distant camps particularly well (e.g. they grew up in distant camp and moved to the current camp upon marriage). For cohorts including ego, ego's picture was displayed first. Participants were first asked if they knew the individual on the photograph (i.e. the target), and if so they were then asked if they knew the target well enough to give their approximate date of birth relative to other individuals. Each photograph was put into one of three categories; 'don't know', 'know but not the age', and 'know with age'. If ego knew both the target and their age, they were asked to rank the age of the target relative to others (with left meaning younger and right meaning older, see Figure 3). Although similar to the method by Hurtado and Hill (1996), rather than having two piles of simply older and younger (with ego as reference), our method produced a relative age list from youngest to oldest. This process was repeated multiple times with different subjects producing a total of 266 partial ranks and including 587 Agta.

The second stage involved deriving age estimates for these 587 individuals. One invaluable source of information, especially for older individuals, was Thomas Headland's database of Casiguran¹³, since some individuals from our population were included in this database, with relatively accurate dates of birth assigned. Absolute ages of individuals were ascertained via various other methods, including; asking individuals if they knew their own or their children's age (which could be from various sources, such as birth certificates, other documentation, school grade, own estimates, etc.), births near dated events (such as martial law in 1970, various known typhoons), and age-mates of individuals with known birthdays. For children up to the age of 12 years, it was also possible to estimate ages by dental development. There are however some issues with methods used to estimate absolute ages, especially estimates given by individual Agta, the tooth age data, and school grade. For example, many individuals gave various conflicting dates/ages, including; saying a child was 4 years old, yet born in 2004, or giving a birth date for one child as 2004 (~8 years old) yet saying a younger child was 9 years old, or age conflicts between individuals (e.g., one

child was given an age of 7 months by one parent, and 2 years by the other). For both teeth ages and school grades, the margins of error were often quite large ($\pm 1/2$ years), which was especially problematic regarding school ages, as the grade reached was often variable for individuals of a similar age, and most children in the community either do not go to school, or start school at older ages than their agricultural neighbours. Therefore, strict criteria were used to select accurate ages/birth dates. First, if an individual was given two markedly different birth dates, that person was excluded from the absolute age list. Second, if ages for an entire sib-set were provided, but at least one age was wrong (e.g., didn't correspond to teeth ages, or didn't allow nine months pre- or post-birth of nearest sibling), then ages for the whole sib-set were excluded. Furthermore, for all children, the birth date had to fall within the range of teeth ages to be accepted, and a similar protocol of matching with teeth ages was established for estimating the ages of individuals from school grade. For individuals with estimated ages from comparisons to individuals with known birth dates, they were given a year of birth with a ± 1 year margin to account for error. Using these methods, 98 individuals were given an exact birthday, while many others were given age estimates within ± 1 year (Table 1). For individuals which we could not attach a secure date or estimate, three of the field researchers (DS, PA, & MD), as well as the principle investigator (ABM) estimated the ages based on cues such as dental development, school grade, birth order (if older or younger siblings have a known age), age of ego's children (if known), number of children, and visual inspection. Independently, each of the four researchers estimated an upper and lower age bound for each individual. In collating these estimates, the youngest lower bound and oldest upper bound of the four estimates were used in order to include as much uncertainty as possible. Obviously, with greater age comes greater uncertainty, as the average difference between upper and lower estimates increases with age (Table 1).

Estimate age at birth based on age distributions of mother and child

Computing the age at birth is trivial when the age of both mother and child are scalar values: simply calculate the difference. However, if the age of the mother, the child, or both, is described by a distribution rather than a scalar, the solution becomes less obvious. This is precisely the case here, as our age estimation procedure results in posterior distributions that capture the uncertainty in the age estimate.

Let the age of mother and child be modelled by random variables M and C , respectively. Analogous to the scalar case, the age at birth—say A —is then described by the difference between the two random variables, $A = M - C$. The full probabilistic description of the age at birth we seek is given by the probability density function (pdf) of A , say $h_A(x)$. It can be derived from the pdfs of M and C by an operation called ‘convolution’: let $f_M(x)$ and $g_C(x)$ be the pdfs of M and C , respectively, then

$$h(x) = \int_{-\infty}^{\infty} f_M(\tau) g_C(\tau - x) d\tau$$

Implementation and statistical analyses

The Gibbs sampler has been implemented in Python 2.7 ¹⁴ and can be downloaded from our website at [TBA].

Regression analyses and plotting were performed using the statistical analysis programming language R version 3.1.3 ¹⁵. Regression analyses were performed using the functions ‘lm’ (Cleveland et al. (1992), chapter 4) and ‘loess’ (Cleveland et al. (1992), chapter 8), Kolmogorov-Smirnov statistical tests with ‘ks.test’, and convolution with the function ‘convolve’ all from the R package ‘stats’.

RESULTS

First, we assess how well the Gibbs sampler approach estimates ages, and then compare it to regression methods. The results are summarised in Figure 4. The distribution of differences between known age and mean age

estimated by the Gibbs sampler across all five partitions shows that the median error of the differences per individual is about 0.29 years (i.e. four months), and the mean 0.91 years (i.e. 11 months). The maximal discrepancy between true and estimate does not exceed 10 years and is reached for old individuals, whose ages are inherently more difficult to estimate due to wider prior age brackets. Interestingly, similar results are achieved even when no age is considered known (no anchors) and the Gibbs sampler only estimates based on rank and age brackets. The near-equivalence in estimation accuracy is also supported by statistical comparison of the two distributions of error: a non-parametric two-sided Kolmogorov-Smirnov (KS) test does not find significant differences between them. In comparison to the Gibbs sampler, the polynomial regression approach has a higher median error of the differences per individual of around 1.16 years (i.e. 14 months), with a high mean of 2.66 years (i.e. 32 months) caused by outliers that are off by up to 28 years. These large errors occur at the boundaries, i.e. for the youngest and oldest individuals, especially when the youngest or oldest individual with known age used for fitting the polynomial is far from these boundaries, as is the case for partition three (see Figure 2, the first individual in partition three has rank 12). Counterintuitively, taking into account the additional information provided by the age brackets does not improve the estimation. The mean error for polynomial regression fitted with midpoints of the age brackets is 52 months, and comparing it to the distribution without midpoints via a KS test yields a significant difference. We also tested a third approach based on local regression (LOESS), that shows intermediate performance with a median error of 0.64 years (i.e. seven months).

These observations remain valid for moments different from the mean (i.e. median and mode) used to summarize the full posterior distribution produced by the Gibbs sampler (data not shown). Furthermore, we tested the influence of the way the data is partitioned, testing two to 13-fold cross validation. As already suggested by the performance of the Gibbs sampler without known ages, the influence of the number of known ages on the Gibbs sampler approach is limited. This is not the case for the polynomial regression approach, for which large differences are observed, especially when fewer

ages are known, mostly reducing the accuracy (see Supplementary Material for details). In summary, we observe that Gibbs sampling achieves the highest accuracy of age estimation, nearly independently of the availability of known ages. Interestingly, the polynomial regression approach is inferior to both LOESS and Gibbs sampling; it is not able to benefit from the additional information provided by the midpoints, which results in even worst performance.

After comparing the accuracy of our approach to existing methods, we illustrate its application with a case study on Agta from the Philippines. In particular, we highlight two aspects: first, the flexibility of our method in dealing with fieldwork data by allowing the use of multiple partial ranks for age estimation; and second, exemplifying how the uncertainties in age estimates can be integrated into downstream analyses, such as understanding age-specific fertility patterns.

One of the difficulties of working with small scale societies, including the Agta, is that individuals living in geographically distant or isolated camps usually do not know each other well enough to be able to rank each others ages. However, as described in the Materials and Methods section, exceptions exist in cases where individuals moved camps, for example upon marriage. The resulting challenge for any age estimation method based on an age ranking is that this loose pattern of familiarity among individuals precludes the assembly of a single age rank. Rather, multiple partial ranks are generated, in our case for example 266, that include different – yet overlapping – subsets of individuals but never the entire population. One of the great flexibilities of our Gibbs sampling approach is that this situation can be accommodated intuitively and rather easily. In a first step, consistent partial lists are merged. For example, (A, B, C) and (B, C, D) are consistent and can be merged to yield (A, B, C, D). In contrast, (A, B, C) and (B, A, D) are not consistent and kept separate. Merging matters to the extent that ranks including more individuals tend to impose stronger constraints on the age of each individual, resulting in narrower posterior distributions and consequently more accurate age estimations. All the distinct lists are then used as input for separate runs of the Gibbs sampler, where a run produces distributions of ages for each individual,

according to their respective partial age rank. In the end, each individual gets an overall age distribution over all its relative ranks, generated by the merging of all these distributions. The upper two panels in Figure 5 exemplify the procedure for two Agta.

Besides its flexibility to deal with multiple partial ranks, a distinctive feature of the Gibbs sampling approach presented here is that it produces full posterior age distributions rather than point estimates, which do not quantify uncertainty. Figures 5 and 6 illustrate how this uncertainty can be integrated into downstream analyses, here with the example of age-specific fertility. In Figure 5, we use convolution to derive the age at birth distribution for a mother, given the uncertainty about the age of both mother and child. This analysis was performed on all mother and child pairs and we averaged the resulting distributions (i.e. stacked and normalised) in order to obtain the overall distribution of the age at birth in that Agta population. Figure 6 depicts this age at birth posterior distribution separately for cases where both the mother's and the child's ages are known exactly from birth certificates (histogram) and for all other cases (density curve). While we do not expect the distributions to be the same as fewer birth certificates are available for older individuals (see Table 1), we nonetheless observe good visual correspondence at least in terms of supports of the two distributions (i.e. those ages that have non-zero probability). We interpreted this as an internal sanity check validating our results.

DISCUSSION

This study introduces a new Bayesian method to estimate ages in a fully probabilistic framework based on Gibbs sampling. This approach permits both improved flexibility in the input data considered, when compared to existing methods^{8,10,11}, and a full account of the statistical uncertainty in the inferences generated. The initial age ranges or prior distributions can be chosen from a wide spectrum of distributions to reflect the level of confidence in the *a priori* estimate for each individual: point masses on the one hand when the birthday is known, to wide uniform distributions on the other when ages

are vaguely estimated and lie in a poorly informed range. The second type of input data used is a ranking of individuals by age, or more flexibly multiple partial ranks. Figure 1 exemplifies how these two data types are integrated to produce posterior distributions that fully capture the uncertainty associated with individual age estimation.

We validate and compare our method against other approaches (see Figure 2). This validation procedure is summarised in Figure 4. We first show that the use of LOESS improves on previously published polynomial regression approaches^{8,11}. LOESS drops the requirement for the data to fit a fifth-order polynomial and therefore allows for more flexible curves that generate more accurate age estimates. Moreover, this permits accommodation of additional information, for example coming from midpoints of age brackets, which only lead to worse performance in case of polynomial regression. More significantly, we show that the Gibbs sampler approach estimates ages of individuals with generally low error, outperforming regression methods. Notably, this is true even when no known dates of birth are provided, a situation when regression cannot be applied at all. Hence, our approach can also work when absolute ages for all or most individuals are not available, i.e. with only partial age rank and prior age range distribution per individual. These can be obtained in short field trips, which should make age estimates for various small-scale societies readily available, facilitating future studies on the evolution of human adaptive variation.

We present a case study on data we collected in the context of actual fieldwork with Agta groups and show our method performs well in these conditions. As described in the Materials and Methods section, age estimation relies on data types with distinct levels of certainty, i.e. either precise ages for some individuals or narrower or wider ranges for others. These are well modelled by different prior age distributions as discussed above. However, specific populations may present additional challenges that may not be accommodated by the basic Gibbs sampling framework. This is the case for the Agta: the isolation of different Agta groups made it impossible to compile a single complete age rank (see Figure 3). Due to the flexibility of the framework, the basic scheme of the Gibbs sampler was easily extended to

deal with partial ranks (see Results section and Figure 5). This demonstrates that specific societal organisations with particular traits can be integrated by relatively simple extensions of our Gibbs sampling framework, making our method widely applicable in diverse fieldwork conditions.

Finally, we analyse the ages we generated for the Agta to showcase how the full posterior distributions produced by our method can be used in downstream analysis. As an example, we consider age-specific fertility patterns, a fundamental aspect of population structure required to understand demography and model population processes¹⁷. Figures 5 and 6 show how the full uncertainties in the posterior age estimates can be propagated through the different steps of the analysis and integrated in the final result. In contrast, approaches based on summary statistics (e.g. mean, median, that by definition do not capture the full information contained in the data), or binning point estimates into arbitrary age classes, may distort and inflate confidence in final results.

The example above illustrates the importance for future work of deriving statistical methods that use the full information content of the data and fully account for the uncertainty in age estimates. Although we show in Figure 4 that point estimates (mean age of the posterior distribution) generated by our method already improve accuracy, the potential of our probabilistic approach is fully reached by incorporating the entire age distribution into downstream analyses. Even though no generic solutions exist for analyses involving ages, standard approaches such as resampling from the posterior distributions can be implemented on top of the output produced by our method. It should be noted that, as with all MCMC-based Bayesian approaches, the MCMC chain, once mixed, is a sample from the posterior distributions, making such approaches very easy to implement.

In summary, the flexible method described here makes full use of the information content of age range and age rank data in a statistically tractable way, leading to improved accuracy and full error integration in age estimation. This will increase the utility of cross-cultural life history datasets for hunter-gatherers and small-scale societies living in various environments, and enable

robust and powerful statistical comparisons between human population groups to shed light on the adaptive processes shaping human life history.

Appendix 5.5

Time	ID(s)	Location	Activity	Distance	Maternal Activity
06:00:20					
06:00:50					
06:01:20					
06:01:50					
06:02:20					
06:02:50					
06:03:20					
06:03:50					
06:04:20					
06:04:50					
06:05:20					
06:05:50					
06:06:20					
06:06:50					
06:07:20					
06:07:50					
06:08:20					
06:08:50					
06:09:20					
06:09:50					
06:10:20					
06:10:50					
06:11:20					
06:11:50					
06:12:20					
06:12:50					
06:13:20					
06:13:50					
06:14:20					
06:14:50					
06:15:20					
06:15:50					
06:16:20					
06:16:50					
06:17:20					
06:17:50					
06:18:20					
06:18:50					
06:19:20					
06:19:50					
06:20:20					
06:20:50					

Appendix 5.6

Individual tables for eight dependents showing the proportion of their proximate interactions which occurred with five categories of kin. Three calculations of 'proximate interactions' are used: interactions closer than 3m as observed during focal follows; interactions with physical contact/touching as observed during focal follows; and finally proximate interactions recorded using motes (remote wireless sensing devices). The purpose of these tables is to verify that the data from the motes do indeed reflect real life proximity data. Dependents' ID (Sex, Age) are indicated in the top left corner of each table. All of the focal follows (obs) data occurred for nine hours per child, split into three three hour segments, which each occurred on a different day and at a different time of day to minimise biases. The total number of beacons received by a given dependent's mote over the course of their participation in a motes sub-study is indicated at the top of the final column: motes (number of beacons).

M729 (F, 1.1)	< 3m (obs)	touching (obs)	motes (2725)
Father	15	17	16
Siblings	19	36	24
Grandmothers	7	3	10
Grandfathers	4	4	1
Aunts/Uncles	0	0	0

M282 (M, 0.2)	< 3m (obs)	touching (obs)	motes (5037)
Father	0	0	0
Siblings	0	0	0
Grandmothers	18	46	20
Grandfathers	0	0	0
Aunts/Uncles	12	36	9

M218 (F, 1.1)	< 3m (obs)	touching (obs)	motes (886)
Father	12	8	8
Siblings	0	0	0
Grandmothers	25	40	22
Grandfathers	4	0	10
Aunts/Uncles	34	35	30

M288 (M, 1.4)	< 3m (obs)	touching (obs)	motes (6783)
Father	20	12	23
Siblings	50	27	47
Grandmothers	6	2	9
Grandfathers	0	0	0
Aunts/Uncles	0	0	0

M323 (F, 1.3)	< 3m (obs)	touching (obs)	motes (7072)
Father	17	50	20
Siblings	0	0	0
Grandmothers	7	11	5
Grandfathers	0	0	0
Aunts/Uncles	0	0	0

M712 (M, 0.9)	< 3m (obs)	touching (obs)	motes (3485)
Father	0	0	0
Siblings	28	35	60
Grandmothers	33	41	12
Grandfathers	3	0	1
Aunts/Uncles	11	10	15

M285 (M, 0.7)	< 3m (obs)	touching (obs)	motes (3950)
Father	43	49	24
Siblings	0	0	0
Grandmothers	3	7	9
Grandfathers	0	0	3
Aunts/Uncles	0	0	0

M306 (F, 4)	< 3m (obs)	touching (obs)	motes (5932)
Father	0	0	0
Siblings	61	46	45
Grandmothers	0	0	0
Grandfathers	1	0	9
Aunts/Uncles	13	19	4

Appendix 5.7

Individual tables for eight dependents showing the proportion of time they spend in proximity with five categories of kin. Three calculations of ‘time in proximity’ are used: interactions closer than 3m as observed during focal follows; interactions with physical contact/touching as observed during focal follows; and finally proximate interactions recorded using motes (remote wireless sensing devices). The purpose of these tables is to verify that the data from the motes do indeed reflect real life proximity data. Dependents’ ID (Sex, Age) are indicated in the top left corner of each table. All of the focal follows (obs) data occurred for nine hours per child, split into three three segments, which each occurred on a different day and at a different time of day to minimise biases. The total number of beacons received by a given dependent’s mote over the course of their participation in a motes sub-study is indicated at the top of the final column: motes (number of beacons).

M729 (F, 1.1)	< 3m (obs)	touching (obs)	motes (2725)
Father	27	7	12
Siblings	35	15	18
Grandmothers	12	1	7
Grandfathers	7	2	1
Aunts/Uncles	NA	NA	NA

M282 (M, 0.2)	< 3m (obs)	touching (obs)	motes (5037)
Father	NA	NA	NA
Siblings	NA	NA	NA
Grandmothers	39	6	18
Grandfathers	NA	NA	NA
Aunts/Uncles	26	5	7

M218 (F, 1.1)	< 3m (obs)	touching (obs)	motes (886)
Father	21	3	3
Siblings	NA	NA	NA
Grandmothers	41	17	17
Grandfathers	7	0	0
Aunts/Uncles	29	7	13

M288 (M, 1.4)	< 3m (obs)	touching (obs)	motes (6783)
Father	42	4	29
Siblings	35	3	19
Grandmothers	12	1	11
Grandfathers	NA	NA	NA
Aunts/Uncles	NA	NA	NA

M323 (F, 1.3)	< 3m (obs)	touching (obs)	motes (7072)
Father	32	12	25
Siblings	NA	NA	NA
Grandmothers	14	3	6
Grandfathers	NA	NA	NA
Aunts/Uncles	NA	NA	NA

M712 (M, 0.9)	< 3m (obs)	touching (obs)	motes (3485)
Father	NA	NA	NA
Siblings	20	3	20
Grandmothers	71	7	12
Grandfathers	7	0	1
Aunts/Uncles	12	1	5

M285 (M, 0.7)	< 3m (obs)	touching (obs)	motes (3950)
Father	52	5	21
Siblings	NA	NA	NA
Grandmothers	4	1	8
Grandfathers	0	0	2
Aunts/Uncles	NA	NA	NA

M306 (F, 4)	< 3m (obs)	touching (obs)	motes (5932)
Father	NA	NA	NA
Siblings	61	3	36
Grandmothers	NA	NA	NA
Grandfathers	1	0	8
Aunts/Uncles	12	1	3

Appendix 6.1

Tables A6.1a- A6.13: All intermediate models between full and final reduced model for kin selection (Table 6.1 in main text); above each table the variable that was removed from the subsequent model is indicated. These are mixed effects models, with ego (child) id and alter (carer) id as random effects to control for repeated measures. The outcome variable is 'Care' – the proportion of time alter spends in proximity to ego according to the notes. Reference values for categorical predictors are indicate in the second columns. Model selection occurred via stepwise removal of variables to minimise AIC, and then stopped when all variables left in the model were significant.

Table A6.1a: Full model

Full Model			
Predictor (n=790 dyads)	Reference factor	β (S.E.)	p
ego and alter r=0.0625	unrelated	0.016 (0.01)	0.001
ego and alter r=0.125	unrelated	0.038 (0.01)	0.000
ego and alter r=0.25	unrelated	0.061 (0.01)	0.000
ego and alter r=0.5	unrelated	0.162 (0.01)	0.000
alter's no. of dependents	not factor	-0.003 (0.00)	0.048
alter's life stage (reproductive)	pre-reproductive	-0.005 (0.00)	0.229
alter's life stage (post-reproductive)	pre-reproductive	-0.012 (0.01)	0.012
alter's sex (male)	female	-0.010 (0.00)	0.002
ego's dependent siblings	not factor	-0.004 (0.00)	0.093
ego's sex (male)	female	0.013 (0.01)	0.125
ego weaned	breastfeeding	0.001 (0.01)	0.919
ego and alter same sex	different sex	0.000 (0.00)	0.881
AIC		-2832.887	

Table A6.1b

Removal of ego and alter same sex			
Predictor (n=790 dyads)	Reference factor	β (S.E.)	p
ego and alter r=0.0625	unrelated	0.016 (0.01)	0.001
ego and alter r=0.125	unrelated	0.038 (0.01)	0.000
ego and alter r=0.25	unrelated	0.061 (0.01)	0.000
ego and alter r=0.5	unrelated	0.162 (0.01)	0.000
alter's no. of dependents	not factor	-0.003 (0.00)	0.047
alter's life stage (reproductive)	pre-reproductive	-0.005 (0.00)	0.231
alter's life stage (post-reproductive)	pre-reproductive	-0.012 (0.01)	0.012
alter's sex (male)	female	-0.010 (0.00)	0.001
ego's dependent siblings	not factor	-0.004 (0.00)	0.093
ego's sex (male)	female	0.014 (0.01)	0.102
ego weaned	breastfeeding	0.000 (0.01)	0.983
ego and alter same sex	different sex	-	-
AIC		-2844.939	

Table A6.1c

Removal of ego weaned			
Predictor (n=790 dyads)	Reference factor	β (S.E.)	p
ego and alter r=0.0625	unrelated	0.016 (0.01)	0.001
ego and alter r=0.125	unrelated	0.038 (0.01)	0.000
ego and alter r=0.25	unrelated	0.061 (0.01)	0.000
ego and alter r=0.5	unrelated	0.162 (0.01)	0.000
alter's no. of dependents	not factor	-0.003 (0.00)	0.048
alter's life stage (reproductive)	pre-reproductive	-0.005 (0.00)	0.229
alter's life stage (post-reproductive)	pre-reproductive	-0.012 (0.01)	0.012
alter's sex (male)	female	-0.010 (0.00)	0.002
ego's dependent siblings	not factor	-0.004 (0.00)	0.077
ego's sex (male)	female	0.014 (0.01)	0.087
ego weaned	breastfeeding	-	-
ego and alter same sex	different sex	-	-
AIC		-2854.594	

Table A6.1d

Removal of ego's sex			
Predictor (n=790 dyads)	Reference factor	β (S.E.)	p
ego and alter r=0.0625	unrelated	0.016 (0.01)	0.001
ego and alter r=0.125	unrelated	0.038 (0.01)	0.000
ego and alter r=0.25	unrelated	0.061 (0.01)	0.000
ego and alter r=0.5	unrelated	0.162 (0.01)	0.000
alter's no. of dependents	not factor	-0.003 (0.00)	0.047
alter's life stage (reproductive)	pre-reproductive	-0.005 (0.00)	0.225
alter's life stage (post-reproductive)	pre-reproductive	-0.012 (0.01)	0.013
alter's sex (male)	female	-0.010 (0.00)	0.002
ego's dependent siblings	not factor	-0.004 (0.00)	0.129
ego's sex (male)	female	-	-
ego weaned	breastfeeding	-	-
ego and alter same sex	different sex	-	-
AIC		-2861.515	

Table A6.1e: final reduced model

Removal of ego's dependent siblings (final model)			
Predictor (n=790 dyads)	Reference factor	β (S.E.)	p
ego and alter r=0.0625	unrelated	0.016 (0.01)	0.001
ego and alter r=0.125	unrelated	0.037 (0.01)	0.000
ego and alter r=0.25	unrelated	0.061 (0.01)	0.000
ego and alter r=0.5	unrelated	0.162 (0.01)	0.000
alter's no. of dependents	not factor	-0.003 (0.00)	0.049
alter's life stage (reproductive)	pre-reproductive	-0.005 (0.00)	0.217
alter's life stage (post-reproductive)	pre-reproductive	-0.012 (0.01)	0.013
alter's sex (male)	female	-0.010 (0.00)	0.002
ego's dependent siblings	not factor	-	-
ego's sex (male)	female	-	-
ego weaned	breastfeeding	-	-
ego and alter same sex	different sex	-	-
AIC		-2871.474	

Appendix 6.2

Table A8.2: In-kind reciprocity in childcare interactions. The dependent variable is care received by ego from alter. The predictor 'Care Reciprocity' refers to the amount of care received by alter's offspring from ego's parents. All significant variables from the initial analysis in table 6.2 are included as controls. Ego id and Alter id are included as random effects to control for repeated measures. For categorical variables, reference factors are indicated in the second column.


Predictor	Reference factor	Coeff. (S.E.)	p
Care Reciprocity	not factor	0.160 (0.05)	0.001
ego and alter r=0.0625	unrelated	0.006 (0.00)	0.174
ego and alter r=0.125	unrelated	0.003 (0.01)	0.656
ego and alter r=0.25	unrelated	0.033 (0.01)	0.000
ego and alter r=0.5	unrelated	0.064 (0.01)	0.000
alter's no. of dependents	not factor	0.001 (0.00)	0.188
alter's sex (male)	female	0.001 (0.00)	0.836

Appendix 6.3

Table A8.3: Not-in-kind reciprocity in childcare interactions. The dependent variable is care received by ego from alter. The predictor 'Food Reciprocity' refers to the average number of calories transferred from ego's household to alter's over 24 hours. All significant variables from the initial analysis in table 6.2 are included as controls. Ego id and Alter id are included as random effects to control for repeated measures. For categorical variables, reference factors are indicated in the second column.

Predictor	Reference factor	Coeff. (S.E.)	p
Food Reciprocity	not factor	0.013 (0.00)	0.000
ego and alter r=0.0625	unrelated	0.019 (0.00)	0.000
ego and alter r=0.125	unrelated	0.051 (0.01)	0.000
ego and alter r=0.25	unrelated	0.037 (0.01)	0.000
alter's no. of dependents	not factor	-0.003 (0.00)	0.084
alter's sex (male)	female	-0.010 (0.00)	0.004
alter's life stage (subadult)	post-reproductive	0.010 (0.00)	0.020
alter's life stage (reproductive)	post-reproductive	0.001 (0.01)	0.090

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Competition for Cooperation: variability, benefits and heritability of relational wealth in hunter-gatherers

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Many defining human characteristics including theory of mind, culture and language relate to our sociality, and facilitate the formation and maintenance of cooperative relationships. Therefore, deciphering the context in which our sociality evolved is invaluable in understanding what makes us unique as a species. Much work has emphasised group-level competition, such as warfare, in moulding human cooperation and sociality. However, competition and cooperation also occur within groups; and inter-individual differences in sociality have reported fitness implications in numerous non-human taxa. Here we investigate whether differential access to cooperation (relational wealth) is likely to lead to variation in fitness at the individual level among BaYaka hunter-gatherers. Using economic gift games we find that relational wealth: a) displays individual-level variation; b) provides advantages in buffering food risk, and is positively associated with body mass index (BMI) and female fertility; c) is partially heritable. These results highlight that individual-level processes may have been fundamental in the extension of human cooperation beyond small units of related individuals, and in shaping our sociality. Additionally, the findings offer insight in to trends related to human sociality found from research in other fields such as psychology and epidemiology.

Many unique aspects of human sociality such as language, theory of mind and cultural norms have been proposed to provide the framework for human cooperative behaviour^{1–4}, which stands alone in its scale and ubiquity between unrelated individuals⁵. Cooperation has been fundamental to the demographic success of our species - resource exchange, collective action and specialisation have increased our efficiency at surmounting a vast array of environmental pressures^{6,7}. Therefore deciphering the context in which human cooperation and sociality evolved is invaluable to understanding what makes us unique as a species.

Inter-individual differences in sociality have been reported to have fitness implications in numerous taxa. For instance, in various non-human primates, greater social integration or social capital has been associated with increased longevity, offspring survival or mating access^{8–10}. However, in humans, the link between individual differences in social integration and reproductive fitness has received little attention. There is substantial evidence that humans have a series of psychological and physiological reinforcement mechanisms encouraging the formation and maintenance of social relationships¹¹. The existence of these proximate mechanisms encouraging social integration, implies social ties must also have some ultimate fitness enhancing function within our species. We pay particular attention to the cooperative function of human social relationships, and investigate the importance of inter-individual differences in relational wealth¹² (access to cooperation from group members) within the group.

Substantial research into the evolution of human sociality and cooperation has focused on group-level explanations. Such explanations emphasise the importance of cooperation between unrelated individuals in large scale warfare and resource competition between groups¹³. These theories assert that human sociality includes a suite of traits such as tendencies to form in-group biases and internalise cultural norms, which evolved to help individuals

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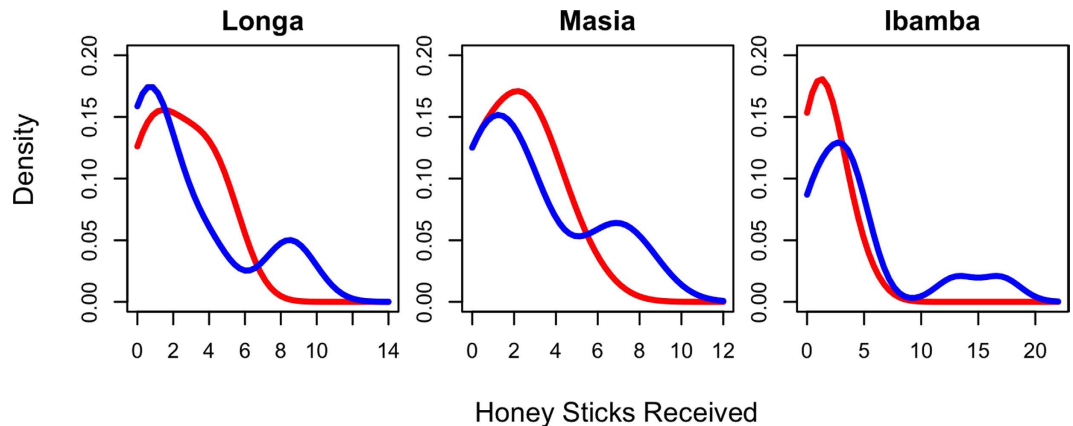


Figure 1. The distribution of relational wealth. Kernel-Density Distributions of the number of honey-stick nominations received per individual for men (blue) and women (red) in three Mbendjele camps. Camp names are indicated above each graph.

function in highly cooperative groups⁴. However, competition and cooperation can also occur at the individual level between members of the same group; and as alluded to above, in numerous non-human taxa differences in sociality within the group have important implications for fitness. Therefore, if certain individuals are better able to accrue cooperative social relationships with others (relational wealth), differences in fitness at the individual level may emerge within groups. We hypothesise that individual level ‘competition for cooperation’ may have been an important driving force in human evolution and fundamental in shaping our sociality.

We attempt to identify the role of inter-individual variation in relational wealth in the dynamics of within-group competition among BaYaka hunter-gatherers. The BaYaka are simple and mobile hunter-gatherers - they consume food they forage soon after acquisition and lack storage mechanisms, and are also politically egalitarian; such societies are the best extant approximation of the ecological conditions under which our species evolved. Therefore, although the BaYaka are an extant population of cognitively modern humans, their forager lifestyle offers a valuable opportunity for inference regarding human evolutionary history.

Whereas in other subsistence modes food storage is an option, simple hunter-gatherers rely profoundly on food sharing to mitigate risks associated with the unpredictability of their foraging niche^{14,15}; thus cooperation is at the heart of these populations. Although these societies are usually egalitarian¹⁶, social interaction and exchange is still structured within these populations^{15,17}, and certain individuals may be better able to accrue cooperative links with others by means not dependent on formal hierarchy. In such a context, where individuals are so reliant on cooperative relationships, those with more relational wealth are likely to have an evolutionary advantage. Women may benefit from more access to allocate and provisioning, in turn increasing the health and survival prospects of their offspring, and aiding in the trade-off between childcare and foraging effort¹⁸. Men with more cooperative partners, may profit from biased resource allocation towards their families, and also have increased access to mates¹⁹. Therefore, in these societies where material wealth is absent, it may be relational wealth that drives documented patterns of individual fitness variance²⁰. Indeed some evolutionary anthropologists have noted the likely relevance of the related concept of social capital to hunter-gatherers²¹. Social capital is traditionally used in economics and sociology, and the term has been used to describe social relationships and interactions with others that generate returns for the individual^{22,23}. Kaplan *et al.* hypothesise that since activities such as food sharing are often not uniform in hunter-gatherer groups, markets for cooperative partners emerge and social capital is likely to become relevant for consumption patterns and fitness²¹.

Here we use economic gift games to construct and compare individual cooperative networks in three BaYaka camps. Our results demonstrate the presence of individual variation in relational wealth, which is particularly striking among men. We show that those with more relational wealth receive food transfers from a larger number of individuals than their peers, and this is reflected in their significantly higher BMI; women with more relational wealth also have significantly higher age-specific fertility. The data also suggest there is a heritable component to relational wealth, and that cooperative alliances may be transmitted inter-generationally. While cooperation may have been important for increasing group resilience in warfare and resource competition, our findings indicate that individual level competition for cooperation within the group may also have been fundamental in shaping human sociality.

Results

Individual variation in relational wealth. We constructed an adult-to-adult gift network by playing a honey stick gift game (HSGG)²⁴ with all adults in three BaYaka camps ($n = 97$, 52 female), where each participant must choose the distribution of three honey sticks amongst other members of his/her camp. Figure 1 shows the distributions of total number of honey sticks received by an individual in the HSGG, which is our measure of relational wealth. It is clear that there is individual-level variation in number of gifts received for both sexes. It is noteworthy that the effect of individual differences in genetic relatedness to members of one’s camp on number of gifts received does not reach significance ($p = 0.067$; $R^2 = 0.036$) (see Supplementary Table 1). The extent of male variation is particularly striking producing multi-modal distributions in all three camps, where certain men

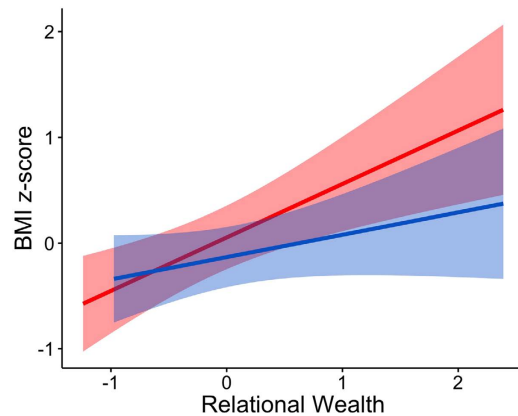


Figure 2. Relational wealth and body mass index (BMI). Relationship between relational wealth and BMI z-score (standardised by sex and age category—pre/post reproductive age for women and over/under 45 for men). Shaded bands indicate 95% confidence intervals. Blue line and shaded band represent males, red line and shaded band represent females.

receive substantially more honey sticks than their peers. Levene's tests highlight a significantly larger variance in male than female relational wealth in two of the three camps – Longa ($p = 0.023$; $n = 47$, 25 female) and Ibamba ($p = 0.011$; $n = 30$, 18 female) (see Supplementary Table 2). The lack of significance in camp Masia ($p = 0.123$; $n = 20$, 9 female) is likely a result of the small sample that is concomitant with the camp size.

This trend may reflect the fact that usually male hunting production is both more variable and shared more widely than female gathered foods in hunter-gatherer societies^{25,26}, thus there are likely to be larger differences between men in opportunities to form alliances via food sharing. In fact, acquisition of social benefits has been postulated as the driving force behind male specialisation in foraging for unpredictable resources that are widely shared²⁷. Additionally, a central aspect of Mbendjele life is the process of undergoing sex-specific initiation rites in order to gain membership to various religious cults, which increase bonding and solidarity amongst members; there is greater variation in membership to these religious cults amongst men. Nevertheless there is substantial variation in gifts received by both sexes, suggesting that if these relationships translate to benefits related to survival or reproduction, both men and women with more relational wealth can gain advantage over fellow camp members.

Relational wealth variation results in individual differences in overcoming environmental risk, and is associated with higher female fertility. Using multiple regression we found a significant association between our measure of relational wealth (HSGG nominations) and the number of camp members from whom an individual receives food in real world transfers ($\beta = 0.24$; $p = 0.005$; $n = 53$) (see Supplementary Table 3 for full results). We also find a significant relationship between BMI and relational wealth for both men ($\beta = 0.53$; $p = 0.032$; $n = 39$) and women ($\beta = 0.90$; $p = 0.003$; $n = 34$) (see Fig. 2; see Supplementary Table 4 for full results). Hunter-gatherer subsistence is highly unpredictable, thus food transfers between households are vital in buffering this high acquisition risk^{14,28}. Although these societies are often characterised by norms promoting widespread sharing^{29,30}, research shows that food transfers are biased by kinship ties, reciprocal relationships and foraging effort of others^{31–33}. The findings here indicate that those individuals with more relational wealth are better able to secure a stable nutritional income, and tackle this fundamental adaptive problem.

Maintaining a healthy body weight may also be particularly important for female fertility as it avoids secondary amenorrhea³⁴. Indeed we find relational wealth is a significant predictor of female age-specific fertility ($\beta = 0.19$; $p = 0.010$; $n = 49$) (see Supplementary Table 5). The result cannot be explained by reverse causality i.e. HSGG participants preferably distributing their honey sticks to women who have more offspring and thus may be in greater need: Female participants were at different stages of their reproductive career and offspring of older participants may have already reached adulthood, thus a participant's total fertility does not necessarily match their current number of dependent (under 16) offspring. We find no significant correlation between a woman's current number of dependent offspring living in the household and relational wealth ($G = 0.14$, $p = 0.280$, $n = 51$), suggesting in the initial association between relational wealth and age-specific fertility relational wealth is affecting fertility rather than vice-versa. Nevertheless the result must be treated as preliminary since our measure of fertility and relational wealth reflect different timescales; specifically relational wealth is a measure reflecting one point in time (the data collection period), whereas fertility reflects the length of ego's reproductive career thus far.

Relational wealth is inherited from fathers. In order to test if relational wealth is heritable, we conducted gamma correlations between the number of honey stick nominations of parents and their adult offspring in the HSGG (see Fig. 2). Ego's (male or female) relational wealth as an adult is positively correlated with ego's father's ($G = 0.65$, $p = 0.002$; $n = 14$), and ego's mother's ($G = 0.17$, $p = 0.294$; $n = 26$) relational wealth (see Fig. 3); but these results are only significant for the former. Although this hunter-gatherer society is egalitarian^{29,35,36}—no

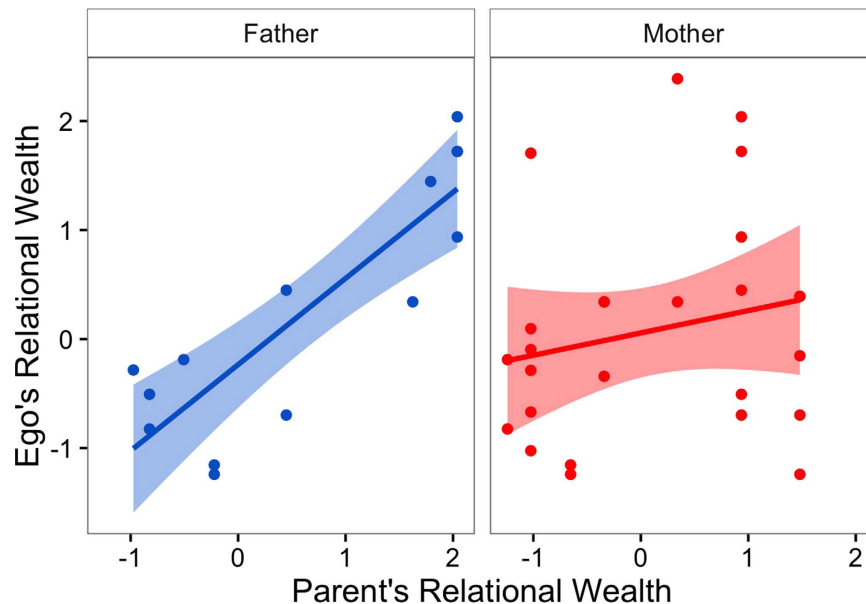


Figure 3. The inheritance of relational wealth. Scatter plots representing the relationship between ego's relational wealth and ego's father's (blue) and ego's mother's (red) relational wealth. Shaded bands indicate 95% confidence intervals.

individuals can exert any authority over others, and there are no hierarchical positions - the results here indicate there is a degree of heritability of relational wealth; we explore the potential mechanisms in the discussion.

Discussion

We find that relational wealth varies by individual, provides health and fertility benefits and is partially heritable. These results highlight that in the absence of material wealth accumulation and social hierarchy, relational wealth may be an important determinant of individual fitness among simple hunter-gatherers. Individuals vary widely in their access to cooperation from fellow camp members, and those with more relational wealth are better equipped to overcome the high risk that characterises the hunter-gatherer lifestyle, since they have a significantly larger pool of food donors to insure against nutritional shortfalls. In addition to augmenting survival and health outcomes, social ties appear to increase reproductive rates of the BaYaka. Women with more relational wealth have higher age-specific fertility, a relationship which may be mediated by BMI since low body-weight disrupts ovulatory processes³⁴. Additionally, we previously demonstrated that men with very high relational wealth are more likely to achieve polygyny in this group, which increases their reproductive rate¹⁹. Studies of other foraging societies have also reported positive associations between male social status and fertility, by examining the effect of hunting ability on mating access and reproductive outcomes^{37,38}.

Egalitarian hunter-gatherers lack the heritable hierarchical positions which are found in agricultural and industrialised societies¹⁶, however, our results indicate partial heritability of relational wealth. We did not investigate the mechanism for this heritability explicitly, but there are several possibilities. Genetic factors have been shown to influence social network positioning in human and non-human primates^{39,40}. Additionally, the inheritance may operate via the direct transmission of cooperative alliances from parents to offspring. This may explain the significant association with paternal but not maternal relational wealth - if relationships are transmitted inter-generationally, an individual's relational wealth would be more closely associated with the parent whose sex has higher variability in number of social relationships. This inheritance of social ties would increase the evolutionary advantage of strengthening one's social network since the associated benefits can accrue over multiple generations. Therefore, in hunter-gatherer groups which are often egalitarian and do not accumulate material resources, relational wealth may drive documented patterns of inter-individual fitness variance and fertility inheritance^{20,41}, and may be the resource that is transmitted inter-generationally.

These findings offer a significant contribution to our understanding of human social evolution. The benefits of social bonds and importance of individual differences in social positioning have been identified for numerous taxa including non-human primates, feral horses and bottlenose dolphins^{10,42,43}. Social ties have been associated with a variety of benefits in different species including increased longevity, offspring survival and mating access, enhanced dominance rank and reduced harassment^{8,9,42,44}. However, similar research investigating the importance of inter-individual differences in sociality among humans is scant. This study differs from those in non-human taxa in its specific focus on cooperative networks (rather than proximity networks for example), nevertheless we still demonstrate that individual variation in an aspect of human sociality (relational wealth) has an important impact on health and fertility in hunter-gatherers.

Many investigations in to the evolution of human cooperation and sociality, specifically its widespread nature and extension beyond kin ties, have emphasised the importance of inter-group competition. These explanations highlight that human sociality evolved to facilitate group wide cooperation, since groups with cultural norms

which are better able to promote cooperation and group beneficial behaviours outcompete others⁴. Our results do not undermine the possibility of selection at the group level, but draw attention to the importance of the role of cooperation in competition within the group. We find substantial inter-individual variability in access to cooperation (Fig. 1), which largely cannot be explained by kinship networks (Supplementary Table 1), and has meaningful consequences for health and fertility outcomes (Fig. 2/Supplementary Table 5). Cooperation is an integral means by which hunter-gatherers deal with their unpredictable environment, and extends across many activities including childcare, foraging and food sharing^{17,45,46}. In the same way that groups with a greater capability to harness cooperation performed well in warfare and resource competition⁴, here we show that individuals within groups who harness more cooperation have increased resilience against the unpredictable foraging niche typifying hunter-gatherer subsistence.

Our findings suggest consideration of within-group competition is crucial to a complete understanding of the evolution of human sociality. These results indicate that over their evolutionary history some hunter-gatherer individuals may have outcompeted other members of their group by expanding their cooperative networks beyond the small close kin units ubiquitous in the animal kingdom. Therefore, although we may have psychological tendencies to form in-group biases and internalise cultural norms as a result of inter-group competition^{4,47}, many of our derived social traits may also reflect within-group competition. Research from psychology and epidemiology on modern populations demonstrate a number of findings consistent with our results such as - positive associations between individual social integration and mental and physical health⁴⁸; a psychological tendency for individuals to evaluate their social positioning relative to their peer group⁴⁹; and neuroendocrine mechanisms encouraging the formation and maintenance of friendships¹¹.

Methods

This study has full approval from the Ethics Committee of University College London, and the methods were carried out in accordance with the approved guidelines. Informed consent was obtained from all participants and research permission granted by the Republic of Congo's Ministry Of Scientific Research. The fieldwork took place between March and July 2014.

Study population. Our study uses data from the Mbendjele BaYaka, a subgroup of the BaYaka who speak Mbendjele language and whose residence spans across the forests of Congo and Central African Republic. BaYaka subsistence techniques include hunting, trapping, fishing, gathering and honey collecting; as well as some trade with neighbouring farmer groups. Food sharing is an integral component of BaYaka subsistence and culture. The BaYaka live in *langos* - multi-family camps constituted of a number of *fumas* (huts) in which nuclear families reside; camp size tends to vary from 10–60 individuals, and genetic relatedness within camps is low³⁶. The BaYaka are predominantly serially monogamous, with some incidence of polygyny¹⁹. We visited three camps in the Likoula and Sangha regions of Congo's Ndoki Forest (see Supplementary Fig. 2 for map).

HSGG. This game was played with all willing members of a camp and was completed as quickly as possible, usually within 2–3 days in each camp. All instructions were spoken in French by the researcher, and then immediately repeated in Mbendjele by the translator. The game was based on the procedure of Apicella *et al.*²⁴. The key features of our protocol for the game were:

1. Participants were asked to accompany the researcher and translator to a private area.
2. Participants were shown three honey sticks, and told that real honey was within each batton.
3. Participants were told they must decide to whom they would like us (the researchers) to give the honey sticks.
4. Participants were told they could give freely i.e. all three sticks to one individual or one stick to three different individuals etc.
5. Participants were told they could nominate any adult in their camp other than themselves.
6. After the games had been completed with all adults in camp, the honey sticks were distributed according to the results.

Food Transfer Observations. Households were observed by JT over a series of two to four hour time blocks, with households observed for a total of 24 or 36 hours depending on the camp. Observations were evenly distributed between 6 am and 6 pm and spread over several days. During observation periods, a record was made of all food produced by a focal household. If division of resource packages occurred, all recipient households were identified. For all food cooked and consumed by the household, the type and amount of food were recorded and all those who ate the food were identified.

Anthropometrics. We measured height and weight of all willing and non-pregnant adults in each camp in order to calculate BMI. Height was measured to the nearest mm using a Harpenden anthropometer, and weight using a Philipps mechanical scale.

Analyses. In all analyses, relational wealth is calculated as the number of nominations received in the HSGG standardised by camp and sex.

We use multiple regression to analyse the relationship between relational wealth and number of food sharing donors. The response variable is the number of different camp members observed to share food with ego during food transfer observations. The predictor is ego's relational wealth, and controls are ego's sex, age (see Supplementary Information for details on calculation of age), and length of time ego was observed in the food transfer observations. In one camp, participants were observed for 24 hours and in the other two camps participants were observed for 36 hours; therefore we use a dummy variable to control for this.

We use multiple regression to analyse the relationship between relational wealth and BMI for each sex. We control for whether ego is post-reproductive (females)/over 45(males) since there is a significant decline in BMI for these age-groups in our sample. We also control for camp membership (categorical).

We use multiple regression to analyse the relationship between relational wealth and female fertility. We use age and age² as controls to account for the quadratic relationship between age and fertility. To check whether reverse causality may explain the significant association found, we conduct a gamma correlation between female relational wealth and the number of dependent offspring in their household. The gamma correlation is conducted using the *rococo* package in R; and is selected as it is appropriate for variables which contain many ties, such as number of dependent offspring.

For correlation analyses of ego's and ego's parents' relational wealth we also use gamma correlations because they are appropriate for small sample sizes and data with ties.

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Author Contributions

A.B.M. idealized the project; N.C., G.D.S., J.T., A.B.M., L.V. and R.M. designed the study; N.C., G.D.S., J.T. and A.R. collected the data with the help of P.G., E.S., M.D., A.P. and D.S. N.C. wrote the manuscript with the help of all other authors. All authors give their final approval for this version to be published.

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Polygyny without wealth: popularity in gift games predicts polygyny in BaYaka Pygmies

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1. Summary

The occurrence of polygynous marriage in hunter–gatherer societies, which do not accumulate wealth, remains largely unexplored since resource availability is dependent on male hunting capacity and limited by the lack of storage. Hunter–gatherer societies offer the greatest insight in to human evolution since they represent the majority of our species’ evolutionary history. In order to elucidate the evolution of hunter–gatherer polygyny, we study marriage patterns of BaYaka Pygmies. We investigate (i) rates of polygyny among BaYaka hunter–gatherers; (ii) whether polygyny confers a fitness benefit to BaYaka men; (iii) in the absence of wealth inequalities, what are the alternative explanations for polygyny among the BaYaka. To understand the latter, we explore differences in phenotypic quality (height and strength), and social capital (popularity in gift games). We find polygynous men have increased reproductive fitness; and that social capital and popularity but not phenotypic quality might have been important mechanisms by which some male hunter–gatherers sustained polygynous marriages before the onset of agriculture and wealth accumulation.

2. Introduction

Before the advent of agriculture 12 000 years ago, humans lived as hunter–gatherers—this subsistence mode occupies more than 90% of our species’ evolutionary history [1]. Throughout this period, humans lived in foraging societies characterized by high mobility

and no accumulation of material resources [2,3]. Given the relative modernity of the Neolithic transition, deciphering the social structure and selective pressures experienced by hunter-gatherers is invaluable in understanding the suite of evolutionary adaptations possessed by humans today. One remaining question regarding human social structure is the evolution of marriage systems, which have been demonstrated to have knock-on effects for inheritance systems, parental investment and intra-sexual aggression within human societies [4–6]. Combined evidence from extant hunter-gatherers, phylogenetic reconstruction and archaeological remains suggests a predominantly monogamous/serially monogamous system in human origins, with polygyny potentially being prevalent at low levels [7–11].

Although differences in male reproductive success have been explored in some foraging populations, these studies have focused on variation in frequency of extra-marital affairs (see [12] for review). However, the occurrence of contemporaneous legitimate partnerships between multiple women and one man, i.e. polygynous marriage, within a hunter-gatherer context remains largely unexplored. In contrast to extra-marital affairs, women engaging in polygynous marriages are incurring the substantial cost of sharing a provider for themselves and their offspring; it is for this reason that polygynous marriage is a particularly interesting phenomenon.

The most common explanation for polygynous marriage employed by human behavioural ecologists is known as the female choice model—an adapted version of the polygyny threshold model [13,14]. The premise is that a female's fitness is determined by the access to resources her mate can offer her. Therefore, polygyny occurs in societies where there are large inequalities in male wealth because, evolutionarily speaking, females are better off becoming the second partner of a wealthy man than the first of a poor one. This explanation has been applied successfully in a large body of within and cross-cultural anthropological research on human polygyny [15–17]. However, it is only relevant to societies in which material wealth is accumulated such as industrialized, agriculturalist and pastoralist, not hunter-gatherers. In fact, there is suggestion that among the Ache, hunter-gatherer families with polygynous marriages operate a resource deficit and depend more than others on food sharing from other households [18], which makes large-scale polygyny seemingly unsustainable in hunter-gatherers that do not have storage. To elucidate the incidence of polygyny in hunter-gatherers, who do not accumulate material wealth or defend individual territories, we must search for alternative explanations.

We first explore the fitness outcomes of BaYaka polygyny. Although previous anthropological research consistently finds that polygynously married men achieve higher reproductive success, these findings are derived from societies that accumulate wealth, and thus some wealthy men are able to afford multiple families [7,16,19]. Given the lack of material resources in BaYaka subsistence, polygynous men may be inadequately equipped to support multiple families. Therefore, here polygynous marriage could instead represent a maladaptive behaviour resulting in increased offspring mortality and lower fitness. In order to address this, we test how marital status affects a man's number of living offspring.

We also explore other possible mechanisms that could facilitate the achievement of polygyny by a few hunter-gatherer men through examination of marriage practices of the BaYaka Pygmies. Women may engage in polygynous marriages because certain men are of a sufficiently high quality that the fitness benefits outweigh the costs of marrying an already married man. Here quality refers to any attributes possessed by a man that ultimately result in increased fitness for a woman marrying him. We investigate whether polygynous BaYaka men differ in quality from their non-polygynous counterparts across two dimensions—phenotypic quality measured by physical attributes of height and hand-grip strength, and social capital quality determined by economic gift games. Phenotypic quality may increase a man's mate value as it reflects genetic quality, which will be inherited by his offspring, thus increasing their viability in a strenuous environment with high mortality risk [20]. Previous studies have mixed results; however, researchers have found positive associations between number of marriages (including serial marriages) and height in Baka Pygmies from Cameroon [21], and strength in the Hadza [22]. Alternatively, in the absence of material wealth, social capital may be the resource that enables certain men to afford multiple families; anthropologists have highlighted the importance of wide social networks to buffer risk associated with hunter-gatherer subsistence [23].

We find polygynous men do have increased reproductive fitness relative to their monogamous peers; and that social capital, but not our measures of phenotypic quality, might have been an important mechanism by which some male hunter-gatherers sustained polygynous marriages before the onset of agriculture and wealth accumulation.

3. Methods

3.1. Study population

Our study uses data from the Mbendjele BaYaka, a subgroup of the BaYaka who speak Mbendjele language and whose residence spans across the forests of Congo and Central African Republic. BaYaka subsistence techniques include hunting, trapping, fishing, gathering and honey collecting. The BaYaka live in *langos*—multi-family camps consisting of a number of *fumas* (huts) in which nuclear families reside; camp size tends to vary from 10 to 60 individuals. They are predominantly serially monogamous like most African hunter–gatherers. Nevertheless, there are a notable proportion of men who are/have ever been married polygynously in our study sample (14.3%). This is a rate of men who achieve polygyny in their lifetime, which may overstate polygyny prevalence as compared to other ‘snapshot’ estimates which calculate the proportion of men/women married polygynously at one specific point in time. However, comparably high levels have been found in other BaYaka Pygmy groups—e.g. Aka [24], using the snapshot method. Such estimates are considerably higher than most well-studied foraging groups, e.g. 4% in Ache; 6% in Kung [6], but probably more representative of foraging societies on the whole, which have a mean male polygyny rate of approximately 14% [25]. When a man has multiple wives simultaneously, they usually reside in different camps, among which he divides his time. We use the term marriage, however it is noteworthy that there is no formal marriage institution. Partnerships are acknowledged by the community when a man and woman begin living in a *fuma* together. This is followed by a period of bride service by the husband for his new in-laws [26].

Our study population consists of 70 men, of whom 10 have been polygynous, from five BaYaka camps in the Likoula and Sangha regions of Congo’s Ndoki Forest (see the electronic supplementary material, figure SI). Not all data were collected in each camp, e.g. gift games were only played in the final three camps we visited; additionally, some individuals were unable to participate—sample sizes for each analysis are indicated.

3.2. Data collection

3.2.1. Measuring the influence of polygyny on male reproductive success

Reproductive histories were recorded from adult men and women. Individuals were asked to list all of their children and spouses, specifying whether they were dead or alive and which partner they conceived each child with. If a man had more than one spouse, he was asked ‘when you started with the second woman, had you already finished with the first, or did you carry on with two women at the same time?’. A man is considered to be polygynous if the answer to this question is that he continued relationships with two women simultaneously. Therefore, men who have ever been polygynous are coded as polygynous even though they may not necessarily be so currently.

3.2.2. Quantifying phenotypic quality

We inspect differences in two physical attributes, specifically hand-grip strength and height. Hand-grip strength was measured using a manual dynamometer. Participants had three attempts with each hand and were instructed to keep their arm straight and perpendicular to the ground. Height was measured using a Harpenden anthropometer. To ensure accuracy, two researchers would take the measurements, with one ensuring that the anthropometer was perpendicular to the ground and that the participant was standing straight, while the other noted the reading.

3.2.3. Quantifying social capital

To measure social capital, we used the Gift Game procedure described in Apicella *et al.* [27]. In this game, participants were asked in private to nominate recipient(s) of three honey sticks. It was explained that participants could allocate the three honey sticks freely, i.e. give one stick to three different individuals or three sticks to one individual, etc. Recipients were permitted to nominate any individual from their camp other than him/herself. This game was played with all adults in the camp. In-degree in the gift game is used as a proxy for social capital, i.e. the more honey sticks an individual receives from other members of his camp, the greater his social capital.

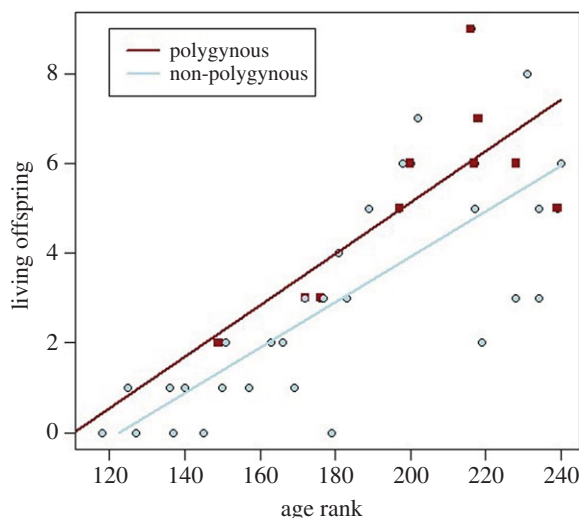


Figure 1. Scatter plot and regression lines of number of currently living offspring by age rank. Purple squares/line are polygynous individuals and blue circles/line are non-polygynous individuals.

Table 1. Multiple regression of number of living offspring on marital status, controlling for age rank. The predictor ‘polygynous’ is a dummy variable—its coefficient represents the change in number of living offspring for age when a man is coded as polygynously married. Thirty-nine refers to total sample size, of which 10 men were polygynous.

<i>n</i> = 39, 10 polygynous	coeff.	<i>p</i> -value
polygynous	1.307	0.025*
log age rank	8.721	0.000***

*** $p < 0.001$, * $p < 0.05$.

3.2.4. Age

In order to analyse whether the polygynous men in our sample had higher reproductive success, it is necessary to control for age. However, none of the individuals in our sample knew their own age, thus we had to create a relative age list and used age rank as a control (see the electronic supplementary material for details).

4. Analyses

- (1) To test whether polygynous men have higher reproductive success we use multiple regression. The response variable is number of living children, with polygynous status (binary) as a predictor and log age rank as a control. Log age rank is used since this fits our data better than age rank squared.
- (2) To determine whether phenotypic quality/social capital explains why certain men are polygynous, we conduct one-way randomization tests with 9999 Monte Carlo re-samplings comparing polygynous and non-polygynous men across these dimensions. For phenotypic quality, we compare their height and hand-grip strength (highest score from all attempts). For social capital, a comparison of *z*-scores for gift game in degree is used; it is necessary to create *z*-scores to control for camp size.

All analyses were conducted using R i386 3.1.1; we use the coin package for randomization tests.

5. Results

5.1. Men in polygynous marriages have higher reproductive success

Our results demonstrate that polygynously married men do have more living offspring for their age than men who are not polygynous (table 1 and figure 1).

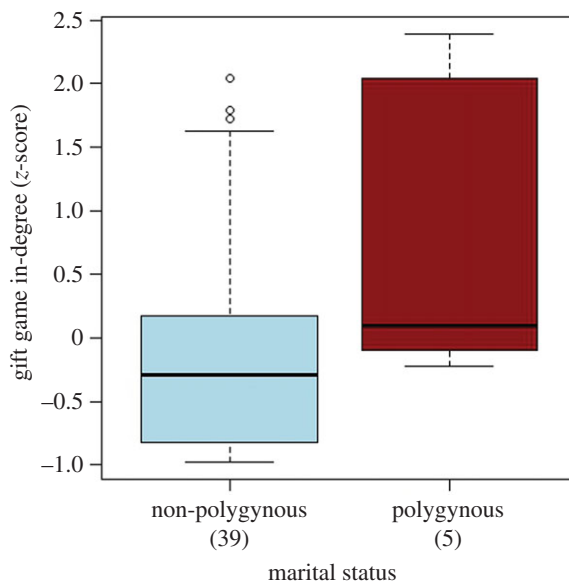


Figure 2. Boxplot comparing gift game in-degree z-scores of polygynous and non-polygynous men. Z-scores are standardized by camp, to allow simultaneous comparison of social capital of men from all camps by controlling for camp size. Hollow circles represent outliers. Sample sizes are indicated in parentheses.

Table 2. One-way randomization tests comparing phenotypic quality and social capital of polygynous and non-polygynous men. Sample sizes are indicated: the first value is total sample size and the value in parentheses refers to the number of polygynous men in the sample.

	<i>n</i>	mean (polygynous)	mean (non-polygynous)	<i>z</i>	<i>p</i> -value
<i>(a)</i> phenotypic quality					
height (cm)	66 (10)	155.7	154.6	−0.500	0.616
hand-grip	62 (10)	46.6	45.7	−0.174	0.871
<i>(b)</i> social capital					
Gift Game z-score	44 (5)	0.842	−0.102	−2.015	0.034*

* $p < 0.05$.

5.2. Phenotypic quality is not associated with polygyny

Our results do not provide support for the hypothesis that men who achieve polygyny are of higher phenotypic quality. Polygynous men in our sample are slightly taller and stronger than non-polygynous men, but these results are not significant (table 2*a*).

5.3. Greater social capital is associated with polygyny

Polygynous men have significantly more social capital than non-polygynous men ($p = 0.034$); see figure 2 and table 2*b* for full results. In two of the three camps where the gift game was played, the individual with the highest number of gifts was polygynous. Both of these men were the *kombetis* (an appointed spokesperson for a camp) of their respective camps. In Longa, this individual received nine honey sticks compared to a camp male average of 2.6; similarly, in Ibamba, these figures are 17 and 4.5, respectively. In Ibamba, there were three polygynous men, who ranked first, third and fourth in popularity out of 12 men in that camp.

6. Discussion

The fact that polygyny rates correlate with wealth inequality in most human populations [5,17] raises the question of whether polygyny was even possible before the Neolithic transition, and whether human origins are strictly monogamous. Here we present a preliminary insight in to this question by exploring

both whether polygynous marriage is actually beneficial to men in a hunter–gatherer context, and how certain men achieve polygyny without material wealth. We find polygynous men have greater reproductive success; and differences in our measures of social capital but not phenotypic quality explain which men achieve polygyny.

It is possible that polygynous marriage is a recent maladaptation among BaYaka men as a result of copying a Bantu pattern of marriage. However, even if higher rates of polygyny are new to the BaYaka Pygmies, they do not seem to be maladaptive for BaYaka men. Polygynous men do experience greater reproductive success in spite of the lack of accumulation of material wealth—they have more living offspring for their age than their non-polygynous counterparts.

With respect to the determinants of which men achieve polygyny, we assessed the importance of phenotypic quality and social capital. Strength and height have been frequently found to increase male attractiveness since they are signals of genetic quality [28–30]. In environments of high pathogen stress, such as those experienced by the BaYaka, women may place more value on genetic quality in order to increase the viability of their offspring [19,31]. Additionally, in contexts where male provisioning is less important, women shift mate selection strategies away from ‘resource shopping’ towards ‘gene shopping’ [9], and male signalling of quality becomes more fundamental in mating dynamics [32]. In contrast to a more typical pattern among forager groups where the majority of provisioning comes from men’s hunting production [33], among BaYaka Pygmies (Aka) from Central African Republic male and female contribution to subsistence is roughly equal in terms of calories [34]; therefore, we might expect BaYaka women to place relatively more value on genetic quality. In spite of this socio-ecological context, our results suggest that polygynous men do not differ significantly in strength or size. Here, we only examine two physical attributes; a recent study on the Hadza with numerous measures found effects on reproductive success that differed in direction and significance [22], highlighting the difficulty in operationalizing phenotypic quality with few variables. Thus, one must be cautious when generalizing these results. Additionally, the short stature of Pygmy groups may be a by-product of other positively selected life-history processes [35], and therefore individual variation in height may not be reflective of differences in phenotypic quality in this population.

The relative importance of social capital or phenotypic quality is also likely to be affected by BaYaka food sharing patterns. A variety of sharing systems have been identified within hunter–gatherer societies, in particular demand sharing and reciprocity [36,37]. With respect to mate value, if demand sharing is the predominant driver of food transfer, then food sharing is completely unbiased and widespread; therefore, a man’s provisioning ability is less important, in turn raising the relative importance of his physical attractiveness. Conversely, under a system of reciprocity food transfer is not unbiased; rather, it reflects long-standing sharing relationships. A meta-analysis of human and non-human primate food sharing highlights that reciprocal transfers are more prevalent in the Central African Republic BaYaka (Aka) than any other group included in the study [38]. Establishing sharing relationships is likely to be crucial to securing a stable nutritional income for one’s family; hence, as shown in our results, we expect that social capital is likely to be a central component of a BaYaka man’s mate value—more so than in other human societies.

We find polygynous men have significantly more social capital than their non-polygynous counterparts. This finding is unlikely to be due to reverse causality, i.e. polygynous men having more affinal kin playing the game, since none of the polygynous men in our sample had multiple wives living in the same camp.

We can only speculate about how social capital assists men in obtaining and supporting multiple reproductive partners at the same time. One possible pathway may be that men with a large social network are more effectively able to buffer food risk. Owing to the absence of food storage in the dietary niche occupied by humans for the majority of our evolutionary history, risk reduction is considered to have been one of the most important adaptive problems faced by our species and the foundation of our sociality [39]. This remains the case for modern day hunter–gatherers, and thus within these communities it is possible that individuals who have more social capital can overcome this adaptive problem more successfully via widespread food sharing networks. These individuals with an abundance of social support may be more attractive marital partners, and the only ones capable of supporting multiple families. Perhaps ensuring bias in food sharing is how social capital translates into the acquisition of multiple wives.

When a polygynous man is staying in another camp with a different wife, his foraging contribution is completely absent. Thus, unless female production covers 100% of provisioning, women incur a cost by marrying polygynously. Moreover, in this group of BaYaka only men hunt, and the protein and fat content of meat they provide are necessary dietary complements to female gathering. Additionally,

fathers in BaYaka groups have been found to provide more direct care than any other society in the world [34]. It is this paternal care that facilitates female production, freeing up mothers to invest time in foraging. Thus, a polygynously married woman, in the absence of her husband, is also likely to encounter more difficulties balancing the trade-off between direct care and foraging. Thus, the wives of polygynous men may rely on their husband's large social network for provisioning and allocare when he is residing in another camp with a different wife.

BaYaka camps have a political position of *kombeti*, which can be described as an appointed spokesperson who has influence, but not absolute authority, over camp decisions regarding subsistence and movement, as well as interactions with farmer and other non-BaYaka groups [24]. There are numerous reasons why these individuals may have higher mate value to women. Although the BaYaka generally do not accumulate material resources, they occasionally receive resources such as money, clothes, machetes, etc., from interaction with tourists, researchers, farmers and government social programmes. *Kombetis* may manipulate the distribution of these resources—in the past when we have given gifts for a camp, the *kombeti* would direct their distribution and usually end up with a larger share (not necessarily overtly); they also receive more goods such as cigarettes from farmers [34]. It is noteworthy that this only occurs with resources that come from outside groups; *kombetis* have no authority over resources produced by camp members themselves. Additionally, these men, through their prestige, may be more able to influence group decisions in their favour thus increasing their mate value further; such an effect has been found in prestigious Tsimane men who in turn have favourable fitness outcomes [40]. Dental research also suggests *kombetis* may have access to a more nutritious diet, and this may be a result of other camp members sharing more high-quality foods with them [41]. This position of *kombeti* is appointed, thus attaining and maintaining this status relies on social capital, and not excessively exploiting it. In our sample, there are only two *kombetis*, both of whom are polygynous and had the most social capital in their respective camps, providing some support for this pathway; confirmation would require conducting pathway analysis with a larger sample size.

This research attempted to identify the determinants and outcomes of polygynous marriage within a society that lacks material wealth. Our findings that polygynous hunter–gatherer men experience advantageous fitness outcomes and have more social capital provide an important step in understanding hunter–gatherer marriage, and whether/how polygynous marriage was even possible before the Neolithic. Some areas of the world like Australia are notorious for high levels of polygyny among hunter–gatherers [42], and cross-cultural research indicates that on average approximately 14% of men are polygynous in foraging groups [25]. Understanding how such systems evolved in spite of unpredictable hunting returns and the need for provisioning has always been a challenge.

To enhance our understanding of this topic further, it would be interesting to investigate why certain men have more social capital than others, and how men compete across this dimension. Australian Aborigine men enhance their status via initiation rites and secret knowledge [42]; perhaps a similar process is occurring with the BaYaka. There are a vast number of initiation rites that occur at different stages of a man's life, some which all men participate in and others which only a fraction of men undergo. Status can be further augmented by becoming a *konja wa mokondi*, where one becomes an authoritative figure in the initiation of others. *Nganga* is another of the few recognized positions held by the BaYaka and refers to healers with advanced knowledge of *bwanga*—forest medicines [24,26]. The attainment of such positions relies on specialist knowledge and individuals who bear such knowledge are perceived to provide benefits to the group, and in turn are likely to accrue social capital. Additionally, in many foraging societies good hunters have high social status, which in turn provides benefits of extra-marital affairs and favourable treatment from camp members who value their contribution and quality [12,43]. Another remaining question is why women choose to enter into polygynous marriages with popular men. Potential starting points to address this question include examining whether men with more social capital have advantageous food sharing networks; or whether social network size is a predictor of becoming *kombeti*, and the extent to which this position facilitates the manipulation of communal resources.

Ethics statement. This research and fieldwork was approved by UCL Ethics Committee (UCL Ethics code 3086/003) and carried out with permission from the Ministry of Scientific Research, Congo. Informed consent was obtained from all participants.

Data accessibility. The data supporting this article are available in the Dryad Digital Repository (doi:10.5061/dryad.0dk3n).

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Conflict of interest. We have no competing interests.

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Polygyny Threshold, The

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Synonyms

[Female choice polygyny](#); [Resource-defense polygyny](#)

Definition

The polygyny threshold model (PTM) provides an explanation for the occurrence of polygyny in the animal kingdom – the mating/marriage of one male with multiple females. This model is principally applied to species, including humans, in which males provide/defend resources to provision their mates and offspring. The *polygyny threshold* refers to the minimum level of inequality in male resource holding, such that a given female's reproductive success is enhanced by becoming the second mate of a resource-rich and already paired male, rather than the sole mate of a resource-poor unpaired male. Once this threshold is surpassed and there is sufficient inequality, polygyny is predicted to occur.

Introduction

Understanding the determinants of mating and marriage systems is vital to a complete understanding of humanity, since they have been demonstrated to have knock on effects at many levels of society. These tenants of social structure bear influence on parenting strategies and family dynamics, violence and crime rates, inheritance systems, and much more. In the case of polygynous societies – where one man mates/marries multiple women – such a system is associated with decreased paternal care for offspring (Strassmann 1981), increased male-male aggression (Schmitt and Rohde 2013), and patrilineal inheritance systems (Hartung et al. 1982). The socially imposed monogamy observed in many industrialized societies today is not representative of the majority of human populations. In fact, polygyny is estimated to be permitted in more than 80 % of human societies (Murdock 1967), and therefore it is still very relevant to our understanding of human behavior.

In order to understand the evolutionary explanation for the widespread occurrence of polygyny in human societies, it is necessary to comprehend the underlying mechanisms behind sex differences in mating behavior and mate choice. The following entry will have five sections: (1) parental investment and female choice; (2) female mate preferences; (3) women's preference for resources; (4) the polygyny threshold model,

theory; and (5) the polygyny threshold in humans – empirical evidence.

Parental Investment and Female Choice

Trivers defined parental investment as *any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring* (Trivers 1972, p. 139). These investments include energetic investments such as producing gametes, material investments such as provisioning an offspring with nutrients, and behavioral investments such as guarding offspring from predators. Males and females have different costs of reproduction, which begin with anisogamy – the fusion of two different gametes in sexual reproduction. The male sex cell is small and metabolically cheap to produce, whereas the female sex cell is larger and more costly. Usually the female is the sex which invests more in the offspring given the initial sunk investment of the more costly sex cell (Trivers 1972). Conversely, the extent of male parental investment (MPI) varies considerably between species, sometimes being limited to the contribution of sperm, e.g., in fish species with internal fertilization, males do not participate in any brood care (Perrone and Zaret 1979); and in other cases MPI includes considerable provisioning and protection for extended periods of time, as observed in many bird species (Møller and Cuervo 2000).

Given that the male gamete is cheap and that it is usually females who invest more in offspring, males have a fast potential reproductive rate; thus, the limiting factor of a male's reproductive success is access to opportunities to fertilize female sex cells (hence, polygyny is advantageous to males since it increases these opportunities). On the contrary, female reproductive rates tend to be restricted by the production of costly sex cells and considerable investments in rearing offspring; hence access to mates is not the primary limiting factor of female fitness (Clutton-Brock and Vincent 1991). Therefore, it is typically females who are the more choosy sex in terms of mate

selection, this phenomenon is referred to as “female choice” (Trivers 1972).

Female Mate Preferences

The traits valued by females of a particular species are largely determined by the necessity of MPI for the successful siring of offspring. Among species where MPI is low and unnecessary, females will predominantly select mates based on their genetic robustness (in terms of survival and reproduction prospects), and complementarity (in terms how well matched a male and female genome are for the production of robust offspring) (Trivers 1972). However, in other species where MPI is more necessary and biparental investment is more crucial to offspring survival, alongside purely genetic characteristics, females give consideration to the ability of a male to provide high-quality parental investment (Trivers 1972). This preference explains the ubiquity of the courting ritual in which males offer females nuptial gifts that serve as demonstrations of their willingness and ability to invest resources. Such behaviors are common in species where females rely substantially on MPI, including many species of bird, and indeed in our own – the diamond engagement ring is an appropriate signal of a man's commitment to invest resources (Lack 1940; Miller and Kanazawa 2007).

Women's Preference for Resources

Narrowing the focus to humans, compared to the rest of the mammalian class, our species are somewhat of an anomaly – in approximately 95 % of mammalian species, MPI is very limited (Geary 2000). In contrast, whether it is manifested in the form of hunting for the next meal or paying tuition fees, paternal investment is ubiquitous and extensive across much of the spectrum of human societies. This high MPI can be attributed to the combination of two factors – the restricted reproductive rate of women and the highly dependent nature of human children.

Due to the 9-month internal gestation period and the subsequent phase of lactational amenorrhea, women are very limited in the quantity of offspring they can produce over the course of their reproductive career. Additionally, the narrow female pelvic canal designed for bipedalism combined with strong selection for encephalization has resulted in the *obstetric dilemma* and human children being born altricial with a substantial proportion of brain growth having to occur post-partum (Rosenberg and Trevathan 2002). Thus children have an extended period of dependence, requiring extensive provisioning to support their metabolically expensive development (Kaplan et al. 2000). Therefore, women have been strongly selected to show mate preferences for men who demonstrate a capacity for high MPI and who can provide resources to maximize the quality of the limited quantity of (highly dependent) offspring they can produce. In a seminal study of 37 cultures across six continents, Buss (1989) showed that women consistently place high value on cues of male resource-holding potential.

Based on the information thus far, the evolutionary puzzle which emerges is deciphering why women would ever partake in polygyny. Polygyny provides an obvious evolutionary advantage to men since sperm is cheap and their potential reproductive rate is not restricted, and therefore access to more mates results in more potential fertilizations and higher fitness. However, for women, who are the choosy sex, it is resource access which is crucial to fitness. This begs the question of why a woman would choose to participate in a polygynous marriage given that such a system requires them to share their husband's resources and parental investment with his other wives.

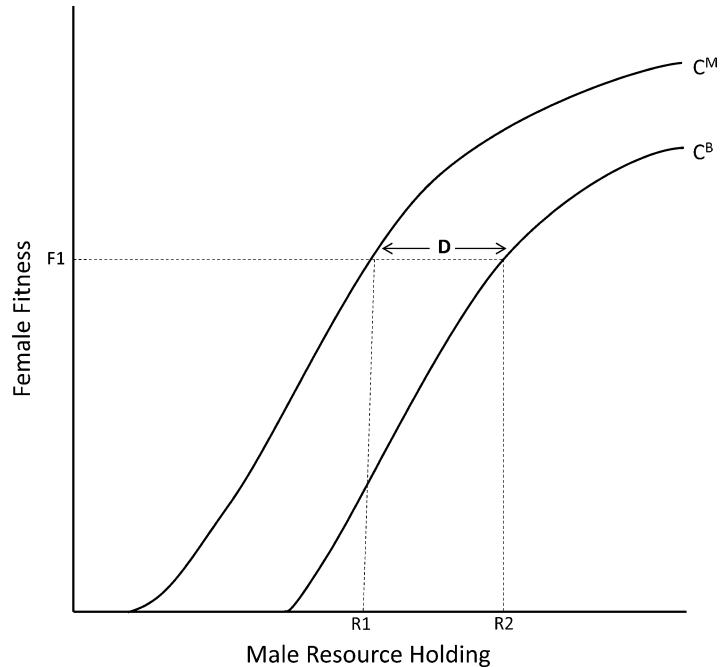
The Polygyny Threshold: Theory

As described above, in species such as humans where MPI is necessary, females require resource provisioning from their mates in order to maximize the quality of their limited quantity of offspring. Therefore, natural selection has shaped female mate preferences to place strong emphasis

on male resource holding. This is the central premise of the *polygyny threshold model* (PTM) (Verner and Willson 1966; Orians 1969) – that a female's evolutionary fitness is determined by the access to resources her mate can offer her; and her mating/marriage behavior should be shaped by natural selection to maximize her fitness. The model was first developed to explain mating systems in birds, and then later applied explicitly to human polygyny (Borgerhoff Mulder 1988). It asserts that there is a level of inequality in male resource holding such that a female will achieve higher biological fitness being paired as the second partner of a resource-rich male than she would as the first partner of a resource-poor male. This is because with sufficient inequality, a fraction of a rich man's resources, which are shared among multiple spouses, may be greater than the total of a poor man's resources. This level of inequality is the *polygyny threshold*, and once it is surpassed, polygyny is predicted to occur. Therefore the PTM predicts that the incidence of polygyny in a society should be closely associated with the degree of stratification of male wealth.

Figure 1 provides a graphical representation of the PTM (modified version of the original figure from Orians (1969)). The curves reflect the relationship between a male's resource holding and the fitness of a female pairing with him (a) monogamously (C^M) or (b) bigamously (C^B). For any given environmental quality, curve C^M is lower than curve C^B because resources must be shared if a female is paired to a male bigamously, and in turn her fitness is lower than if she was monogamously paired with him and had exclusive access to his resources. However, for each level of resources provided by an unpaired male, there is a corresponding higher level of resources provided by an already paired male which would result in a given female achieving the same fitness. For instance, a female would achieve the same fitness (F1) being paired monogamously to a male with resource holding R1 as she would being paired bigamously with a male with resource holding R2. Thus if this level of inequality (D) exists within a society, a female can achieve the same fitness via bigamous mating as monogamous mating and polygyny can emerge

Polygyny Threshold, The, Fig. 1 Graphical representation of the polygyny threshold model (Adapted from Orians (1969))



via female choice. Therefore, D represents the *polygyny threshold*.

The Polygyny Threshold in Humans: Empirical Evidence

The PTM makes three main predictions: (a) the incidence of polygyny across human societies should correlate with their relative levels of male inequality in resource holding; (b) in societies where polygyny does occur, it is resource-rich men who achieve polygyny; and (c) women marry polygynously when it is optimal for their fitness and therefore should not achieve lower fitness than monogamously paired women. All of these predictions have empirical support; however, the evidence for the final prediction is more mixed.

To begin with, there is strong support for the prediction that polygyny is more likely to occur in societies with greater male wealth inequality. At contact, Native American societies demonstrated a positive association between polygyny prevalence in a community and the extent to which males could monopolize food extraction sites,

such as resource-rich fishing or hunting areas (Sellen and Hruschka 2004). This trend has even been applied at the macro level of nation-states. Schmitt and Rohde (2013) calculated a “human polygyny index” (HPI) for 38 nation-states based on the number of sexual partners reported by men and women and found a strong positive association between a nation’s HPI and their Gini index of income inequality.

Within societies with sufficient inequality, as predicted, it is the resource-rich males who marry polygynously. For instance, in Uganda, which is highly dependent on agriculture, ownership of land is a strong predictor of a man’s likelihood of having more than one wife (Pollet and Nettle 2009). Nettle and Pollet (2008) also analyzed selection gradients of wealth in 11 societies and found strikingly high selection on male wealth in the two polygynous societies from their sample, thus providing further evidence that it is indeed resource-rich males who benefit from increased mating access. Even more pronounced examples can be found in historical empires where male resource holding was extremely skewed, and emperors had access to immense wealth and in turn a vast number of mates. Dynastic leaders in

Asia had prolific concubines, and Y-chromosome research estimates that ~40 % of living Asian men may be descendants of just eleven powerful rulers from the last few thousand years (Balaesque et al. 2015).

Polygyny rates in extant hunter-gatherer societies, whose lifestyle reflects the way our species lived for the majority of human evolutionary history, are approximately 14 % (Marlowe 2005). The incidence of polygyny in this subsistence mode had previously posed a problem for the PTM since hunter-gatherers do not accumulate resources; hence, no inequality in male resource holding is assumed. However, recent research reconciles hunter-gatherer polygyny with the PTM, finding it is men with stronger social networks who marry polygynously in these groups, and these men may have superior resource access due to larger food sharing networks (Chaudhary et al. 2015).

With respect to the final prediction of the PTM, the evidence is less consistent. A woman's evolutionary fitness is determined by both her fertility and offspring survival. There is some research indicating that polygyny can be detrimental to both of these components of female fitness and thus cannot be explained by the PTM, which asserts that it is an adaptive female choice. The polygyny-fertility hypothesis refers to the occurrence of lower fertility among polygynously married women than their monogamous counterparts, which is most likely caused by reduced coital frequency (Bean and Mineau 1986). In a review of 86 studies, 64 found evidence for the polygyny-fertility hypothesis (Josephson 2000). Moreover, the offspring of women married polygynously may also incur increased mortality risk since they have access to a smaller proportion of their father's parental investment. The results concerning offspring mortality are inconsistent and vary cross-culturally. For instance, a study using demographic and health surveys from Ghana found that children whose fathers are married polygynously experience higher childhood mortality (Gyimah 2009); conversely, among the agropastoralist Kipsigis from Kenya, there is no significant effect of marital status on offspring survivorship (Borgerhoff Mulder 1989).

Despite considerable evidence for the polygyny-fertility hypothesis, which contradicts the PTM, the latter should not be disregarded. There are numerous potential confounding factors, which could result in the polygyny-fertility effect even if polygyny is an adaptive choice for women. For instance, women who marry polygynously are often older than those who marry monogamously, and men married to sterile wives will often marry polygynously (Pebbley et al. 1988). Additionally, Josephson (2002) found that although polygynously married women in the nineteenth-century Utah had fewer offspring than monogamously married women, they actually had the same number of grandchildren due to enhanced reproductive performance of their offspring. Thus the polygyny-fertility effect may fail to account for complex patterns governing the relationship between polygyny and women's long-term fitness.

Nevertheless, the possibility that polygyny may be detrimental to women's fitness in certain circumstances can certainly not be disregarded. Such cases may occur in settings where the rule of female choice is superseded by male coercion and thus the PTM is not applicable. In these contexts, dominant males are able to exert control over female reproductive behavior and monopolize multiple women. Among the Dogon of Mali, child mortality is a major determinant of female fitness, and the offspring of mothers married polygynously are 7–11 times more likely to die by the age of five (Strassmann 1997). Despite this, polygyny is extremely prevalent and has been attributed to the dominant position of men in Dogon society who are able to suppress female reproductive interests, i.e., male coercion rather than PTM/female choice explains polygyny (Strassmann 1997).

Conclusion

In humans, due to the restricted reproductive rate of women and the necessity of biparental care for altricial offspring, when selecting a mate, women are particularly concerned with a man's ability to provide resources. Therefore, the PTM

hypothesizes that in societies where there is sufficient inequality in men's resource holding, polygyny will emerge. This is because women will preferentially enter polygynous marriages with rich men than monogamous marriages with poor men.

The predictions of this model have mixed support from research on human populations. There is strong evidence that polygyny is more likely to occur in stratified populations and that it is rich men who marry polygynously within these societies. However, the PTM also predicts that women will choose polygyny when it is optimal for their fitness and therefore should not achieve lower reproductive success than monogamously paired women. Many studies indicate this may not be the case and that polygynously married women experience lower fertility or higher offspring mortality. These contradictory findings highlight that it is necessary to consider other models of polygyny, such as the male coercion model, in combination with the PTM for a full understanding of human marriage practices.

Cross-References

- ▶ [Female Choice](#)
- ▶ [Mate Preferences](#)
- ▶ [Mating Systems](#)
- ▶ [Parental Investment and Sexual Selection](#)

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