Social structure and knowledge sharing networks in hunter-gatherers

A case study on the plant knowledge of the Mbendjele BaYaka Pygmies

Gül Deniz Salalı

A dissertation submitted in partial fulfilment

of the requirements for the degree of

Doctor of Philosophy

Department of Anthropology

University College London

February 2017

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

Abstract

Hunters and gatherers occupied 95% of the human history. Despite the forces of globalization, current-day hunter-gatherers can shed light on how we adapted to different environments and generated complex cultural traits. Their changing ways of life, on the other hand, may let us understand cultural change. In this thesis, I explore the cultural evolution of plant knowledge in an extant hunter-gatherer population, the Mbendjele BaYaka Pygmies from the Northern Republic of Congo. In Chapter 4, I show that the Mbendjele use wild plants for various reasons from treating digestive system disorders to punishing norm violators. In Chapter 5, I investigate whether there are adaptive benefits to the use of certain medicinal plants and explore the common uses of medicinal plants across different Pygmy populations and great apes. I also explore the known bioactive compounds, and test the effects of mothers' use of certain medicinal plants on their children's body-mass-index. In Chapter 6, I investigate how the Mbendjele have evolved such a rich plant use repertoire by exploring sharing of medicinal and non-medicinal plant knowledge with respect to features of social structure. I argue that the long-term pair bonds, marital ties and cooperative breeding have allowed the Mbendjele to combine and accumulate rich medicinal plant uses. Additionally, co-residence of multiple families provides a context for the sharing and accumulation of plant uses that concern cooperative foraging and social norms. In Chapter 7, I explore the socioeconomic transitions in the Mbendjele that live in a logging town and examine how plant knowledge declines with their changing life-style. I argue that change in subsistence activities, emerging inequalities and decreased mobility hinder the transmission of traditional knowledge. Nevertheless, I argue that adoption of new cultural traits may be inevitable and beneficial for the resilience of modern day hunter-gatherers.

Contents

List of Figures

List of Tables

Acknowledgments

This thesis would not be possible without the help and support of the great people in my life. I am deeply grateful to all of them.

First, I would like to thank my PhD supervisor, Dr. Andrea Migliano, for her guidance and support throughout my PhD. I am very fortunate that she gave me the opportunity to be part of the Hunter-Gatherer Resilience Team. She did not only advise me for my research, but also supported me through important life decisions. I cannot possibly imagine a better supervisor than her. My sincere thanks to Prof. Ruth Mace for her co-supervision and advice throughout my PhD, and Dr. Lucio Vinicious for his help in my statistical analyses and lively discussions.

Thank you to Nikhil Chaudhary for always being there and lifting me up whenever I need help. I cannot be more grateful for his support, friendship and our stimulating discussions. I believe that our PhDs are only the beginning, and that we will continue working and having amazing adventures together. I am also deeply grateful to my friends and fellow PhD students in the Hunter-Gatherer Resilience Team, James Thompson, Mark Dyble, Abigail Page, Janis Strods, and Daniel Smith. It has been a great four years interacting with these brilliant people, sharing laughter, ideas and adventures.

Many thanks go to Dr. Jerome Lewis who introduced us to the Mbendjele, gave us invaluable information about their culture, and put his time and effort to arrange our research permits. I really appreciate his help and advice on conducting fieldwork in Congo. Thanks also go to Aude Rey, who greatly helped us in our data collection during the 2014 fieldwork and shared unforgettable adventures with us. My special thanks go to post-doctoral researchers Pascale Gerbault and Jed Stevenson who greatly supported us during parts of our fieldwork. I am also indebted to Prof. Mark Thomas at UCL for giving me inspiration to conduct research on hunter-gatherer plant use and diet. Special thanks go to the botanists at Kew Gardens, Dr. Olwen Megan Grace and Dr. Xander van der Burgt, for identifying plant species from photographs and guiding me in my literature research on medicinal plants. This research was made possible by the funds received from the Leverhulme Trust Foundation, and Funds for Women Graduates. I am indebted to these organizations.

I am deeply grateful to the Mbendjele for their hospitality, friendship and patience. It has been an amazing experience being part of this community and learning about life in the forest with them. My special thanks to Semoi and Tokidya’s family who were extremely

welcoming and supportive during our stays in Longa and Masia. Many thanks also go to Bakima Arnaux and Ngulawe who were kind enough to show me the trees in the forest.

I am extremely fortunate that the PhD programme at UCL has allowed me to get to know some amazing people who have become close friends over the last three years. I have had one great year sharing a beautiful house with PhD friends, now all doctors (!), Cathryn Townsend, Bram van Leeuwen and Matthew Thomas. I am especially grateful to Cathryn Townsend for always being there whenever I needed support and guiding me with her valuable advice. Specific thanks to Bram van Leeuwen for sharing the office with me at late evenings and on weekends, and being such a warm and supportive friend. Many thanks to Matthew Thomas for always suggesting interesting books and encouring me to engage in science communication. I am very fortunate to have shared an office with Rafael Morais Chiaravalloti and engaged in exciting conversations about life, writing books and future projects where we visit fieldsites around the world. Many thanks go to Emily Emmot (now Dr.), who has been a great and reliable friend, for introducing me to the great places in London and engaging in fun conversations with topics ranging from evolution to relationships.

I cannot express how much grateful I am for the warm friendship of my officemates Sahil Nijhawan and Juan Du. Their friendship has been the major source of joy in my life and given me much strength. I am especially grateful to Sahil Nijhawan for his guidance and wise advice throughout my PhD that helped me to gain perspective at times I needed it.

I am deeply grateful to my flatmate Jessica Jennings with whom I shared many good memories, intellectual and fun conversations over the last year. Special thanks go to Dave Morrison and Sushil Rajagopalan for hosting me in their house in Tempe Arizona while I was completing this thesis. Their warm friendship and support have greatly helped me to complete my writing in a new environment. Many thanks also go to Prof. Rob Boyd for lending his computer to me at a much-needed time, and for hosting me at ASU where I had a chance to engage in stimulating conversations with brilliant researchers.

Finally, my foremost thanks go to my dear parents, Latife Salalı and Gültekin Salalı, who supported me throughout my life in every decision I have made. Only with their endless love, support and guidance, was I able to fulfil my dreams and do this research. I would like to dedicate this work to the memory of my aunt Ayşegül Süldür whose big heart and kindness will continue to guide my life.

Chapter 1: Introduction

Humans exhibit a remarkable capacity for social learning and culture. Cultural complexity is one of the key features of human sociality that has enabled humans to surmount ecological pressures and occupy habitats from desserts to the Arctic pole (Richerson & Boyd, 2005). The capacity for culture has substantially accelerated human evolution as cultural adaptations can evolve faster than genetic ones. How humans have evolved such complex culture is one of the central questions in evolutionary anthropology. This thesis investigates adaptiveness, evolution of and change in cultural traits by using plant knowledge and plant use in an extant hunter-gatherer group as a case study. In particular, I explore: 1) the diversity of plant uses in forest hunter-gatherers, 2) adaptive benefits of medicinal plant knowledge, 3) the inter-play between social structure and sharing of plant knowledge, which has implications on the evolution of cultural complexity, and 4) socio-economic transitions and cultural change. I do so by examining variation in the knowledge of plant uses in the Mbendjele BaYaka forest hunter-gatherers. I first examine the adaptive benefits of knowledge of medicinal plant uses. I then ask whether defining features of human social structure such as strong pair-bonds, interactions through marital ties, cooperative breeding, and living in groups facilitate sharing of knowledge. Moreover, I examine whether the content of knowledge influences how it is shared. Finally, I investigate how socio-economic transitions (market integration, change in subsistence activities and mobility) affect social structure and explore cultural changes associated with these transitions. To do so, I use data collected over seven months during my fieldwork with the Mbendjele BaYaka Pygmy hunter-gatherers in the Northern rainforests of the Republic of Congo.

1.1 Evolutionary approaches to culture

Culture, like genes, is transmitted and subject to change with time. Scholars have long promoted the use of evolutionary approaches to study cultural transmission and change, which led to the emergence of the research field of "cultural evolution" (Boyd & Richerson, 1985; L. L. Cavalli-Sforza & Feldman, 1981). There are several analogies between cultural and biological evolution (Mesoudi, Whiten, & Laland, 2004). First, cultural transmission is analogous to reproduction and mutation in biological evolution (L. L. Cavalli-Sforza &

Feldman, 1981). Innovations and random changes in cultural transmission parallel to mutation (L. L. Cavalli-Sforza & Feldman, 1982). Cultural transmission mechanisms such as imitation are adaptive, especially in stable environments, because they reduce the costs associated to individual learning and allow individuals to acquire the locally adaptive behaviour (Boyd & Richerson, 1985). Second, cultural traits vary and this variation can be subject to selection (Boyd & Richerson, 1985; Mesoudi, 2011).

The evolution of cultural traits depends on how those traits are transmitted among individuals (L. L. Cavalli-Sforza & Feldman, 1981). In evolutionary biology, transmission often implies Mendelian genetic transmission (L. L. Cavalli-Sforza & Feldman, 1981). For the study of cultural transmission and evolution the fields of epidemics and population genetics have been influential. By adopting some terminology from epidemiology, researchers identified different modes of cultural transmission (L. L. Cavalli-Sforza & Feldman, 1981). Accordingly, vertical transmission is used to describe transmission from parent to offspring and horizontal transmission denotes transmission between any two (usually unrelated) individuals of the same generation. Following Cavalli-Sforza and Feldman (1981), oblique transmission describes transmission from an unrelated member of the older generation to a member of the younger generation. Different modes of transmission affect the pace of cultural change differently. For example, vertical transmission is relatively solid and resistant to change over time. Moreover, since the information is passed down within families, it maintains cultural variation within groups (L. L. Cavalli-Sforza & Feldman, 1981). On the other hand, horizontal transmission is similar to transmission of infectious diseases and the spread of the cultural trait in the population may be fast, in comparison to vertical transmission. Variation may occur via random manner like a mutation, or it can be guided, in which case the acquired information is modified by individuals (Richerson & Boyd, 2005). Table 1-1 lists some of the processes in cultural evolution that were modelled by Cavalli-Sforza, Feldman, Boyd and Richerson, and shows their effects on the cultural trait of the group.

Table 1-1: Processes of cultural evolution, adapted from Cavalli-Sforza and Feldman 1981, and Mesoudi 2011.

Process	Description	Effect on group structure
TRANSMISSION		
Pathway		
Vertical	Transmission from biological parents (either uniparental or biparental)	Maintains within group variation
Oblique	Transmission from unrelated members of the parental generation	Can reduce within group variation
Horizontal	Transmission from unrelated members of the same generation	Can reduce within group variation
Scope		
One-to-one	Face to face learning from one individual to another	Slow cultural change
One-to-many	One individual influencing many others via mass education or mass media	Reduces within group variation, rapid cultural change
Concerted or many-to-one	Older members of social group to younger members of social group	Reduces within group variation, most conservative (slow cultural change)
Mechanism		
Blending	Adopting the average value of a continuous trait from more than one model	Reduces within group variation
Particulate	All-or-nothing transmission of discrete cultural traits	Can reduce within group variation
VARIATION		
Cultural mutation	Generating innovations entirely at random	Can increase within group variation
Guided variation	Individuals modify acquired information according to individual cognitive biases	Can decrease within group variation, if cognitive biases are similar
CULTURAL SELECTION		
Content biases	Preferentially adopting traits based on their intrinsic attractiveness	Can decrease within group variation
Model-based biases	Preferentially adopting traits based on characteristics of the model, e.g. their prestige, age, similarity	Can decrease within group variation
Frequency-dependent biases	Preferentially adopting traits based on frequency, e.g. conformity (copying the most popular trait)	Reduces within group variation
CULTURAL DRIFT	Random changes in cultural trait frequencies due to cultural mutation, random copying and sampling error	
NATURAL SELECTION	Cultural traits spread due to their effect on biological survival and reproduction	
MIGRATION		
Demic diffusion	Cultural traits spread as their bearers move	Reduces between group

	between groups	variation
Cultural diffusion	Cultural traits spread across group boundaries due to cultural transmission	Reduces between group variation

The evolutionary approach to culture is useful because it provides a systematic framework that enables researchers to examine how cultural traits are transmitted and distributed in a population and why certain traits or information are favoured over others with respect to the environment (L. L. Cavalli-Sforza & Feldman, 1981).

1.1.1 Is culture adaptive?

Cultural variation may be subject to natural selection (Boyd & Richerson, 1985). This is because some inherited cultural traits (through social learning), have an effect on individual's survival and reproduction (Boyd & Richerson, 1985; L. L. Cavalli-Sforza & Feldman, 1981). According to the cultural evolutionists, social learning allows humans to accumulate a repertoire of adaptive information over many generations, resulting in the evolution of cumulative culture that may be highly adaptive (Boyd & Richerson, 2005). This is parallel to the biological phenomena called "niche construction". Niche construction refers to the changes in environmental selection pressures as a result of an organism's behaviours (Kendal, Tehrani, & Odling-Smee, 2011). Uses of technology, emergence of writing as a tool to transmit information are examples of cultural traits that are part of human niche construction. This is because those cultural traits help humans to better adapt to their environment by influencing the strength of natural selection (Kendal et al., 2011).

Studies on small-scale societies showed adaptiveness of some cultural traits. For example, mothers with higher levels of plant knowledge and use are found to have healthier children in Tsimane' forager-horticulturalists, independent of potentially confounding variables related to education, market integration and acculturation (McDade et al., 2007). Tsimane' researchers also found that they shared ethnobotanical knowledge widely, but people in the same village shared more knowledge than people from different villages (Reyes-García, Godoy, Vadez, & Apaza, 2003). In Fiji, researchers showed that food taboos for pregnant and lactating women selectively target the most toxic marine species and effectively reduce a woman's chances of fish poisoning (Henrich & Henrich, 2010). Adaptive knowledge may be shared more widely in a population through gene-culture co-evolution or cultural selection. However, there are not many empirical studies examining the sharing patterns of cultural traits with respective to their adaptive value. In the next section, I will further discuss about how human life history traits and features of social structure may facilitate transmission of adaptive information.

1.2 Social structure, human life history traits and cultural transmission

Humans are a social species. Most features of human behaviour have been shaped under the influence of living in groups. There is an evolutionary explanation why we care about our reputation, why we tend to see famous people as role models and interested in what they wear or do, and why our conversations are dominated by social information and gossip. Evolutionary scientists have suggested that defining human features such as high intelligence and language have evolved to regulate social interactions under increasing group sizes (Aiello & Dunbar, 1993; Byrne, 1996; Dunbar, 1992, 1998). Group composition, mating systems, residence patterns and between-group interactions all define the social structure of a species. These defining characteristics of human social structure might have played a key role on the evolution of cultural traits that separate humans from other great apes. In this section, I will explore how human social structure and life history traits might have contributed to cultural evolution.

1.2.1 Human social structure & life-history

"To define what is specifically human and what is not, one must compare human societies with nonhuman societies. Such a comparative analysis leads me to define human societies as federations of multifamily groups." Bernard Chapais

1.2.1.1 What is social structure?

The terms social structure and social organization have been inter-changeably used in the evolutionary anthropology literature (Chapais, 2008, 2010, 2013; Gowlett, 2008). Although some authors used a narrower definition of social structure by stating that it is the patterns of social interactions in a society, thus distinguishing it from social organization (Kappeler & Van Schaik, 2002), I will use the term to encompass the characteristics of group composition, mating systems, residence patterns, kin recognition patterns and between-group relations in humans.

1.2.1.2 Universal characteristics of human social structure

What are the defining features of human social structure? It is not easy to describe human unitary social structure because of variation across cultures. Chapais (2010), however, argues that the common features of culturally diverse human social structure can be described by investigating the deep structure of the human society, that is the shared structural features of all human groups. Chapais was not the only anthropologist who sought universal features in human social organization. Structural anthropologists such as Levi-Strauss have long attempted to identify the core features (Lévi-Strauss, 1969). According to Levi-Strauss's "alliance theory", exogamy, incest prohibitions and reciprocal circulation of women are the universal structural features of human societies (Lévi-Strauss, 1969). Unlike Chapais, however, Levi-Strauss did not attempt to find the ultimate cause for these universal features.

Evolutionary approaches are important because comparisons between closely related species may inform us why certain traits have evolved in one species, but not in the other. In this respect, we must first provide a unified definition of human social structure. Then, we can discuss the differences of social structure in humans and other primates and how these differences may help us explain uniquely human features. In the next sections, I will lay out each of the key characteristics of human social structure in comparison to nonhuman primates.

1.2.1.2.1 Long-term pair bonds

One of the key features of human social structure is the existence of long-term pair bonds between males and females (Chapais, 2008; Dyble et al., 2015). Compared to other primates, humans have a more flexible mating system: polygyny, monogamy and polyandry are all observed (Chapais, 2013). More than 80% of the human societies have a mixed prevalence of polygyny and monogamy, whereas only 17% are strictly monogamous (Chapais, 2013; Chaudhary et al., 2015; Henrich, Boyd, & Richerson, 2012; Marlowe, 2000). Polyandry, where a woman has multiple husbands is very rare, at only 1% (Marlowe, 2000). Nevertheless, polygynandry (where two or more males have sexual relationships with two or more females) and accompanied partible paternity is common among the South American indigenous groups of Amazonia (Walker, Flinn, & Hill, 2010). Although polygyny is the most ubiquitous, only few men in polygynous societies actually have multiple wives rendering the monogamous marriages the dominant mode of human mating system (Chapais, 2013; Chaudhary et al., 2015; Henrich et al., 2012; Marlowe, 2000). Moreover, monogamy is the predominant mating system across all hunter-gatherer populations (Kaplan & Lancaster, 2003). Note that I use the term monogamy here to refer to social rather than sexual monogamy, as social monogamy does not exclude extra-pair sexual activity (Chapais, 2013; Opie, Atkinson, Dunbar, & Shultz, 2013).

Monogamy is rare in mammals (less than 3% of species) and evolutionary puzzling (Lukas & Clutton-Brock, 2013; Opie et al., 2013). This is because in a monogamous setting a male's reproductive success is tied by his mate's: he may be foregoing his higher reproductive potential (Strier, 2000). Monogamy is more common in primates compared to other mammals, accounting for more than a quarter of primate species (Opie et al., 2013). It has evolved relatively late in primate history (Opie, Atkinson, & Shultz, 2012; Shultz, Opie, & Atkinson, 2011) and presented a stable social system, in that the transition from monogamy back to polygyny was rare (Opie et al., 2012). How monogamy has evolved in mammals and primates is a hotly debated topic with theories linking its evolution to risk of male infanticide (Opie et al., 2013); low female density and impossibility of defending more than one female (Lukas & Clutton-Brock, 2013); female fidelity and choice for low-ranked but high-provisioning males (Gavrilets, 2012a).

The evolution of long-term pair bonds played a significant role in the emergence of unique life history traits in humans. Long term pair-bonding is likely followed by the higher paternal investment (Lukas & Clutton-Brock, 2013; van Schaik & Kappeler, 2003) that supported the transition towards a life-history with high-cost offspring and extended childhoods (Kaplan, Hill, Lancaster, & Hurtado, 2000; Opie et al., 2013). Lovejoy (1981), for example, argued that male-provisioning of food to females in pair-bonded pairs resulted in decreased inter-birth intervals and lead to the increased selective pressure for bipedalism. This is because bipedal locomotion allows for food carrying and increases the efficiency in transportation of food items (Carvalho et al., 2012). Pair-bonding also plays a role in the evolution of kinship recognition and affinal relations in humans, which I will discuss in the next section (Chapais, 2008, 2013).

1.2.1.2.2 Exogamy and kinship recognition

Human societies have the rule of exogamy. Exogamy is defined as marrying outside a specific group. For example, the Mbendjele have the rule of clan-exogamy, where a clan refers to a patrilineal group with genealogies that are often three or four generations deep. In addition to exogamy, humans have the ability to recognize both maternal and paternal kin. The extent of kinship recognition in humans is incomparable to that of other primates. In primate species with no stable pair bonds maternal kin recognition is common, but not paternal kin (Chapais, 2008, 2013; Silk, 2002). This is due to the close association with maternal kin early in life and paternity uncertainty (Silk, 2002). For instance, while male chimpanzees (*Pan troglodytes*) prefer to affiliate and cooperate with their maternal brothers, this is not the case for the paternal ones suggesting that paternal brothers cannot be accurately recognized (Langergraber, Mitani, & Vigilant, 2007). Even in pair-bonded species with multi-level social structure, paternal kin recognition is restricted. In most of those species, such as gelada baboons (*Theropithecus gelada*) and Asian colobines (*Nasalis, Presbytis, Pygathrix, Rhinopithecus, Semnopithecus, Simias, Trachypithecus*) males disperse, withholding the formation of patrilineal kin networks (Grueter, Chapais, & Zinner, 2012; le Roux, Beehner, & Bergman, 2011). Only in hamadryas baboons (*Papio hamadryas*) there is paternal kin recognition, due to male philopatry (Chapais, 2013; Grueter et al., 2012; Swedell & Plummer, 2012). However, in this species female dispersal is controlled by males as males coerce females to leave one group and join another (Grueter et al., 2012; Swedell & Plummer, 2012). Therefore, the interaction with kin among females is restricted (Grueter et al., 2012; Swedell & Plummer, 2012). Finally, affinal kinship (i.e. linkage of unrelated individuals through pair-bonds- such as in-laws) is uniquely human (Chapais, 2008, 2013; Foley & Gamble, 2009).

The ability to recognize both biological and affinal kin along with the rule of exogamy have important consequences in the formation of human's multi-level social structure. The links between bonded pairs and their biological kin allow for the formation of wide kinship networks (Chapais, 2013). Wider kinship networks coupled up with multi-local co-residence patterns in hunter-gatherers (Dyble et al., 2015; Hill et al., 2011; Marlowe, 2004) further enable wide, friendly networks between different groups (Hill, Wood, Baggio, Hurtado, & Boyd, 2014). For instance, the exchange of individuals through marriage creates obligations of reciprocity for resources and political alliances between groups (Dyble et al., 2015; Hill et al., 2011). This social structure might have potentially set the stage for human's extended cooperation beyond the family (Dyble et al., 2015, 2016). In the next section, I will explore the multi-level social structure and between group interactions in more detail.

1.2.1.2.3 Multi-level organization

Chapais defines human society as "federations of multifamily groups" (Chapais, 2013). In fact, the above features of human social structure altogether set the stage for the formation of a nested social structure (Foley & Gamble, 2009). The smallest unit, the female-male pair, nests in a multi-family group. Multi-family groups are further linked by affinal and kinship ties (Chapais, 2010). Unlike other animals, several human groups can also coordinate their actions and constitute "federations" (Chapais, 2013; Grueter et al., 2012). In theory, there is no upper limit on the number of nested structures in human social organization, which renders our social structure unique (Chapais, 2010, 2013), and forms the basis of human social complexity (Salali, Whitehouse, & Hochberg, 2015). This unique structure has also played a role in the evolution of human cooperation (also refer to as "hyper-cooperation" (Burkart et al., 2014) or "ultrasociality" (Richerson & Boyd, 1998) and culture (Dyble et al., 2015; Hill et al., 2011; Salali et al., 2016).

1.2.1.3 Life-history traits

Life history theory investigates the evolution of the timing of key events such as reproduction and senescence in an organism's lifetime. Human life-history is characterized by extended period of juvenile dependence, long life-spans and post-reproductive life-spans, and allo-maternal care (i.e. the help that females receive from other community members during child-raring) (Kaplan et al., 2000; Mace, 2000; Migliano, Vinicius, & Lahr, 2007; Vinicius & Migliano, 2016). These features cannot be considered separate from the features of human social structure. For example, long-term pair bonds, presence of affinal kin, and living in groups might have all contributed to the patterns of human development and childcare. Help in child-care from spouses and other community members ("cooperative breeding") has allowed women to be able to look after costly human infants (with greater brain size, and longer developmental time) and have shorter inter-birth intervals (Kramer, 2011; Meehan, Quinlan, & Malcom, 2013; Sear & Mace, 2008). As a result of cooperative breeding, hunter-gatherer women have higher fertility compared to chimpanzee females and human babies are larger than chimpanzee infants at birth (Kramer, 2010; Sear & Mace, 2008).

1.2.2 Effects on cultural transmission

Scholars have proposed that the multi-level social structure observed in hunter-gatherers, with stable sexual bonds, exogamy, and bilateral kin recognition (Chapais, 2008, 2013; Dyble et al., 2015; Foley & Gamble, 2009; M. J. Hamilton, Milne, Walker, Burger, & Brown, 2007; Hill et al., 2011), has facilitated the evolution of cultural complexity and modern human behaviour. First, long-term pair bonds, exogamy and affinal kin recognition might have facilitated the transfer of information between otherwise unconnected families. Moreover, partially-connected groups are proposed as playing a key role in the evolution of complex cultural traits, and the multi-level social structure in humans has this partially-connected nature (Derex & Boyd, 2015, 2016). In partially-connected groups, individuals within the groups have sufficient opportunities necessary for the emergence of group-specific information. The connections between different groups then allow for the combination of group-specific information, which may lead to the formation of more complex traits. Finally, extended childhoods and cooperative breeding may provide opportunities for social learning of information that may have adaptive benefits. I will expand on the links between human social structure, life history traits and cultural transmission in Chapter 6.

In the next section, I will explain how studying plant knowledge as a cultural trait in hunter-gatherers may enable us to answer questions on the association between social structure and cultural evolution with respect to the content of information.

1.3 Why study culture in hunter-gatherers?

Field experiments are important in studying cultural transmission because they capture the actual behaviour of people in their everyday lives and solve the problem of external validity that laboratory experiments may lack (Mesoudi, 2011). Hunter-gatherers are particularly interesting since: 1) they represent the main mode of living for the majority of modern human history, which can provide explanations for certain cultural adaptations and how these adaptations came into place with respect to the core features of human social structure, 2) they lack literacy, mass media, and formal education; the factors which make it harder to track the cultural transmission of particular skills and knowledge, 3) most of them are in transition to a more sedentary life style which makes it easier to observe and test hypotheses on cultural change. Despite these facts, there are only a few quantitative studies analysing cultural transmission in hunter-gatherers. As Hewlett et al. (2011) asserts, “Given the potential importance of hunter–gatherers for understanding social learning in humans, it is ironic that more books and other publications exist on chimpanzee social learning than that on hunter–gatherer social learning.”

Hunting and gathering lifestyle occupied 95% of human evolutionary history. Only in the last 12,000 years of modern humans’ 200,000-year existence on earth have we started changing our hunter and gatherer ways (R B Lee & Daly, 2004). Although there has been a vast change in human’s ways of life since the emergence of agriculture, dozens of hunter-gatherer societies have persisted. Despite their resilience, modern day hunter-gatherers are getting more and more exposed to non-forager societies due to the forces of globalization, environmental degradation and cultural imperialism. Their resilience can shed light into the ways we adapted and generated extensive culture. Their changing lifestyles, on the other hand, may let us reveal the cultural adaptations associated to the shift from the hunter-gatherer subsistence to the agricultural ways of life.

In this section, I will provide information on hunter-gatherers and their social structure to establish the necessary framework for my research questions and hypotheses on the inter-play between social structure, cultural transmission, and cultural change.

1.3.1 Current day hunter-gatherers

There is much variation in the ecology of current day hunter-gatherers from desert dwelling populations such as the Kung in Namibia and Botswana, to the ones occupying tropical rainforests such as the Central African Pygmies and the coastal populations such as the Agta in the Philippines, or the ones inhabiting colder habitats such as the Haida of Northern coasts of North America (Kelly, 2013). Associated with ecological variation, there are differences in hunter-gatherer populations, namely in their social and political organization, residential mobility, and the presence of food storage. In general many hunter-gatherer populations are marked by their high residential mobility, friendly interactions between bands, lack of material possessions, limited food storage, and an egalitarian social structure. Anthropologists used the term *simple*, *affluent* or *immediate-return* to refer to the populations who share those common features (Kelly, 2013; Woodburn, 1982). On the other hand some hunter-gatherer populations (*complex*, *nonaffluent* or *delayed-return* ones) live in large groups, are sedentary, have food storage, social hierarchies, and a non-egalitarian social structure (Kelly, 2013). Table 1-2 presents the common features of egalitarian and non-egalitarian hunter-gatherer populations.

In egalitarian societies the obtained food is consumed in a short time (hence, they are also called immediate-return). The main characteristics of those societies are egalitarian social organization, high residential mobility and low resource accumulation (Woodburn, 1982). People do not process or store, but eat the food on the same day they obtain; they use simple, portable and replaceable tools and weapons that are made with skill, but do not require complex labour. Non-egalitarian societies, on the other hand, are marked by high levels of food storage, where there is a delay between the acquisition and consumption of food, high wealth accumulation and sedentism (remaining residentially static year-around) and more hierarchical political structures with the presence of group leaders (Woodburn, 1982). Most farmers, herders and Western societies, along with some hunter-gatherer populations (also referred to as complex, affluent or delayed-return ones) have those features (Table 1-2).

Table 1-2: Simple versus complex hunter-gatherers.

Feature	**Simple** **(Immediate-return or non-affluent)**	**Complex** **(Delayed-return or affluent)**
Resources	Unpredictable and /or variable	Highly predictable, less variable
Political organization	Egalitarian	Hierarchical; classes based on wealth and/or descent
Social structure	Small groups nested within bands. Groups come together for ceremonies and rituals some time to time.	Larger groups
Residential mobility	Medium to high	Low to sedentary
Sex equality	High	Low
Food storage	Little to no dependence	Medium to high dependence
Example hunter-gatherer population	Mbendjele BaYaka, Hadza, Kung, Martu	Kwakwak'awakw, Tlingit, Ainu

Source: based in part on Kelly 2013

My study population, the Mbendjele BaYaka Pygmies, are traditionally an egalitarian society (J. Lewis, 2014b). They exhibit high residential mobility and live in small groups. Nevertheless, some Mbendjele are moving toward a more non-egalitarian way of life. The next section further outlines the social structure of the Mbendjele, and changes in social structure, along with their effects on cultural evolution.

1.3.2 Hunter-gatherer social structure

1.3.2.1 Group size, residence patterns, and organizational levels

Egalitarian hunter-gatherers live in small groups, which form fluid meta-groups. Research on compiled empirical datasets have suggested the average group size to be fewer than or around 30 individuals (Hill et al., 2011; Kelly, 2013; Marlowe, 2005). Those groups exhibit high residential mobility (which will be examined later) and group composition change by fusions and fissions. In fact, studying the organizational levels in 339 hunter-gatherer societies, Hamilton et al. (2007) found a “magic” number that determines the increments in group size regardless of the cultural diversity. Accordingly, group size seem to increase by a factor of 4: families consist of 4-5 people, a residential group is 14-17 people, social aggregations involve 50-60 people and periodic aggregations (i.e. infrequent multi-group, socio-economic aggregations) are 150-180 people (M. J. Hamilton et al., 2007).

Did group size in hunter-gatherers evolve in a way to maximize food and information flow? Hamilton et al. (2007) argues that the observed regularity in groupings of hunter-gatherers from diverse environments may result from density-dependent trade-offs. According to these researchers, individuals face trade-offs between resource availability and competition from conspecifics. Therefore, people had to group in a way that optimized the flow of food, culturally transmitted information and potential mates. One limiting factor for group size, which may lead to group fission, is the difficulty in consensus decision-making above a certain group size (Johnson, 1982). For example, a hunter-gatherer group of 25 individuals could contain about four to five families; however, an increase in group size would require leaders to coordinate social life and foraging activities. Even so, the egalitarian ethics in hunter-gatherers might result in people moving away from a dominating leader (Kelly, 2013). Therefore, unless social hierarchies emerge, hunter-gatherers solve the problem associated with growing population sizes by splitting groups.

What is the kinship structure of hunter-gatherer camps? Hunter-gatherers were suggested as having either virilocal or multilocal residence patterns (Marlowe, 2004). In virilocal residence a married couple lives in the same camp as the husband’s parents, while in multilocal residence, couples choose to reside with either husband’s or wife’s kin. Marlowe (2004) has argued that to fully investigate the residence patterns in hunter-gatherers one must consider the change in residence throughout the course of life. This is logical especially for cases where the groom performs bride service by residing in his wife’s camp until the birth of their first child, when they return to the husband’s camp (Bahuchet, 1999; J. Lewis, 2002). This change in residence is important because it reflects the patterns as being multilocal. In fact, by analysing 36 hunter-gatherer and fisher-foragers Marlowe (2004) concluded that foragers are significantly less virilocal and more multilocal compared to non-foragers. This conclusion was supported by a study on the residence patterns of 24 hunter-gatherer populations where the researchers found that either sex may disperse or remain in their natal group with brothers and sisters often co-residing (Hill et al., 2011).

Moreover, our own work on the Agta and the Mbendjele hunter-gatherers has confirmed the reported co-residence patterns found in previous studies (Dyble et al., 2015). Our analyses of co-residence patterns of the 191 Agta across 11 camps, and 103 Mbendjele across nine camps have shown that around 25% of dyads were biological kin, 25% were close affinal kin, and the remaining half of the dyads were distant affinal kin or unrelated individuals (Dyble et al., 2015). These co-residence patterns are in contrast with those of farmers. For instance, Paranan farmers in the Philippines presented a significant male bias in co-residence where men lived with a significantly larger number of kin than women did (Dyble et al., 2015). Furthermore, the group consisted of more related individuals compared to hunter-gatherer groups. We have suggested that sex equality in residential decision making in hunter-gatherers may have been the driving force behind the emergence of multilocal residence patterns and lower within group relatedness (Dyble et al., 2015).

As well as flexible residence patterns, hunter-gatherers exhibit high residential and individual mobility. Who moves with whom and under what circumstances? The next section addresses this question.

1.3.2.2 Flexible Residence patterns and mobility

When talking about hunter-gatherer mobility it should be noted that mobility can refer to different dimensions such as: individual foraging, movement of the residential base camp, movement of individuals around and between residences or long-term territorial shifts (Kelly, 2013). In this thesis, I will only consider the movement of individuals between residences, as these movements affect spread of information and may have effects on the evolution of cultural traits.

Not all the hunter-gatherer groups move frequently. Residential mobility is related to environment (Kelly, 2013). In general, hunter-gatherers occupying the tropical forests and the extreme Arctic tend to be very mobile, whereas those living in temperate forests and deserts are less mobile due to the seasonal or environmental constraints (e.g. availability of a water resource) (Kelly, 2013). The reasons to move may depend on the distribution of resources such as food, raw materials, intolerable insects, but may also be socially or politically motivated. Ethnographies and compiled datasets show that when hunter-gatherer groups fuse or split up, the movements happen along similar family lines with families moving together to exploit resources efficiently, or to avoid conflict and inter-personal tension (M. J. Hamilton et al., 2007; Turnbull, 1961).

Mobility patterns of modern day hunter-gatherers are also affected by socioeconomic changes. Many contemporary hunter-gatherers, for instance, are tied to agricultural plots (their own or those of sedentary neighbours), sources of wage labour, alcohol and cigarettes, government agencies or mission posts. Rather than residential movements, they make treks into the forest that last from a few days to several weeks (Kelly, 2013). The more sedentary a group gets, the greater the distance foragers must go to search for resources (Kelly, 2013). As Bahuchet and Guillaume (1982) reports, natural resources and hunting and gathering efficiency declines with increasing sedentism. This means that men and women will invest more time in search for food, which may result in increased peer-rearing (e.g. sibling care) and cultural change (Kelly, 2013). Chapter 7 of this thesis examines the effects of sedentism and market integration on cultural change in the Mbendjele. Sedentism also influences the political structure of the populations, as the option of dispute resolution by simply moving away disappears in sedentary populations. In the next section, I will examine the political organization of immediate-return hunter-gatherers.

1.3.2.3 Egalitarianism

In egalitarian hunter-gatherers there are no group leaders and hierarchical structures. Not every hunter-gatherer society is egalitarian. Those with delayed-return systems are found to have institutionalized leadership and centralized political formations (for a review see Bird & Bird, 2010; Kelly, 2013). In fact, Boehm (1999) has argued that egalitarianism arose in the distant past from some kind of social hierarchy that is seen in many non-human primates. If this was the case, then egalitarian relations did not come easily; groups needed to have specific mechanisms to enforce and maintain egalitarian structure (Kelly, 2013).

Before discussing about the paths leading to egalitarianism, I will describe what egalitarian means. Kelly (2013) asserts, "The term egalitarian does not mean that all members have the same of everything – goods, food, prestige, or authority". In this respect, egalitarianism does not equate to equality as egalitarian hunter-gatherers may exhibit inequality. This inequality may be in the form of relational wealth: that is the web of connections of friends and family that an individual has, a concept that is also called "social capital" (Kaplan, Gurven, & Lancaster, 2007). For instance, our research on the relational wealth (the number of individuals that a person receives gift from) of the Mbendjele has shown that higher relational wealth is associated with polygyny and increased reproductive fitness in men (Chaudhary et al., 2015), and higher body-mass index and fertility in women (Chaudhary et al., 2016). Moreover, those men with higher relational wealth have been found to inherit their relational wealth, as their sons also had more gift donors (Chaudhary et al., 2016). Therefore, in egalitarian societies a person may gain popularity or prestige and fitness benefits associated with this. Nevertheless, social norms prevent popular or prestigious people to dominate others, preventing the formation of social hierarchies.

Many hunter-gatherer societies emphasize the importance of individual autonomy in their culture (Kelly, 2013; Woodburn, 1982). For instance, when I was conducting interviews regarding tabooed animals, one of my questions was why the person refused to eat a certain animal. Most of the time, the Mbendjele replied to me saying “Ame kondja,” which literally means “I am the boss.” They chose not to eat that particular animal because it was their own choice, no one else’s. Similarly, other hunter-gatherer societies perceive their societies as those where each individual “is headman over himself” (R. B. Lee, 1982).

Maintenance of egalitarian ethos requires specific mechanisms to control overassertive, dominant, or very successful individuals. These include variety of cultural practices such as using humour to keep people in line (J. Lewis, 2002), coalition of the weaker (Boehm, 1999; Gavrilets, 2012; Wiessner, 2002) and rituals (see Kelly, 2013, p. 244 for examples). In highly-mobile groups simply moving away from the dominants is a common practice to avoid power inequality (Marlowe, 2010).

Why did egalitarianism evolve in the first place? Some researchers suggested that subordinate individuals formed up political coalitions to prevent dominants taking away resources from them and having higher fitness (Boehm, 1999; Gavrilets, 2012b). They argue that this coalition psychology was favoured by natural selection since it increased individuals’ fitness especially in small groups. Another explanation concerns big-game hunting. Accordingly, because the hunting success for big game was unpredictable and the meat was valuable for everyone in the group, male hierarchies were undercut and this resulted in egalitarian patterns (K Hawkes, 2000).

The emergence of hierarchies would not only change the political but also social structure of the groups by changing the dynamics of interaction patterns. How does the transition from an egalitarian to a hierarchical social structure happen? According to Kelly (2013), the key factor is “a reduction in residential mobility due to increasing population density, which eventually results in sedentism”. In fact, population size, decreased mobility and food storage all interact in a self-reinforcing cycle. As the group size increases and the detection of free-riders gets harder, the group may solve the problem by assigning leaders. By using a game theoretical model, Hooper et al. (2010) concluded that the optimum solution for individuals in a large group to have successful cooperation (where free riding and coordination errors are avoided) is to be in a group with a leader. Furthermore, sedentism accompanied with high population pressure may lead to a decline in between group interactions with only a few individuals maintaining links with other groups as opposed to nomadic hunter-gatherers (Kelly, 2013). In Section 1.4, I will further discuss the change in social structure in current day hunter-gatherers and its effects on cultural change.

1.3.3 Plant knowledge in hunter-gatherers as a case study

Plant knowledge is a good medium to study knowledge sharing and cultural evolution in hunter-gatherers, as it constitutes a rich cultural domain. Investigating plant uses in the Mbendjele will allow me to answer the main questions that I raise in this thesis for the following reasons: 1) plant knowledge represents a rich cultural repertoire. There are various different types of use, and the variation in plant uses among individuals within a group may help to reveal the patterns of cultural transmission with respect to the features of social structure. Different use types also allow us to test how content and function of information affects its sharing patterns; 2) plant knowledge is important for survival; therefore it confers adaptive benefits and may inform us on how adaptive knowledge is shared. Comparisons of plant knowledge among different groups may inform us on both the history and shared culture of those groups and the importance of particular plants in traditional medicine (Betti, 2004; Terashima & Ichikawa, 2003); 3) it is part of traditional ecological knowledge; allowing one to test whether socioeconomic transitions and changes in social structure in hunter-gatherers lead to a change in traditional knowledge. I will provide more information on this latter point in the following section.

1.4 Changes in social structure and cultural transmission

Kelly (2013) demonstrates how increased sedentism in egalitarian hunter-gatherers may trigger a change in the social structure, foraging activities, and allomaternal care. With market integration and sedentism some men may choose to spend more time in prestige-seeking activities (Kelly, 2013). For instance, some Mbendjele men living in a market town work at the logging company or the radio station for indigenous people. Those people earn more money than many others do in their camp, and possibly are regarded as prestigious. Such processes may bring about wealth inequalities, which I will discuss in detail in Chapter 7. Sedentism may also require men to go on long-distance hunting and fishing trips that take longer time, decreasing their time spent with their family (Kelly, 2013; Riddell, 2013). Moreover, in the current study population we observe higher rates of wage labour for farmers in larger, more sedentary and market integrated Mbendjele camps (Riddell, 2013; Salali & Migliano, 2015). This may also have an impact on the time a mother and other caregivers will spend with the offspring. Kelly (2013) argues that such changes in subsistence activities may result in higher involvement of peers as opposed to parents in childcare. These shifts may potentially affect cultural transmission patterns and lead to cultural change in subsequent generations.

Can certain cultural domains be an indicator of change in the social structure? Studies show that market integration is associated with cultural change in many indigenous populations (Godoy, Reyes-García, Byron, Leonard, & Vadez, 2005). Market integration may affect cultural transmission patterns by affecting the subsistence activities and the time allocated to different activities. For instance, our studies and others have found that the Mbendjele spend more time in wage labour in larger camps located at market towns (Riddell, 2013; Salali & Migliano, 2015). If adults start spending more time in the agricultural fields, there may be fewer opportunities for children to learn about forest skills. Recently researchers showed that Tsimane' adults experienced a net decrease in the report of plant uses and this decline in traditional knowledge was more prominent in people living close to farmer towns (Gómez-Baggethun & Reyes-García, 2013; Reyes-García, Guèze, et al., 2013). Similarly, transition to a market economy in Donana national park in Spain was associated with the rapid decline in the traditional agricultural knowledge among the local people (Gomez-Baggethun, Mingorria, Reyes-García, Calvet, & Montes, 2010). Although market integration may cause a loss in traditional knowledge via influencing the social structure of a population, it may set the stage for the formation of new cultural adaptations. I will further discuss the impacts of social change on cultural evolution in Chapter 7.

1.5 Aims and overview of the thesis

This thesis attempts to gain insight into the evolution of and change in cultural traits by investigating plant knowledge in an extant hunter-gatherer society- the Mbendjele BaYaka of the Northern Congo-Brazzaville. Because the hunting and gathering life-style dominated much of human history, studying culture in the Mbendjele enables me to test various hypotheses on cultural evolution. I will begin by providing an ethnographic description of the study population (Chapter 2). In Chapter 3, I outline the fieldwork process, and the details of methods used. The four chapters that follow constitute the analysis and research section of the thesis.

In Section 1.1, I noted that certain cultural traits may provide fitness benefits to their bearers. I further noted that those cultural traits may spread in the populations through cultural selection, a process in which adaptive cultural traits are shared more widely compared to other traits. I highlighted that there are not many empirical studies examining the sharing patterns of cultural traits with respect to their adaptive value. Therefore, in the first two analysis chapters, I investigate various plant uses in the Mbendjele and whether there is any adaptive value in the use of medicinal plants. My hypothesis is that uses of certain medicinal plants affect health and survival in the Mbendjele.

Section 1.2 highlighted the potential role of human social structure and life history traits on the evolution of complex cultural traits. In particular, I hypothesize that strong pair-bonds, affinal kin recognition and exogamy promote the transmission of information that is family-specific. In this context, extended childhood, post-reproductive life-spans, and allo-maternal care further provide an environment that facilitates the transmission of knowledge that may have adaptive benefits. Moreover, I further hypothesize that living in cooperative groups with links to other groups also enable both the specialization and combination of cultural traits that enhance cultural complexity. In Chapter 6, I test these hypotheses by analysing the co-occurrence of plant uses (indicating their shared knowledge) in Mbendjele dyads and test whether dyads that have biological or affinal kin relationships, or reside in the same camp have increased odds of sharing plant knowledge. Following the results obtained in previous chapters, I further examine how adaptive knowledge is shared by testing whether the content of knowledge (medicinal versus non-medicinal) affects its sharing patterns.

In Section 1.4, I noted how socioeconomic transitions may lead to a change in the egalitarian social structure of hunter-gatherers and how these changes may affect cultural transmission. I further address this topic in Chapter 7 by first examining the changes in social structure in the Mbendjele that live in market towns. I hypothesize that the Mbendjele that are born and raised in market towns have decreased levels of plant knowledge compared to the Mbendjele that come from forest regions.

Following these four analysis chapters, I provide a summary and discussion of the overall findings and how they contribute to our knowledge of human cultural evolution. Key areas of discussion include adaptive benefits of certain cultural traits, sharing of knowledge with respect to social structure and life-history traits in hunter-gatherers, cultural change in response to socioeconomic transitions, and the scope of health data and social network analyses in future research. I end with a brief discussion on the future of hunter-gatherer populations.

Chapter 2: The Mbendjele BaYaka

In this chapter, I will first introduce the study population; the Mbendjele BaYaka hunter-gatherers of Northern Congo (Figure 2-1).

Figure 2-1: Kamba- an Mbendjele woman from the camp Masia- with sharpened teeth.

2.1 Overview of the Study population

The study population is the Mbendjele hunter-gatherers of the tropical forests of Northern Congo-Brazzaville (Congo). Some researchers use the name "Aka" rather than "Mbendjele", however in general the name Aka refers to the hunter-gatherers living in Central African Republic (CAR), and the Mbendjele living in Congo. The Mbendjele are one of the Western Pygmy groups that occupy forest west of the Ubangi River, in CAR, Congo, Cameroon, and Gabon (J. Lewis, 2014b). These groups include Mbendjele in Congo (15-20,000), Baka (45-60,000) in Cameroon and Gabon, Aka (15-20,000) in CAR, and several smaller groups such as Mikaya, Luma, Kola, Gyeli, Bongo, and others (maybe 10-15,000) (J. Lewis, 2014b). It is important to note that the population numbers are the estimates, and vary between different resources. For example, Bahuchet indicates the population size of the Aka and Mbendjele together to be 60,000 (Bahuchet, 2012). I will follow the terminology used by Jerome Lewis and use BaYaka to include all the Western Pygmy groups (J. Lewis, 2014b). The Mbendjele also refer to themselves as *BaYaka* more often than Mbendjele. According to Lewis, they use "Mbendjele" only when they want to differentiate themselves from neighbouring Pygmy groups such as the Mikaya, Ngombe or Baka (J. Lewis, 2014b).

The Mbendjele live in the rainforests of Congo Basin; the second largest (after the Amazons) and least degraded area of contiguous tropical rainforest in the world (Olivero et al., 2016). Figure 2-2 shows the location of the logging town, Pokola, from which we visited several Mbendjele camps located in Sangha and Likouala regions in Northern Congo. This area is sometimes referred to as the Ndoki Forest or Likouala aux Herbes and characterized by swamp forests and recognized as one of the biggest swamps in the world (J. F. Gillet & Doucet, 2012). Throughout this thesis I will use the term *Mbendjele* or *BaYaka* to refer to the Pygmy hunter-gatherers living in this region.

Figure 2-2: Location of the logging town, Pokola (marked with yellow pin), where we based our fieldwork with respect to surrounding countries.

2.2 Central African Pygmies and their languages

Central African Pygmies are the largest and most diverse group of modern day hunter-gatherers (Barry S. Hewlett, 2014). A recent study estimated the total number of Pygmies living in Central African forests to be around 920,000 (Olivero et al., 2016). According to their estimations about 60% of these live in Democratic Republic of Congo (DRC) (Olivero et al., 2016).

The word "Pygmy" comes from the Greek word *pugon* (cubit or about 30 cm), and was first used by Homer in the Iliad to refer to mythical short people who fought cranes (Barry S. Hewlett, 2014). The word was reintroduced during the 19th century by American and European explorers to refer to the rainforest people with a short stature and a nomadic lifestyle living in Central Africa (Bahuchet, 2014). Some academics and government officers does not approve the use of the word Pygmy as it is derogatory or does not correctly represent the people (Barry S. Hewlett, 2014). In Congo, it is forbidden to use the term; instead hunter-gatherers are referred to as autochthones. For the same reason, some Cameroonian officials refer to the four hunter-gatherer groups (Baka, Bakola, Bagyeli, and Bedzan) as "four Bs" (Barry S. Hewlett, 2014). Nevertheless, Pygmy is a popular and commonly used term by the researchers across the world, as well NGOs.

The naming and definition of Pygmies is problematic. First, there is a degree of cultural diversity among different hunter-gatherer groups in Central Africa (Bahuchet, 2014). Moreover, some groups are more sedentary and rely less on hunting and gathering. In early 1900s researchers have suggested that only people below 150 cm should be referred to as Pygmies (Cavalli-Sforza, 1986). Although on average shorter than farmer groups in Central Africa, there is a variation in height among Pygmies with some people taller than 150 cm (Cavalli-Sforza, 1986). There is also an asymmetrical admixture between Pygmy groups and farmers (often a Pygmy woman marrying a non-Pygmy man), contributing to the variation in height (Cavalli-Sforza, 1986; Patin et al., 2009; Tishkoff et al., 2009; Verdu et al., 2013). Nevertheless, population genetics studies have found that all Central African Pygmy groups had once shared a common ancestor that is separate from the non-Pygmy African populations. Next section will further detail the studies on the origins of Pygmies, but the results from these studies indicate that referring all hunter-gatherers across Central Africa as Pygmy groups is not entirely incorrect. In general, most African Pygmies share the following characteristics: shorter stature, semi-nomadic life-style with hunting and gathering as the main subsistence (at least until very recently), regular exchange and interaction with neighbouring farmers (Cavalli-Sforza, 1986).

The Central African Pygmies correspond to the combination of scattered ethno-linguistic groups (Figure 2-3), which numbers about 20 (Bahuchet, 2012). Bahuchet lists the following group of Pygmies who continue to subsist on hunting and gathering, and have a semi-nomadic life style: BaYaka (Baka, Aka, Mbendjele- following Lewis's terminology), and BaMbuti (Efe, Asua and BaSua) (Bahuchet, 2014). Following Cavalli-Sforza, most researchers refer to BaYaka as Western Pygmy groups, and Mbuti of Ituri forest as Eastern Pygmies groups (Cavalli-Sforza, 1986). On the other hand, the following groups have settled in villages and practice a combination of foraging and farming subsistence: BaKola, BaBongo, BaKoya, and BaTwa (Bahuchet, 2014). Several names are in use to differentiate these groups (Bahuchet, 2012) (Table 2-1).

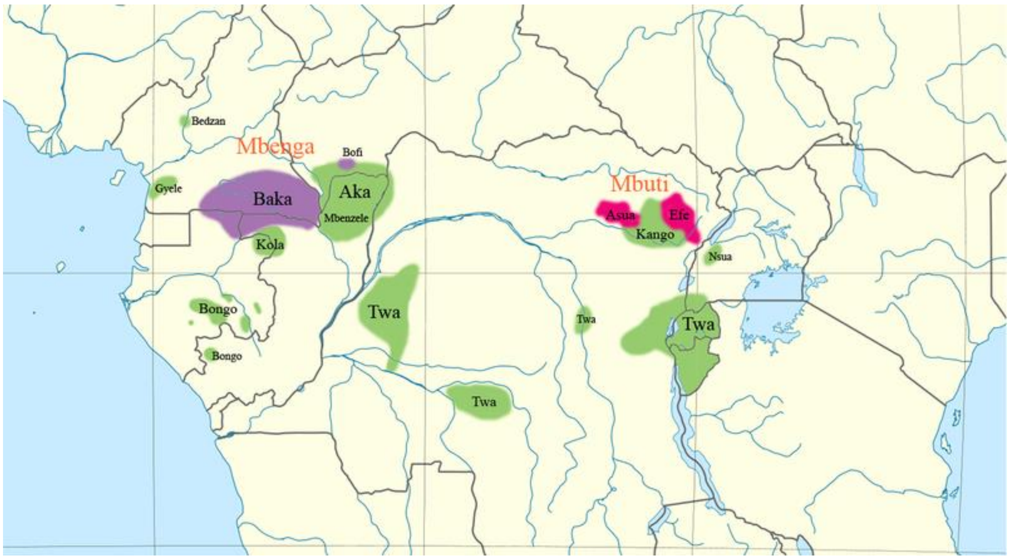


Figure 2-3: General map of the Pygmy populations in Central Africa. This map shows the dispersion of the various Pygmy groups and the respective size of the areas they occupy. In the map, the Bantu-speaking Pygmies are green, the Ubangian-speaking ones are purple and the Central Sudanic speaking ones are red (drawn by Paul Verdu on indications by Bahuchet)**.**

Central African Pygmies speak languages closely related to Bantu, Ubangian (both part of Niger-Congo) and Central Sudanic (Nilo-Saharan) languages (Table 2-1), all of which are spoken by non-Pygmy populations. The BaYaka in our research area speak Mbendjele (or Mbendzele); one of two dialects of the Aka (the other one is called the Aka dialect, but some researchers think they are the same language). However, there can be regional variants of words between different Mbendjele groups and sometimes people use words from languages other than their own – such as the languages of their farmer neighbours: Lingala, Bongili or Kabounga (J. Lewis, 2002). Interestingly, the Aka, Baka and Asua speak a language that cannot be understood by their surrounding farmers. The Mbendjele share a territory with 19 groups of farmers, but only 6 of these farmer groups speak a variety of Bantu C10, similar to the Mbendjele (Bahuchet, 2012). Moreover, as Lewis (2014a) explains the Mbendjele BaYaka are very talented imitators and they can mimic sounds of many other languages as well as animal sounds including duikers, pigs, crocodiles, and monkeys.

Table 2-1: Terminology of Pygmy groups and their languages, adapted from (Bahuchet, 2012).

Name	Country	Other Names	Language Family
(Ba*)Kola	Cameroon	(Ba)Gyeli	Bantu A80
Bedzan	Cameroon	Medzan, Tikar Pygmies, Pygmées des Tikar	Bantoïd-non Bantu/Tikar
Baka	Cameroon, Congo, Gabon	Bangombe, Bibayak, Babinga	Ubangian/Gbanzili group
(Ba)Rimba	Gabon	Babongo	Bantu B40
(Ba)Bongo	Gabon	Akoa, Barimba	Various Bantu B30,60,70
(Ba)Koya	Gabon, Congo	(Ba)Kola	Bantu B20
Mikaya	Congo	Bambenga	Bantu C10
(Ba)Aka	CAR, Congo	Bayaka, Biaka, Babinga, Bambenga, BaMbenz(/dj)ele, Babenz(/dj)ele	Bantu C10
Bofi Pygmies	CAR	Babinga	Ubangian/gbaya
(Ba)Twa	DRC	Konda Twa	Bantu C60
(Ba)Cwa	DRC	Bushong Twa, Kuba Cwa	Bantu C80
(Ba)Cwa; (Ba)Tembo	DRC	Luba Cwa, Batwa, Bambote	Bantu D30
Asua	DRC	Bambuti, Akka, Aka, Tikki-tikki	Sudanic/mangbetu-asua
Efe	DRC	Bambuti	Sudanic/mangbetu-efe
(Ba)Twa; (Ba)Rhwa	DRC	Batwa, Kivu Twa, Western Twa	Bantu JD50
(Ba)Twa	Uganda	Batwa	Bantu J11
(Ba)Twa	Rwanda, Burundi	Batwa, Eastern Twa	Bantu JD60

CAR: Central African Republic; DRC: Democratic Republic of Congo; Congo: Congo (Brazzaville). The letters in language family column indicate geographic zones and decades, based on the Guthrie classification of Bantu languages.

*In many Bantu languages the prefix “ba” signifies a group of people, or the plural of a noun.

2.3 Pygmy origins

The first population genetics studies on Central African Pygmies were done by Cavalli-Sforza and his collaborators (Cavalli-Sforza 1986). During their extensive fieldwork starting in 1960s, these researchers collected demographic and health data as well as blood samples from Pygmies in Cameroon, CAR, DRC, and Rwanda (Cavalli-Sforza, 1986). Their seminal work provided the first evidence suggesting that all Pygmy populations had a common origin followed by a more recent divergence between Eastern and Western Pygmy populations (Cavalli-Sforza, 1986; Cavalli-Sforza et al., 1969).

The following studies with richer genetic markers and more advanced statistical and methodological tools verified the results of the initial population genetics studies conducted on African Pygmies (Verdu, 2014). By sequencing the non-coding regions of genome, geneticists have estimated the date of ancestral Pygmy non-Pygmy population divergence to be around 60,000 (Patin et al., 2009). A further study using complete mitochondrial genomes estimated this date to be around 70,000 years ago (Batini et al., 2011). Moreover, the more recent divergence between Eastern and Western Pygmy populations was estimated to occur around 27,000 years ago (Batini et al., 2011). Genetic data based on autosomal sequencing also indicated that there has been rapid genetic diversification among Western Pygmy populations during the last 3,000 years (Verdu et al., 2009). In addition, microsatellite analysis of all African populations suggested that Khoesan speaking hunter-gatherers and Central African Pygmies had a shared ancestry, and might have diverged more than 35,000 years ago (Tishkoff et al., 2009). In fact, the results pointed at a possibility that the South African Khoesan (San and !Xun/Khwe), Hadza, Sandawe and Pygmy populations had once belonged to a proto-Khoesan-Pygmy populations of hunter-gatherers (Tishkoff et al., 2009). The authors proposed that before losing their indigenous language, Pygmy hunter-gatherers might be speaking a Khoesan-related language, which is evident in their shared polyphonic music styles (Tishkoff et al., 2009). Figure 2-4 shows the schematic model for the origins of Pygmy populations derived from the population genetics studies.

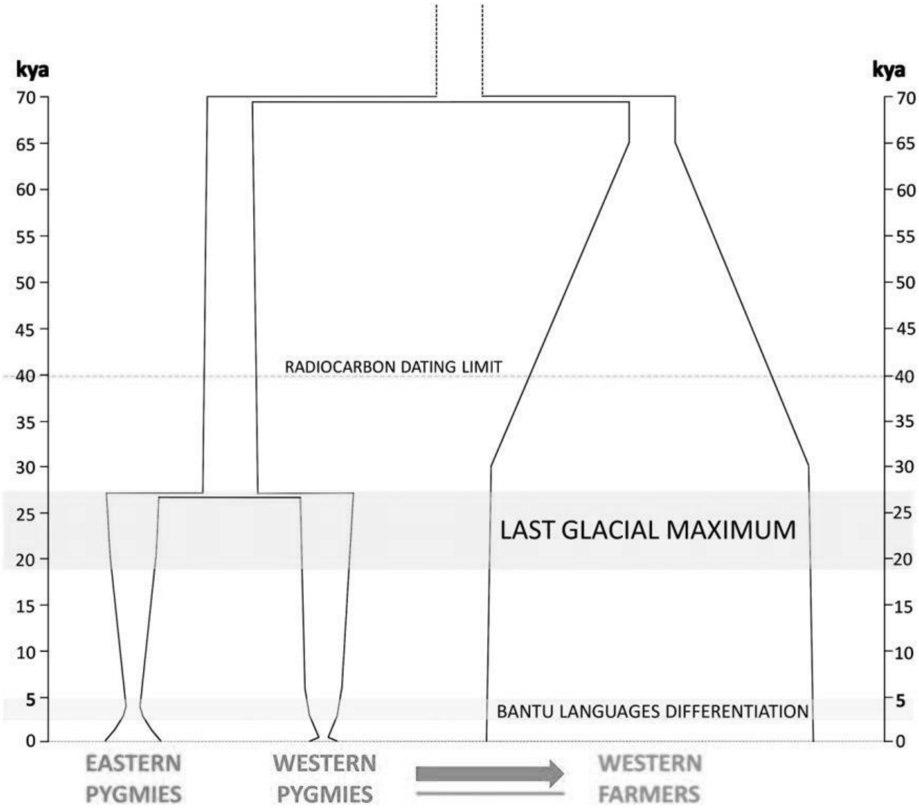


Figure 2-4: Evolutionary scenario proposed for the origin of Pygmies and their relations with the present-day Bantu-speaking farmers (Batini et al., 2011).

Although it is difficult to determine the causes for the ancient Pygmy, non-Pygmy divergence, there are some theories on the causes of divergence within Pygmy lineages. Archaeological and paleoclimatological data suggest that the Eastern and Western Pygmy divergence coincided with the Last Glacial Maximum. This period was characterized by forest fragmentation and formation of isolated forest patches. For this reason, researchers have suggested that the reduction in forest areas might have triggered the isolation of Eastern and Western Pygmy populations (Batini et al., 2011; Patin et al., 2009). Similarly, a climate change occurring 4,000-5,000 years ago and resulting in the contraction of forest areas might have triggered the formation of isolated populations among Western Pygmy groups (Verdu, 2014). Another likely cause of divergence among Western Pygmy groups is the Bantu expansion that started around that time. Verdu and his colleagues (2009) proposed that the emergence of agriculture and accompanied migrations of Bantu farmer populations triggered extensive social and demographic changes among these Western populations. Nevertheless, a recent population genetics study revealed that the first socio-economic interactions between farmers and hunter-gatherers during the Bantu expansion were not accompanied by genetic exchanges immediately. According to this study, substantial admixture only started within the last 1,000 years (Patin et al., 2014).

2.4 Mbendjele BaYaka

This section examines the social structure, subsistence strategies and cultural features of the Mbendjele.

2.4.1 Mbendjele subsistence

All Mbendjele groups are hunter-gatherers to varying degrees and each group has its own territory in the forest (Lewis, 2005). Tropical rainforest where the Mbendjele live is not homogenous. For instance, in the flat areas of the Congo Basin, wide beds of waterways get flooded regularly or permanently leading to the formation of marsh zones. Vegetation varies with respect to the wetness of the soil, which in turn affects the distribution of different animal species in the forest. The biggest mammals such as the elephant and the *situtunga* antelope (*Tragelaphus spekei*) are found in marshy forest; whereas the *bongo* antelope (*Boocercus euryceros*) is found in the mixed forests (wet slopes that are only flooded for short periods). Other animal species such as duikers (*Apholophus*), red hogs (*Potamochoerus porcus*) and apes (*Gorilla gorilla gorilla* and *Pan troglodytes*) live in the semi-deciduous parts of the solid-ground forest, and a species of duiker (*Cephalophus leucogaster*) and the bongo are common in the evergreen parts of the solid-ground forest. These environmental differences affect the modes of subsistence of various hunter-gatherer groups (Bahuchet & Guillaume, 1982). For instance, the Aka living in the Lobaye region of the CAR, where semi-deciduous forest is predominant mainly hunt anthropoids, red hogs and duikers with spear-tracking techniques in rainy season, whereas the Motaba Pygmies living in the marsh zone hunt elephants and sititungas with the same techniques, but in any season (Bahuchet & Guillaume, 1982). Table 2-2 shows the names of the animals that may be hunted and consumed by the Mbendjele. I made this list with the help of my Mbendjele translators to use in my research on food taboos. Later, I found out that some animals, such as the chimpanzee, were heavily tabooed and were not consumed frequently. Figure 2-5 shows some animals that the Mbendjele hunted during my stay with them.

Figure 2-5: A hunted *musome* (Peters' duiker) and *bondji* (giant pangolin).

Table 2-2: List of animals that the Mbendjele may consume. The list is made for a project examining the variation in food taboos in Mbendjele.

Mbendjele name	Animal	Latin name
Mboko	Blue duiker	*Philantomba monticola*
Musome	Peters' duiker	*Cephalophus callipygus*
Mbamu	Bay duiker	*Cephalophus dorsalis*
Bemba	Yellow backed duiker	*Cephalophus silvicultor*
Senge	Gabon duiker	*Cephalophus leucogaster*
Munjombe	Black fronted duiker	*Cephalophus nigrifrons*
Bengene	Antelope	-
Mbongo	Bongo antilope	*Tragelaphus eurycerus*
Mbule	Yellow backed duiker	*Cephalophus silvicultor*
Ngua	Red river hog	*Potamochoerus porcus*
Bia	Giant forest hog	*Hylochoerus meinertzhageni*
Koi	Greater spot-nosed monkey	*Cercopithecus nictitans*
Beti	Monkey	-
Mambi	Crested mona monkey	*Cercopithecus pogonias grayi*
Ngada/ Gandu	Grey-cheeked mangabey	*Lophocebus albigena*
Kalu	Black-and-white colobus	*Colobus guereza occidentalis*
Singi	Monkey	-
Mosila	Brazza's monkey	*Cercopithecus neglectus*
Nyau	Monkey	-
Tamba	Crested mangabey	*Cercocebus galeritus agilis*
Ebobo	Gorilla	*Gorilla gorilla gorilla*
Sumbu	Chimp	*Pan troglodytes*
Leke	Crested guineafowl	*Guttera spp.*
Kokofence	Bird	-
Tende	Sunbird	*Nectarinia spp.*
Esako	Bulbul	*Pycnonotidae spp.*

Kulangu	Great blue turaco	*Corythaeola cristata*
Ngunduma	Bird	-
Mokuakue	African pied hornbill	*Tockus fasciatus*
Edua	Bird	-
Pupa	Bird	-
Djayanga	Bird	-
Kata	Bird	-
Kosu	Bird	-
Koko	Chicken	-
Mukuake	Dwarf crocodile	-
Ngombe	-	-
Ngando	Crocodile	-
Ndjia	Turtle	-
Elenge	Turtle	-
Ekadi	Pangolin	*Manis (Phataginus) tricuspis*
Bondji	Giant pangolin	*Smutsia gigantea*
Mboka	Genet	-
Iyoka	Tree hyrax	-
Mboko	Buffalo	-
Ngomba	Porcupine	-
Nganda	Mongoose	-
Ekela	Slender mongoose	-
Motomba	Big mouse	-
Nyangoku	-	-
Embembe/ Binya	Pangoline	-
Kendu	Small forest mouse	-
Joko/Londu	Marsh mongoose	-
Buse	Civet	-
Mungele	Ratel	-
Embongo	Leopard	-
Ndoku	Golden cat	-
Njoku	Elephant	-
Kudu	Tortoise	-
Bama	Flying squirrel	-

Kitanishi (1995) divides the BaYaka subsistence activities into the following categories: hunting, the collecting of invertebrates, the collecting of wild plants and honey, fishing, and agricultural work. The farmer populations neighbouring the BaYaka practice farming, slash-and-burn cultivation, hunting in the forest with guns, fishing with nets, hooks, traps and poison (K Kitanishi, 1995).

Seasonality in Northern Congo: Dry season in Northern Congo starts in December and goes through February with the mean monthly rainfall levels less than 100 mm. In the rainy season, from March to November, the mean monthly rainfall exceeds 100 mm. The rainfall is heaviest in September and October, however monthly rainfall levels vary considerably from year to year (K Kitanishi, 1995). Another peak in rainfall can be experienced in May, and a shorter drier period in July (J. F. Gillet & Doucet, 2012). The temperature remains almost constant throughout the year.

Cultivation and wild food production in the forest are influenced by the onset and duration of the dry season. The BaYaka use different hunting techniques in different seasons and collect certain foods in certain times. For example, honey is collected from the dry season to the early rainy season, when bees are most active and the caterpillars are collected during the late rainy season, with the peak in August and September (K Kitanishi, 1995). By affecting the food distribution, seasonality also affects the movement patterns of the BaYaka. For instance, according to BaYaka the caterpillars are more abundant in the secondary forest near the village and this may result in some members of a BaYaka group moving closer to the village in the caterpillar season (e.g. in Figure 3.4, on September 1992 the group splits into forest and village camps) (K Kitanishi, 1995). It should be noted, however that, unlike the Mbuti of the DRC where subsistence activities change with a clear seasonal cycle (Turnbull, 1961), the subsistence activities of the BaYaka and their movement patterns could not be represented by a single annual cycle (K Kitanishi, 1995).

Among wild plants, the most commonly collected ones are the *koko* leaves (*Gnetum bucholzianum*), various types of wild yams (*mea, ekule* and others) and nuts (Figures 2-6, 2-7, 2-8). The gathering of those wild plants is women's task, and often done in groups (Appendix A, video 1). Fishing is also done by women with several different techniques employed. During fieldwork, the most common fishing method that I observed was dam fishing. Women, accompanied by young girls, go to riversides together and build dams. Once dams are made they empty the water out from dammed areas so that the river gets shallow. This makes it easier for women to catch fish with their machetes. Fishing is done more frequently during the dry season, as the water levels make it easier to catch fish. They also use plants as fish poison (Appendix A, video 2). Chapter 4 provides more details on the use of plants for killing fish.

Figure 2-6: Young girls collecting *wusa* seeds (*Treculia africana*) in the forest.

Figure 2-7: A young Mbendjele woman cutting *koko* leaves.

Figure 2-8: An Mbendjele child carrying the wild yams (*mea*) that she dug in the forest.

Makombo (wild mushrooms) is also a common source of food that is known and collected by everyone. Mbendjele also collect plants to be used as *bwanga* (medicine).

2.4.2 Mbendjele social structure

Group size and residence patterns: The Mbendjele live in *langos*- multi-family camps, where a number of nuclear families reside, each in their *fumas* (huts) (Figure 2-9).

Figure 2-9: Two newly-made Mbendjele huts. The huts are made of flexible branches and *Phrynium* leaves.

Camps size varies between 10 and 60 individuals; however there may be a larger variation depending on the location of the camps. Hunter-gatherer camps in market towns tend to be larger, while the camps deep in forest are the smallest (Figure 2-10, see Chapter 7 for details). Our analysis on the social structure of the nine Mbendjele camps showed that the mean camp size was about 19 adults (Dyble et al., 2015). On average, 25% of the camp members were biological kin, 25% were close affinal kin, and around 50% of dyads were distant affinal kin or unrelated individuals (Dyble et al., 2015).

Figure 2-10: An Mbendjele camp- Masia**-** that we visited in 2014

Traditionally, after marriage the groom lives in his wife's camp for several years to perform bride service by hunting and collecting honey for the bride's family (J. Lewis, 2002). After the birth of the first children, the young couple return to the husband's camp, however the groom may remain in his in-law's camp where he may be joined by one of his siblings. Elderly widowed women often return to their brother's camp (Bahuchet, 1999). Bahuchet (1999) describes the residence of the BaYaka as "virilocal, with a strong tendency to bilocality". As previously discussed in Chapter 1, *virilocal* is the residence pattern where married couples live in the same camp as the husband's parents, and *bilocal* or *multilocal*, is where couples choose to reside with some kin, but which kin varies (Marlowe, 2004). Our analysis based on the genealogies of over 100 Mbendjele showed the Mbendjele residence pattern to be multilocal (Dyble et al., 2015).

Marriage: The Mbendjele do not have a formal marriage institution. When a woman and a man start living together in a *fuma* their partnership is acknowledge by the community. Nevertheless, the rule of clan exogamy applies for marriages (J. Lewis, 2002). There is often the payment of some bride price (traditionally a few thousand CFA francs or US$ 4-5 (J. Lewis, 2002), but see Chapter 7 for variation in bride price payments). Majority of the Mbendjele practice serial monogamy, nevertheless polygyny is also observed. Our genealogical interviews showed that 14% of the Mbendjele are or have once been married polygynously (Chaudhary et al., 2015). Those men in polygynous marriages have higher reproductive success (Chaudhary et al., 2015).

Mobility: Contrary to farmer groups, the Mbendjele are highly mobile. Frequent changes occur in group composition and visits are common between groups. Several groups aggregate during some weeks of the year, engage in collective hunting, and celebrate large festivals by singing together (Bahuchet, 1992). When they live close to the village, they build “village camps” behind villager houses, near fields, or in the secondary forest within 30 minutes’ walk from the village. Deep in the forest they build “forest camps”. According to observations of Kitanishi (1995) in Northern Congo, the Mbendjele spend four to eight months a year in the forest camps and stay around the farmer village during the remaining months. The movement pattern of an Mbendjele group changes from year to year. This is because the Mbendjele move opportunistically between well-known resource centres such as the salt licks popular with large game, areas rich in yams, seasonal caterpillars, fruit trees, rich fishing sites, abandoned palm-nut plantations, farmers’ villages, logging towns or prospecting camps (J. Lewis, 2005). Camp movement is influenced both by the availability of the food resources and the availability of the food products for exchange with the villagers (K Kitanishi, 1995). For instance, groups that engage in net hunting gather together in dry season (between January and March) to set up hunting camps that cover an area of 10 km in the forest (Bahuchet, 1988; Takeuchi, 2012).

People tend to move in family groups. For example, couples travel with their family to stay with in-laws for several weeks or months, or distant relatives come to stay with them (Bahuchet, 1999). In addition, hundreds of people may come together during the dry-season ceremonies where isolated groups have a chance to meat each other (J. Lewis, 2002). Finally, individuals can choose to move to avoid or resolve problems like hunger, illness, conflict, political domination or disputes among themselves (J. Lewis, 2008b).

During our fieldwork spread over two years, we observed that the Mbendjele often moved between certain camp locations. Therefore, the movements are not random, but to fixed locations in forest, by roadsides or in farmer villages. Sometimes a larger camp located by a roadside can split into smaller groups of families, each going to a forest camp to engage in hunting for several weeks. These locations are known by all Mbendjele in the region, and each has a specific name. In dry season, camps tend to get larger around water resources as many families come together and exploit the rivers for fishing. Moreover, people from far away regions can get together during important initiations and ceremonies such as *Ejengi*.

Political organization: Mbendjele society is acephalous (a society which lacks political leaders or hiearachies) (Bahuchet, 1999). Lewis (2008b) describes the Mbendjele egalitarianism as assertive where people shun the superior status which could attract jealousy and cursing. However, there are three fundamental socially recognized positions:

the *kombeti* (elder) who provides information for the group's moral standards and speaks during times of conflict; the *tuma* (master-hunter) who ensures the material and spiritual success in elephant hunting; and the *nganga* (healer) who communicates with the world of spirits, cures illnesses and seeks the causes of disorder (Bahuchet, 1999). In addition, older, experienced men and women may have more control over others in the camp and possess leadership abilities (Takeuchi, 2012).

2.4.3 Mbendjele - farmer relations

The Mbendjele term *Bilo* (village people) refers to over 40 different ethnic Bantu and Ubangian language-speaking, village dwelling agriculturalist (J. Lewis, 2002). According to Lewis (2002), the Mbendjele maintain formal relations with around ten ethnically different farmer groups in the region where my fieldwork took place. Bahuchet states that the BaYaka outnumber the farmers in the region between the Congo and Sangha River (Ngando, Bondongo, Mbati, Enyele, Mbomotaba, Pande, and Ngundi) by a factor of 10 (Bahuchet, 2012).

Mbendjele-farmer relationships are predominantly based on economic transactions (Lewis, 2002). According to older ethnographies, there is a patron-client relationship between the Aka Pygmies of the Central African Republic and the neighbouring farmer communities (Bahuchet & Guillaume, 1982). Every Aka individual is associated, from birth to death, with a villager. The Aka individual has to bring to his farmer "patron" forest products such as meet, honey and nuts and also has to help him in the farm. In return the farmer has to give "his" Pygmy iron tools, cooking pots, salt, palm oil, tobacco, cloths and starchy food such as plantains, cassava and taros. If a conflict occurs between the Aka and the farmers, the Aka may choose to leave the village and move to another area temporarily or permanently depending on the severity of the conflict (Bahuchet & Guillaume, 1982). The inter-marriages may occur most often with non-Aka males marrying Aka women (Bahuchet, 2012).

Colonial administration increased the dependency of the BaYaka to farmer populations and resulted in the integration of the BaYaka into farmer production activities by encouraging the increase in production for the external market, stimulating exchange and creating new needs (Bahuchet & Guillaume, 1982). The accounts of the interactions between farmers and the Aka in CAR from the 1980's match well with what is happening today. With the increase and expansion of agriculture, the BaYaka became a workforce mainly to be used in agriculture and trade. As a result, the subsistence activities of the BaYaka groups are affected by the activities of the neighbouring farmer populations. For example, Ngando farmers claim meat products from the Aka and sell the hunted meat to urban centres and to large coffee and forest enterprises. In these hunter-gatherer groups much hunting time is devoted to producing meet for the farmers. Moreover the use of snares (and nowadays rifles) and tending of snares that belong to farmers lead to the reduction in camp mobility (Bahuchet & Guillaume, 1982). A quantitative study on the mobility of the Aka in CAR also showed that acculturation of the Aka involved not only the adaption of language and clan names for a farmer identity, but also becoming more sedentary (Hewlett, Koppel, & Cavalli-Sforza, 1982). The effects of the Aka integration to the farmer production activities are summarized by Bahuchet and Guillaume (1982) as follows:

> “1) Nomadism decreases and 'the time spent in settled camps on the edge of the forest,' close to villages, increases. Hunting and gathering are increasingly carried on from these bases, and no longer from temporary forest camps. 2) The territory of exploitation is more and more restricted. Great hunting expeditions are slowly replaced by shorter trips of limited distance. 3) There is a decrease in natural resources and Iowered hunting efficiency occurs because of over-hunting in the most frequented areas. Big game, such as elephants, bongo, and red hog are becoming scarce, and only survive deep in the forest.”

The patron-client description of Pygmy – farmer relations has been criticized by some anthropologists (Kohler & Lewis, 2002; Turnbull, 1961). These scholars argue that Pygmies use their mobility and flexibility to avoid any coercion by farmers. Although the farmers may pretend that they are the patrons, in reality the Mbendjele can choose to stay in or leave an economic partnership with a group of farmers (Kohler & Lewis, 2002). They are often strategic about their relations with Bilo. In presence of farmers, they can be respectful and polite, in their absence they may talk about farmers in a very negative way. As such, the Mbendjele also refer to Bilo as *ebobo* (gorilla) because of their large bodies and aggressive demeanour. Gorillas are large animals with abundant meat, and they are dangerous to hunt. Similarly, for the Mbendjele, Bilo are rich and aggressive (Kohler & Lewis, 2002). Nevertheless, the Mbendjele are scared of Bilo sorcery, and that is why they tend to act politely in their presence (Kohler & Lewis, 2002).

Farmers see the Pygmies as primitive, dirty, lazy and sometimes as thieves, but they also know and respect hunter-gatherers for their supernatural abilities, herbal and forest knowledge, singing and dancing, and high fertility (Barry S. Hewlett, 2014). In fact, farmers often go to Pygmies for important ceremonies and ask to get initiated in Pygmy cults such as *Ejengi*, which I will explain in the following section.

The Mbendjele do not only interact with farmers, but other politically important minorities. These include foreign loggers, NGO agents, Muslim traders, non-regional administrators and non-African researchers (Kohler & Lewis, 2002). Mbendjele call all white people *Mundele*- a Lingala word that is also commonly used by farmers. White people are also called red river hogs, which have huge amounts of fat, referring to the substantial wealth of white visitors (Kohler & Lewis, 2002).

2.4.4 Mbendjele Culture

Music and rituals:

Mbendjele's rich culture is a mirror to the life in the forest. It is marked by complex polyphonic singing and various initiations and forest spirit rituals.

Mbendjele singing is polyphonic that involves particular clapping techniques and women singing in turns. Most of the time polyphonic musical performances are intended to communicate with forest spirits and game animals (J. Lewis, 2014a). Women also yodel during foraging trips to scare the animals away and prevent attacks from dangerous animals such as gorillas, elephants, buffalos, and leopards (Appendix A, video 1). Polyphonic singing requires high degree of coordination, since the quality of the songs depends on the synchrony of the singers (J. Lewis, 2015). Therefore, it also serves as a medium to maintain social bonds and group identity. Moreover, physical proximity marks those ritual associations and musical performances. Women sit in such a close proximity that their bodies almost always touch each other during singing performances, while children sit or lay beside them either participating in by clapping and drumming or just sleeping.

Mbendjele ritual associations are called *mokondi* (forest spirits), and forest spirit performances are called *massana*. These associations are only accessible by a group of initiates (*bangonja*). The initiates have sacred places in the forest, called *njanga*, where they talk important issues, practice rituals and call *mokondi* (J. Lewis, 2002). Depending on the ritual association, these forest spirits may appear in the body of an Mbendjele and dance among the wider community upon singing and calling. Some forest spirits have particular costumes that are made from different types of leaves or may wear masks. During fieldwork, commonly practiced ritual association among all the camps we stayed in was the *massana* of *Bobe*. In camp Ibamba, the Mbendjele were also performing the forest spirit ritual called *Monano* (or *Bonanne*). Moreover, there are two ritual associations of Mbendjele that are considered as the most important for each sex. For men, it is the *Ejengi*, and for women the *Ngoku* initiations. I will give brief information for each of these ritual associations.

Bobe (*malobe*, *bolobe* or *mobe*) is a ritual that is performed for hunting success. Although it is a men's ritual association, the ritual performance proceeds with women calling the spirit into the camp by singing. It is done at night, in dark. Women's polyphonic songs often make reference to their hunger, since it is believed that *Bobe* will bring meat to the camp (J. Lewis, 2002). The songs may also concern the events in the camp. For example, it was common for us to hear our names during *Bobe* performances, as some songs were about our presence in the camp. *Bobe* rituals start with all camp members gathering together at the camp centre, and with women sitting down and starting singing. The singing goes for hours, calling for *Bobe* to enter into camp. During this time the *Bobe* initiates go to their *njanga* (sacred path in the forest), which is forbidden to enter for the others. The initiates must remain silent about the events happening in the sacred path. When the time is ready *Bobe* comes out from the forest and enters the camp dancing. A number of forest spirits may be dancing at the same time (Figure 2-11). Dancing and singing can go for hours, sometimes till dawn. Lewis's description of the forest spirit performances explains the social bonding and the unity with the forest that one experiences during these rituals very well (J. Lewis, 2015):

> "When done well, the music takes on a life of its own as the co-ordination between the singers reaches astounding synchronicity. The effect is synergistic and euphoric. People dance out from the group and trance-like states begin to engulf participants. It is at this stage that the forest begins to yield its charms and small leafy parts of it begin to enter into the horseshoe-shaped group of singers in camp. As the forest spirits repeatedly move into the horseshoe of singers and back out into the forest again it is as if the forest is making love to the camp. It is at this stage that the distinctive euphoria of the spirit-play is most strongly experienced."

Figure 2-11: Bobe forest spirits dancing.

Ejengi may be the most important ritual association for the Mbendjele. All Mbendjele men must be *Ejengi* initiates. This ritual association is also present in the Baka, Aka and Kola Pygmies (J. Lewis, 2002). *Ejengi* spirit belongs to men, although it is believed that initially it was women's. Later when women encountered men, they gave the spirit to them (either by force, or with the help of honey that men gave to women. The story changes depending on the sex) (J. Lewis, 2002). Ejengi has a costume made up from long raffia leaves (Figure 2-12). The Mbendjele believe that as *Ejengi* dances babies fall from its raffia clothing. When *Ejengi* comes into camp, it is accompanied by male initiates. Women sing, clap hands and dance around the spirit, but they should never come closer and touch *Ejengi*. If a woman wants to know the secrets of *Ejengi*, or touches its raffia, Mbendjele believe that she will die. *Ejengi* is danced when a clan returns to a permanent campsite from a long journey in the forest or for commemoration ceremonies. During these times a young boy can be initiated, but if there are a number of neophytes the *Ejengi* may be danced for the sole purpose of initiation (J. Lewis, 2002). These initiations last for three days, and a lot preparation is needed. The neophyte's relatives must provide alcohol, cigarettes and food (depending on *Ejengi*'s demands) during the ceremony. Neighbouring farmers respect *Ejengi* and ask Pygmies to perform funeral ceremonies for them, as they believe the dances will remove the pollution of death (J. Lewis, 2002).

Figure 2-12: Ejengi initiation ceremony.

Ngoku is the women's ritual association and all Mbendjele women get initiated into this association. It is this time a young Mbendjele girl is taught the secrets of the women's *molimo* (spirit). Men do not participate in *Ngoku* performances, and are in danger if they do not stay away respectfully. *Ngoku* does not materialize in public with a specific costume, rather it is believed to be embodied by the initiates (J. Lewis, 2015). The performance starts with elder women leading the singing and younger women running up and down in the camp, arms attached, calling all other women to come and informing that *Ngoku* has started (Figure 2-13). As more women joins, they occupy the communal places of the camp and impose their authority. It is during this time women celebrate their power and solidarity and use it as a device to shame men (J. Lewis, 2002). As such, the *Ngoku* songs often insult men, concerning sexual relations. Some of the lyrics include (J. Lewis, 2002):

> "*Mapindi ma mu bola!*' (Their testicles are broken!) or '*ba ena mojambi na yobe mapeni*' (They cut the water liana with a sharp knife – referring to men's need for circumcision), or '*baito wonda to njombo, doto ba die ebe*!' (Women only chase young men, old men are no good!), and so on".

Figure 2-13: Women's Ngoku initiation.

It is worthwhile to note here that *mokondi*s (spirits) can be sold and bought (J. Lewis, 2015). The Mbendjele often share food, clothing and other material items freely on demand, however, according to ethnographies the knowledge is not free (J. Lewis, 2015). Different Mbendjele groups own different spirits, and if a group wants to perform a forest spirit ritual owned by another group, they must get the permission to do so. These spirits are believed to be captured or found in the forest by spirit guardians (*konja mokondi*). A spirit guardian may capture a spirit by promising that it will be fed by singing and dancing in return for its help to people (J. Lewis, 2015). Later, the guardian may sell the spirit that he captured to other BaYaka groups. Lewis (2015) accounts a story of a conflict that arose upon the theft of the *Monano* spirit that we got to observe during our fieldwork in Ibamba (Figure 2-14). Accordingly, the Mbendjele from the Minganga region saw the *Monano* performance during their visit to Ibamba and introduced it under a different name when they returned back to their village. The word got spread and caused a conflict between the initial owner of the spirit and the men from Minganga (J. Lewis, 2015). According to Lewis, the spirit-plays may be traded among the BaYaka from Northern Congo, Southern Cameroon and CAR, and Western Gabon (J. Lewis, 2015).

Figure 2-14: Monano spirit dancing with an initiated man.

Children are always present in different spirit performances, and they have their own *massana* (forest spirit performances). One that we encountered in the camp Masia was the children's version of *Bobe*. Mbendjele children are great imitators, and infant learning occurs more via practice and imitation, than active teaching (Appendix A, Video 3). Children form mixed-aged groups (ranging from 3 to 15) during these spirit-plays, which allow younger children to learn from the older ones. During children's *Bobe*, I observed that older boys directed younger boys and used the *njanga* (sacred path) to prepare the forest spirit, while girls sang and drummed, calling the spirit to come out from the forest (Figure 2-15). These observations suggest that there is much social learning through horizontal, peer-to-peer cultural transmission and practice during Mbendjele childhood.

Figure 2-15: Children's massana (forest spirit performance).

Social norms:

Mbendjele have the concept of *ekila*, a set of beliefs and social norms that concern interactions between men and women, babies' health and sharing. Mbendjele may call *ekila* for blood, menstruation, taboo, a hunter's meat, animal's power to harm humans, and particular hazards to human reproduction, production and health (J. Lewis, 2008a). I have found from my surveys on the food taboos that certain animals are considered as *ekila* and avoided to be consumed, especially by pregnant or breastfeeding women and their husbands. For example, giant forest hog was avoided by pregnant and breastfeeding women, because the Mbendjele believed that the consumption of it would cause the baby to have disturbed teeth, shaped like the animal's tusk.

Mbendjele have taboos that concern sexual behaviour. For example, a couple with a breastfeeding baby is forbidden to have sex until the baby is weaned. Otherwise, the Mbendjele believe that the baby would get severely ill. Moreover, adultery is punished (Chapter 4 details how plants are used for punishing cheaters) and sleeping around with multiple women is believed to ruin a hunter's success (J. Lewis, 2008a). Woman's menstruation is also considered *ekila*, and a man should not go to forest for hunting if his wife is menstruating. It is believed that dangerous animals can smell the blood of his wife on him, and may attack (J. Lewis, 2008a).

Chapter 3: Fieldwork and Data Collection

In this chapter, I provide detailed information on the fieldwork that I undertook in 2013 and 2014, and the research methods that I used during my fieldwork. I stayed in Congo in total for 7 months spread over two field trips. The first field trip was in 2013 between April-June, and the second one was in 2014 between March-July. During this time, I stayed in eight Pygmy camps with my colleagues from UCL and the Mbendjele field assistants and translators (Figure 3-1). I was together with my PhD friends Nikhil Chaudhary and James Thompson during the entire fieldwork. Post-doctoral researchers Pascale Gerbault and Jed Stevenson, and the Master's student Aude Rey accompanied us during some parts of our trip.

Figure 3-1: Map of the campsites and villages that are visited during fieldwork in 2013 and 2014. Camp Enoko (not shown) was located between Masia and Longa, while camp Mbaya (not shown) was located between Masia and Minganga. Pokola is the logging town, and Minganga is a village where many Mbendjele reside with Bantu farmers.

3.1 2013 Fieldwork

My first trip to Congo-Brazzaville started in April 2013 with Charan Chaudhary, James Thompson, Pascale Gerbault and Jed Stevenson. The aim of this trip was to collect demographic data that was required for each of our individual projects and to conduct pilot studies to test the feasibility of our research designs. After much preparation for the equipment and the arrangement of research permits we arrived in Brazzaville. Obtaining research permits was made easy with the help of Jerome Lewis, a social anthropologist at UCL who conducts fieldwork in Congo with the Mbendjele for over 20 years. From Brazzaville, we took a small plane to Ouesso, a small town in Northern Congo, and also the capital of the Sangha region. We met Jerome Lewis in Ouesso, and introduced ourselves to the local authority at the prefecture in Ouesso and show him our research permits. It was very important to meet the local authorities and introduce ourselves everywhere we go in Congo, even in small villages, to avoid any conflict and for security purposes. From Ouesso, we took a public canoe to cross the Sangha river to the side where Pokola is located (Figure 3-2). From the riverside, we took a minibus to Pokola centre, which took about half an hour.

Figure 3-2: Crossing the Congo river from Ouesso to Pokola.

Pokola is a rapidly growing town (*n*= 12,000), where an international logging company, Congolaise Industrielle des Bois (CIB) is located (Figure 3-3). This is also the country's largest logging company and the presence of it attracts people from nearby villages for employment opportunities. There is also a fairly reliable hospital that is run by the logging company. We used Pokola as our base to reach to various Pygmy camps. We returned to this town in between our stays in forest camps to stay at a hotel that provided us the comforts of a bed, shower and nice breakfasts. We bought all necessary cooking equipment and food supplies from the market in Pokola (Figures 3-4, 3-5).

Figure 3-3: The logging town Pokola.

Figure 3-4: The market in Pokola.

Figure 3-5: A woman selling dried fish in the market, Pokola.

We also hired our field assistants in Pokola. The official language in Congo is French but there are many local languages. The Mbendjele speak a Bantu language, therefore it was necessary for us to use a translator. In this first field trip, we were able to find an Mbendjele translator and field assistants through Jerome Lewis, as he has previously worked with them.

Thus, apart from us, the researchers, our team 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 cook (Figure 3-6).

Figure 3-6: Part of our team in 2013.

We often travelled to the forest camps by hiring local taxis or minibuses, and followed the logging roads (Figure 3-7). All three camps that we visited during our trip in 2013 were located along the logging road between Pokola and the farmer village, Minganga (Figure 3-1). Some campsites, such as Longa and Mbaya, had satellite camps- usually made of close family- that were within walking distance to the main camp. The Mbendjele in all three camps associate themselves with Minganga village and are known as the Mbendjele from the Minganga region. Table 3-1 shows the population size and distance from Pokola for each camp we visited in 2013.

Figure 3-7: On the way to Ibamba. The dirt road was covered by fallen trees.

Table 3-1: Summary of the campsites that were visited in 2013.

Campsite	Camp Number	Population size	Number of adults	Number of children	Distance from Pokola (market town) (km)	Distance from Minganga (farmer village) (km)
Longa*	1	58	30	27	55	33
	2	3	2	1	55	33
	3	28	16	12	55	33
	4	10	7	3	55	33
	5	9	2	7	55	33
Enoko	6	30	11	5	68	20
Mbaya*	7	40	21	19	81	8
	8	31	14	17	81	8

*Camps Longa and Mbaya consisted of small satellite camps that were within walking distance from each other. All individuals in those camps interacted frequently.

3.1.1 Longa

The first Pygmy camp that we visited was Longa, which was about 55 km away from Pokola (Figure 3-8). People in Longa greeted us with great joy and hospitality. Dr. Lewis introduced us to the community and he and his family stayed with us during the initial days of our stay, which made it easier for us to adapt to life in the forest. We build our camp 5 minutes away from the main camp with the help of Mbendjele. During our fieldwork, we often chose 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 not surrounded by many tall, unsteady trees, which were serious hazards during storms and undoubtedly the most terrifying aspect of the fieldwork.

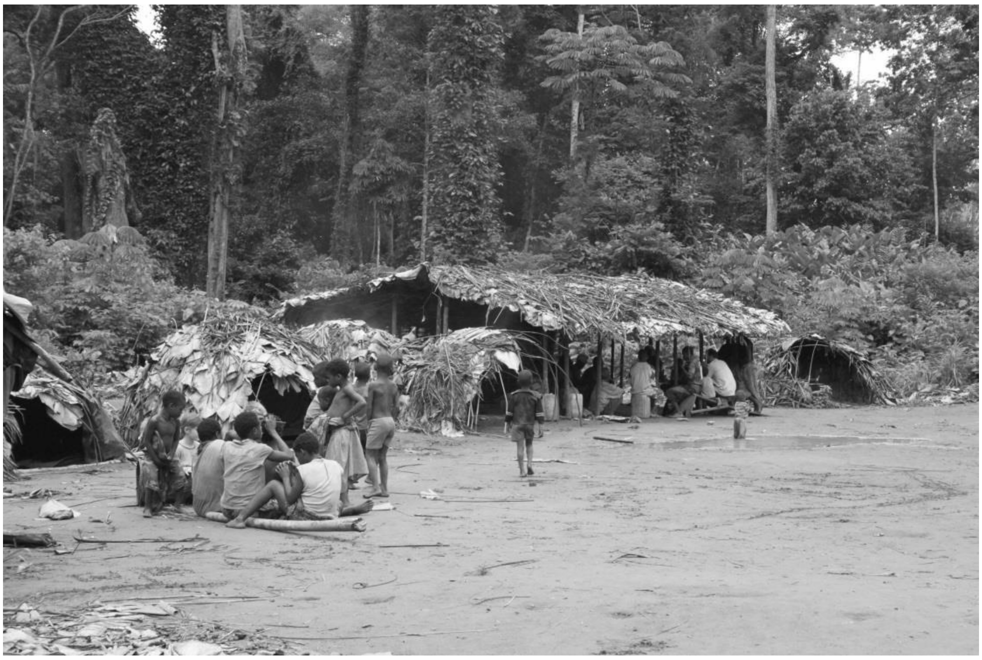


Figure 3-8: Longa in 2013.

Longa is located by the logging road and the Mbendjele may choose to come and go between Longa, other camps deep in forest or farmer villages. For this reason, the camp composition changes frequently, but the location of the camp is permanent. For example, towards the end of our first field trip we returned to Longa after two months and realized that some families have left the camp, while others have arrived from Minganga. Moreover, there was one main camp in Longa, and number smaller camps that were within walking distance to the main camp (Table 3-1). When living in larger groups, the Mbendjele often divide into smaller family groups that camp together in close proximity to other family groups.

Mbendjele build roadside camps like Longa to be able to trade their forest products. The logging road between Pokola and Longa is a frequented road by bush meat traders, who come either by minibuses or taxis to collect bush meats and some other forest products such as the *koko* or *ngongo* leaves from the Pygmies (Figures 3-9, 3-10). The Bantu gave shotguns and cartridges, and wire snares to the Mbendjele as they are the best hunters in the region. There is a high demand for bush meat in Pokola with its growing population since the establishment of the logging company. The Mbendjele get alcohol, cigarettes, manioc flour or tubers, bread, and occasionally clothes in return. Bantu traders often make payments in advance, and write down individual hunter's debt. The Mbendjele use the money most frequently for alcohol- the local palm wine *ngolongolo*, or Pastis. Sometimes conflict arises over debts.

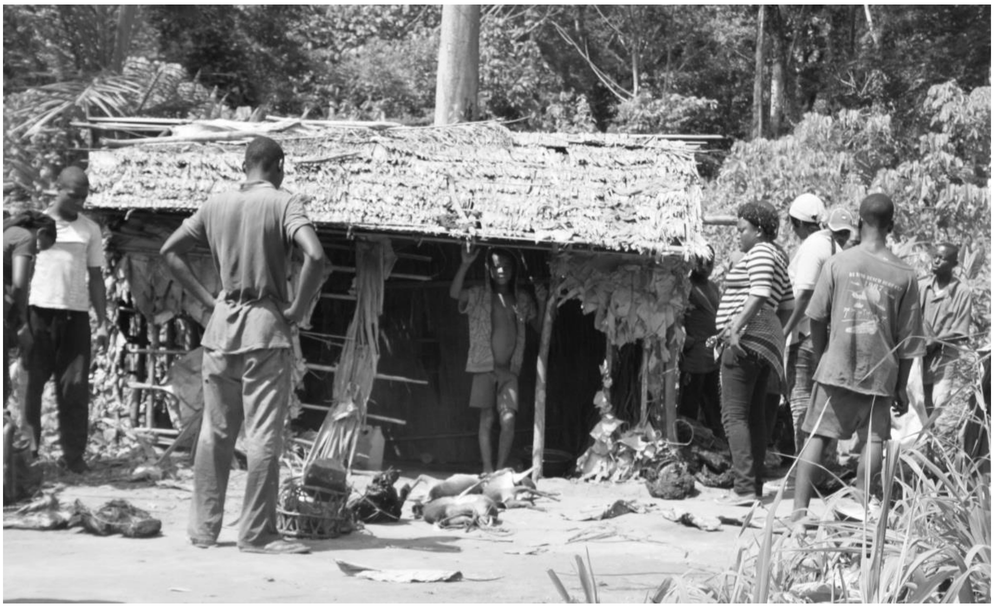


Figure 3-9: Bantu traders buying bush meat from the Mbendjele in Mbaya.

Figure 3-10: Minibus that transports bush meat from forest to towns.

The Mbendjele face serious problems about their land rights, mainly because of the bush meat trade. They are being forced to relocate from camps like Longa for the purposes of wildlife conservation. Many actors are in play, from conservation NGOs, to multinational logging companies and local administrators (J. Lewis, 2005). For example, the logging company, which has concessions in the Minganga region, wants Pygmies to settle down in farming villages so that they can control the bush meat trade in this region. The company needs to control the bush meat trade as a requirement for their FSC (Forest Stewardship Council) certificate that indicates sustainable forestry. Pygmies are easy targets for eco-guards, wildlife conservation NGOs, since they lack the necessary political power to defend their land rights. Unfortunately, the obvious causes for the bush meat trade, growing population sizes and high international demand that supports illegal trafficking, are not addressed properly. Instead, the Mbendjele are being targeted, sometimes violently, by eco-guards that are employed by the government with support from international NGOs (Salali, 2014).

We stayed in Longa for over 3 weeks, during which we got more accustomed to living in the forest.

3.1.2 Enoko

The second Mbendjele camp that we stayed in was Enoko, which was located along the same road as Longa, but further down towards Minganga. This was a smaller and a more temporary camp compared to Longa (Figure 3-11). As such, the camp was not occupied during our second trip. We stayed in this camp for about 10 days.

Figure 3-11: A young man showing us a hunting spear in the camp Enoko.

3.1.3 Mbaya

Mbaya was also located about half an hour drive from Enoko towards Minganga. This camp was comprised of three groups of huts; two located at either sides of the road, and one located within a couple of minute walk down the road from the other two (Figure 3-12). There were palm trees in the forest around the camp, probably have grown from the seeds that were spread by the Mbendjele. For this reason, it was a frequently visited campsite by other Mbendjele who came to collect palm fruits. We arrived in Mbaya in May, which was a shorter rainy season and our trip was marked by heavy thunderstorms. Our camp was located in the forest, at a short walk from the road, but we were not able to find a clear opening and were surrounded by some tall trees. One night during a heavy rain, we were so frightened by the thunderstorms and danger of falling trees that we spent the night in the house of Bilombi and his family, the *kombeti* (spokesperson) of Mbaya. We stayed in Mbaya for nearly 4 weeks.

Figure 3-12: Getting my hair done with the women in Mbaya.

3.1.4 Daily routine and relations with the Mbendjele

Our daily routine included waking up around 5:30am and having breakfast of some oats or instant soup before going to the Mbendjele camp around 6:00am (Figure 3-13). Most of the Mbendjele wake up with the first lights of the day. Not in forest, but in clearings and roadsides midday is very hot, which makes it very difficult to carry on work, especially taking anthropometric measurements. For this reason, most often we would have a break for lunch and wait until afternoon. Moreover, this time of the day may get even more difficult to concentrate by the *mbongo mbongo* stingless bees (also known as sweat bees) that repeatedly stick to your head and body and fly in to your eyes. We would then get back to work until about 5:30. Nevertheless, my data collection pattern has changed during the second trip when I started my interviews on plant uses. Then, I could also work inside a hut or a shadowed place during warm hours of the day.

Figure 3-13: Our camp in Longa.

In the evenings the whole team would sit down together for dinner. Lunch and dinner meals consisted of supplies bought from Pokola such as spaghetti, corned beef, sardines and occasionally beans and dried fish. We did not exchange/buy food from the Mbendjele since our research included collecting data on foraging and food sharing. Nevertheless, when none of the team was collecting such data we would buy forest food from the Mbendjele, which were more delicious than the supplies we brought from Pokola. A delicious Mbendjele dish was bush meat cooked in sauce made from *koko* leaves and supplies of peanut butter or palm oil obtained by crashed palm fruits (*mbiya*) (Figure 3-14).

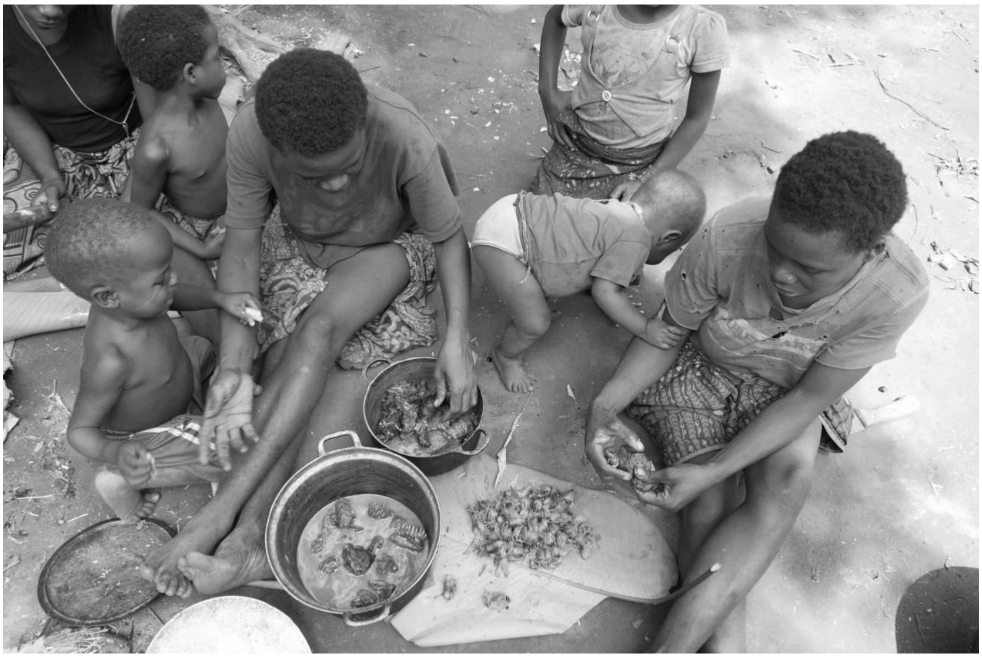


Figure 3-14: Semoi and Egbay preparing pangolin in palm oil extracted from crashed fruits.

We would go to bed around 9:00pm unless there was a *Bobe massana*. The Mbendjele performed *Bobe* some nights, either for celebrating our arrival or for hunting success. During these times, we were often expected to provide alcohol. Being part of these performances was an unforgettable experience.

Living in the forest was tough at times. We had termites eating the bottom of our tents, and trying to make a nest inside. Various flies and stingless bees during midday and around our camp toilet were a major discomfort. On the other hand, we did not have any dangerous encounter with a wild animal. Congo has big snakes such as viper and python, but the ones we saw were already killed. The most frightening moments were the thunderstorms and the strong wind that would come just before rain and make trees fall.

The Mbendjele greeted us with joy and were very welcoming at every camp we stayed. I was fascinated by their stamina and joy. Staying at a camp for several weeks enabled us to get to know each person and establish social bonds. Children were especially curious to know us, and always willing to teach us about the life in the forest (Figure 3-15). As we were helpless in the forest, they would teach us how to make fire, where to look for mushrooms, the names of the plants, how to hold a machete and so on.

Figure 3-15: Looking at photographs of animals with children in Longa.

Organizing a *massana* each week was a great way of bonding with the Mbendjele. We were also lucky enough to participate in initiation ceremonies. In Longa, I was initiated in *Ngoku*. Whenever I find a break from data collection, I followed women in their foraging and fishing trips. I enjoyed these times very much and learnt a great deal about women's life in the forest. These activities allowed us to build trust and friendship with people who are unfortunately accustomed to discrimination and exploitation.

Occasionally, there was social tension due to requests for money and gifts. The Mbendjele understandably perceived us as extremely wealthy, and given the norm of sharing in their culture it is not surprising that we were continuously asked for food, money, cigarettes, clothes etc. At times I found it extremely hard to reject those demands, but over time we learnt to manage them. 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. This latter part sometimes caused tension, as the Mbendjele did not want to wait until the end. We resolved these by calling a camp meeting and explaining we are students, and detailing exactly what gifts we can give. Moreover, our experience in Longa taught us not to give a large sum of money to a camp spokesperson to divide between camp members, which caused discussions among them. Later, we divided the money into smaller amounts to be given to each household at the end of our stay at a camp.

3.2 2014 Fieldwork

Nik, James and I went on this second fieldtrip with the aim of collecting the main data that each of us planned to collect for our specific research purposes (Figure 3-16). We also continued collecting the demographic data that all of us needed. In terms of logistics, over time, we built up a small network of local acquaintances for routine tasks such as buying and delivering supplies, and drivers who knew what dates we needed transport to and from particular camps. I also got a semi-professional video camera with a grant from UCL and our research project that enabled me to film various aspects of the Mbendjele life during my second trip.

Figure 3-16: Nik, James and I with Semoi and her children and granddaughter in Longa, 2014.

On this trip, we added two more translators to our team – Gifanhou and Nicolas Yupi after numerous French competency interviews with Mbendjele students in Pokola (Figure 3-17). Nik, James, and I had a translator each, greatly improving our efficiency relative to our first trip when we were all reliant on Paul. Although I never got fluent in speaking Mbendjele, I could understand and speak some common words during this second trip, which was helpful for a deeper understanding of the Mbendjele life. In addition to Nik, James, the field assistants, and I we had a Master's student, Aude Rey, in our team for the parts of this trip.

Figure 3-17: My translator, Nicolas in the town camp Sembola

Over 4 months of fieldwork, we visited 5 Mbendjele camps: Longa, Ibamba, Masia, Bolobo and Sembola (Table 3-2, Figure 3-18).

Figure 3-18: Our equipment in 2014.

Table 3-2: Summary of the campsites that were visited in 2014.

Campsite	Population size	Number of adults	Number of children	Distance from Pokola (market town) (km)
Longa	60	29*	26	55
Ibamba	62	35	27	100
Sembola and Bolobo	306	139	167	0
Masia	33	19	14	60

*Missing data on age groups

3.2.1 Longa

When we arrived in Longa for the second time in late March 2014, we quickly realized how different the camp composition was compared to our first time there. There remained some familiar faces, such as the *kombeti* Mbame, but there were many new families as well. As in 2013, there were some Bantu traders living with the Mbendjele. This time there was one Bantu family in the main camp, and another couple living in a smaller camp that is two-minute walk from the main camp.

We had an unfortunate event during our early days in Longa. As mentioned earlier, all foreign researchers in Northern Congo are expected to introduce themselves to the local authorities and police. A couple of days after our arrival in Longa we were visited by a policeman from Mbua, a Bantu village that is about 1,5 hours drive from Longa, and nearby Minganga. We were planning to pay a visit to him to introduce ourselves and give fees that are charged by local authorities; however we realized that we were too late. He was quite drunk and accompanied by a group of men from Mbua. He was upset that we did not ask his permission to stay in Longa, and started beating our translator, Paul. We managed to calm him down by showing him our research permits and giving him money for petrol to Pokola. Luckily it was the only difficulty with the local authorities during our entire trip, and a lesson for us to be careful about the local official requirements.

During our time in Longa, Nik and James got initiated to the famous *Ejengi* ritual (Figure 3-19). The ritual ceremony lasted for three days, where much singing, dancing, drinking and eating happened.

Figure 3-19: Bakima, James, an Mbendjele boy and Nik during the *Ejengi* initiation.

3.2.2 Ibamba

After Longa, we wanted to go to a camp where the Mbendjele did not trade with Bantu. Although almost all Mbendjele trade with Bantu at some point during the year, we heard that Pygmies in Ibamba region might be trading with Bantu less frequently. Ibamba is located 100 km away from Pokola, on an old, currently unused logging road. The camp that we stayed in was called Ibamba, nevertheless, Ibamba is actually the name of the region which consists of big swamp forests, where many Mbendjele reside.

Reaching Ibamba was 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 an encounter with two gorillas; but we got there in the end.

Soon we realized that the people in Ibamba were not hunting game (at least when we were there), because they were too frightened by the eco-guards. Some weeks before our arrival, an Mbendjele man from Ibamba was accused of illegal hunting and got arrested and sent to the prison in Ouesso. There were manioc fields and plants around the camp, and people were collecting tubers and leaves frequently. Thus, the main meals that were eaten in Ibamba were cultivated tubers, manioc leaves (*djabuka*), fish and crocodiles (Figures 3-20, 3-21).

Figure 3-20: Women and girls poundering manioc leaves, *djabuka* in Ibamba.

Figure 3-21: A dwarf crocodile caught in the swamp forests of Ibamba.

I found staying in Ibamba physically the hardest for two reasons. First the camp was in a swamp forest, therefore it was very difficult to supply find drinking water. We managed this by employing two Mbendjele men as field assistants to collect water and bring them to camp. Second, there were many *mbongo bongo* flies, honeybees and mosquitos, much more than those in other camps (Figure 3-22).

Figure 3-22: Filming honey collection in Ibamba with hundreds of flies (*mbongo bongo*) around.

Despite of these difficulties, we had joyful times with Mbendjele; participating in *Bobe*, *Monane*, and *Molimo* ritual performances, going on fishing and honey-collection trips, trekking in the forest to see elephants (although we did not have luck). I stayed in Ibamba for two weeks, and after finishing my work there came to Pokola with Aude Rey to start working with the Mbendjele living in town for our research on socioeconomic transitions.

3.2.3 Town camps: Bolobo and Sembola

Mbendjele build large camps in Pokola. The ones I conducted research in were called Bolobo and Sembola, which were located within two minutes walking distance from each other. Because those two camps were very close to each other, I will refer to them as the town camp. Aude and I shared a hotel room in Pokola and walked to the Mbendjele camp every day with the first lights of the day (Figure 3-23).

Figure 3-23: On the way to the town camps, Bolobo and Sembola.

The Mbendjele have permanent houses made of old timbers in the town camp (Figure 3-24). Some houses also have gardens, where people grow sugar cane, manioc, and banana. Although some families come and go or stay there for visiting relatives, some Mbendjele live in the town camp permanently. For example, all our field assistants had permanent houses in Sembola. I observed people going to the local market to buy food and frequently working as wage labourers in farmers' fields or for the logging company.

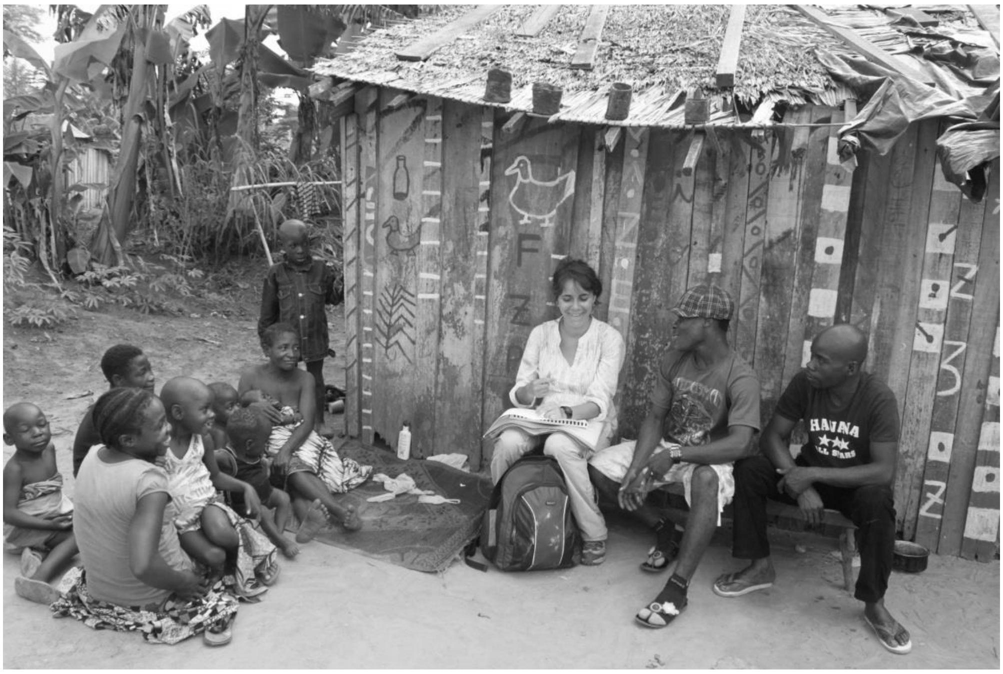


Figure 3-24: Aude and her translator Gifhanou in the town camp Sembola.

The Mbendjele that were living in the town camp at the time came from various regions, although some younger adults were born and raised in Pokola (see Chapter 7 for details).

3.2.4 Masia

The last Mbendjele camp that we stayed in was Masia. This was a smaller camp about an hour and a half walk away from Longa towards Minganga (Figure 3-25).

Figure 3-25: The camp Masia.

Moreover, there was a satellite camp where Semoi and her husband were living with their children. We knew Semoi and her family from Longa. Both in Longa and Masia they preferred to make their own camps at a walking distance from the main camps. We have already established a very good connection with Semoi and her family, and decided to build our camp behind their camp in Masia (Figure 3-26).

Figure 3-26: Our camp nearby the huts of Semoi and her family in Masia.

Our stay in Masia was very comfortable and full of joy (Figure 3-27). I accompanied Semoi and her family in their foraging trips and had an opportunity to film various events. Semoi and her daughters showed me how to find and dig different types of wild yams and plants in the forest. We also participated in several *Bobe massana*. A day before our departure, I participated in *Ngoku* ceremony with women.

Figure 3-27: Children bathing in the river near Masia.

There was always a Bantu trader in Masia, who would buy the hunted meat from the Mbendjele. Moreover, women were collecting *koko* and *nganga* leaves to sell to traders that frequently drove by Masia (Figure 3-28, 3-29).

Figure 3-28: Noel, a hunter, with bush meat behind him. The meat is smoked to be sold to traders.

Figure 3-29: Mbendjele women carrying the *ngongo* leaves that they collected in the forest to be sold to Bantu.

During our stay in Masia, we heard that people were forced to abandon Longa. Some Mbendjele passing from Masia informed us that some families from Longa have now moved to a forest camp to wait for the atmosphere in Longa to calm down. As we nearly completed the data collection and were preparing for our return, we decided to pay a visit to the forest camp. We left our tents in Masia and started walking towards Longa. On the half way, we managed to get on a minibus that was passing by. In Longa, Mabiala (the *kombeti* Mbame's son) greeted us and walked us to the forest camp. This camp, called *Mokole*, was two hours walk from Longa. The camp mainly comprised of Mbame's family: his sons and their wives with children, his first wife and daughter. The Bantu family in Longa was also there, probably for hunting and employing some Mbendjele hunters. Everyone was very upset about the relocation and asked us to send news to Dr. Jerome Lewis for taking an action. We stayed there for a night.

3.2.5 Minganga

A group of people from Masia were going to Minganga to visit a relative who was severely ill. A truck was passing by and I seized this opportunity to visit Minganga with them, asking Nicolas (my translator) to come with me. Although Minganga is a farmer village, there are many (maybe more than the farmers) Mbendjele living there, at the outskirts of the village. Their camps are big, like the ones in Pokola, comprised of houses scattered around a large area (Figure 3-30). There, I saw many familiar faces, some friends and children from Longa and Mbaya that I have not seen since our first trip.

Figure 3-30: Mbenjele houses in the farmer village Minganga.

I went to Minganga, because I was interested in the residence patterns and time preferences in Bantu farmers. With the help of Mbendjele and local people, I found a small neighbourhood where I collected demographic data and played a time-preference game that I will explain in the next section.

3.3 Data Collection

This section provides detailed information about the research methods my colleagues and I used during fieldwork. I collected the genealogical, anthropometric and age data together with my colleagues Nikhil Chaudhary, James Thompson, Aude Rey, Jed Stevenson and Pascale Gerbault. The interviews on the knowledge and uses of plants and food taboos, along with the future discounting game were conducted by me with the help of my Mbendjele translator, Nicolas. I conducted the "gift game" experiment together with Nikhil Chaudhary and Aude Rey. All the data analyses presented in this thesis are conducted by me.

3.3.1 Ethical Approval and Informed Consents

The research presented in this thesis and fieldwork was approved by UCL Ethics Committee (UCL Ethics code 3086/003). Moreover, we obtained a research permit from the Congolese Ministry of Scientific Research and Technology (Appendix B).

We carried out our research protocols after informed consent was obtained from all participants. Before we started our research, we explained the Mbendjele our research purposes by using posters that had illustrations about the research (Figure 3-31). If the participant agreed to participate in research, we took written consents. The written consents were required because of the saliva samples that we collected for genetics analyses. Although the Mbendjele were illiterate, we read the consent form through our translators. The information sheet for participants on the consent form can be found in Appendix C. If the participant agreed, we asked for his/her signature, after explaining what a signature is. If the participant did not know how to sign, our translators signed the form as witnesses.

Figure 3-31: Our translator Mekounu Paul is explaining the purpose of our research to the Mbendjele.

3.3.2 Genealogies & Kinship

We started our research by conducting genealogical interviews (Figure 3-32). Based on our interviews we drew family trees, which allowed us to define the relationship type (mother/father/sibling/spouse/cousin/affine etc.) and genetic relatedness for all dyads in our study sample, as well as their residence patterns. Mbendjele have multiple names and nicknames, so we asked all the names of an individual on the genealogy to prevent duplicates. When entering the data on a computer, we also identified the cases where the same individual was named differently by different participants by cross checking the names of other relatives.

Figure 3-32: Planning work in Longa.

Genealogical interviews were conducted with all adults in each camp. 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, including the deceased, their sex, and with which spouse each offspring was conceived
- The birth order of offspring (including the deceased)
- 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

Initially we also planned to ask some questions about mobility and residence patterns, however, we came into the conclusion that the answers would not be as robust as the data that we would obtain from genealogies and observations. First, the Mbendjele did not have the same concept of time as we did, therefore questions like “When did you last move to another camp/location? Do you move frequently?” did not make sense for them. Moreover, some questions such as “How long did you live with your parents?” required accurate re-collection of events, which could not be verified.

Analysing the kinship and residence patterns of the Mbendjele:

By using the genealogical data from the pilot fieldwork, I constructed kinship matrices by using the R packages kinship2 and pedigree (Coster, 2012; Therneau, Atkinson, Sinnwell, Schaid, & McDonnell, 2013). These matrices were used to determine the genetic relatedness between all dyads in our sample. Together with Mark Dyble (a PhD student at UCL), I constructed relatedness networks to analyse the camp composition and residence patterns of the Mbendjele and Agta hunter-gatherers. The results that are obtained from the analysis of these networks have been published as a research paper (Dyble et al., 2015). Figure 3-33 shows how marital ties (depicted in red) connect clusters of people from different camps.

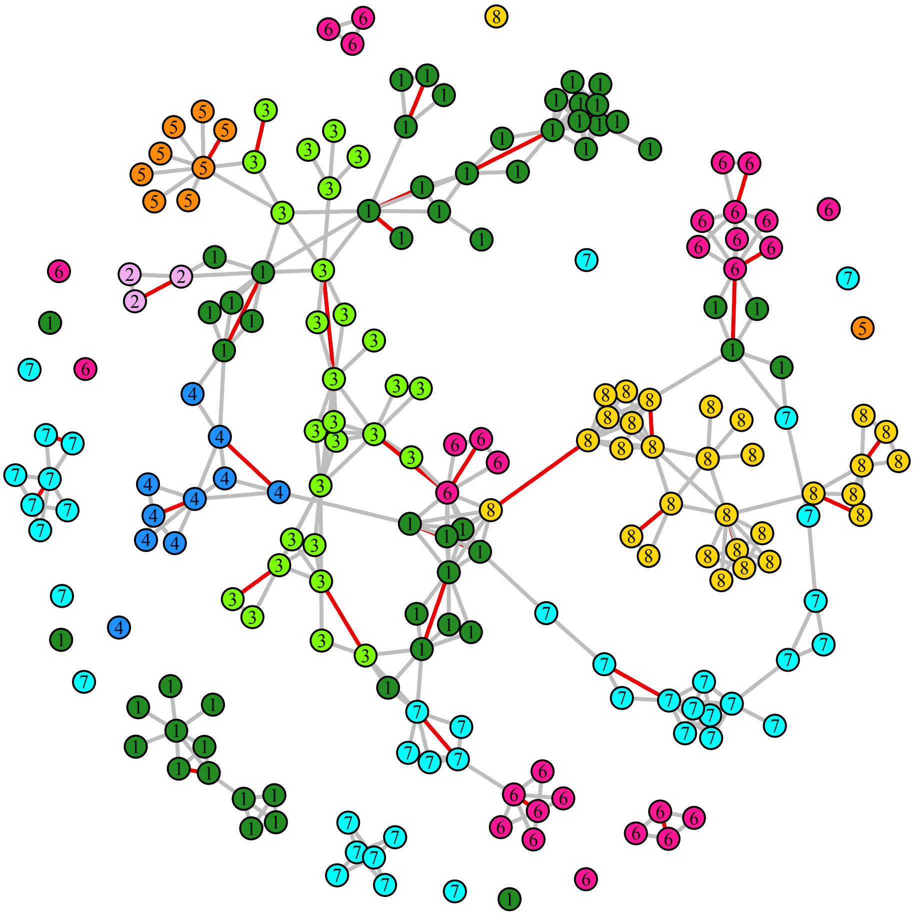


Figure 3-33: Relatedness network for the entire study population in 2013. Camp membership is represented by node colour. Numbers inside the nodes are the camp numbers that are shown on Table 3-1. Grey ties show the primary kin relationships (i.e. mother, father, child, sister or brother). Red ties correspond to the marital relationships.

3.3.3 Anthropometrics

We often collected genealogical and anthropometrics data at the same time. For each household, one of us would draw the family trees, while the other two would take anthropometric measurements of the members of the household. We used a Harpenden anthropometer for measuring height, and waist and shoulder width (Figure 3-34). We would always demonstrate how we take the measurements on ourselves first, since the Mbendjele were not familiar with the equipment we used for measurements. This way, we tried to ensure safety of the equipment. Moreover, we would measure older siblings before young children to mitigate any fear of young participants.

The following measurements were taken:

- Height (adults and children).
- Height (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. We weighed ourselves 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 (children and adolescents only) was recorded using a reference sheet.

3.3.4 Aging

The analyses conducted in Chapters 6-7 of this thesis included data on participants' age. For these, I used age groups rather than actual ages. This is because the Mbendjele are not familiar with our calendar and do not keep track of their age. We estimated participants' ages by using a method called "consensus aging" that is developed by anthropologists working on the Ache hunter-gatherers (Hill & Hurtado, 1996).

To construct a relative age list, we took photographs of all camp members at each campsite, except for the town camp. These were then divided in to 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 our estimations. We then laid out all the photographs of a given cohort (starting from the youngest cohort) at the centre of the camp and first asked the participants to identify the oldest member of the cohort (Figure 3-34). Then, we picked up the remaining photographs and displayed them one by one asking the participants the name of the individual on the photograph to confirm they recognize the person. If the participants recognized the person, we asked them 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. This process was repeated for all cohorts.

Figure 3-34: On the left, Nik is collecting anthropometric data. On the right, consensus aging in Mbaya.

We obtained three relative age lists for participants in the Minganga region. The first two were constructed during our first fieldtrip in 2013 (n= 180), and the third one was constructed in 2014 by including all members from Minganga region in the entire study population (i.e. camps Longa, Masia, Mbaya, Enoko) – 240 individuals. The Mbendjele in this region were familiar with all the 240 members in our study population, since they frequently visit relatives in other camps and move between camps across the region. On the other hand, because Ibamba was far away from Minganga region, the participants there 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 (n= 60).

After obtaining relative age lists, one must assign actual ages to some individuals to enable the calculation of estimated ages (Hill & Hurtado, 1996). 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, we estimated a lower and upper bound of their age. These age ranges were informed by dental development, reproductive histories, birth order and visual appearance. By using the relative age lists and anchor points for actual ages, Prof. Mark Thomas and Dr. Yoan Diekman from UCL have developed a new method based on Bayesian statistics to obtain the final age estimates for each participant from the Minganga and Ibamba regions. By using the obtained results, I broke the age of the participants into four categories for all my analyses: child (0-15 years), young adult (15-25 years), adult (25-45 years) and old adult (45+ years). For people in the town camp, I used the age groups above based on my own estimates with respect to visual appearance at the time of interviews.

3.3.5 Interviews

3.3.5.1 Plant knowledge and use data

On our second fieldwork, I conducted interviews that aimed at examining participants' plant knowledge and use. These interviews were based on a list of 35 plants that I chose from an initial list that contained the vernacular names of 83 plants. I obtained the initial plant list by asking 15 adults in Longa to list the name of the plants that they use for medicinal purposes. Chapter 4 details how I constructed the final list that contained 35 plants from this initial list. Two plants on the list had different names in different camps, and participants in the town camp did not recognize the name on the questionnaire. For this reason, I omitted the data on these two plants from my analyses.

After preparing the list of plants for the interviews, I asked each participant about their use of these plants with my translator. For each plant we asked, i) whether the participant knew the plant, ii) if they knew whether they used the plant, iii) if so for what purposes they used the plant. At the end of each interview we also asked from whom the participant learnt about the plants. The information on the sample size is provided in Chapter 4.

Before going to Congo in 2014, Dr. Sandy Knapp, a botanist from the Natural History Museum in London, advised me to take as many photos of the plants as possible. Following her advice, I took detailed photos of the leaves, bark, and where available, fruits of the 33 plants on my list with the help of two Mbendjele informants from Longa, and one from Ibamba (Figure 3-35). Upon return from fieldwork, I collaborated with two botanists, Dr. Olwen Grace and Dr. Xander van der Burgt, from the Kew Gardens. They identified 31 out of the 33 plant species on my list from the photos. The data obtained from the plant interviews are used throughout this thesis.

Figure 3-35: Ngulawe, an Mbendjele healer from Longa, is showing me the plants that he uses. The photographs I took during this forest trip were used to identify various plant species.

3.3.5.2 Food taboos

During the interviews about plant uses, I also asked the participants about the animals they eat. This was for a project that is examining the food taboos in the Mbendjele, aiming to understand how food taboos are shared and differed among individuals from different camps and age, and sex groups. Although, this thesis does not include the results obtained from this project, the list of 60 animals that was presented in Chapter 2 was used to determine which animals the Mbendjele have a taboo of (Table 2-2).

3.3.5.3 Questions on socioeconomic transitions

In addition to the interviews about the plant uses and food taboos, we asked the participants the following questions; usually after the genealogical interviews or before the behavioural games we played (explained in the next section). The answers to some of these questions were used in the analyses about the market integration of the Mbendjele, presented in Chapter 7.

The following questions were asked to each of the participants:

1. Do you own a field?
2. Have you ever paid a bride price *[for males]*? If so, how much was it?
3. Do you go to school?
4. Do you engage in wage labour? If so, do you engage in frequently (e.g. once or multiple times a week) or non-frequently?

3.3.6 Behavioural Games

3.3.6.1 Future discounting game

I collected data on inter-temporal time preferences (i.e. future discounting) to examine the variation in the participant discounting levels across different camps. In behavioural economics this procedure is used frequently to investigate whether an individual is willing to wait to receive a larger sum of money (or any type of currency) in the future, or prefer to receive a smaller amount sooner. It measures how much a person discounts the future and can be used to understand individuals' willingness to accumulate resources. The procedure employs a choice task between two or more options such as "Do you prefer to receive 1 monetary unit in 5 days, or 10 monetary units in two weeks?” The participant, who chooses 1 monetary unit over 10 to be received in nearer future, is said to discount the future more than the one who would wait to receive 10 monetary units.

Initially, I planned to play this economic game by using money. In Longa I conducted pilot experiments where I asked participants whether they preferred to receive 500 CFA in two days or 1000 CFA in five days. Everyone chose to receive the smaller, but sooner option no matter how much I varied the options. I even tried 500 CFA today or 1000 tomorrow, and everyone chose the “today” option. I came to the conclusion that with the money as currency, I would not have any variation in response in an immediate-return society that greatly values the immediate options.

Nevertheless, I decided to use stock cubes instead of money and conducted some experiments in Ibamba. Stock cubes (also known as bouillon cubes) are used widely in West and Central Africa as a food-flavouring agent, and highly valued by the Mbendjele. In fact, we were always asked to provide some stock cubes every Mbendjele camp that we stayed in. Although majority of the people chose the sooner option, there was a variation in time preferences with the choice task between receiving one stock cube today or five tomorrow. I continued using this choice task in all other camps that we stayed in.

I have asked this question to each participant at the end of completing an interview, stating that we will be giving stock cubes as a gift for their participation in our research. I then asked whether they would like to receive one cube today, or five cubes tomorrow (as usual translated from French to Mbendjele by my translator). The participants were told if they chose to receive one cube today, the researcher would give them one cube at the end of the interview. If they chose to receive five cubes tomorrow, then she would give them five cubes tomorrow during the day. I gave the stock cube(s) to the participants according to their preference. The results from this study are discussed in Chapter 7.

3.3.6.2 Gift game

Nikhil Chaudhary, Aude Rey and I collected this data to discern adult-adult social networks, and determine the social capital (i.e. how willing other camp members were to cooperate with them) of each participant. We followed the Gift Game procedure that was used in another study on the cooperation networks of Hadza hunter-gatherers (Apicella, Marlowe, Fowler, & Christakis, 2012). This protocol uses sticks of honey as gifts and the researcher asks the participant to name up to three people to give three honey sticks as gifts.

We played this game with all willing members of the Longa, Masia, Ibamba and the town camp. The key features of the 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 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.

We published the results from the honey sticks game in two papers, examining the effects of social capital on reproductive success (Chaudhary et al., 2015), and the heritability of social capital (Chaudhary et al., 2016).

3.3.7 Filming

In 2014, I documented various aspects of the Mbendjele life by filming the Mbendjele who gave their consent to be recorded on camera. I video recorded the verbal consent of participants before filming. My aim was to make a short documentary about the Mbendjele camps by the roadsides, documenting the bush meat trade, and lives of hunter-gatherers in modern days. I edited various short videos, some of which I put online on my blog (congokongo.wordpress.com) to communicate our research to wider audiences. Moreover, some of the videos have been used as supplementary materials in research articles (Salali et al., 2016), and some as data. For instance, some of the footage documented infant-caregiver interactions in the Mbendjele (Appendix A, video 3) and were used in a collaborative project examining those interactions across various cultures. The results from this project have recently been accepted for a publication (Mesman et al., 2017).

Chapter 4: Plant uses in the Mbendjele BaYaka

4.1 Introduction

The use of plants is a crucial part of life for forest-dwelling hunter-gatherers. In fact, African Pygmies, like many other traditional societies, largely rely on plants for food and medicines. For this reason, it is not surprising that Pygmies are famous for their knowledge of medicinal plants and healing abilities among their neighbouring groups (Bahuchet, 2014). In Congo, Bantu farmers often go to Pygmy healers when they are sick (Jerome Lewis, personal communication). Although the Mbendjele BaYaka are exceptional in their knowledge and skills related to forest, there is not much work conducted on the uses of plants in this population. The aim of this chapter is to document various uses of wild plants by the Mbendjele. In particular, I will address the following questions: 1) For what purposes do the Mbendjele BaYaka use plants?, 2) Which are the plants used as medicine and for what diseases they are used for?, 3) Do men and women differ in their plant uses?, 4) Do different Mbendjele camps differ in their plant uses?

4.1.1 Plant use research in Central African Pygmies

Most of the studies documenting plant uses of various African Pygmy groups are conducted by Japanese researchers (Hattori, 2006a, 2006b; Kimura, 2013; Terashima, 2003; Terashima & Ichikawa, 2003; Terashima, Ichikawa, & Sawada, 1988). Terashima and Ichikawa (2003) documented the uses of plants in the Efe and Mbuti Pygmies from Ituri forest in DRC by collecting and identifying over a thousand plant species and recording their uses. Their surveys have revealed that the plants were used as food, medicines, as poisons to hunt and fish, as materials to make huts, beds of logs, leaf mats and as equipment for cooking, transporting or foraging. Some plants were eaten by animals and Pygmies use this knowledge to ambush animals that approach those plants for feeding. Some others had social or symbolic meanings. For example, a plant species was considered as part of the "master of forest" who controls all the life in the forest and was forbidden to be collected (Terashima & Ichikawa, 2003). In a separate study Terashima compared the names, uses and attributes of plants and animals among the Efe and the Mbuti (Terashima, 2003).

Hattori investigated the variation in plant uses among 10 Baka Pygmies in Cameroon (Hattori, 2006a). Among the 602 plants she collected, the majority were used as medicine and others as food or in material culture. Like the Efe and the Mbuti, the Baka also used some plants in their social and spiritual life. For example, one folktale recounted how *Komba* (the god of the forest) stuck a leaf and stalk of a Marantaceae plant (*ngongo*: *Megaphrynium macrostachyum*) into the anus of a Baka man who then transformed into a yellow-backed duiker (*bemba: Cephalophus silvicultor* (Afzelius)) (Hattori, 2006a). It is interesting that the stalk and the leaf of the plant resemble the oval-shaped tail and the yellow pattern that is on the back of the animal. Another ethnobotanical study on the Baka in Cameroon concerned their medicinal plant use. Betti recorded the uses of 107 medicinal plants and found that the most common uses were for treatment of cough, lactation failure, malaria, wound and toothache (Betti, 2004). Betti and his colleagues also surveyed 6 Baka adults from Gabon about their medicinal plant uses and found that the majority of the uses concerned treatment of malaria, sexual dysfunction and diarrhoea (Betti, Yongo, Mbomio, Iponga, & Ngoye, 2013). The results from the above studies have been compiled in an exciting plant use database that is maintained by the researchers from the Kyoto University (AFlora Committee, 2013; Kimura, 2013). This database contains over 6,000 records from tropical Africa and is very useful for comparisons of plant uses among various African groups.

4.1.2 Importance of plant use

Why is plant use important in tropical forests in the first place? Moist and hot, tropical rainforests act as an incubator for parasitic microbes and viruses that cause intestinal and respiratory infections (Froment, 2001, 2014). In fact, the main causes of mortality in Aka Pygmies of Central Africa were found to be respiratory and digestive system infections (accounting for nearly 50% of the fatality cases) (B.S. Hewlett, van de Koppel, & van de Koppel, 1986). Similarly, among Baka Pygmies of Cameroon digestive and respiratory system disorders are the primary causes of death in infants and children (Froment, 2014). African Pygmies are found to be infected by up to twenty, and Malayan Semang hunter-gatherers up to twenty-two different parasites (Dunn, 1968). In Cameroon, the prevalence of intestinal worm infections goes from 2 percent in Saharan to 98 percent in equatorial zones, where Pygmies reside (Froment, 2014).

Although we did not collect direct health data on the prevalence of parasitic infections in the camps that we lived in, we all got infected by parasites ourselves. Upon return from fieldwork, I found out that I got infected by whipworms, roundworms and hookworms. One of my fieldwork colleagues got threadworm (*Strongyloides sp.*) infections and Schistosomiasis, while my other colleague got Filariasis (caused by an infection with roundworms). In the absence of modern medicine, medicinal plants are the only treatment option that is available for rainforest dwelling human groups. Although it is difficult to measure the effectiveness of medicinal plant use, researchers working on Tsimane forager-horticulturalists have found that mothers with higher ethnobotanical knowledge had children with better health indices (McDade et al., 2007). Therefore medicinal plant uses may provide direct health benefits in small-scale societies with limited access to modern medicine.

4.2 Methods

4.2.1 Initial plant list

At our first campsite, I asked individuals to list the names of the camp members who are known to have good knowledge of plants. The Mbendjele have healers known as *ngangas*. Although families may specialize and are known to be experts in certain treatments, an individual can develop a high reputation and become *nganga* because of his/her skills in healing people. After choosing 15 adults (one of which was the *nganga* of the camp, five females) as informants I asked them to list the names of the medicinal plants they use. This initial list consisted of 83 vernacular names (Table 4-1). I calculated how many times each of the 83 vernacular names was mentioned by informants. To avoid biasing our questionnaire sample with either plants that are used very frequently or seldom, I chose 35 plant species with mixed use-frequencies. For example, one plant on the list was mentioned by only one informant, whereas another was mentioned by 7 informants (Table 4-1). After choosing 35 plants to use in our questionnaires, three informants (two from camp one (Longa), one from camp three (Ibamba), at different times, walked me and my translator around the forest and showed us the trees to take photos for identification and to ensure consensus for the vernacular names. Two plants on the list had different names in different camps, and participants in the town camp did not recognize the name on the questionnaire. For this reason, I omitted the data on these plants from my analyses.

Table 4-1: Initial list of 83 plants (vernacular names) and the number of informants (n= 15) that reported using them.

Plant	Frequency	Plant	Frequency	Plant	Frequency
Bamba	1	**Ijo**	1	**Mongemba**	2
Banga	4	**Imbanda**	4	**Mongo**	3
Bangi	1	**Imbenya**	1	**Mongoko**	1
Benya	1	**Imbi**	2	**Moningo**	1
Bobamba	8	**Indengo**	5	**Mopo**	1
Bobate	1	**Indjele**	1	**Mosebe**	1
Bokambonga	2	**Ingoka**	2	**Mosombo**	3
Bokana	1	**Jongo**	2	**Mototoko**	6
Bokoko	1	**Juese**	1	**Motunga**	3
Bondonge	1	**Kokoso**	3	**Muese**	1
Bosao	1	**Kombo**	1	**Muinda**	1
Boso	1	**Kulu**	1	**Mundanga**	2
Boyo	5	**Kungu**	2	**Munjumbu**	1
Bulaki	3	**Lembe**	1	**Mutunga**	1
Ekango	1	**Lindja**	1	**Ndeme**	1
Ekoka	5	**Mbaso**	1	**Ngama**	1
Ekungu	2	**Moba**	2	**Ngata**	3
Elendi	1	**Mobey**	4	**Ngolu**	1
Eloi	1	**Mokakake**	3	**Ngomangoma**	2
Elomba	1	**Mokata**	2	**Ngombe**	1
Embema	1	**Mokole**	2	**Njobe**	2
Embondo	5	**Mokosa**	1	**Somboli**	1
Epema	1	**Mokula**	3	**Toko**	5
Etebe	1	**Molenge**	1	**Tombo**	1
Euey	1	**Molulumba**	2	**Toto**	2
Evua	1	**Mombeke**	1		
Guka	7	**Mombo**	1		
Iboko	1	**Mongamba**	2		
Igbendje	1	**Mongangai**	2		

4.2.2 Data collection

After preparing the list of plants for the interviews, I asked each participant about their use of these plants with my translator. For each plant we asked, 1) whether the participant knew the plant, 2) if they knew, whether they used the plant, 3) if so, for what purposes they used the plant. At the end of each interview we also asked from whom the participant learnt about the plants. We had 219 participants (118 females- 54%) from four campsites (forest camps: Longa: n = 59, Masia: n = 22, Ibamba: n = 31; town camp: Sembola: n = 107). Majority of the participants (90%) were adults (older than 15 years).

4.2.3 Plant identification

When I return to London, I made connections with two botanists at the Royal Botanic Gardens, Kew and showed them the photographs of the plants on my questionnaire. They were able to identify 31 out of 33 plants from the photographs. I also compared the vernacular and Latin names of the plants in my list with those that were reported by Gillet and Doucet in their documentation of woody plants in the Northern Congo which also included the vernacular names given by the Mbendjele (J.-F. Gillet & Doucet, 2012).

4.2.4 Categorization of plant uses

The initial answers contained over 200 use types, some of which concerned the same use purpose. I first categorised the open answers into the following main use categories: medicinal, foraging related (plants that are used for killing animals or known to reserve honey or caterpillars), social beliefs and norms, and other uses that concerned making materials, food and animal food. These main use categories were largely based on the classifications of plant use in previous ethnobotanical studies of African Pygmies (AFlora Committee, 2013; Hattori, 2006a; Terashima, 2001; Terashima & Ichikawa, 2003). I then sub-categorised the use types within each main plant use category. For medicinal and foraging related uses, I used sub-categories based on the Economic Botany Data Standard (Cook, 1995). This is important because using a standardised plant use categories benefits researchers when conducting comparative analyses. Appendix B shows the initial reported use types and their corresponding main and sub- use categories. Below, I explain the main use categories in more detail.

4.2.4.1 Medicinal

This category included the plant uses that concerned treatment of digestive (e.g. stomach-ache, hernia, nausea, intestinal parasites, mouth ulcers, or for brushing teeth), respiratory (coughing and respiration problems) and circulatory system disorders, wounds, skin (facial wash and for itching), infections (e.g. eye, ear infections, malaria and fever), poisonings, pregnancy related problems (e.g. abortion and birth facilitation), genitourinary problems (e.g. vaginal infections, erectile dysfunction) and ill-defined causes (vertigo). I categorized a plant use as medicinal only when the use included treating a specific health problem. On the other hand, if the use concerned preventing someone from falling sick because a social norm is broken, I categorized it as social beliefs and norms.

4.2.4.2 Foraging

Some plant parts were used as poisons to kill monkeys or fish. Some trees were known to have beehives or caterpillars so they were recognized as potential honey or caterpillar reserves.

4.2.4.3 Social beliefs and norms

Other uses concerned social norms and beliefs. For example, some plants were used to identify liars: if someone is accused of committing adultery or stealing from someone, the bark of a tree is boiled to make a drink. This drink is believed to be selectively poisonous: they poison liars and leave truthful people well. The Mbendjele also have social taboos concerning sex and menstrual bleeding (J. Lewis, 2008a). For example, a couple that have a breastfeeding baby is forbidden from having sexual intercourse until the baby is weaned. Otherwise, it is believed that the baby will become unwell and may die. Some plants are used when a couple break this norm based on the belief that they will prevent the baby from getting sick. Similarly, if a woman has sexual intercourse with multiple men and gets pregnant, it is believed that the baby will be sick. Some Mbendjele reported using plants to prevent the baby becoming unwell when the woman had multiple partners. Under the category of beliefs, there were other use types: some people mentioned their use of a particular plant because it brought luck in their search for a partner or they got better at singing.

4.2.4.4 Other uses

Other plant uses included making materials such as baskets, rugs, canoes or drums. Some plants are consumed as food or eaten by animals. Others were used as food additives: a seed pondered to be consumed as salt, or leaves added in water to make a drink resembling coffee. There were some plant uses that were only mentioned by only one participant or were difficult to categorize due to poor translation. I classified them as uncategorized uses. These uses concerned making traps or house (each mentioned by only one participant), and a belief that concerned washing in dirty water.

4.2.5 Preparation methods

Although I did not collect systematic information on the preparation methods for plant uses, I gathered information through my observations and two informants who showed me the plants in the forest (Table 4-2). The most commonly used part of the trees for medicine is the bark. The Mbendjele either cut a couple of pieces of bark, or grate the bark of a tree with a machete (Figure 4-1). When the bark is grated, the pieces are often put into a cone-shaped container made with *ngongo* leaves (*Megaphrynium macrostachyum*; see the detailed uses of marantacea plants by Pygmies in (Hattori, 2006b)) along with some drops of water. Then the juice is squeezed into nose, ears or eyes depending on the purpose of use (e.g. due to ear or eye infection, or when a baby is expected to get sick because of violation of a norm, the juice is dropped into the baby's nose). Often, for treatment of limb or chest pain, the grated bark is wrapped in a large *ngongo* leaf (*bomba*: packages that contain food or medicine) and put on fire. Once heated, the pieces are smeared on the painful body part and attached with a piece of cloth. If pieces of bark are cut, they are often boiled in water to be drunk as medicine (Figure 4-1). Many plants for treating digestion problems are used in this way. In some cases, the leaves are boiled and the water is consumed. In other occasions the leaves are burnt and the ash is mixed with water and smeared on body for wounds. The annual herb, *Cyathula prostrata*, was used in this way. Often, the Mbendjele use a red paste called *mongole* made from the dead bark of *Pterocarpus soyauxii* (J. Lewis, 2002) as a base to many medicinal plant preparations.

Table 4-2: Use type and preparation methods of some of the study plants as explained by an Mbendjele informant.

Plant- vernacular name	Use type and preparation method	Part used	Description
Bulaki	Headache. Squeeze the juice out of the grated bark with a bit of water. Drop into nose	bark	small tree
Ekoka	Digestion. Mix the grated bark with chili pepper and boil in water. Drink	bark	small tree
Embondo	Respiration. Grate the bark, mix it with water and squeeze or drink the juice. It makes you vomit after drinking.	bark	tall tree
Euey	Broken limbs. Mix the grated bark with *mongole* paste and a bit of water and boil. Apply the mixture on the broken bone, attach with a piece of cloth.	bark	small tree
Guka	Digestion. Put two pieces of bark in cold water and drink the water.	bark	tall tree
Imbanda	If a couple have sex when they have a breastfeeding baby. To avoid baby getting sick you take the grated part of the bark, mix with water and squeeze the juice into baby's nose.	bark	tall tree
Imbenya	Respiration. Boil the leaf with water and drink.	leaf	tall tree
Kokoso	Wounds. Burn the leaf and put the ash on the wound.	leaf	shrub
Kulu	Limb aches. Mix the grated bark with *mongole* paste and water. Put the mixture in *ngongo* leaves and heat by the fire. Smear the mixture on the body where it aches. Put the rest on the aching part.	bark	NA
Kungu	Teeth- if you have a cavity. Squeeze the juice of grated bark on the tooth. Also if you have a problem with your wife to see if she had cheated you squeeze it in her eyes. If the eyes get affected then it shows that she had cheated.	bark	tall tree
Mobey	Fontanelle (*potu potu*). Grate the bark and mix with *mongole* paste and a bit of water. Put the mixture on baby's head.	bark	tall tree
Mokakake	Cough. Smash the stalk and drink the juice.	stalk	bamboo type
Mokata	Cough. Mix the grated bark with cold water and chilli pepper and drink.	bark	small tree
Mongamba	Headache. Grate the bark and squeeze the juice into your nose. For digestion, grate the bark, boil in water and drink. Also monkeys eat the fruit.	bark	small tree
Mopo	Teeth. Take the fibre of the bark and attach it on the neck.	bark	small tree
Ngata	If a couple have sex when they have a breastfeeding baby. To prevent baby from becoming ill take the grated part of the bark, mix with water and squeeze the juice in baby's nose.	bark	tall tree
Mongo	Digestion. Mix the grated bark with cold water and drink the juice.	bark	tall tree
Mokula	Erectile dysfunction. Eat the root.	root	shrub
Juese	Wounds which are many, red on the skin. Smash the leaf on hand and smear on the wound.	leaf	small tree
Mongangai	Cough. Boil the leaf in water and drink	leaf	tall tree

Figure 4-1: Preparation methods for the medicinal uses of plants. A) Shredded bark of *Entandrophragma cylindricum* (*Boyo*) is put into a cone-shaped container made with ngongo leaves (*Megaphrynium macrostachyum*). B) A piece of *Autranella congolensis* (*Banga*) is cut to be boiled in water. C) Nyambe is preparing medicine from the bark of *Entandrophragma cylindricum* (*Boyo*). She first grates the bark, D) and wraps the grated pieces in an *ngongo* leaf and puts it on fire, E) she attaches the warm pieces on the chest of her baby, and F) breastfeeds to sooth her.

4.3 Results

4.3.1 Majority of plant uses concerned medicinal purposes

I calculated the frequency of different use types among 7227 responses (219 participants, each having 33 reports). The majority of plant uses concerned medicinal purposes (47.20% among all data points, and 80% among all cases when a plant was used). Table 4-3 shows the reporting frequency of each plant use category. Among medicinal uses, majority (35%) concerned treating digestive system disorders. This is followed by the treatment of respiratory system disorders (25%), pain and injuries (15%) and infections (12%). Among all the cases when a plant was used, 7% concerned uses related to beliefs and social norms. The main plant use related to beliefs was to detect cheaters.

Table 4-3: Uses of plants by Mbendjele BaYaka Pygmies.

Category	Sub category	% Percentage in all answers (219 individuals x 33 plants)
Medicinal	digestive	16.60
	respiratory	11.86
	pain and injuries	7.07
	infections	5.77
	wounds	3.27
	genitourinary	1.34
	pregnancy	0.75
	ill defined	0.32
	Skin	0.12
	poisonings	0.06
	circulatory	0.04
	Subtotal medicinal	**47.20**
Social beliefs	social norms concerning liars	1.65
	social norms concerning sexual taboos	1.29
	luck in finding a partner	0.35
	luck in hunting	0.32
	luck in fishing	0.32
	better sing	0.06
	better fight	0.03
	for rain	0.03
	better share	0.03
	better work	0.03
	Subtotal beliefs	**4.08**
Foraging	bee plants	0.73
	fish poison	0.62
	caterpillar tree	0.50
	monkey poison	0.48
	Subtotal foraging	**2.34**
Other uses	food	3.45
	mat	1.29
	food additives	0.35
	pirogue	0.32
	firewood	0.14
	uncategorised	0.12
	animal food	0.11
	axe	0.11
	hut	0.10
	avoid animal attacks	0.07
	drum	0.07
	basket	0.03
	Subtotal other uses	**6.14**
Not available		**0.10**
Plant not used		**40.14**
	Total	**100.00**

4.3.2 Some plants were used by a large number of people but others not

There was a large variation in whether a plant is used or not (average percentage of participants that reported using a plant based on the use percentages for 33 plants: *mean*= 60, *sd*= 18). There were some plants for which more than half of the participants reported using in one way or the other, and there were some other that only a few people reported using.

4.3.3 Some plants had a larger consensus on their use purpose

There was also a variation in the number of different uses a plant had (Figure 4-2). For instance, some species such as *Alstonia boonei* (*guka*) had a large consensus on what it is used for. Accordingly, 82% of the participants used this plant for treating digestive system disorders. There were 3 other purposes of use for this plant, all of which concerned medicinal reasons (Figure 4-3). Other plants, however, had much diverse use types (Figure 4-2). For example, *Microdesmis puberula* (*mokula*) had 12 different use types ranging from medicinal purposes to social beliefs (Figure 4-3).

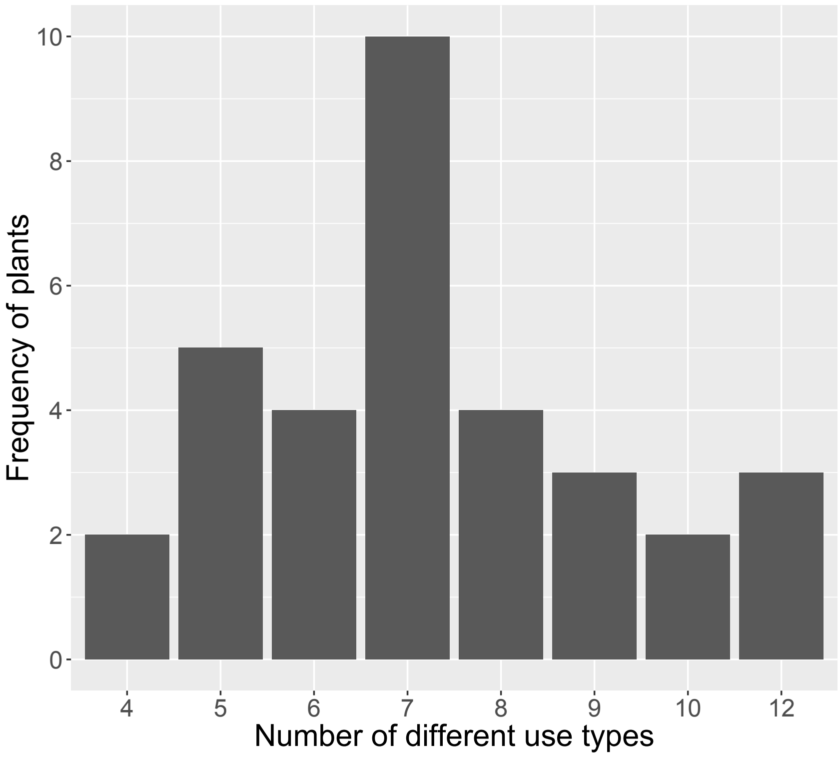
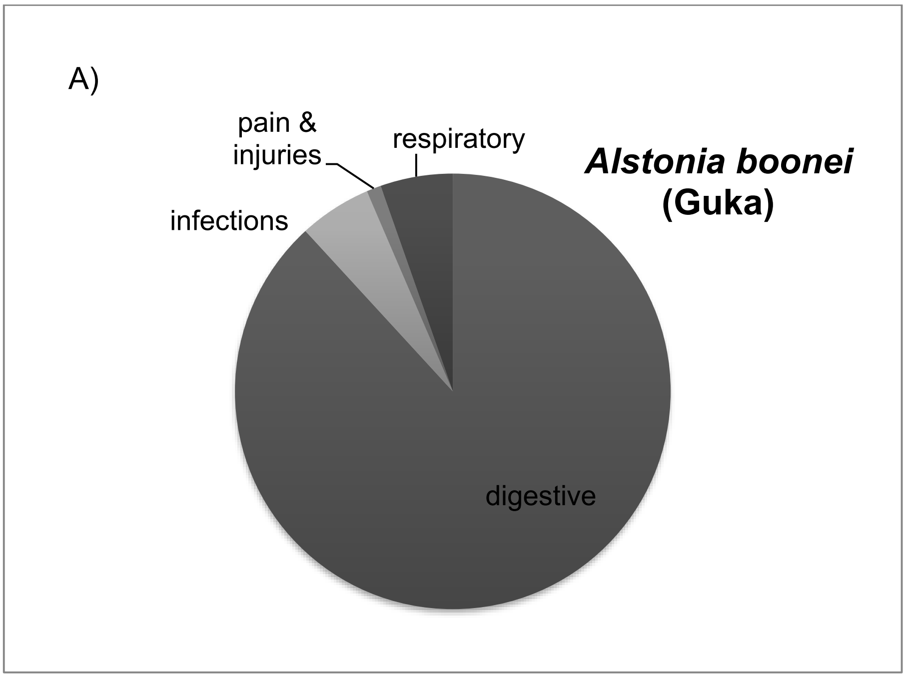


Figure 4-2: Frequency of plants per number of different use types (based on sub use categories that are presented in Table 4-3). Most plants had seven different uses. The number of different use types for a given plant varied between 4 and 12.

Overall, more than half of the plants had between 6 to 8 different use purposes and only a few had either many or a few different use types (Figure 4-2).



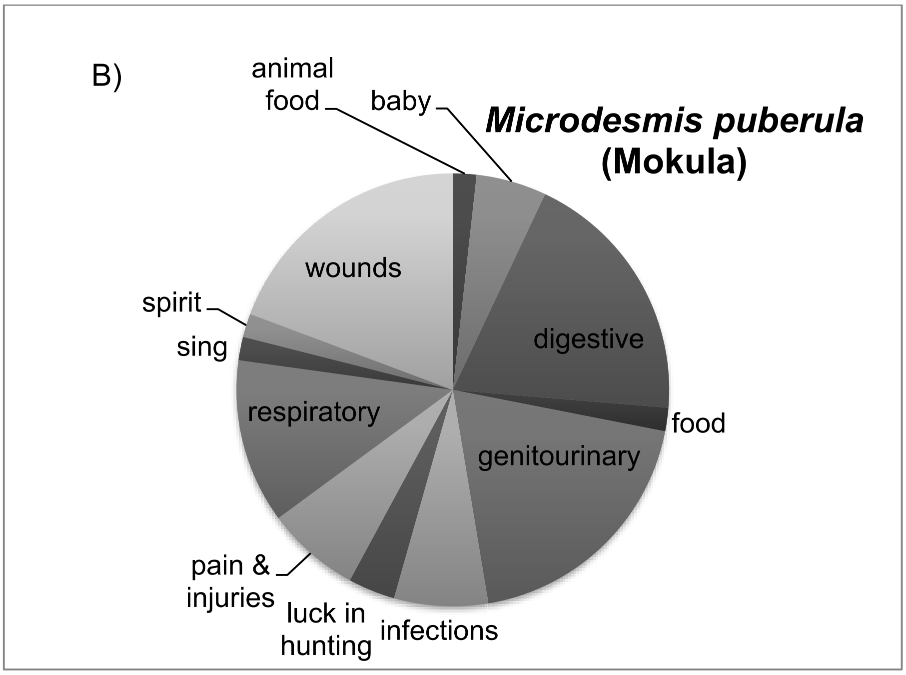


Figure 4-3: Reported use purposes for two plants: A) *Alstonia Boonei*, B) *Microdermis puberula.*

Although all the plants on the list were used as medicine by at least some of the participants, a smaller number of species were used for foraging or social beliefs (Table 4-4). For instance among the 33, only 12 plants had some uses that concerned foraging. The most commonly used plant for foraging was *Eriocoelum macrocarpum* (vernacular name:

Toko), of which the fruits were used for poisoning fish. This species is also used for poison fishing by people in DRC (Neuwinger, 2004).

Table 4-4: Latin and local name of the plants and their most common use purposes.

Plant	Mbendjele name	Two most common medicinal uses*	Use purpose for foraging and social beliefs**
Autranella congolensis	Banga	digestive, pain and injuries	
Entandrophragma cylindricum	Boyo	infections, respiratory	caterpillars feed on it
Caloncoba welwitschii	Bulaki	pain and injuries, digestive	
Thomandersia hensii	Ekoka	digestive, infections, respiratory	
Milletia laurentii	Embondo	digestive, respiratory	
Rauvolfia vomitoria	Euey	pain and injuries, digestive	used as arrow poison to kill monkeys
Alstonia boonei	Guka	digestive, infections, respiratory	
Dioscorea smilacifolia	Iboko	digestive, pain and injuries	
Erythrophleum ivorense	Imbanda	pain and injuries, digestive	judicial ordeal
Unknown	Imbenya	digestive, pain and injuries	
Marantochloa congensis	Imbi	respiratory, pain and injuries	
Croton haumaniamus	Indengo	respiratory, digestive	
Ricinodendron heudelotii	Jongo	infections, pain and injuries	caterpillars feed on it
Trema orientalis	Juese	respiratory, wounds	preventing babies getting sick
Cyathula prostrata	Kokosa	wounds, digestive	
Musanga cecropioides	Kombo	respiratory, digestive	
Piptadeniastrum africanum	Kungu	digestive, infections	judicial ordeal
Pentaclethra macrophylla	Moba	digestive, pregnancy	
Anonidium mannii	Mobey	pain and injuries, digestive	
Costus sp.	Mokakake	respiratory, digestive	
Garcinia (e)punctata	Mokata	respiratory, digestive	
Microdesmis puberula	Mokula	digestive, genitourinary, wounds	
Dichostemma glaucescens	Mongamba	pain and injuries, respiratory	attracts bees, the flowers give the honey a bitter taste
Alchornea sp.***	Mongangai	respiratory, digestive	
Zanthoxylum tessmannii	Mongo	respiratory, digestive	
Millettia sanagana	Mopo	infections, digestive	
Irvingia grandifolia	Mosombo	pain and injuries, digestive, digestive	luck in fishing

Picralima nitida	Mototoko	digestive, pain and injuries	
Nauclea diderrichii	Muese	digestive, infections	
Myrianthus arboreus	Ngata	respiratory, digestive	preventing babies getting sick
Strombosia grandifolia	Njobe	pain and injuries, digestive	
Penianthus longifolius	Somboli	infections, digestive	used as arrow poison to kill monkeys
Eriocoelum macrocarpum	Toko	pain and injuries, digestive	poisoning fish

*If two categories had the same percentages of use, I included both.

** Only use purposes that are mentioned by more than or equal to 5% of the participants are included.

***Genus name is not definitive.

4.3.4 Women and men differed in their plant use only in a few cases

I examined differences in plant uses between men and women to see whether there is sex-specific information sharing in the Mbendjele. Knowledge may be shared differentially depending on its function. For example, I predict knowledge on foraging related plant uses to be shared within the same sex as there is division of labour in hunter-gatherers. Boys may be more exposed to using certain plants to hunt animals simply because they accompany hunters more often than girls would do. For this reason, I expected to see different use frequencies for plants that are used for killing fish or monkeys. Hunting monkeys is a predominantly male activity therefore the plant poisons used for this reason may be reported more often by men than women. On the other hand, I predicted to find no differences in plant use frequencies for medicine except for sex-specific use purposes. To test these predictions, I examined whether there were differences between men and women in their purposes for using plants by calculating the percentages of cases a use purpose was mentioned by each sex (Figure 4-4). Because there were more female participants than male (118 vs. 108), it was more accurate to compare percentages to investigate whether certain use types were more represented in one sex.

Women and men had similar percentages for the majority of use types. For instance, 17% of the women's and 16% of the men's responses concerned treating digestive system disorders (see Appendix Table A for all the sex-specific reporting percentages per use category). 40% of the women's and 41% of the men's responses indicated no use of plants. Moreover, there was not a significant difference between women and men in their reported usage of plants as monkey poison (percentages of use 0.4% and 0.6% by women and men respectively, proportion test, p = 0.25). Fishing is often done by groups of women and children, however sometimes men and women go on fishing trips together. For example, the fruits of *Brenania brieyi* (in Mbendjele, “mo.lunju” or “mo.unju”; prefix “mo” is for the singular of a noun, and “ba” is for the plural) are used as fish poison and cut into pieces and mixed with ashes to be put in the dams. In the camp Ibamba, I observed that although women conducted the fishing related tasks (cutting the fruit, and making dams in the river and waiting for the fish) men were also present during the trip but they later left the group for hunting dwarf crocodiles (Appendix A, video 2). I found that the reported usage of plants for poisoning fish (e.g. the study plant *Eriocoelum macrocarpum*, in Mbendjele: *Toko*) did not differ between men and women (0.6% for both sexes, $p = 0.94$). Some plants were used to bring luck in foraging activities. Women reported usage of plants (mainly *Irvingia grandifolia*, in Mbendjele: *mosombo*) to bring luck in fishing more often than men, although the difference was not significant (0.44% and 0.18% for women and men respectively, proportion test, $p = 0.08$). Men, on the other hand, reported using plants to bring luck in hunting significantly more often than women (0.05% and 0.63% for women and men respectively, proportion test, $p < 0.001$).

Expectedly, women reported usage of plants for pregnancy related purposes, e.g. for abortion or facilitating birth, more often than men (1.16% and 0.27% for women and men respectively, proportion test, $p < 0.001$). On the other hand, men reported using plants for genitourinary problems more often than women (0.85% and 1.92%, for women and men respectively, proportion test, $p < 0.001$). This category contained usage of plants that was believed to give men sexual strength, or treat erectile dysfunction and to treat vaginal disorders. The higher percentage of use by men in this category is because one of the listed plants, *Microdesmis puberula*, was frequently used by men for impotence.

Finally, women reported usage of plants that concern beliefs about babies’ well-being more often than men (1.54%, 0.99% for women and men respectively, $p < 0.05$). As mentioned in the previous sections, the Mbendjele believe that a couple with a breastfeeding baby should refrain from intercourse until the baby is weaned. The plants in this category are used for preventing the baby from becoming ill when a couple breaks this norm.

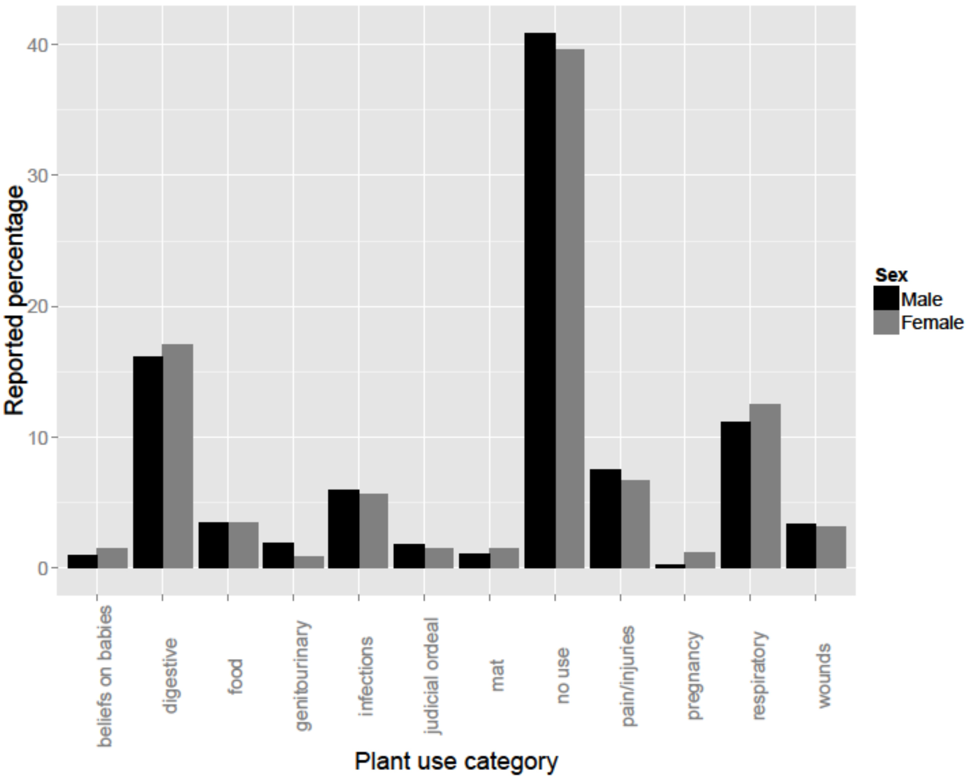


Figure 4-4: Percentage of reported usage per category by women and men. Only percentages that are higher than one are shown.

4.3.5 Participants who resided or were born in the town camp reported using plants for medicine less frequently

Mbendjele camps that I visited differed in their distance to the market town. One of the questions I aim to explore in this thesis is how social structure of the Mbendjele change with market integration and how the change affects cultural transmission. I predicted traditional knowledge to be in decline in the Mbendjele who experience socioeconomic transitions. For this reason, I examined the number of reported plant uses across different Mbendjele camps.

Participants that resided in the town camp reported using plants less frequently than the other three camps (Figure 4-5, percentage of responses when a plant was not used: 39, 32, 32, 45% for forest camps 1-3 and town camp, respectively. Pairwise proportion test, $p < 0.001$ for all comparisons between the town camp and the forest camps). Among the forest camps, people residing in Longa (camp 1), reported using plants less frequently than people in camps Masia (camp 2) and Ibamba (camp 3; pairwise proportion test, $p < 0.01$).

Among common plant uses for medicine, participants residing in the town camp often reported less frequent usage. For instance, the three forest camps did not differ in their use percentages for treating digestive system disorders (Figure 4-5). Participants in the town camp reported using plants for treating digestive problems less often than participants from the forest camp Masia ($p < 0.05$), but not compared to other forest camps, Longa and Ibamba. People in the forest camp Ibamba used plants for pain and injuries more often than people in the town camp, and in forest camp Masia (for forest Masia and Ibamba: $p < 0.01$, for Ibamba and the town camp, $p < 0.001$). Moreover, people in forest camps Masia and Longa reported using plants for respiratory disorders more often than people in the forest camp Ibamba and the town camp ($p < 0.001$, for all comparisons).

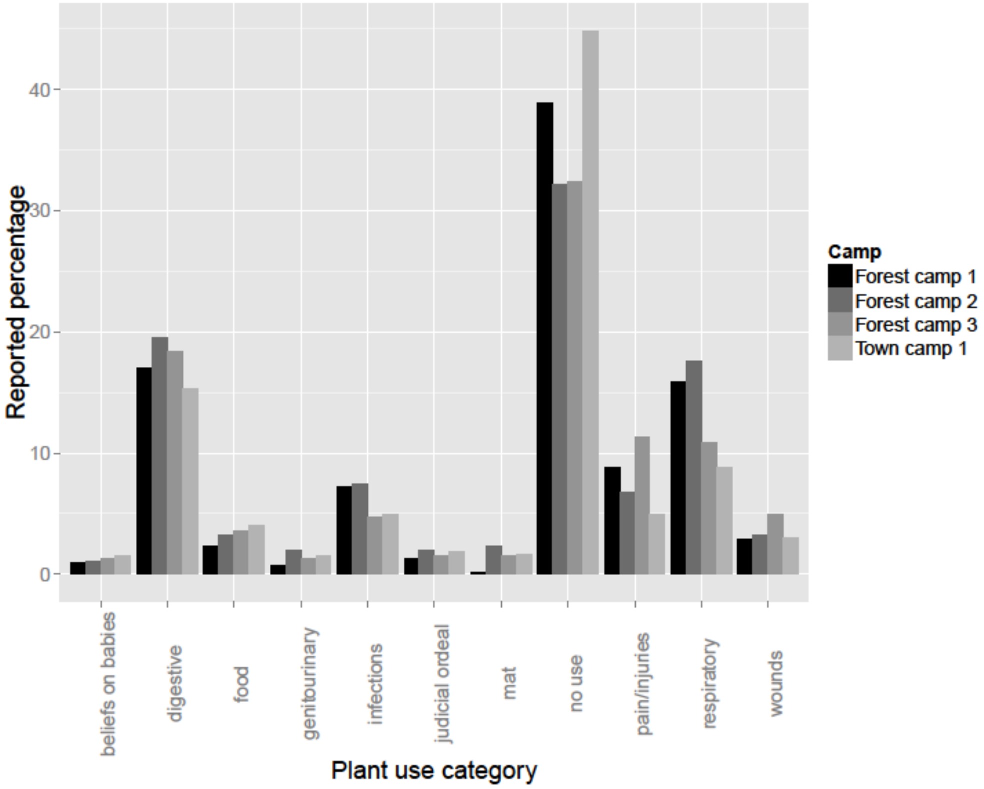


Figure 4-5: Percentage of reported usage per plant use category by current camp residence. Only reported percentages that are higher than one are shown.

Similarly, people who reported their birthplaces as the town Pokola used plants less frequently compared to all the other birthplaces (Figure 4-6, percentage of responses when a plant was not used: 32, 38, 31, 57% for Ibamba, Minganga, Other and Pokola respectively, $p < 0.001$). People that were born in Minganga (most people from forest camps Masia and Longa), reported using plants less frequently than people who were born in Ibamba or in other unvisited locations ($p < 0.001$). Moreover, people that were born in the town reported using plants for the most commonly treated disorders less often than other participants (Figure 4-6). While people that were born in the town reported using plants for digestive problems 12% of the cases, the corresponding mean was 18% for all the other participants ($p < 0.001$ for all the pair-wise comparisons). Similarly, participants that were born in the town reported using plants less frequently for infections, respiratory problems and pain and injuries compared to all the other participants (Figure 4-6).

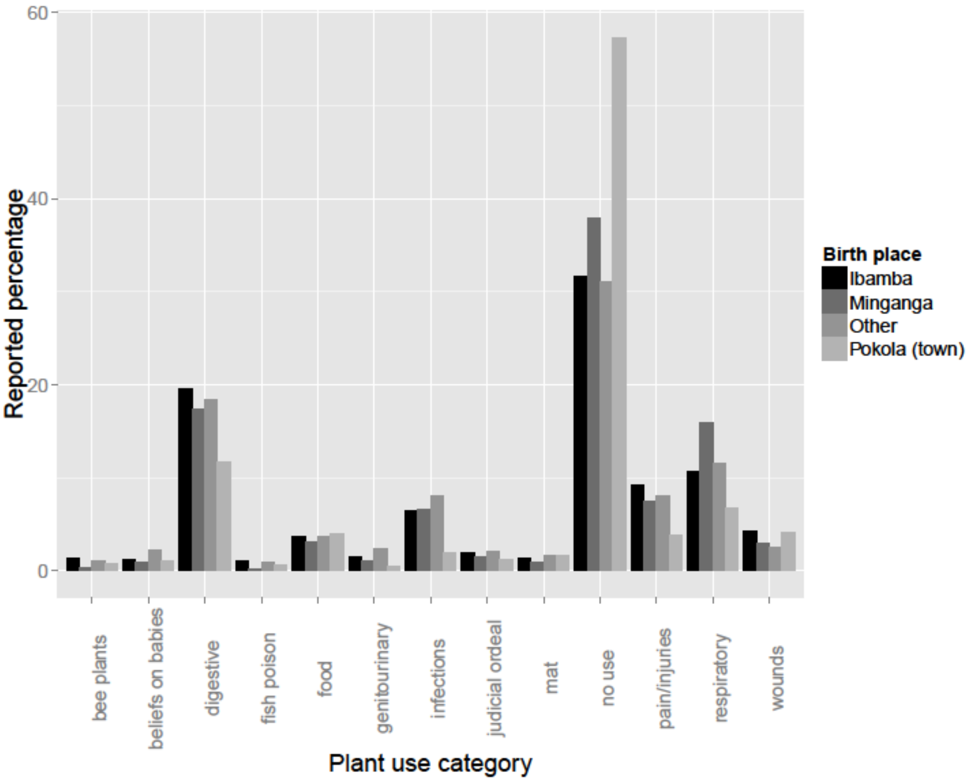


Figure 4-6: Percentage of reported usage per category by birthplace. Only reported percentages that are higher than one are shown. Ibamba and Minganga are the regions in the forest. Pokola is the logging town. Other refers to the villages or campsites where I did not visit during fieldwork. Most people from camps Longa and Masia were born in Minganga region (see Chapter 3 for more information about the different campsites).

4.3.6 Poisonous plants were used to detect cheaters

Plant uses in the Mbendjele were diverse and some of them concerned social norms. As mentioned in the introduction, this variation in the uses enables me to reveal the patterns of cultural transmission and explore how the content of information affects its transmission patterns.

Among the plants that were used for social purposes, two species were commonly used to detect cheaters: *Piptadeniastrum africanum* (Mbendjele name: *Kungu*) and *Erythrophleum ivorense* (Mbendjele name: *Imbanda*). The Mbendjele reported using *Kungu* by dropping the juice extracted from the bark in a person's eye. The Mbendjele believe that this process selectively blinds adulterers. The bark of the *Piptadeniastrum africanum* has toxic properties and is known to be used as ordeal poison (Bosch, 2008). Other resources indicate that Pygmies in Cameroon and DRC use this plant as arrow poison, and some populations use it to poison fish or mice (by mixing with rice) although the participants did not report these additional uses as poison (Bosch, 2008; Neuwinger, 2004).

In a similar fashion, *Erythrophleum ivorense* is used to selectively poison people who are accused of adultery or stealing from others. The Mbendjele believe that if the accused person drinks the juice of the boiled bark and vomits, s/he is free of guilt. Otherwise the person gets poisoned and may die. This judicial ordeal, also known as "sassywood", is also practiced in other African countries such as Sierra Leone and Liberia. Both *Erythrophleum suaveolens* and *Erythrophleum ivorense* are known as the sassywood tree, indicating their common use as judicial ordeal (Bosch, 2008; Leeson & Coyne, 2012). Therefore, Pygmies might have acquired those uses from neighbouring Bantu groups. Moreover, anthropologists studying Efe and Mbuti Pygmies of DRC's Ituri forest have also accounted uses of plants related to social norms. An Efe man, for example, was observed smearing pounded leaves of a plant around his mouth to avoid sharing his rice with other people. The Efe believed that if the plant was used it would avoid others to demand their highly prized food (Terashima & Ichikawa, 2003).

4.4 Discussion

In this chapter, I investigated the uses of plants by the Mbendjele. I explored the variation in plant uses that is going to form the basis of the analyses in the next chapters. Specifically, the findings that is presented in this chapter will enable me to 1) investigate whether there is adaptive benefits of using medicinal plants (Chapter 5), 2) discern knowledge sharing patterns in the Mbendjele (Chapter 6), 3) explore how content and function of information affect this sharing patterns (Chapter 6), 4) examine how socioeconomic transitions and change in social structure affect traditional knowledge

(Chapter 7). The results from this chapter showed that the plant uses in the Mbendjele were diverse. Plants were used as medicine, for foraging activities, making materials, to maintain social norms and beliefs, and consumed as food. Below, I will discuss my findings with respect to the questions I will focus on in the next chapters.

4.4.1 Medicinal uses of plants and their implications

The medicinal uses of plants indicated potential health benefits of plant knowledge. This is because, the most common medicinal uses of plants concerned treatment of high prevalence diseases; digestive and respiratory system disorders. As I mentioned in the Introduction of this chapter, even during our relatively short stay of four months in the forest, we all got infected by multiple parasites. *Loa Loa* (*microfilariae*) that infected one of us, was indeed found to be present in 46% of Mbuti Pygmies from DRC (Pampiglione & Ricciardi, 1986). Moreover, researchers working on parasitic infections among the African Pygmies have found the presence of intestinal helminths "so much so that their absence is exceptional" (Pampiglione & Ricciardi, 1986). In our genealogical interviews, the most reported cause of child mortality was diarrhoea and respiratory problems.

12% of the medicinal uses of plants concerned treatment of infections. Among those, malaria treatment was the primary reason. Parasitological surveys conducted by Italian researchers in the late 60's and early 70's on African Pygmies in the Central African Republic, Cameroon and DRC showed that 44 to 60% of children had malarial parasites in their blood (Pampiglione & Ricciardi, 1986). Because Pygmies have only little or no access to modern medicine, even diseases that have almost disappeared from the rest of the world are still observed among them. One of such diseases is yaws, caused by the bacterium *Treponema pertenue*, and can easily be treated with penicillin. In 60s and 70s, about 10% of all Pygmy subjects from the three countries mentioned above was found to have symptoms of yaws. During my fieldwork, I also encountered people with yaws (Figure 4-7). In the absence of modern medicines, the only treatment option for those forest hunter-gatherers is the use of medicinal plants. The match between the prevalence of diseases and the common uses of medicinal plants encourages the investigation of the adaptive benefits of medicinal uses, which will be the main topic of the next chapter.

Figure 4-7: A young child with yaws in Ibamba.

There was a variation in how much a plant was used. Not all the plants were used in similar frequencies and some plants had larger consensus on what they are used for than the others. Larger consensus on the medicinal properties of a plant may be indicative of its treatment potential. Moreover, medicinal use of the same plant by multiple populations may indicate the plant's therapeutic properties (Saslis-Lagoudakis, Klitgaard, et al., 2011). For this reason, I will further explore whether plants that are used by the Mbendjele are also used in similar fashion by other Central African Pygmies and great apes in the next chapter.

Although some plants may have potential health benefits, the origins of certain plant uses may be due to human's cognitive biases (e.g. due to our tendency to associate certain features in different organisms). The fact that some plants had as many as 12 different uses suggests that some of the uses may not have an effective therapeutic reasoning. For example, the morphological features of a plant such as its shape or colour may attract human attention and contribute to its use purpose. The Efe Pygmies in the Ituri forest are reported to use *Citropsis articulata*, which has sharp spines on the stem, for treating a disease caused by eating catfish, because these spines resemble those of catfish (Terashima & Ichikawa, 2003). In fact, those beliefs also serve as the reasons for food taboos in many societies. For instance, horticulturalists in Ituri forest avoid eating certain animals because if consumed, they believe their baby would acquire the anomalous characteristic of the forbidden animal (Aunger, 1994, 2000). Aunger referred to those food avoidances as "homeopathic" taboos (Aunger, 1994, 2000). Similarly, during my fieldwork I observed that the Mbendjele who are pregnant or have breastfeeding babies avoided eating the giant forest hog, which has big tusks; because they believed their babies would develop a tooth resembling the tusk of the hog. Such cross-culturally held beliefs are strong evidence for humans' natural tendency to categorize and seek patterns in nature, and may result in the emergence of some plant uses.

4.4.2 Plant uses of men and women and sex-specific knowledge sharing

I explored differences in plant uses between men and women to see whether there is sex-specific knowledge sharing in the Mbendjele. I predicted to find differences in certain plant uses between men and women because of division of labour in foraging activities. Although fishing is mainly done by women and hunting monkeys by men, reported frequencies of using plants as poisons to kill fish and monkeys did not differ between men and women. One reason is that fishing trips to forest sometimes involve the participation of all members in the camp, therefore plants that are used to poison fish may be known by the majority of people, regardless of sex. 60% of the reports that involved using plants as poisons for monkeys were done by men, and the remaining 40% by women. The reporting difference between men and women was not significant, but this may also be due to the fact that this use was not very common (only 0.5% of all the data points concerned plant uses for hunting monkeys). Nowadays, the Mbendjele use shotguns to kill monkeys and they consider using crossbows with plant-based poisons as something that was done in the past. Nevertheless, gender differences were more common for the uses of plants that were believed to bring luck in sex-specific foraging activities. Although the difference was not significant, women reported using plants to bring luck in fishing more often than men. On the other hand, significantly more men reported using plants to bring luck in hunting than women. I will further explore the patterns of knowledge sharing with respect to sex, age group, camp co-residence, biological and affinal kin ties, and based on different use types in Chapter 6.

4.4.3 Market integration and plant uses across the Mbendjele camps

One of the main questions I ask in this thesis is how knowledge sharing and traditional knowledge change with socioeconomic transitions in the Mbendjele. For this reason, I explored the frequency of different plant uses across the Mbendjele camps that are located in forest regions, and in a logging town. I found that people residing at or were born in the town camp reported using plants in lower frequencies than people from forest regions. Unlike other camps, Pygmies in the town have easy access to the market, and they frequently engage in wage labour (Salali & Migliano, 2015). The findings in this chapter point at a cultural change among the Mbendjele that live in the town. I will investigate the socioeconomic transitions that the Mbendjele in the town go through, and further explore the change in traditional plant knowledge associated to these transitions in Chapter 7.

4.4.4 Conclusion

In this chapter I explored different types of plant uses in the Mbendjele by analysing the reported uses of 33 plants by 219 participants. The variation in the percentage of participants that used a plant and the consensus on the use purposes suggests certain medicinal plants may have more therapeutic potential than the others. In the next chapter I will explore adaptive benefits of medicinal plant uses further by comparing the uses of the same plants by the other Central African Pygmy groups and also by chimpanzees and gorillas. I will also use children's BMI (body mass index) as a health indicator and discuss whether the Mbendjele mothers that use more plants to treat certain disorders have children with higher BMIs.

Chapter 5: Is medicinal plant use adaptive? Cross cultural and cross species analyses of medicinal plant uses and their effect on health

5.1 Introduction

A central question in this thesis is whether certain knowledge provides adaptive benefits to its bearers and if so, with whom this knowledge is shared. Evolutionary approaches to culture predict that certain cultural traits are transmitted with respect to their adaptive importance. Accordingly, a cultural trait may spread in a population as a result of cultural selection (Mesoudi, 2016). Cultural traits, like biological ones, may go extinct as a result of competition for memory, attention and expression. Cultural selection occurs when a certain cultural trait is successfully inherited over other cultural traits (Mesoudi, Whiten, & Laland, 2006). In this chapter, I investigate whether medicinal plant knowledge has any fitness benefits. Answering this question will then enable me to test whether medicinal plant knowledge in the Mbendjele evolves with respect to its fitness benefits or via cultural drift. Below I will discuss how certain cultural traits may provide fitness advantage and how the adaptive value of those traits may affect their transmission and evolution.

Cultural traits can be adaptive. For instance, food taboos in Fiji are shown to prevent fish poisoning during pregnancy (Henrich & Henrich, 2010). Similarly, the use of medicinal plants can provide fitness benefits, especially in remote populations where there is no access to modern medicine. Central African Pygmies rely on plants as their primary source of medicine. Therefore, individuals who know and use more medicinal plants may have higher reproductive success and offspring with higher survival rates. Medicinal plants have already been shown to have adaptive value and to improve health in other traditional populations with limited or no access to modern medicine (McDade et al., 2007). Although, the use of medicinal plants in Central African Pygmies has been well documented (AFlora Committee, 2013; Betti, 2004; Betti et al., 2013; Hattori, 2006a; Terashima & Ichikawa, 2003), to my knowledge, there is no research on the effects of use on people's health and fitness.

The secondary metabolites are what give a plant its medicinal properties. These are organic compounds that do not directly take role in the organism's growth and reproduction, but help the plant against herbivores and pathogens and attract pollinators (Bernhoft, 2010). That is why these metabolites can have both toxic and pharmaceutical properties, often depending on the usage dose. Glycosides, flavonoids, tannins and alkaloids are among the many secondary metabolites which have biochemical effects in animals and are referred to as bioactive compounds (Bernhoft, 2010). Researchers screen plants that are used in traditional medicine for detecting their bioactive compounds. One study shows that 80% of the 122 active compounds that are derived from 94 plant species and used as drugs had identical use purpose in traditional medicine to the current use of the drug (Fabricant & Farnsworth, 2001).

Common medicinal uses of the same plants may indicate potential benefits on health and fitness (Saslis-Lagoudakis et al., 2012; Saslis-Lagoudakis, Klitgaard, et al., 2011; Saslis-Lagoudakis, Williamson, Savolainen, & Hawkins, 2011). Knowledge about the highly toxic or therapeutic plants may be discovered independently in multiple places or shared more widely because of their influence on survival. There are estimated 920,000 Pygmy people living in Central African forests across nine countries (Olivero et al., 2016). Various uses of forest plants have been documented in some of these Pygmy populations (AFlora Committee, 2013; Betti, 2004; Betti et al., 2013; Hattori, 2006a, 2006b; Kimura, 2013; Terashima & Ichikawa, 2003). Nevertheless, there is only one study comparing the plant uses of two Pygmy populations, Efe and Mbuti from DRC (Terashima & Ichikawa, 2003). A wider comparison among Pygmy populations may inform us on the potential adaptive benefits of using those plants.

Not only humans, but also non-human primates use plants as self-medication (Michael A Huffman, 1997, 2001; Masi et al., 2012; Pebsworth, Krief, & Huffman, 2006). Although great apes may benefit from the secondary metabolites of the plants that they merely consume as food, they also exhibit what primatologists call “unusual feeding behaviour” (Masi et al., 2012). This is when primates consume plants that are low in nutritional value but high in bioactive compounds. Primatologists have suggested that the infrequent intake of plant species outside diet in African great apes is mainly to treat intestinal parasites and cure gastrointestinal discomfort (Michael A Huffman, 1997; Michael A Huffman & Wrangham, 1994). Two behaviours that are identified as self- medication in African great apes are bitter pit chewing and leaf swallowing. For instance, chewing the bitter pits of *Vernonia amygdalina* is observed when chimpanzees are infected by nematode (e.g. thread worm, whip worm and nodule worm), trematode or protozoa (e.g. amoeba species) (Michael A Huffman, 1997). The bioactive compounds found in this species are thought to treat parasitic and gastrointestinal illness (M A Huffman, Gotoh, Izutsu, Koshimizu, & Kalunde, 1993), however the evidence for bioactive secondary metabolites is yet to be found (Alawa et al., 2003).

Chimpanzees have also been observed to swallow whole leaves of certain species without chewing them (Wrangham, 1995). A common property of the swallowed plants is that they have rough and hispid leaves. Chimpanzees in many sites increase their leaf swallowing behaviour, and may swallow between 1 to 100 folded leaves, when infected by tapeworms or nematodes (Michael A. Huffman & Hirata, 2004; Michael A Huffman, 1997; Wrangham, 1995). Leaf swallowing help chimpanzees expel the parasites they have, as whole leaves are found with parasite fragments in the dung (Michael A Huffman, 1997; Wrangham, 1995). Although this behaviour was later discovered in gorillas and bonobos as well (Michael A. Huffman & Hirata, 2004; Michael A Huffman, 1997), there is only one study comparing the frequency of unusual feeding behaviour in chimpanzees and gorillas, and citing the human use of those plants (Masi et al., 2012). These comparisons are important as common uses of plants across different species may inform us on their adaptive value.

In this chapter, I am going to examine whether medicinal plant knowledge is adaptive by seeking answers to following questions: 1) Are plant species on my questionnaire also known and used by other Central African Pygmy groups?, 2) Do chimpanzees and gorillas use them as medicine?, 3) Do they have known bioactive compounds?, 4) Do the Mbendjele mothers' use of medicinal plants affect their children's health? I first present my literature research on the medicinal plant use across Central African Pygmies and great apes. The second section concerns my analysis on the effects of maternal plant use on children's body mass index (BMI).

5.2 Cross-population and cross-species use of the same plants indicates potential medicinal properties

5.2.1 Methods

I conducted literature research on the uses of these plants among other Central African Pygmy populations as well among chimpanzees and gorillas. I did much of the plant use comparisons among the Central African Pygmies by using the AFlora database, a plant use database for Africa, established by the researchers from Kyoto University (AFlora Committee, 2013; Kimura, 2013). Moreover, I also examined the known bioactive properties of these species by scanning the literature for each of the plants. Plant databases, "Global Plants" on JSTOR and "PROTA4U" which was developed by the international program Plant Resources of Tropical Africa (PROTA) have been very useful in my research.

5.2.2 Results

Out of 31 identified plant species, 26 were used by at least one other Central African Pygmy population, including the Mbuti and Efe from Democratic Republic of Congo (AFlora Committee, 2013; Terashima & Ichikawa, 2003), the Aka from Central African Republic, and the Baka from Cameroon and Gabon (AFlora Committee, 2013; Betti, 2004; Betti et al., 2013). Table 5-1 shows the list of plants and the references to the papers on their use in other Pygmy groups and great apes along with known bioactive properties. 15 were documented to be used by Baka Pygmies from Cameroon and Gabon (Betti, 2004; Betti et al., 2013). For each of those 15 plants, I calculated the percentage of BaYaka reporting medicinal use of that plant and the number of times the same plant was used as a treatment by the Baka Pygmies from Cameroon and Gabon (Betti, 2004; Betti et al., 2013). There was a positive correlation among the use frequencies of those plants between the two Pygmy groups (Figure 5-1, n= 15, Beta= 0.81, P< 0.01). In other words, both the Mbendjele and Baka Pygmies used the same plants at higher frequencies.

Table 5-1. List of plants, their use by other Pygmy populations, chimpanzees and gorillas and known biological activity.

Common Mbendjele name	Genus	Species	Gorilla use	Chimpanzee use	Which Pygmy group	Known biological activity	References
Banga	Autranella	congolensis	0	0	CB, DRC-M, DRC-E, Cam-Bak	1	(AFlora Committee, 2013; J.-F. Gillet & Doucet, 2012; Memvanga, Tona, Mesia, Lusakibanza, & Cimanga, 2015; Musuyu Muganza et al., 2012)
Boyo	Entandrophragma	cylindricum	0	0	Cam-Bak, CB, DRC-M, DRC-E	1	(AFlora Committee, 2013; J.-F. Gillet & Doucet, 2012; Kouam, Kusari, Lamshöft, Tatuedom, & Spiteller, 2012)
Bulaki	Caloncoba	welwitschii	1	0	CB	0	(AFlora Committee, 2013; Cousins & Huffman, 2002; J.-F. Gillet & Doucet, 2012)
Ekoka	Thomandersia	hensii	1	0	CA, CB	1	(AFlora Committee, 2013; Bickii, Tchouya, Tchouankeu, & Tsamo, 2006; Masi et al., 2012)
Embondo	Milletia	laurentii	0	1	NA	1	(J.-F. Gillet & Doucet, 2012; Havyarimana, Ndendoung, Tamokou, Atchadé, & Tanyi, 2012; Ngamga, Fanso Free, Tane, & Fomum, 2007; Pebsworth et al., 2006)
Euey	Rauvolfia	vomitoria	0	0	Cam-Bak, DRC-E, CB	1	(Betti, 2004; Bisong, Brown, & Osim, 2011; J.-F. Gillet & Doucet, 2012; Olatokunboh, Kayode, &

							Adeola, 2009; Zirihi, Mambu, Guédé-Guina, Bodo, & Grellier, 2005)
Guka	Alstonia	boonei	0	1	Cam-Bak, Gb, DRC-E, DRC-M,CB	1	(Betti, 2004; Betti et al., 2013; Mesia et al., 2007; Musuyu Muganza et al., 2012; Pebsworth et al., 2006; Zirihi et al., 2005)
Iboko	Dioscorea	smilacifolia	0	0	DRC-M, DRC-E, CB	0	
Imbanda	Erythrophleum	ivorense	1	0	Cam-Bak, CA, DRC-M,CB	0	(Betti, 2004; Betti et al., 2013; Kamanzi Atindehou, Schmid, Brun, Koné, & Traore, 2004)
Imbenya	Unknown	Unknown	NA	NA	NA	NA	NA
Imbi	Marantochloa	congensis	1	1	CA, DRC-E, Cam-Bak, CB, DRC-M	0	(Masi et al., 2012; Pebsworth et al., 2006)
Indengo	Croton	haumaniamus	0	0	Gb, DRC-M,CB, DRC-E	0	(Betti et al., 2013; J.-F. Gillet & Doucet, 2012)
Jongo	Ricinodendron	heudelotii	0	0	DRC-E, Cam-Bak, CB, DRC-M, CA	1	(J.-F. Gillet & Doucet, 2012; K Kitanishi, 1995; Tekwu, Pieme, & Beng, 2012)
Kokosa	Cyathula	prostrata	0	0	DRC-E, Cam-Bak, CB	1	(AFlora Committee, 2013; Ibrahim, Sowemimo, Van Rooyen, & Van De Venter, 2012; Kamanzi Atindehou et al., 2004)
Kombo	Musanga	cecropioides	0	0	Cam-Bak, DRC-M, DRC-E, CB	1	(AFlora Committee, 2013; Betti, 2004; J.-F. Gillet & Doucet, 2012; Memvanga et al., 2015; Musuyu Muganza et al., 2012)
Kungu	Piptadeniastrum	africanum	0	0	Cam-Bak, Gb, DRC-M, DRC-	1	(AFlora Committee, 2013; Ateufack et al., 2015; Betti, 2004; Betti et al.,

					E, CB		2013; Brusotti et al., 2013)
Mobey	Anonidium	mannii	1	0	Cam-Bak, Gb, DRC-E, DRC-M, CB	1	(AFlora Committee, 2013; Betti, 2004; Betti et al., 2013; Memvanga et al., 2015; Musuyu Muganza et al., 2012)
Mokakake	Costus	lucanusianus	1	1	Cam-Bak, Gb,DRC-E, DRC-M, CB	1	(AFlora Committee, 2013; Betti, 2004; Betti et al., 2013; Cousins & Huffman, 2002; Kumar, Sharma, Bairwa, Roy, & Kumar, 2010; Pebsworth et al., 2006)
Mokata	Garcinia	punctata	0	0	Cam-Bak, Gb, DRC-E, CB	1	(AFlora Committee, 2013; Betti, 2004; Betti et al., 2013; Memvanga et al., 2015; Musuyu Muganza et al., 2012)
Mongamba	Dichostemma	glaucescens	0	0	DRC-E, Cam-Bak,CB	1	(AFlora Committee, 2013; J.-F. Gillet & Doucet, 2012; Memvanga et al., 2015; Mesia et al., 2007)
Mopo	Millettia	sanagana	0	0	NA*	0	(J.-F. Gillet & Doucet, 2012)
Mosombo	Irvingia	grandifolia	0	0	Cam-Bak, CB	1	(AFlora Committee, 2013; Betti, 2004; J.-F. Gillet & Doucet, 2012; M Lamidi et al., 2005)
Mototoko	Picralima	nitida	0	0	Cam-Bak, Gb, DRC-M, DRC-E,CB	1	(AFlora Committee, 2013; Betti, 2004; Betti et al., 2013; Bickii et al., 2006; J.-F. Gillet & Doucet, 2012)
Muese	Nauclea	diderrichii	1	0	Gb, DRC-M, CB	1	(AFlora Committee, 2013; Betti et al., 2013; Cousins & Huffman, 2002; J.-F. Gillet & Doucet, 2012; Maroufath Lamidi et al., 1996)
Moba	Pentaclethra	macrophylla	0	0	Cam-Bak, Gb, DRC-E, DRC-M,CB	1	(AFlora Committee, 2013; Betti, 2004; Betti et al., 2013; Kamanzi Atindehou et al., 2004; Kumar et al.,

							2010)
Ngata	Myrianthus	arboreus	1	1	Cam-Bak, DRC-M, CB, DRC-E	1	(AFlora Committee, 2013; Betti, 2004; Cousins & Huffman, 2002; J.-F. Gillet & Doucet, 2012; Krief, Hladik, & Haxaire, 2005; Masi et al., 2012; Memvanga et al., 2015; Pebsworth et al., 2006)
Somboli	Penianthus	longifolius	0	0	Cam-Bak, DRC-M, DRC-E, CB	1	(AFlora Committee, 2013; J.-F. Gillet & Doucet, 2012; Memvanga et al., 2015; Musuyu Muganza et al., 2012; Onguéné et al., 2014)
Toko	Eriocoelum	macrocarpum	0	0	CB	0	(AFlora Committee, 2013)
Mongo	Zanthoxylum	tessmannii	0	0	Cam-Bak, Gb, CB	1	(Betti, 2004; Betti et al., 2013; J.-F. Gillet & Doucet, 2012; Mbaze et al., 2007)
Mokula	Microdesmis	puberula	0	0	Cam-Bak, Gb, CB	1	(Betti, 2004; Betti et al., 2013; J.-F. Gillet & Doucet, 2012; Mesia et al., 2007; Okany, Ishola, & Ashorobi, 2012)
Juese	Trema	orientalis	0	1	Cam-Bak, CB	1	(Abiodun et al., 2011; Betti, 2004; Dimo, Ngueguim, Kamtchouing, Dongo, & Tan, 2006; J.-F. Gillet & Doucet, 2012; Michael A Huffman, 1997)
Mongangai	Unknown**	Unknown	NA	NA	NA	NA	NA
Njobe	Strombosia	grandifolia	0	0	CB	0	(J.-F. Gillet & Doucet, 2012; Hohmann, Robbins, & Boesch, 2006)

CA= Central Africa, Aka; Gb= Gabon, Baka; Cam-Bak= Cameroon, Baka; CB= Congo-Brazzaville, Mbendjele; DRC-M= Mbuti, DRC; DRC-E= Efe, DRC
*Many cases of Milettia use in the Aflora database, but the species are unknown.
** Maybe Alchornea sp.

The plant species that were used frequently by both populations were *Alstonia boonei*, *Pentaclethra macrophylla*, *Costus sp.*, *Picralima nitida*, *Alchornea sp.*, *Microdesmis puberula*. 82% of the participants used *Alstonia boonei* for treating digestive system disorders, and the uses for this plant among the Baka involved treating intestinal helminths, malaria and snake bites. The Mbendjele reported using *Pentaclethra macrophylla* mainly for digestion and pregnancy related treatments and the Baka used the same plant for digestive problems and malaria. Both Mbendjele and the Baka used *Costus species* frequently to treat respiratory problems. The Baka reported using *Picralima nitida* for treating diarrhea, gonorrhea and malaria and the Mbendjele mainly for digestive problems and pain/injuries. *Alchornea sp.* was used by the Mbendjele for respiratory and digestive problems, and by the Baka for digestive problems and for pain/injuries. Finally, the Mbendjele reported using *Microdesmis puberula* for digestive and genitourinary problems as well as for treating wounds, and the Baka for genitourinary problems and for cough. In summary, there was a considerable overlap between the Baka and the Mbendjele in their use of some of the reported plant species.

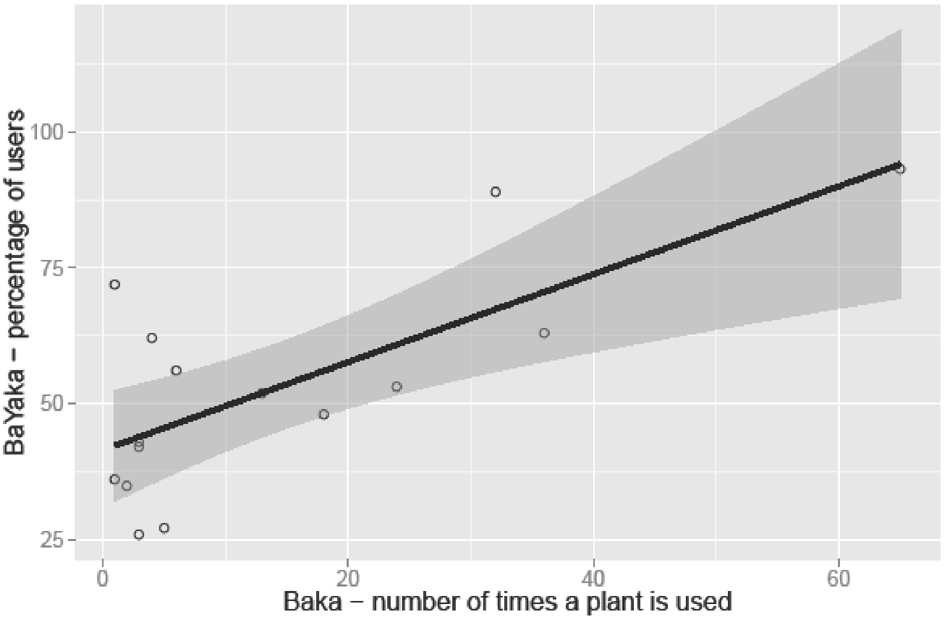


Figure 5-1: Cross population use of medicinal plants. Percentage of Mbendjele BaYaka (n= 219) that used a particular plant as a medicine and the number of times the same plant was used as a

treatment by the Baka Pygmies from Cameroon (n= 37, data from Betti 2004 (Betti, 2004)) and Gabon (n= 6, Betti et al. 2013 (Betti et al., 2013)). Each dot refers to a plant species (n= 15).

Some plants on the list were also used by chimpanzees and gorillas as medicine. Eight of the identified species were used by gorillas (Cousins & Huffman, 2002; Michael A Huffman, 1997; Masi et al., 2012); and six by chimpanzees (Krief et al., 2005; Masi et al., 2012; Pebsworth et al., 2006) (Table 5-1). Among the plants listed, young gorillas were observed eating *Costus sp.* and *Caloncoba welwitschii* when suffering from diarrhoea or parasites (Cousins & Huffman, 2002). The leaves of *Trema orientalis* were observed to be swallowed without being chewed by chimpanzees in Tanzania and Guinea, suggesting that they relieve the symptoms of nematode and tapeworm infections (Michael A Huffman, 1997).

Additionally, 24 plants (77% of the identified species) in our list had known bioactive properties according to pre-existing literature (Table 5-1).

5.2.3 Discussion

This section examined the common medicinal plant uses across various Central African Pygmy population and great apes. I found that 84% of the identified plant species were also used by at least one other Pygmy population. Moreover, eight of the identified species were used by gorillas, and six by chimpanzees. Majority of the species had known bioactive properties.

5.2.3.1 Common uses among different Pygmy populations and their implications

Common cultural traits observed in different human populations may result from different reasons. One reason is convergent cultural evolution: a cultural trait may have independently emerged in two unrelated populations as an adaptation to similar environments. For instance, the cultural tradition of teeth sharpening in the Mbendjele is also observed in a distant and unrelated hunter-gatherer group, Aeta hunter-gatherers from the Philippines (Figure 3-1). Although when asked, the Mbendjele say that it is for aesthetic reasons, filed teeth may help hunter-gatherers to chew meat more efficiently. Similarly, independent discovery of same medicinal plants in different populations may result from convergent cultural evolution and indicate their adaptive value (Saslis-Lagoudakis et al., 2012).

Cultures are not independent, however, and similar cultural traits may be the result of common ancestry or geographical proximity (Holden & Mace, 2003, 2009). This non-independence of cultures is known as "Galton's problem". Some scholars have suggested the application of phylogenetic methods to studies on cultural evolution to overcome this problem. This application applies the tree-like branching way of biological evolution to cultural evolution (Collard, Shennan, & Tehrani, 2006). By using language phylogenies researchers can identify whether two cultural traits are related because of shared ancestry or convergent cultural evolution (Holden & Mace, 2003).

As detailed in Chapter 2, Section 2.3, the population genetics studies on various African Pygmy populations supported the hypothesis that those populations have once shared a common ancestry (Batini et al., 2011; L. L. Cavalli-Sforza et al., 1969; Patin et al., 2009; Verdu et al., 2009). At some point, Western (e.g. Baka from Cameroon and Gabon, Mbendjele from Congo and Aka from CAR- altogether BaYaka) and Eastern (e.g. Efe and Mbuti from DRC) Pygmy populations diverged. Later on, these Western and Eastern groups further fragmented into various populations that we see as current-day Pygmy groups.

Does this mean that common plant uses in various African groups do not necessarily indicate their potential medicinal value? Those common uses may be due to the fact that the Pygmy groups had a common origin, hence shared many cultural traits regardless of the traits' adaptive value. To address this issue, we may refer to the times of divergence of various Central African Pygmy populations. It has been estimated that ancestral Pygmy and non-Pygmy populations had diverged roughly 60,000 years ago, which was followed by the divergence of Eastern and Western Pygmy populations about 20,000 years ago (Batini et al., 2011; Patin et al., 2009). Due to the emergence of agriculture and Bantu expansion, Western Pygmies have later on isolated into sub-populations around 3,000 years ago (Verdu et al., 2009).

Despite of the early divergence of Eastern and Western Pygmy groups, 21 out 31 (68%) plant species on my surveys were used as medicine by both the Mbendjele and the Eastern Pygmy groups, the Efe and Mbuti in DRC. The persistent use of the same plants may result from the cultural selection of those plants that display effective treatment outcomes. This is because if those traits were observed in the ancestral population, they must have survived for thousands of years despite of the divergence of populations. There is undoubtedly, some variation in medicinal plant uses even within the same Pygmy lineages. For example, an ethnobotanical study that investigated the uses of 771 identified plant species among four Eastern Pygmy groups in the Ituri forest found that the Efe and Mbuti differed in the composition of the medicinal plants that they use (Terashima & Ichikawa, 2003). Nevertheless, the researchers have also found that certain plant species were used as medicine more commonly among all the Eastern groups. Among those *Alstonia boonei* and *Picralima nitida* were reported frequently. I suggest that those plants that are most commonly used in many different hunter-gatherer groups merit further investigation for their adaptive value. A recent review on the diverse medicinal uses and pharmacological properties of *Picralima nitida* has indeed showed the plant's potential for the treatment of malaria as the extracts from the seed, fruit and stem bark demonstrated remarkable inhibitory activity against drug resistant clones of *Plasmodium falciparum* (Erharuyi, Falodun, & Langer, 2014).

Although, the similarity in plant uses between the Baka and the Mbendjele can be explained by common origin and the relatively recent divergence, the similarity in the use frequencies of certain plant species between those two populations may indicate these species' therapeutic potential. Accordingly, certain plant species were reported to be used as medicine very frequently both by the Baka and the BaYaka (Figure 5-1). For example, *Alstonia boonei* was one of such frequently used species by the two populations. A phylogenetic study that analysed cross-cultural uses of different genera for various medicinal purposes suggested the *Alstonia* genera to be given high priority for bioprospecting for conditions related to skin problems (Saslis-Lagoudakis et al., 2012). Nevertheless, in another study the plant extract showed moderate to weak antiplasmodial activity (related to the treatment of malaria) (Musuyu Muganza et al., 2012). On the other hand, the common use of this plant for treating diarrhoea not only by Pygmy populations, but also by African farmer groups, such as the Kako and Bangando of Cameroon and Bongando of DRC, requires further investigation into its bioactive properties (AFlora Committee, 2013).

5.2.3.2 Common medicinal plant uses across species and their implications

Some medicinal plants on our list were not only used by Central African Pygmies, but also by other great apes. The uses of plants as medicine in non-human animals may inform us on the emergence of medicine (Cousins & Huffman, 2002). One explanation is the idea of “food for medicine”. Some plant species that are already consumed as food may also have medicinal properties that later get discovered by the species consuming it (Michael A Huffman, 1997). There is also the possibility that humans discovered the uses of some plants by observing other animals. Some scholars have argued that man discovered the effects of drug plants by observing the behaviour of animals (Huffman 2001, 2002, Siegel 1979). For instance, Huffman speculated that Pygmies in Gabon discovered the hallucinogenic plant iboga (*Tabernanthe iboga*) by watching wild boars going into a wild frenzy and jumping around after digging up and eating the roots (Huffman 2001). Moreover, indigenous people in Africa also reported observing gorillas and porcupines changing their behaviour after consuming the roots of the plant. The consumption of the roots of this plant in gorillas is also observed by primatologists who consider the use to be of medicinal purpose (Huffman 2002).

There is evidence that chimpanzees and gorillas pick up self-medication through social learning (Cousins & Huffman, 2002; Masi et al., 2012). The extent of medicinal plant use in non-human great apes is not well studied since it happens very rarely (present in <1% of yearly feeding time of all food items consumed (Masi et al., 2012)). The fact that eight plants are medicinally used by gorillas (Cousins & Huffman, 2002; Michael A Huffman, 1997; Masi et al., 2012) and six by chimpanzees (Krief et al., 2005; Masi et al., 2012; Pebsworth et al., 2006) makes it unlikely that learning happens solely through trial-and-error in those species. However, their medicinal plant uses are not comparable to the vast diversity of plants used by the BaYaka and other human populations. How such rich cultural traits have emerged in humans is one of the main questions in cultural evolution studies. It may be that evolved social learning mechanisms (such as high fidelity copying) and patterns of cultural transmission might have helped humans to accumulate more cultural traits compared to other animals. Next chapter addresses these topics in further detail and explores how knowledge sharing patterns in the Mbendjele might have contributed to the diversity of plant uses.

Much of the common plant uses among Central African Pygmies and other great apes concerned treating digestive system disorders. This is due to the high prevalence of parasitic infections among Pygmies and the great apes, and the effects of these parasites on the behaviour and reproductive fitness of an individual (Blackwell et al., 2015; Froment, 2014; Michael A Huffman, 1997) (see also Chapter 4, Discussion). The common uses of medicinal plants reported in this study by Central African Pygmies and African great apes may indicate that medicinal plant knowledge is likely adaptive. However, unless we conduct a systematic study measuring health outcomes of those who use certain plants as medicine and those who do not, we cannot be sure whether the medicinal use is effective. For this reason, the next section will use a more direct measure to examine potential health effects of medicinal plant use in the Mbendjele. In particular, it will examine whether maternal medicinal plant use has an effect on children's body mass index (BMI).

5.3 Mothers' medicinal plant use for respiratory system disorders affects children's body mass index (BMI)

In this section, my aim is to examine the link between the Mbendjele mothers' medicinal plant use and their children's health outcomes. I use BMI as a proxy for children's health. BMI is often used as a reliable health measure in children in the absence of other health data (Cole, Flegal, Nicholls, & Jackson, 2007). I use several different measures to quantify mothers' medicinal plant use.

5.3.1 Methods

I calculated the BMI z-scores (using intervals of 1 year) of children aged 0 to 5. As BMI is affected by age, it is necessary to standardize BMI value by age. That is why I use z-scores of BMI. A z-score of 1.5 means that a child is 1.5 standard deviations above the average value, and a z-score of -1.5 means a child is 1.5 standard deviations below the average for a particular age.

I investigated the mothers' use of medicinal plants by using the following measures, each of which constitute a different set of analysis: 1) I calculated the total number of medicinal plants each mother used- regardless of plant's use purpose- and assigned an overall medicinal use score to each mother. 2) I calculated a plant use score for each mother for the most commonly used plants for treating respiratory or digestive system disorders. The most commonly used plants were determined as the ones, which were used by at least 20% or more participants for the given category, and there were seven such plants for each category. To give an example, if a mother used three of the seven plants that are most commonly used to treat respiratory system disorders, her use score was three. 3) Instead of assigning use scores to mothers, I examined whether the mothers' use of particular plants affected children's BMI. I chose those plants that are either used very commonly (by >20% of the participants) for treating certain disorders, or are used by both Central African Pygmies and great apes.

For each analysis, I used linear mixed-effects models for testing the effect of a mother's plant use score or the use of particular plants on their children's BMI, controlling for mother's ID (random effect, as there were 33 mothers and 42 children), age, camp residence and child's sex.

5.3.2 Results

I first examined whether mothers' overall medicinal plant use score (i.e. how many of the 33 plants a mother used as medicine) influenced their children's BMI. There was not a significant effect of mother's medicinal use score on their children's BMI z-scores (mixed-effects linear regression model, coefficient= 0.003, SE=0.03, *p*= 0.9). As discussed in the previous chapter, there is a variation in medicinal uses of plants and not all the plants have a large consensus on their use purpose. Therefore, while some uses may confer adaptive benefits, others may not be as useful. Moreover, not all the treatments are expected to have an effect on individuals' BMI.

For these reasons, I investigated whether mothers' medicinal use of the most commonly used plants for treating digestive and respiratory system disorders (plants that are used by more than 20% of the participants) affected their children's BMI. I found that mothers with higher plant use scores for treating respiratory system disorders had children with significantly higher BMI z-scores (Table 5-2, Model 1-2). However, there was no effect of mother's use score for treating digestive system disorders on their children's BMI z-scores (Table 5-2, Model 2-1). These results reinforce that certain medicinal plant uses may provide fitness benefits.

Table 5-2: Mixed-effects linear regression models of maternal plant use on children's BMI. Models 1-1 to 1-4: mothers' use score of 7 plants for respiratory system disorders on children's (aged 0 to 5) z-BMI. Models 2-1 to 2-3: mothers' use score of 7 plants for digestive system disorders on children's z-BMI. Control variables: mother's age group, camp residence, and children's sex.

	Respiratory uses							
	Model 1-1		**Model 1-2**		**Model 1-3**		**Model 1-4**	
	Coeff. (SE)	**P**	**Coeff. (SE)**	**P**	**Coeff. (SE)**	**P**	**Coeff. (SE)**	**P**
(Intercept)	-0.84 (0.67)	0.22	-1.24 (0.54)	0.03	-0.3 (0.31)	0.35	-0.37 (0.32)	0.26
Use score	0.21 (0.1)	**0.04**	0.2 (0.09)	**0.05**			0.1 (0.08)	0.21
Age 25-35	-0.28 (0.48)	0.56						
Age 35-45	-0.34 (0.51)	0.51						
Age 45-55	0.26 (0.79)	0.74						
Forest camp 2	0.61 (0.5)	0.23	0.55 (0.47)	0.25	0.73 (0.49)	0.15		
Forest camp 3	1.51 (0.54)	**0.01**	1.47 (0.54)	**0.01**	0.88 (0.49)	0.08		
Town camp	0.4 (0.4)	0.32	0.44 (0.38)	0.26	0.13 (0.37)	0.73		
Sex- male	-0.46 (0.3)	0.14						
AIC	119.83		117.64		120.36		120.17	
N observations	42		42		42		42	
N groups	33		33		33		33	

	Digestive uses						
	Model 2-1		**Model 2-2**		**Model 2-3**		
	Coeff. (SE)	**P**	**Coeff. (SE)**	**P**	**Coeff. (SE)**	**P**	
(Intercept)	0.35 (0.65)	0.59	-0.3 (0.31)	0.35	-0.04 (0.34)	0.91	
Use score	-0.03 (0.13)	0.85					
Age 25-35	-0.51 (0.5)	0.32					
Age 35-45	-0.54 (0.54)	0.33					
Age 45-55	0.09 (0.89)	0.92					
Forest camp 2	0.9 (0.54)	0.11	0.73 (0.49)	0.15	0.7 (0.48)	0.15	
Forest camp 3	0.92 (0.52)	0.09	0.88 (0.49)	0.08	0.86 (0.48)	0.08	
Town camp	0.15 (0.41)	0.72	0.13 (0.37)	0.73	0.05 (0.36)	0.89	
Sex- male	-0.36 (0.34)	0.31			-0.46 (0.28)	0.15	
AIC	125.41		120.36		119.52		
N observations	42		42		42		
N groups	33		33		33		

The models were fit by maximum likelihood. Models 1-1 and 2-1 were the full models. For respiratory use score, the optimum model was Model 1-2 which included mother's use score for respiratory problems and her camp residence. Dropping the variable *Use score* from Model 1-2 significantly decreased the model's fit (for Model 1-2 and 1-3: $P[\chi^2(1) > 4.72] < 0.05$). For digestive use score, the optimum model was Model 2-2 which included mother's camp residence. Dropping the variable *Sex* from Model 2-2 did not affect the model fit (for Model 2-2 and 2-3: $P[\chi^2(1) > 2.84] = 0.09$).

Since there was a positive effect of mother's use score for respiratory problems, I performed an additional analysis by breaking down the effects of the use of each plant. In this analysis, I used mixed effects logistic regression models as above with children's BMI z-scores as the response variable. The main predictors were the mother's use of each of the seven plants (categorical variable coded as 0- not used or 1- used), and the control variables were the same as the previous analyses. The optimum model showed that mothers who used *Myrianthus arboreus* (local name, *Ngata*) to treat respiratory problems had children with BMI z-scores approximately 0.75 standard deviation higher than those whose mothers did not use the plant (Figure 5-2, Coefficient= 1.1, SE= 0.27, $p < 0.001$). Moreover, children who resided at the camps Masia and Ibamba had higher BMI z-scores compared to children who resided at Longa. The use of other six plants for respiratory problems did not have an effect on children's BMI.

Myrianthus arboreus was one of the three plant species that were used by both Central African Pygmy groups and gorillas and chimpanzees (Table 5-1). The other two species were *Marantochloa congensis* (*Imbi*) and *Costus sp.* (*Mokakake*). I did not examine the effects of *Marantochloa congensis*, since majority of the participants who reported using this plant used it for making mats (only 18 people reported using it as medicine as opposed to 93 who reported using it for making materials). On the other hand, I examined the effect of mothers' medicinal use of *Costus sp.* (*Mokakake*) on their children's BMI. Among 33 mothers only 3 did not use this plant, therefore there was not much variation in its use. The medicinal use of this plant by mothers did not have an effect on their children's z-BMI (Coefficient= 0.44, SE= 0.62, $p = 0.49$). This may be due to the small variation in mothers' use of this plant, which renders detecting its effect more difficult. Nevertheless, my analyses above indicated that mothers who specifically used this plant for treating respiratory problems did not have children with increased z-BMI compared to other children (Coefficient= 0.24, SE= 0.36, $p = 0.5$). Similarly, mothers who specifically used this plant for treating digestive system disorders did not have children with increased BMI z-scores (Coefficient= -0.07, SE= 0.43, $p = 0.87$). In fact, none of the seven plants that the mothers used to treat digestive system disorders were correlated with increased z-BMI in children.

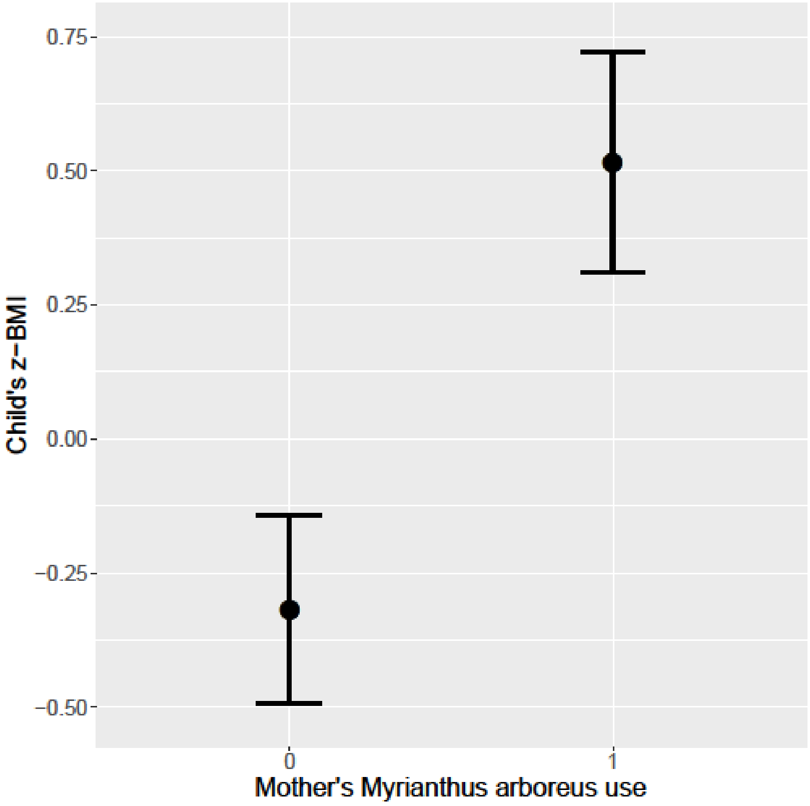


Figure 5-2: Mother's use of *Myrianthus arboreus* on children's z-BMI. Mothers who reported using the plant (coded as 1) had children with higher BMI compared to mothers who did not report using the plant (coded as 0).

5.3.3 Discussion

In this section, I examined whether the Mbendjele mothers' use of medicinal plants influenced their children's BMI. My results showed that the number of medicinal plants a mother used did not have an effect on their children's BMI. I also investigated the use of most commonly reported medicinal plants among the Mbendjele for treating digestive and respiratory system disorders. Among those, only the use of *Myrianthus arboreus* to treat respiratory system problems was associated with higher BMI in children.

Myrianthus arboreus (*Ngata*) was one of the most commonly used plants by the Mbendjele. 68% of the participants reported using it. Among those 44% reported using it for treating respiratory problems and 22% for consuming as food, since it has tasty edible fruits

(Figure 5-3). 10% reported using it for digestive problems. It is interesting that among the Baka of Cameroon the fruit is believed to encourage the growth of children, especially twins (AFlora Committee, 2013). The leaves are used as analgesic for teeth and throat pain by Congolese people (Masi et al., 2012), and for treating cough, fever, dysentery and skin infections by other African populations (Masi et al., 2012; Memvanga et al., 2015; Tshibangu, Chifundera, Kaminsky, Wright, & König, 2002). Moreover, not only humans but also other great apes use the plant as medicine (Masi et al., 2012). Anti-malarial activity is found in the leaf extracts (Masi et al., 2012; Memvanga et al., 2015; Tshibangu et al., 2002).

Figure 5-3: *Myrianthus arboreus* (*Ngata*) fruits, also called as *ekamu*.

Although the majority of the reported usage of medicinal plants concerned treatments of digestive problems, mothers' use of plant medicine for these problems did not have an effect on their children's BMI. One limitation of my analysis was the absence of direct health measurements. Without more systematic research designs on people's use of medicinal plants and their families' health outcomes, it is difficult to assess the effectiveness of medicinal plant use. Nevertheless, my results here can be used as a stepping-stone for further investigations on the adaptive value of medicinal plant use.

5.4 Conclusion

In this chapter, I investigated whether medicinal plant use has adaptive benefits that enable the Mbendjele to better cope with pathogens in their environment. I found that majority of the medicinal plants were also used by other Central African Pygmy groups and some of them by gorillas and chimpanzees as medicines. The common plant uses across human groups and great apes mainly overlapped for treating digestive disorders. Moreover, the Mbendjele mothers' use of *Myrianthus arboreus* as a treatment for respiratory problems was associated with higher BMI in their children. Overall, these results suggest that the use of particular plant species as medicine may have health benefits hence may increase individuals' fitness in the absence of modern medicine.

Among their neighbors, Pygmies are known for their forest skills and their extensive knowledge on plants (Bahuchet, 2014). One interesting question is: how do they get to accumulate such diverse plant knowledge? Why are there so many different use purposes? I believe that how the Mbendjele share their knowledge about plants can inform us on how this cultural diversity came into place. The next chapter examines how knowledge on different types of plant uses is shared among the Mbendjele. In particular, it asks how the Mbendjele's social structure- biological and affinal kin ties, and ties among camp co-residents- affect the sharing of plant knowledge and whether function and adaptive value of knowledge have an effect on its sharing patterns.

Chapter 6: Knowledge-sharing networks in the Mbendjele and their implications on the evolution of culture

6.1 Introduction

This chapter examines how knowledge on plant uses with different functions is shared among the Mbendjele. By examining the knowledge sharing patterns, I aim to explore how the Mbendjele acquired this rich cultural repertoire and test hypotheses on the effects of social structure and life-history on cultural transmission. The work presented in this chapter is published as a research paper in the journal *Current Biology* entitled “Knowledge sharing networks in hunter-gatherers and the evolution of cumulative culture” (Salali et al. 2016). A copy of this paper is provided in Appendix C. Author contributions for this paper are as follows: G.D.S designed the research, collected and analysed the data, A.B.M., R.M., N.C., J.T., M.D., A.E.P., and D.S. helped with protocol design and collection of genealogical, anthropometric and age data; O.M.G. and X.M.vdB. identified the plant species and helped with the plant literature research; J.L. assisted in fieldwork; G.D.S., A.B.M., and L.V. wrote the manuscript with the help of all other authors.

6.1.1 Human culture and its origins

What is culture? While there are various definitions of culture in the social sciences (Durham, 1991), I will use a definition which is widely used by biological anthropologists: culture is socially transmitted information or behaviour that is specific to a group (Dean, Vale, Laland, Flynn, & Kendal, 2014; Richerson & Boyd, 2005). Following this definition, culture is not unique to humans (Laland & Hoppitt, 2003). Female sperm whales use acoustic signals (“codas”) for communication, and those codas are found to be socially transmitted (Whitehead & Rendell, 2014). Moreover, researchers suggest that the codas shape the social structure as whales tend to group together with others that have similar coda repertoires (Mauricio Cantor & Whitehead, 2013). Chimpanzee groups exhibit variation in tool usage, grooming and courtship behaviour (Whiten et al., 1999), however to what extent this variation is due to social learning or ecological variation is not clear (Laland & Hoppitt, 2003). Capuchin monkeys in Costa Rica display group-specific traditions that are seen as social rituals (Perry, 2011; Perry et al., 2003). These include hand-sniffing (where a pair of individuals insert fingers in or on nostrils of each other for a duration of time), prolonged sucking of body parts, eye-poking, and games (i.e. where one animal strongly bites an object belonging to the other animal and the other tries to retrieve it back) (Perry, 2011; Perry et al., 2003). Those interesting rituals are thought to serve as a bond-testing, enabling a pair of animals to assess the degree of commitment and trust in their relationship (Perry, 2011).

Although social learning and culture is observed in non-human animals (Maurício Cantor et al., 2015; Galef & Laland, 2005; Jaeggi et al., 2010; Whiten et al., 1999; Whiten, Horner, & de Waal, 2005), the size of cultural repertoires are small and cultural change is almost never cumulative (Tennie, Call, & Tomasello, 2009; Michael Tomasello, Kruger, & Ratner, 1993). Nevertheless, a recent study has suggested that chimpanzees have the foundations of cumulative culture by showing that they were able to combine two different techniques to generate a more efficient technique (Davis, Vale, Schapiro, Lambeth, & Whiten, 2016). Whether or not it is unique; a key aspect of human culture is our ability to ratchet up the complexity of cultural traits over time (Dean et al., 2014; Tennie et al., 2009).The end result of the accumulation of beneficial modifications to knowledge is what defines cumulative culture: culturally transmitted knowledge or traits so complex that they cannot be invented by a single individual (Dean et al., 2014; Michael Tomasello et al., 1993). It has been argued that evolution of cumulative culture does not only require high cognitive abilities, but also ability to cooperate with others and work together towards a shared goal (M. Tomasello, 1999; Michael Tomasello, Carpenter, Call, Behne, & Moll, 2005; Michael Tomasello & Rakoczy, 2003). Supporting this view, a laboratory experiment showed that unlike chimpanzees and capuchins, the success of children in solving a task was associated with pro-sociality along with teaching through verbal instructions and imitation (Dean, Kendal, Schapiro, Thierry, & Laland, 2012).

Humans are indeed exceptionally good at imitating other individuals (Tennie et al., 2009; Michael Tomasello et al., 1993). Unlike other great apes, humans even copy actions of others that appear causally irrelevant for the purpose of a given task- a phenomenon called "over-imitation" (Horner & Whiten, 2005; Lyons, Damrosch, Lin, Macris, & Keil, 2011; Lyons, Young, & Keil, 2007). Therefore human social learning is more oriented towards process than product (Tennie et al., 2009), and this feature plays an important role in the spread of skills, behaviours and social norms (Salali, Juda, & Henrich, 2015; Tennie et al., 2009). In fact, some scholars have argued that high-fidelity transmission is the key driver behind the cumulative culture; and the progress in cultural complexity depends more on the combination of different traits than on new inventions or modifications (H. M. Lewis & Laland, 2012).

Evolution of cumulative culture cannot be discussed without a discussion on the evolution of language (Harari, 2011). Indeed, language is one, if not the most, powerful tool in transmitting information with high fidelity and might have been selected for this purpose (Pinker, 1994; Pinker & Bloom, 1992). According to Dunbar, language has evolved to facilitate the transmission of social information that was crucial to maintain social bonds under increasing group sizes (Aiello & Dunbar, 1993; Dunbar, 1993, 2016). In non-human primates, grooming serves to maintain social relationships and the amount of time spent during grooming linearly correlates with the group size (Dunbar, 1991). Dunbar states that in humans, language replaced the function of grooming, because otherwise 40% of the hominin time would have to be dedicated to grooming under increasing population sizes (Dunbar, 1993). Whereas grooming has to be a one-to-one interaction, speaking made simultaneous connections with many individuals in the group possible (Aiello & Dunbar, 1993; Dunbar, 2016).

One key aspect of human language that differentiates it from any other forms of animal communication is the use of metaphors (Pinker, 2010; Ramachandran, 2011). Use of metaphors not only requires abstract thinking, but also the ability to understand other's intentions and mind state. Dunbar cites an interesting example from Happe (1994) about an individual with severe autism who is told to "pull the door behind him" (Dunbar, 1998). And he did so literally, failing to comprehend the metaphoric aspect of the order. Indeed, language is tightly connected to our ability to understand other's mental states and intentions (Dunbar, 1998). This is not surprising given that the main function of language is purely social (Dunbar, 1993, 2004). The language itself therefore is not sufficient to explain cultural evolution. One must consider the evolution of human's shared intentionality and theory of mind, language and pro-sociality all together to be able to fully understand the evolution of cultural complexity. Moreover, the progress of cumulative cultural evolution also depends on who shares the information with whom and requires information on the population's social structure. Given that the progress in cultural complexity may depend more on transmission fidelity and the combination of traits, rather than new innovations or modifications (H. M. Lewis & Laland, 2012), a population structure that allows both knowledge specialization and combination would support cumulative culture. In the next section, I will discuss how social structure contributes to the trajectory of cultural evolution in detail.

6.1.2 Role of social structure

One aspect of social structure that is thought to have a direct effect on the evolution of cumulative culture is group size (Richerson, Boyd, & Bettinger, 2009). According to some scholars cultural complexity, or the extent of cultural repertoire, requires sufficient pool of individuals to exchange, combine and modify information (Henrich, 2004; Shennan, 2001). Using an historical data on the decline of cultural complexity in Tasmania, some scholars suggested that the decline was associated to the decrease in effective population size, hence the size of the pool of social learners (Diamond, 1978; Henrich, 2004; Jones, 1977, 1995). According to Henrich's model based on the Tasmanian case, at larger population sizes there is a greater chance of a random error in cultural transmission leading a social learner to acquire a skill that is even more efficient than his/her model's skill (Henrich, 2004). The same process may lead to maladaptive loses of information at shrinking population sizes, a process that was believed to have happened in the Tasmanian case (Diamond, 1978; Henrich, 2004). Experimental studies observing the emergence of cultural complexity in the laboratory have found that larger groups accumulated more cultural traits (Derex, Beugin, Godelle, & Raymond, 2013; Kempe & Mesoudi, 2014), but see (Caldwell & Millen, 2010). Archaeological and anthropological analyses have produced mixed results, some showing an evidence to increased cultural complexity with increasing population sizes (Kline & Boyd, 2010), and others with environmental risk but not the population size (Collard, Buchanan, O'Brien, & Scholnick, 2013; Read, 2012).

Perhaps, rather than the group size per se, the structure of the group (i.e. the presence of sub-groups and the interactions among them) is more crucial in explaining the cultural complexity. Supporting this view, Powell and colleagues have shown in their simulation models that demography played a significant role in the emergence of modern human behaviour (Powell, Shennan, & Thomas, 2009). Emergence of modern human behaviour is marked by archaeological evidence displaying substantial increase in technological and cultural complexity with abstract art, ritualistic artefacts and body decorations, rapidly at about 45ka in Europe (Mellars, 2005), and earlier on and more gradually in Africa (Powell et al., 2009). According to Powell and colleagues' model, what caused greater skill complexity was not the meta-population size per se, but the amount of interactions among the sub-populations comprising the meta-population (Powell et al., 2009). This sub-population effect still required a certain size of a meta-population (50 individuals in their model), suggesting that the arguments on the effect of group size in the Tasmanian case might hold true (Powell et al., 2009).

Why would a population structure with sub-groups be more efficient than the population size itself? The answer may lie in the power of partial connectivity (Derex & Boyd, 2015, 2016). In a fully connected population, the group may converge on a suboptimal solution to a problem, especially considering human's tendency to learn from prestigious or skilful individuals (Derex & Boyd, 2016; Henrich & Gil-White, 2001a). On the other hand, if there are sub-groups, each sub-group may develop a different solution contributing to cultural diversity. The connections among sub-groups may then give way to new combinations and hence potentially more complex cultural traits or tools. Testing the ability of different groups to develop solutions to a complex problem in a laboratory experiment, Derex and Boyd showed that groups that were partially connected developed more complex solutions in the long run compared to the fully connected groups (Derex & Boyd, 2016). Since human social structure is characterized by strongly bonded sub-groups consisting multiple families, hunter-gatherer population structure might have been one of the key contributors to the evolution of cultural complexity (Derex & Boyd, 2016; Dyble et al., 2015; Hill et al., 2011, 2014; Migliano et al., 2017; Powell et al., 2009; Salali et al., 2016).

If the above theory is true, then the follow-up question would be how the connections among sub-groups are maintained, and with whom the information is shared? Pair bonding and marital connections are very important in the formation of our nested social structure. In small-scale societies, such as hunter-gatherer bands, those marital ties may be crucial in the transmission of information and accumulation of cultural skills and knowledge that is important for survival. Nevertheless, the importance of monogamy, exogamy and marital ties is often neglected in discussions of cultural evolution. Strong pair bonds in humans do not only link males and females, but also their families. Spouses bring information from their natal groups. Therefore, marital ties may have been the initial information transmission vectors among different sub-groups, contributing to the emergence of cultural complexity.

6.1.3 Role of life-history traits and cooperative breeding

Another aspect of human evolution that is neglected in the discussions of cultural evolution is the human life-history traits. In their seminal paper, Kaplan and colleagues have suggested that a shift to high-calorie, large-package resources has triggered the co-evolutionary processes for higher intelligence, longer childhoods and life-spans (Kaplan et al., 2000). According to their theory, extended juvenile dependence, and childhood have allowed humans to socially acquire the complex skills that were necessary to obtain high-calorie resources (Kaplan et al., 2000).

Since childhood is an important period of time for learning skills that are necessary for survival, cooperative breeding must have been important in the transmission of information from older to younger generations. In fact, some scholars have argued that long post-reproductive period in humans might have evolved because of the adaptive benefits associated to the transmission of skills from the older, more skilled and knowledgeable individuals to the younger ones (Kaplan, Gurven, Winking, Hooper, & Stieglitz, 2010). Although it has been argued that cooperative breeding is the driving force behind the evolution of theory of mind and shared intentionality in humans (Burkart, Hrdy, & Van Schaik, 2009; Hrdy, 2009), its role in cultural transmission has been neglected. Child-care, however, would provide the necessary time and context for transmission of knowledge between the caregivers and also from caregivers to caretakers. Since caregivers primarily constitute mother and father, grandparents and older siblings (Kramer, 2010, 2011; Sear & Mace, 2008), we would predict much knowledge sharing among those pairs of individuals (Figure 6-1). One feature of human social structure is very crucial in this respect: the interactions among affinal kin. Often those interactions are based around the offspring with the shared reproductive value. Consider a mother receiving help in child-care from her sister-in-law: As the sister-in-law is 0.25 related to the offspring (aunt-niece pair), she gains inclusive fitness benefits by helping the mother (W. D. Hamilton, 1964). Interactions among affinal kin around childcare, therefore, may not only provide fitness benefits, but also opportunities for exchanging knowledge and transmitting it to the offspring.

Figure 6-1: Mbendjele interactions are often shaped around childcare. Mamoi, an Mbendjele woman, is bathing her grandson. At the entrance of the hut Mamoi's daughter Carmen is looking after her brother's baby. Anga, the young girl in the middle, is playing with a flip-flop while her younger brother is watching her.

6.1.4 Sharing of knowledge based on the content of information

Studies of cultural evolution have mainly focused on mechanisms such as fidelity, combination, innovation and modification (H. M. Lewis & Laland, 2012). The content and function of cultural information, however, also affects knowledge-sharing mechanisms (Mesoudi, Whiten, & Dunbar, 2006; Reyes-García, Luz, et al., 2013). Content bias (also called as "direct bias") occurs when individuals select to copy traits based on their utility (Boyd & Richerson, 1985). Since human cumulative culture is diversified into functional domains (Henrich & Broesch, 2011; Mesoudi, Whiten, & Dunbar, 2006; Reyes-García et al., 2009; Reyes-García, Luz, et al., 2013), it may also require corresponding differentiation of knowledge-sharing mechanisms and underlying social structure (Díaz-Reviriego et al., 2016). For example, long-term pair bonding, exogamy and biological and affinal kin recognition in hunter-gatherers might contribute to within-family transmission and accumulation of knowledge that is relevant for childcare, which may have fitness benefits. Knowledge required for camp-wide activities such as cooperative foraging, or social norms and rituals that are necessary for group cohesion should instead be shared more widely across all individuals in a camp.

Plant knowledge in the Mbendjele provides an ideal context to study the mentioned effects of social structure, life-history traits and the content of information on the sharing of knowledge and the evolution of cultural complexity. First, Mbendjele social structure is marked by pair-bonded couples living in multi-family groups. Moreover, childcare is provided cooperatively. Second, plant knowledge represents a rich cultural repertoire with diverse functions. As discussed in Chapter 4 plant uses in the Mbendjele have many different functions, from killing animals for food to punishing cheaters that violate social norms. Moreover, as examined in Chapter 5, certain medicinal plants might provide fitness benefits to the individuals who bear the knowledge. Therefore, investigating the sharing patterns of knowledge on different types of plant uses in the Mbendjele will help us understand the link between the content and function of information and how it is shared.

With this aim, this chapter examines the reported uses of 33 plants by 219 Mbendjele from four camps. I use three main categories, as reported in Chapter 5, to classify plant uses: medicinal, foraging, and social norms and beliefs. I chose those three categories, as the medicinal uses concern health and potentially provide fitness benefits, while foraging and social beliefs concern group-level activities. I predict that the knowledge on medicinal plants will be shared among biological and affinal kin who have common reproductive interests as medicinal uses may bring about fitness benefits. On the other hand, I predict the plant knowledge on foraging or social beliefs to be shared widely with other group members as they concern group related activities and social norms. I test these predictions by analysing the co-occurrence of plant uses between individuals in dyads (which I define as their ‘shared knowledge’ of plant uses). I investigate the effects of biological and affinal kin ties (e.g. mother-offspring, siblings, spouses, in-laws and etc.), co-residence (residing at the same camp), age and sex on the odds of two individuals sharing knowledge of a particular plant use in a sample of 23,868 dyads.

6.2 Methods

Study population. Data from all four Mbendjele camps that I visited is used (three forest camps, Longa: n = 59, Masia: n = 22, Ibamba: n= 31; and one in a logging town Sembola: n = 107; see Chapter 3 for detailed information on the camps).

Measuring plant knowledge and use. I asked 219 individuals (118 women, 101 men) across four campsites whether they knew each of the 33 species, and if so, whether they used it for any purpose (see Chapter 4 for detailed information on the selection of those species and the classification of the use types).

Dyadic sample. From 219 individuals I obtained 23,871 dyads. Each dyad had responses for uses of 33 plants, resulting in possible 787,743 data points. If an individual used a plant for multiple purposes I only used the first use type in my analyses. This only occurred in 2% of all the responses of 219 participants. 151,038 data points (19%) contained responses where none of the individuals in a dyad used a given plant. These points were omitted from the analyses, resulting in a sample of 636,705 data points and 23,868 dyads.

Measuring co-occurrence of plant use ('shared knowledge'). The similarity in use type for each plant was coded based on the sub-categories presented in Chapter 4, Table 4-4. For each dyad, if individual A and individual B reported the same use for a given plant, their dyadic response was coded as 1 ('shared knowledge'). On the other hand, if the individuals in a dyad used a plant for different purposes their response was coded as 0 (knowledge not shared). If one individual used a plant, but the other did not use it for any reason their response was coded as 0. Similarly, if one individual used a plant for any use type under one category (e.g. foraging), and the other used the same plant for a use type under another category (e.g. medicinal) their response was coded as 0.

Statistical analysis. I used mixed effects logistic regression to predict the reported co-occurrence of plant use in a dyad. Because for each pair of individual I had 33 different responses (the reported uses for each of the 33 plants), I controlled for dyad's ID as a random effect. My fixed predictors were biological kin ties (measured first as coefficient of relatedness, and subsequently as presence of a specific biological kin tie, e.g. mother-offspring; I analysed and described models based on each measure separately), affinal kin ties (spouse, spouse's primary kin, spouse's distant kin), camp ties (residing in the same camp), age group and sex (female-female, male-male, female-male dyad). "Spouse's primary kin" are the parents, children, or siblings of an individual's spouse. "Spouse's distant kin" are consanguineal kin of an individual's spouse of up to four steps of genealogical distance.

I performed separate analyses for three categories of plant use (medicinal, foraging, and social norms and beliefs). For instance, for medicinal uses, I compared the dyads that shared knowledge on the medicinal use of a plant with dyads that did not share knowledge on how to use a plant (Figures 6-2A, 6-3A, Table 6-1). For other use types, I compared dyads that shared knowledge on either the foraging related uses or the uses associated with social beliefs with dyads that did not share knowledge (Figures 6-2B, 6-3B, Tables 6-2, 6-3).

6.3 Results

6.3.1 Medicinal plant knowledge is shared within families

Mixed effect models revealed that dyads represented by biological or affinal kin ties had increased odds of reporting the same medicinal plant use (Figures 6-2A, 6-3A and Table 6-1). A 0.25 increase in the coefficient of relatedness within a dyad increased the odds of reported co-occurrence of medicinal plant use by 22% (Odds ratio (OR)= 1.22, 95% CI= 1.17, 1.27; Risk ratio (RR)= 1.19; Risk difference (RD)= 3%; Figure 6-2A; Table 6-1 Model 1). Breaking down the effects of kinship, dyads including mother and offspring had an increase of 57% in the odds of co-occurrence of medicinal plant use (OR= 1.57, 95% CI= 1.33, 1.84; RR= 1.46; RD= 6%; Figure 6-3A; Table 6-1 Model 2). The effect was much smaller (28%), but still significant for father and offspring (OR= 1.28, 95% CI= 1.04, 1.56; RR= 1.23, RD= 3%). Being siblings increased the odds by 40% (OR= 1.40, 95% CI= 1.18, 1.65; RR= 1.33; RD= 5%).

Affinal ties were also important in explaining co-occurrence of medicinal plant uses (Figures 6-2A, 6-3A, Table 6-1). The odds of co-occurrence of medicinal plant use increased by 61% between spouses (OR= 1.61, 95% CI= 1.32, 1.96; RR= 1.49; RD= 7%). Even distant affinal kin were more likely to report similar medicinal uses of plants (Figures 6-2A, 6-3A). The odds of co-occurrence of medicinal plant use increased by 41% (OR= 1.41, 95% CI= 1.26, 1.58; RR= 1.34; RD= 6%) between an individual and their spouse's primary kin, and 24% (OR= 1.24, 95% CI= 1.17, 1.31; RR= 1.20; RD= 3%) between an individual and their spouse's distant kin.

Unlike the large effect of family ties, camp ties (when the two individuals in the dyad reside in the same camp) increased odds of co-occurrence of medicinal plant use by only 6% (Figures 6-2A, 6-3A; OR= 1.06, 95% CI= 1.04, 1.08; RR= 1.05; RD= 1%; Table 6-1). Dyads where individuals belonged to the same age group had increased odds of reporting the same medicinal plant use by 36% (Figure 2A; OR= 1.36, 95% CI= 1.33, 1.39; RR= 1.30; RD= 4%; Table 6-1). Female-female dyads had increased odds of co-occurrence of medicinal plant knowledge compared to female-male dyads, but the effect size (7%) was small (Figure 6-2A; OR= 1.07, 95% CI= 1.05, 1.09; RR= 1.06; RD= 1%; Table 6-1).

6.3.2 Plant knowledge related to cooperative foraging and social beliefs is shared among campmates

Unlike medicinal plant knowledge, plant uses related to foraging and social norms/beliefs co-occurred more frequently among camp members, regardless of family ties (Figures 6-2B, 6-3B). Kin and non-kin effects on odds of reporting similar plant uses were similar in the two categories (Table 6-3), which were therefore merged. Being from the same camp increased the odds of co-occurrence of plant use in foraging and social norms and beliefs by 84% (Figures 6-2B; OR= 1.84, 95% CI= 1.72, 1.97; RR= 1.83; RD= 0.3%; Table 6-2 Model 1). In contrast, neither relatedness (Figures 6-2B, 6-3B; OR= 0.91, 95% CI= 0.78, 1.06; RR= 0.92; RD= 0%; Table 6-2) nor spousal ties had an effect on odds (Figures 6-2B, 6-3B, OR, RR= 0.82; RD= 0.1%; Table 6-2). The odds of co-occurrence of plant use decreased by 26% between a person and his/her spouse's distant kin (OR, RR= 0.78, 95% CI= 0.64, 0.96; RD= 0.1%). Similarity in age group (OR, RR= 1.51; RD= 0.02%) and sex (for male-male dyads: OR= 1.13; RR= 1.12, RD= 0.01%; for female-female dyads: OR= 0.91; RR=0.92; RD= 0%) had significant effects, but the effect sizes for sex were small (Figures 6-2B, 6-3B and Table 6-2). Patterns of co-occurrence of plant use are similar for foraging and social norms and beliefs (Table 6-3).

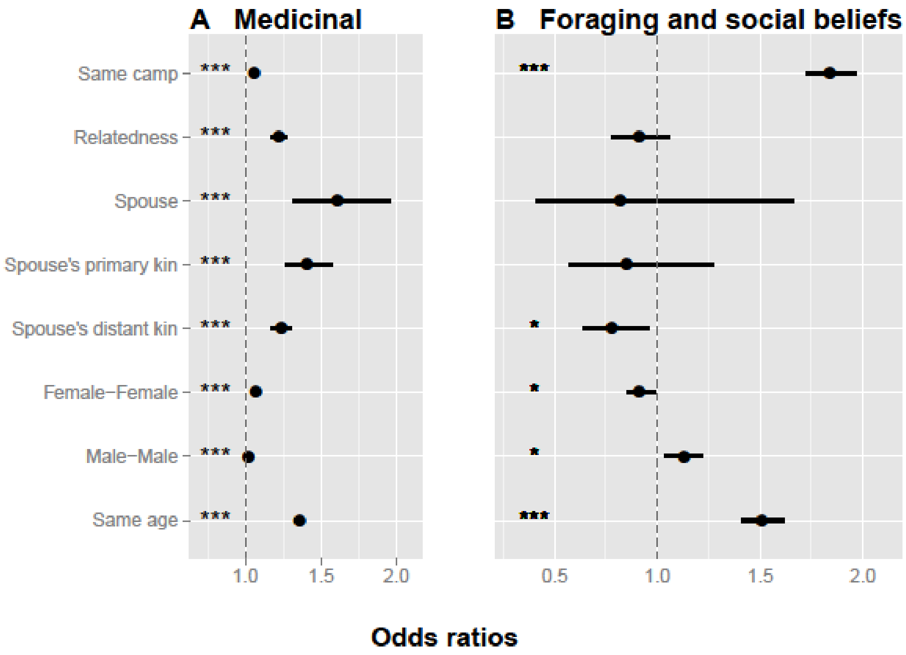


Figure 6-2: Odds Ratios for the predictor variables based on Model 1, Tables 6-1 and 6-2. Response variable is reported co-occurrence of plant use for A) medicinal purposes or B) purposes related to foraging and social beliefs. The dots show the odds of co-occurrence of plant use when individuals in a dyad belong to the same camp; are genetically related (odds ratio calculated for a 0.25 increase in coefficient of relatedness); have one of the following affinal kin ties: spouse, spouse's primary kin, or spouse's distant kin; are females; are males; belong to the same age group. Error bars show 95% confidence intervals. ***$p < 0.001$, *$p < 0.05$.

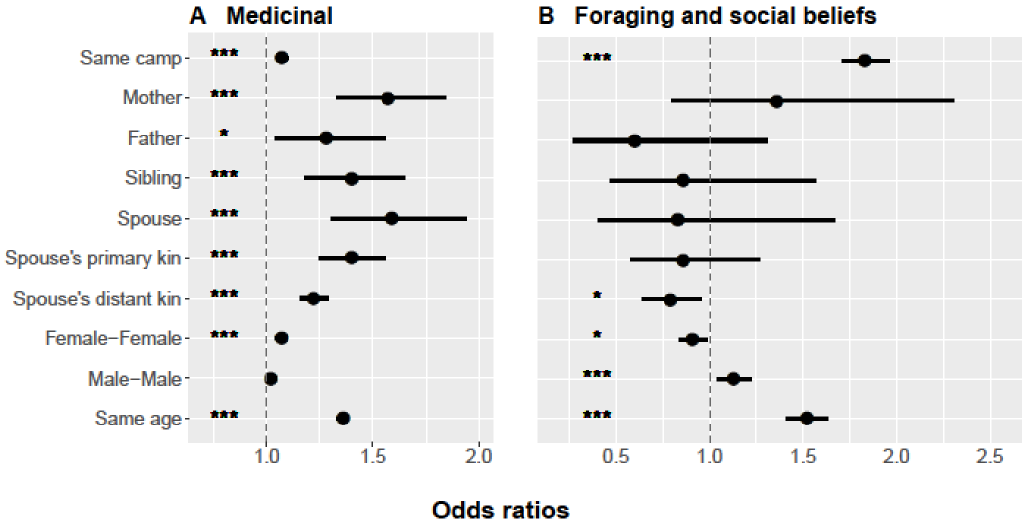


Figure 6-3: Odds Ratios for the Predictor Variables based on Model 2, Tables 6-1 and 6-2. Response variable is reported co-occurrence of plant use for A) medicinal purposes or B) purposes related to foraging and social beliefs. The dots show the odds of co-occurrence of plant use when individuals in a dyad belong to the same camp; have one of the following biological kin ties: mother, father, sibling; have one of the following affinal kin ties: spouse, spouse's primary kin, or spouse's distant kin; are females; are males; belong to the same age group. Error bars show 95% confidence intervals. ***$p < 0.001$, *$p < 0.05$.

Table 6-1: Results from mixed effects logistic regression models on probabilities of reported co-occurrence of medicinal plant use.

		Model 1		Model 2	
	% in dyads with the same plant use	ODDS (CI)	P	ODDS (CI)	P
Intercept		0.15 (0.15, 0.15)	0.00	0.15 (0.15, 0.15)	0.00
Same camp	34%	1.06 (1.04, 1.08)	0.00	1.07 (1.05, 1.1)	0.00
Same age group		1.36 (1.33, 1.39)	0.00	1.36 (1.33, 1.38)	0.00
Female-female		1.07 (1.05, 1.09)	0.00	1.07 (1.04, 1.09)	0.00
Male-male		1.02 (1, 1.05)	0.08	1.02 (1, 1.05)	0.06
r (0.25 increase)		1.22 (1.17, 1.27)	0.00		
Mother	0.4%			1.57 (1.33, 1.84)	0.00
Father	0.2%			1.28 (1.04, 1.56)	0.02
Sibling	0.4%			1.4 (1.18, 1.65)	0.00
Spouse	0.3%	1.61 (1.32, 1.96)	0.00	1.59 (1.3, 1.94)	0.00
Spouse's primary kin	0.9%	1.41 (1.26, 1.58)	0.00	1.4 (1.25, 1.56)	0.00
Spouse's distant kin	3%	1.24 (1.17, 1.31)	0.00	1.22 (1.16, 1.29)	0.00
AIC		540,396		540,430	
Log likelihood		-270,188		-270,203	
N (dyads)		23868			
N (total dyadic responses)		617465			
N (dyadic responses for shared plant use type for medicinal uses)		100149			
N (dyadic responses for not shared use types)		517316			

Percentage in dyads shows the percentage of dyadic data points for each of the theoretically important independent variables. For instance, among the 100149 dyadic data points where co-occurrence of plant use was present 34212 (34%) were the dyads that resided at the same camp, and 410 (0.4%) had mother-offspring relationship.

Table 6-2: Results from mixed effects logistic regression models on probabilities of reported co-occurrence of plant use related to foraging and social-life (combined).

		Model 1		**Model 2**	
	% in dyads with the same plant use	**ODDS (CI)**	**P**	**ODDS (CI)**	**P**
Intercept		0 (0, 0)	0.00	0 (0, 0)	0.00
Same camp	46%	1.84 (1.72, 1.97)	0.00	1.83 (1.71, 1.96)	0.00
Same age group		1.51 (1.41, 1.62)	0.00	1.52 (1.41, 1.63)	0.00
Female-female		0.91 (0.85, 0.99)	0.03	0.91 (0.84, 0.99)	0.02
Male-male		1.13 (1.04, 1.22)	0.01	1.13 (1.04, 1.22)	0.00
r (0.25 increase)		0.91 (0.78, 1.06)	0.24		
Mother	0.4%			1.36 (0.8, 2.31)	0.26
Father	0.2%			0.6 (0.27, 1.31)	0.20
Sibling	0.3%			0.86 (0.47, 1.57)	0.62
Spouse	0.3%	0.82 (0.41, 1.66)	0.58	0.83 (0.41, 1.67)	0.60
Spouse's primary kin	0.7%	0.85 (0.57, 1.27)	0.43	0.86 (0.58, 1.27)	0.44
Spouse's distant kin	3%	0.78 (0.64, 0.96)	0.02	0.79 (0.64, 0.96)	0.02
AIC		615,417		615,438	
Log likelihood		-307,609		-307,599	
N (dyads)		23,868			
N (total dyadic responses)		523,061			
N (dyadic responses for shared plant use type for foraging and social beliefs)		5,745			
N (dyadic responses for not shared use types)		517,316			

Table 6-3: Results from mixed effects logistic regression models on probabilities of reported co-occurrence of plant use related to foraging (Models 1-2) and social-life (Models 3-4).

		Model 1		**Model 2**	
	% in dyads with the same plant use	**ODDS (CI)**	**P**	**ODDS (CI)**	**P**
Intercept		0 (0, 0)	0	0 (0, 0)	0
Same camp	57%	2.94 (2.49, 3.49)	0	2.91 (2.46, 3.44)	0
Same age group		1.78 (1.5, 2.11)	0	1.78 (1.5, 2.11)	0
Female-female		0.88 (0.72, 1.07)	0.21	0.88 (0.72, 1.07)	0.21
Male-male		1.05 (0.85, 1.3)	0.64	1.05 (0.85, 1.3)	0.65
r (0.25 increase)		0.89 (0.62, 1.27)	0.51		
Mother	0.4%			1.02 (0.26, 3.9)	0.98
Father	0.3%			1.03 (0.23, 4.74)	0.96
Sibling	0.4%			1.16 (0.33, 4.03)	0.81
Spouse	0.4%	0.65 (0.12, 3.45)	0.61	0.66 (0.12, 3.49)	0.62
Spouse's primary kin	0.8%	0.76 (0.3, 1.95)	0.57	0.77 (0.3, 1.97)	0.58
Spouse's distant kin	3%	0.74 (0.46, 1.2)	0.22	0.75 (0.47, 1.21)	0.24
AIC		25464.3		25468.6	
Log likelihood		-12722.1		-12722.3	
N (dyads)		23,868		23,868	
N (total dyadic responses)		519,412		519,412	
N (dyadic responses for shared plant use type for foraging)		2,096		2,096	
N (dyadic responses for not shared use types)		517,316		517,316	

Table 6-3 continues

		Model 3		**Model 4**	
	% in dyads with the same plant use	**ODDS (CI)**	**P**	**ODDS (CI)**	**P**
Intercept		0 (0, 0)	0	0 (0, 0)	0
Same camp	39%	1.41 (1.29, 1.53)	0	1.4 (1.29, 1.51)	0
Same age group		1.38 (1.27, 1.5)	0	1.38 (1.27, 1.5)	0
Female-female		0.95 (0.86, 1.04)	0.25	0.95 (0.86, 1.04)	0.23
Male-male		1.15 (1.05, 1.27)	0	1.15 (1.05, 1.27)	0
r (0.25 increase)		0.95 (0.79, 1.15)	0.58		
Mother	0.4%			1.57 (0.84, 2.92)	0.16
Father	0.1%				
Sibling	0.2%			0.77 (0.35, 1.68)	0.51
Spouse	0.2%	0.87 (0.36, 2.11)	0.76	0.88 (0.36, 2.12)	0.77
Spouse's primary kin	0.7%	0.98 (0.61, 1.58)	0.95	0.99 (0.62, 1.58)	0.97
Spouse's distant kin	2%	0.78 (0.61, 1.01)	0.06	0.79 (0.61, 1.01)	0.06
AIC		42965		42965	
Log likelihood		-21472.5		-21471.5	
N (dyads)		23,868		23,868	
N (total dyadic responses)		520,965		520,965	
N (dyadic responses for shared plant use type for social beliefs)		3,649		3,649	
N (dyadic responses for not shared use types)		517,316		517,316	

6.4 Discussion

The main purpose in this chapter was to examine how hunter-gatherers shared knowledge that is important in their day-to-day lives, and whether features of human social structure and life-history traits affect knowledge sharing patterns in a way to facilitate the evolution of cumulative culture. One of the main features of human social structure is the presence of strong pair bonds in a multi-level society, where individuals are able to recognize both their maternal and paternal kin (Chapais, 2008, 2013). Monogamous sexual bonds, and multi-layered societies where smaller groups of animals are nested in larger groups, are also observed in other primates (Grueter et al., 2012). Nevertheless, only in humans we observe extended kin recognition of both paternal and maternal relatives. In fact, both social and biological anthropologists have documented the importance of enduring pair bonds and affinal relationships in the maintenance of between group interactions in modern day hunter-gatherers (Lévi-Strauss, 1969; Marlowe, 2005).

According to recent experimental studies, how groups are structured affect their ability to accumulate and generate complex culture. Derex and Boyd (2015, 2016) have shown that larger groups are better able to accumulate information and generate more efficient solutions to complex problems; nevertheless it is the groups that are connected “partially” that generated the most efficient solutions. This is because cultural diversity reduces with time in fully connected groups due to humans’ tendency to learn from successful individuals (Henrich & Gil-White, 2001b), or conformist learning (Henrich & Boyd, 1998). On the other hand, in partially connected groups cultural diversity can be maintained by each group generating a solution (or cultural trait) that can be later combined with solutions from other groups, potentially leading to complexity (Derex and Boyd 2016). Hunter-gatherer social structure can be seen as an example to “partially connected” groups with independent groups being linked via marital relationships.

How the marital ties and group living affect the sharing of plant knowledge in the Mbendjele was the main question of this chapter. My results showed that 1) knowledge of medicinal plants is mainly shared between spouses, biological and affinal kin; and 2) knowledge of plant uses associated with foraging and social norms is shared more widely among campmates, regardless of relatedness. I will discuss each of these findings in detail below.

6.4.1 Sharing of medicinal plant knowledge

I hypothesized that the strong pair bonds and extended kin recognition in humans' were among the key driving forces behind the evolution of cultural complexity. This is because marital links connect otherwise isolated families, as well as groups that contain those families. My findings on the sharing of medicinal plant knowledge supported this hypothesis. Spouses and affinal kin (such as in-laws, or spouse's second or third degree relatives) in the Mbendjele use the same plants for the same medicinal purposes, suggesting that there is much knowledge transmission among these individuals. I suggest that this is because when a couple starts living together they exchange medicinal uses of plants that they have learnt from their families. This allows them to combine knowledge and potentially develop new combinations of medicinal plants and preparation techniques. Moreover, my finding of frequent co-occurrence of medicinal uses between spouses is consistent with my field observations of parents collecting medicinal plants and preparing medicines together (Appendix A, video 4).

In addition, I observed that the Mbendjele uses medicinal plants often for childcare (Appendix A, video 4). When a child is sick, it is common that not only mothers, but also other caregivers involve in the preparation of plant based medicine. During fieldwork, I witnessed a number of occasions where mothers, their older children and affinal kin, or grandmothers were preparing medicinal plants for sickly young children (Figure 6-4). With respect to the cooperative breeding hypothesis, humans' rapid production of highly dependent offspring is only possible by assistance to mothers in childcare. Previous literature have documented the importance of allo-maternal care by fathers (Lovejoy, 1981) and grandmothers (Kristen Hawkes, O'Connell, Blurton Jones, Alvarez, & Charnov, 1998), as well as explored the adaptive value of cooperative breeding in terms of increased child survival or maternal fertility (Meehan, Helfrecht, & Quinlan, 2014; Sear & Mace, 2008; Snopkowski & Sear, 2013). Cooperative breeding has also been suggested to be the driving force behind the evolution of human cooperation (Burkart et al., 2009; Hrdy, 2009), however it is a much-neglected topic in discussions of cultural transmission. My findings on sharing of medicinal knowledge in the Mbendjele suggest that this form of childcare may provide the context for sharing of adaptive information (i.e. knowledge that may influence one's survival and reproductive success).

In Chapter 5, I discussed the adaptive value of medicinal plant knowledge in hunter-gatherers, and concluded that there may be health benefits to using certain plants as medicine. Spouses, in-laws, and people that are connected via marital ties often have shared reproductive interests. Therefore, kin selection and inclusive fitness theory is one of the main mechanisms how cooperative breeding might have evolved in humans. For example, a person and his sister-in-law have a common reproductive interest, because they are both related to the offspring of the person (coefficient of relationship (*r*) is 25% between the sister-in-law and her nephews and nieces). The reason why I find knowledge sharing of medicinal plant uses among affinal kin may be due to the inclusive fitness benefits that the knowledge on medicinal plants may confer. The cooperative childcare, therefore, provides a context for cultural transmission.

Figure 6-4: Nyambe preparing medicine from the bark of *Boyo* for her sick baby, while her older children watching her.

Not only the affinal kin learn new information on the uses of medicinal plants during childcare, but also the children themselves. Human life history is marked by extended period of juvenile dependence and childhood (Kaplan et al., 2000). It is been argued that long childhood allowed humans to socially acquire the complex skills that are necessary for finding food, hence survival (Kaplan et al., 2000). Since most medicinal plant uses occur around childcare, the

Mbendjele children may also acquire various uses of medicinal plants by simply observing adults in times of sickness (Figure 6-4; Appendix A, video 4). Indeed social interactions create the conditions for cultural transmission through various modes of social learning (Barry S. Hewlett et al., 2011). Among the Mbendjele, social learning predominantly happens through observation and imitation (Appendix A, video 3), through being a recipient of actions relying on cultural knowledge (a child being treated with a particular medicine by parents), or through sharing experiences (e.g. co-participation in rituals). Active teaching is also present, although learning through observation, participation and practice is more common among African Pygmies (Barry S. Hewlett et al., 2011; Barry S Hewlett & Roulette, 2016). My preliminary analysis of the video data I collected on social learning in the Mbendjele children aged 0-5 showed that the majority of the learning occurred through observations (38% of all social learning cases). This was followed by copying an actor (27%), play in mixed-age children groups (13%), active teaching (12%) and trial and error (10%).

Another feature of human life history that is important for knowledge transmission is the presence of long post-reproductive period (Kaplan et al., 2000; Mace, 2000; Vinicius & Migliano, 2016). According to a theory, long post-reproductive period in humans have evolved because of the adaptive benefits associated to the transmission of skills from the older, more skilled and knowledgeable individuals to the younger ones (Kaplan et al., 2010). This is consistent with my field observations where grandmothers prepare plant-based medicine for their grand offspring. Therefore, two main features of human life history, long periods of childhood and post-reproductive lifespan, together create an environment for knowledge transmission.

6.4.2 Sharing of plant knowledge on foraging and social beliefs

So far, I showed how pair-bonding, affinal ties and life-history features of humans contribute to the sharing of information that concerns medicinal plant uses in the Mbendjele. As well as investigating the sharing of medicinal plant knowledge, I also examined how knowledge on non-medicinal uses of plants was shared among the Mbendjele. My analysis in this chapter showed that knowledge on plant uses that concerned foraging and social beliefs was shared among the camp members, regardless of relatedness. This finding demonstrates the relationship between group-living and the transmission of information that is relevant for social life and cooperative activities. Like many other immediate-return (or simple) hunter-gatherers, the forest-dwelling Mbendjele live in groups of 10-60 individuals (although the camp size varies depending on the season and in the case of gatherings for funerals or initiation ceremonies). My results suggest that multi-family camps with low inter-relatedness between camp members provide a framework for the exchange of functional information related to cooperative activities beyond the family unit, such as foraging and regulation of social life.

Variation in foraging related plant uses among the Mbendjele camps may reflect distinct levels of foraging activities in each camp (J. Lewis, 2002; Salali & Migliano, 2015). Although I do not have quantitative data on the frequency of different foraging activities among the Mbendjele camps, ethnographies indicate that the variation in the distribution of animals across forest affects the modes of subsistence of various hunter-gatherer groups (Bahuchet & Guillaume, 1982). For instance, the Aka living in the Lobaye region of the CAR, where semi-deciduous forest is predominant mainly hunt anthropoids, red hogs and duikers with spear-tracking techniques in rainy season, whereas the Motaba Pygmies living in the marsh zone hunt elephants and sititungas with the same techniques, but in any season (Bahuchet & Guillaume, 1982). Differences in the frequency of foraging activities may result in the observed variation among the Mbendjele camps in plant uses that concerned foraging. For example, camps from the Minganga region (Masia and Longa) reported about the plants that they look for honey in 0.2% of their responses, while people from Ibamba reported using plants to look for honey in 1.6% of their responses. This difference may result from the variation in the levels of honey-collecting among Pygmies in different regions. Nevertheless, the Mbendjele from Minganga region are known as "children of the flowers" because of their forest-oriented life style and skills in honey collecting (J. Lewis, 2002). Quantitative data is needed to test the proposed association between level of different subsistence activities and the reported uses of plants for foraging.

The variation in social-belief related plant uses among different Mbendjele camps may result from cultural drift. The camps where the data was obtained included Masia, Longa, Ibamba and the town camp. Masia and Longa were located about an hour and a half walk from each other, and participants in those camps associate themselves with the farmer village Minganga. On the other hand, the Mbendjele in Ibamba are associated with the Ibamba region.

In Chapter 3, I quoted an argument between the Mbendjele from Minganga and Ibamba regions, over a stolen forest spirit. Accordingly, a hunter from Ibamba region captured the *Monane* spirit, which later got stolen and used in ritual performances by the Mbendjele from Minganga, who saw the spirit performance during their occasional visit to Ibamba (J. Lewis, 2015). Such events document the emergence of different cultural traits across Pygmies in regions that are further away from each other, as a result of cultural drift. Occasional contact between Pygmies during large gatherings for ceremonies and funerals may result in the exchange of different traditions, adding to the cultural complexity.

If someone breaks a social norm (e.g. cheating partners), or a conflict arises the Mbendjele speak out the issue during *Mosambo* speeches (J. Lewis, 2002, 2014a). *Mosambo* is a form of public speaking that occurs in the mornings and evenings. A person who is upset or angry with someone speaks loudly informing the whole camp about the problem, hence getting his/her annoyance out. As well as announcing conflicts, information related to forest activities is also shared and decisions are made. For example, Lewis (2002) states that during *Mosambo* elders may remind young boys to forage for palm-nuts and honey, and a hunter, who has seen wild yams during hunting, may inform women where to go for foraging. *Mosambo*, therefore provides an excellent example of how social norms are reinforced and knowledge on foraging related activities (e.g. which trees to look for honey) are shared among the Mbendjele. Cooperative foraging also provides a context for sharing of information on foraging related plant uses. During fieldwork, I observed multiple occasions where members of a camp, including children, went for fishing together and used plant poison (Appendix Movie 2).

One limitation to my analysis on the sharing of non-medicinal plant knowledge was the low frequency of such uses. Accordingly, 80% of the plant uses concerned medicinal purposes, while 7% concerned social beliefs, and 4% foraging (Table 4-4). Among 787,644 dyadic responses, 0.7% (n= 5,745) corresponded to the case where a dyad used the same plant for the same foraging or belief related purpose. This may be why when dyadic relationships were broken into specific categories of kinship the obtained results had large confidence intervals, rendering them insignificant. For example, only 0.4% of the dyads that used the same plant for the same non-medicinal purpose had a mother-offspring relationship. Nevertheless, there was a relatively higher number of dyads that had a distant affinal relationship (i.e. consanguineal kin of an individual’s spouse, of up to four steps of genealogical distance), where the effect on sharing of non-medicinal plant knowledge was significantly negative (Figure 6-2B). This is in contrast to the results for sharing of medicinal plant knowledge, reinforcing the importance of camp co-residence over family ties in the sharing of information that concern foraging and social beliefs.

6.4.3 Findings from other populations

One of the first quantitative studies on cultural transmission patterns in hunter-gatherers was the one conducted by Hewlett and Cavalli-Sforza in the 80s (Barry S. Hewlett & Cavalli-Sforza, 1986). This study examined how skills and knowledge related to food gathering, shelter, reproduction and social life were transmitted among the Aka Pygmies of Central African Republic. To capture transmission patterns, the researchers asked each participant whether they had the skill in question and if so from whom they acquired the skill. Their analyses showed that transmission from parents to offspring was the predominant mode of social learning, especially for forest related skills such as net hunting and food gathering, also for child care (Barry S. Hewlett & Cavalli-Sforza, 1986). Dancing and singing skills, on the other hand, were acquired partly from parents (52% of the contributors) and partly from other unrelated individuals (42% of the contributors). In general, these findings are in line with the overall hypothesis suggested in this chapter. While cultural traits that are highly adaptive and concern childcare are transmitted within families, traits that concern social activities and contribute to group cohesion are transmitted regardless of relatedness. It should be noted that detecting patterns of cultural transmission by asking people from whom they learned particular information (the ‘retrospective method’) is known to be problematic, as this method is affected by memory biases and social norms (Henrich & Broesch, 2011; Mesoudi, 2011). For this reason, assessing similarity of cultural knowledge among individuals is thought to be a better way of mapping pathways of cultural transmission (Aunger, 2000; Reyes-García et al., 2009).

Aunger (2000) investigated the cultural transmission of food taboos in horticulturalists living in the rainforests of Democratic Republic of Congo by using the similarity in food taboos to assess pathways of cultural transmission. His results have shown that food taboos were acquired differently depending on the type of the taboo (Aunger, 2000). Some food avoidances had ancestral reasons: particular foods were believed to be incompatible with the bloodline of that individual's male relatives. Aunger found that those "ancestral" food taboos were mostly similar between fathers and sons (Aunger, 2000). Because of strong vertical transmission in the male line, there was low within household, but high between household variations in those taboos. On the other hand, some food avoidances concerned pregnancy and lactation, and targeted pregnant or breastfeeding women and sometimes their husbands. Aunger called those taboos "homeopathic" ones, as often the reason of avoidance was because if the pregnant woman ate a particular animal, then the baby would be born with some feature of that animal. Similarity in homeopathic taboos showed that there was a strong transmission from mothers to their sons and daughters, and also partially from fathers to their daughters (Aunger, 2000).

The effect of the content of information on its transmission patterns is also found in the differential transmission of knowledge on plant uses in the Baka of Cameroon (Hattori, 2006a). Hattori (2006) compared the uses of 90 plants by 10 Baka men and found that while the knowledge on medicinal uses of plants largely varied, knowledge on plant uses for food or making materials was widely shared. Based on the self-reports on the acquisition of medicinal plant knowledge of those participants, Hattori (2006) suggested that the Baka learnt about the medicinal properties of plants from their parents or family members when they or their children became sick. Similarly, anthropologists comparing plant uses in the Efe and Mbuti Pygmies have found that medicinal plant uses largely varied, however uses of plants as food resources or raw materials were more common between these two groups (Terashima & Ichikawa, 2003).

The effects of social structure on patterns of cultural transmission have been found in other studies. For example, Aunger's above study on the food taboos has also shown that the "homeopathic" food taboos had very small variation between villages due to the residence patterns (Aunger, 2000). Because the study population was patrilocal horticulturalists, women left their natal villages upon marriage, taking the knowledge on homeopathic food taboos with them. The female dominant transmission patterns coupled with high female mobility resulted in lower between village variation in taboos related to pregnancy and lactation (Aunger, 2000; Mesoudi, 2011). Nevertheless, this lower between-village variation may also be due to the adaptive benefits of avoiding certain animals. As discussed in Chapter 5 some cultural traits that may have direct fitness benefits and may spread in the population more widely due to cultural selection. Another study, that revealed the effects of social structure on cultural transmission patterns concerned cultural evolution of Iranian textile patterns. Tehrani and Collard found a strong vertical transmission (especially from mother to daughter) of textile patterns and techniques during childhood, and horizontal transmission from unrelated women during adulthood (Tehrani & Collard, 2009). Despite of the prevalence of horizontal transmission after childhood, there was a large variation in textile patterns among tribes (Tehrani, 2011; Tehrani & Collard, 2009). This was because women weavers did not marry out of their local tribes, limiting the transmission of textile patterns among the members of different tribes (Tehrani, 2011; Tehrani & Collard, 2009). Another study that analysed social networks and richness of plant knowledge in Tsimane' horticulturalists found that people who had greater centrality in the social network had more diverse medicinal plants in their home gardens (Díaz-Reviriego et al., 2016).

6.5 Conclusion

My results suggest that marital ties in hunter-gatherers are crucial in the transmission and accumulation of cultural skills and knowledge that is important for fitness. Strong pair bonds in humans do not only link males and females, but also their families. Spouses bring information from their natal groups. Therefore, marital ties may have been the initial information transmission vectors among different sub-groups, creating an environment for cultural transmission as well as knowledge specialisation and innovation exclusive to humans. Those ties also connect people around cooperative childcare allowing younger generations to get exposed to different cultural models. In addition, co-residence of multiple families allows for the transmission and accumulation of plant knowledge related to group-wide activities such as foraging and rituals, which enhance group coordination. All these factors may have contributed to the adaptive differentiation of cultural domains and the diversity of human cumulative culture.

In this chapter, I examined how the Mbendjele Pygmies share their knowledge on different plant uses with respect to their family and camp ties. I demonstrated the importance of social structure, extended childhoods and cooperative breeding on the transmission of plant knowledge. In the next chapter, I will explore how plant knowledge changes with the changes in social structure due to socioeconomic transitions.

Chapter 7: Socioeconomic transitions and the decline in plant knowledge and use

The time in which these charming people will continue living in an economic system presumably similar to that of earlier ancestors is limited indeed.

Luigi Luca Cavalli-Sforza in African Pygmies (1986)

7.1 Introduction

This chapter examines how plant knowledge and use is affected by socioeconomic transitions in the Mbendjele. It asks how changes in subsistence activities and levels of market integration break the egalitarian system and lead to a change in social structure. It then explores how changes in social structure affect cultural transmission of plant knowledge. In the first section, I will investigate the socioeconomic transitions and changes in social structure of the Mbendjele by using various measures. In the second section, I address how the socioeconomic transitions lead to cultural change. The work presented in the first section is published as a research paper in the journal *Plos One* entitled “Future discounting in Congo Basin hunter-gatherers declines with socio-economic transitions” (Salali et al. 2015). A copy of this paper is provided in Appendix D. Author contributions for this research paper are as follows: Conceived the project: G.D.S., A.B.M. Designed and performed the experiments: G.D.S. Analysed the data: G.D.S. Wrote the paper: G.D.S., A.B.M.

7.2 Changes in socio-economic structure in the Mbendjele

The Mbendjele is traditionally an immediate-return society. Immediate return hunter-gatherers are marked by high mobility and egalitarian political organization, which is believed to facilitate extensive food sharing as opposed to resource accumulation (Woodburn, 1982). In delayed return systems (most farmers, herders and western systems) on the other hand, the food yield is obtained over long periods and stored; individuals accumulate wealth; and the political structure is less egalitarian and more hierarchical (Woodburn, 1982). Immediate return societies sustain their egalitarian structure through levelling mechanisms that prohibit saving, accumulation and dominance (Boehm, 1993, 1999; Gavrilets, 2012b; Polly Wiessner, 2005). These levelling mechanisms are believed to be important adaptations to ensure food sharing and in turn survival in unpredictable environments (Erdal & Whiten, 1994; Gavrilets, 2012b; H. M. Lewis, Vinicius, Strods, Mace, & Migliano, 2014; Winterhalder, 1986). Transitions from immediate- to delayed-return systems are most likely triggered by new storage systems and domestication (Alvard & Kuznar, 2001; Kelly, 2013). Changes in subsistence mode and food surpluses break down social systems of sharing, resulting in inequalities (Erdal & Whiten, 1994). In a similar way, market integration, sedentism and high population density push immediate return hunter-gatherers towards a delayed-return system (Kelly, 2013).

Mbendjele's way of life is changing because of increasing pressure from logging activities (Laporte, Stabach, Grosch, Lin, & Goetz, 2007), commercial hunting, and protected forest areas for conservation (J. Lewis, 2005; Riddell, 2013). Because camps vary in their proximity to market towns, groups differ in their market integration and livelihood activities (J. Lewis, 2005; Riddell, 2013). For example, the camp Masia was located by a logging road, 60 km further away from the logging town Pokola. Bush meat trade is common (the reason why many camps are located close to mud roads rather than deep in the forest), and sometimes individuals travel to the nearest farmer village to engage in wage labour (J. Lewis, 2005). The main trading items are meat (mainly species of antelopes, but trading of illegal animals also occurs) and *Marantochloa* (local name: *ngongo*) and *Gnetum bucholzianum* (local name: *koko*) leaves. Nevertheless, the main subsistence is hunting and gathering, and the money that is earned by selling meat and forest leaves is often spent immediately on goods such as alcohol, cigarettes, clothing and agricultural products. The camp Ibamba was located near an old, currently unused logging road. In the past, when the logging road was being actively used by the loggers, Pygmies used to engage in bush meat trade. Therefore, Ibamba participants were also familiar with monetary exchange, but similar to people from Masia they mainly hunt and gather forest plants for subsistence and move between camps depending on the resource availability. In addition, people also had access to fields where they collected their own manioc tubers from time to time. Unlike Masia and Ibamba, the camp Sembola was located near the centre of the logging town Pokola. Pokola is a growing town because of the employment opportunities of country's largest logging company, Congolaise Industrielle des Bois (CIB), and attracting people from nearby villages. During my time with the Mbendjele in Sembola, I observed people going to the local market to buy food and frequently working as wage labourers in farmers' fields or as employers for the logging company.

In this section, I am going to investigate the socioeconomic differences between the Mbendjele living close to town centres (which I will refer to as the town camp), with those that live closer to forest (which I will refer to as forest camps) by using three measures: 1) frequency of wage labour, 2) amount of bride price paid, 3) inter-temporal choices (i.e. future discounting). I use frequency of wage labour to determine the levels of change in hunting and gathering subsistence way, and amount of bride price paid as an indicator of wealth accumulation and emerging inequalities. Inter-temporal preference is a concept in behavioural economics that measures individual's willingness to save for future. Similar to the change in wealth accumulation, I gathered participants' inter-temporal choices to test whether socioeconomic changes are associated with the Mbendjele becoming more future-oriented.

7.2.1 Indicators of socioeconomic transitions

7.2.1.1 Frequency of wage labour and the amount of bride-price paid

I investigated the frequency of farming work in the town and forest camps as a proxy for integration in a delayed-return system (Koichi Kitanishi, 2006). For assessing the resource accumulation in different camps, I used sums paid as bride prices since bride price has to be accumulated and planned ahead (Koichi Kitanishi, 2006). I predicted that the frequency of wage labour and the amount of bride-price paid would be higher in Pygmies living in the town camp compared to Pygmies living in the forest camps.

7.2.1.2 Future discounting

Organisms often prefer immediate rewards over future ones, a preference that is known as "future discounting" (Daly & Wilson, 2005). A person with a higher discount rate (or higher impulsivity or lower patience) might choose 5 monetary units now, over 10 monetary units in a week. Although, the ability to fight impulsivity has been observed in non-human animals such as chimpanzees (Evans & Beran, 2007), pigeons (Ainslie, 1974) and guppies (Mühlhoff, Stevens, & Reader, 2011), humans appear to have evolved greater capacities for patience (Tobin & Logue, 1994). Here, I measured the levels of future discounting in the Mbendjele from different camps and in farmers, to use it as an additional measure of socioeconomic transitions. My prediction is that the Mbendjele who mainly subsist on hunting and gathering, and maintain an immediate-return system where food storage is absent and egalitarianism is enforced through levelling mechanisms will discount the future more. In this context, future discounting is an adaptive strategy to prevent wealth accumulation and the emergence of hierarchies. This ensures food sharing and allows for survival in unpredictable environments where there is risk of an energy shortfall. On the other hand, I predict that a shift to a delayed-return system will make hunter-gatherers more future-oriented. This is because with the emergence of agriculture and possibilities for food storage wealth accumulation, hierarchies and lower discount rates become the adaptive strategy. This will ultimately change sharing mechanisms and social interactions.

Although there is a large body of literature investigating the determinants of future discounting in Western populations (Apter et al., 1990; Becker & Mulligan, 1997; Frederick, Loewenstein, & O'Donoghue, 2002; Griskevicius & Tybur, 2011; Wilson & Daly, 2004), there are only a handful of studies examining the level of future discounting in small-scale societies (Godoy et al., 2004; Godoy & Jacobson, 1999; Kirby et al., 2002; Reyes-García et al., 2007; Tanaka, Camerer, & Nguyen, 2010; B Tucker, 2006; Bram Tucker, 2012). For example, Tucker (Bram Tucker, 2012) tested whether individual-level wealth and income variables or conformity to social norms better predicted time preferences in Mikea forest forager-farmers and their fisher and farmer neighbours. Godoy et al. (Godoy et al., 2004) investigated whether the effects of years of schooling, age or income affected the levels of patience in Tsimane' forager-horticulturalists. They also compared rates of discounting in Tsimane' with those from two samples from the United States. While both studies found higher discount rates in forager-horticulturalist groups, they did not directly test whether a shift in social structure from an egalitarian one to a hierarchical one affects levels of future discounting. Finally, the ethnographic observations on the changes associated to cacao cultivations in Baka hunter-gatherers of Cameroon showed that some Baka were more future oriented than the others, enabling them to accumulate more money (Oishi, 2012).

Investigating inter-temporal preferences in the Mbendjele will enable me to explore socioeconomic transitions and change in social structure associated to these transitions. With this information in hand, I will then investigate change in the levels of plant knowledge and use across different camps and its implications on cultural transmission.

7.2.2 Methods

7.2.2.1 Study Population

For this study, I collected data in the Mbendjele camps Masia, Ibamba and Sembola, and a farmer village. Longa was excluded from this study, because it was the first camp that I visited and I conducted pilot experiments there to determine the medium (money or food) and time interval to use in the future-discounting experiments. There were in total 186 adult (> 15 years old) participants (91 females); 23 (14 females) from Masia, 30 (18 females) from Ibamba, and 111 (46 females) from Sembola (the town camp). The last location was a Bantu farmer village called Minganga (n = 22, 13 females).

I spent equal amounts of time, 3-4 weeks, in each camp regardless of whether they were located in the forest or in the town. In the forest camps, our camp was established right next to the Mbendjele camp, and I was actively participating in the daily/social activities such as foraging for various forest products and evening dances. Participants were aware that I was staying there not for a day, but a longer period of time. Moreover, I performed this study after trust had been built and the groups were familiar with me.

7.2.2.2 Measuring frequency of wage labour and the amount of bride-price paid

I used two indicators to quantitatively test the transition from an immediate to a delayed-return system amongst Mbendejele living in the town: 1) sums paid as bride prices (n = 18 for forest camps, n = 26 for the town camp, 2) frequency of farming work (n = 56 for forest camps, n = 63 for the town camp). For the frequency of wage labour, I asked individuals how frequently they work for farmers, coding responses as 1) no/infrequent farm work, and 2) frequent farm work. I compared these responses using the Chi-square test of independence with Monte-Carlo re-samplings. For the bride prices I asked married men how much money in CFA they paid as a bride price. I used a one-way permutation test based on Monte-Carlo simulations to compare the means of bride prices across locations.

7.2.2.3 Future-discounting experiment:

The participants were informed that they were going to receive stock cubes (also known as bouillon cubes that are used widely in West and Central Africa as a food flavouring agent) for their participation in another study. Stock cubes are highly valued by Mbendjele to spice up food and obtained from traders, or local markets. At the end of the interviews, I asked participants whether they would prefer to receive one stock cube today or five tomorrow, and gave the stock cube(s) accordingly.

I designed a choice task between receiving one stock cube today versus five stock cubes tomorrow because my pilot experiments conducted in Longa with a larger temporal gap and varying amounts of reward resulted in no variation, where all participants discounted the future. In addition, most Mbendjele do not have experience in counting large numbers, therefore I kept the study design as simple as possible.

Data were analysed using R 3.2.0. To test whether people's choices differed between locations, I performed logistic regression analyses. My response variable was future discounting: the choice of one cube today was coded as 1; the choice of five cubes tomorrow was coded as 0. My predictor variables were *Group type* (forest camps, town camp and Bantu village) and *Sex*. To obtain the optimal model, I removed non-significant variables based on the likelihood ratio test statistic and its associated p-value.

Other factors such as the level of food sharing, the proportion of food that is obtained from the market versus that is hunted or gathered, the frequency of movement between camps may all reflect the socioeconomic transition. Since the transition is a group-level phenomenon that results from various intervening factors, I used group type (forest, town or farmer) as a predictor in my main analysis.

For a subsample of the study population, I had information on both the frequency of wage labour in farms and the future discounting at the individual level (n = 100, 55 females). To test whether farming frequency (coded as either "non/infrequent" or "frequent") predicts the levels of future discounting I performed a separate logistic regression analysis, controlling for the sex of the participants. Similarly, I conducted an additional analyses to test the amount of bride price a man paid predicted their future discounting (n= 44, 18 from forest camps, 26 from the town camp).

To control for the age effects on future discounting, I performed a separate analyses. In my sample, I had consensus relative age lists (see Chapter 3) for the two forest camps. I used these two age ranks to break the data into three age categories: young adult, adult and old adult. Since I did not have a relative age list for the town camp, I used eyeball estimates of ages that were recorded during data collection. Accordingly, I listed any participant that looked between 15-25 as young adults, others older than 25 and younger than 45 as adults, and everyone else (45+) as old adults. I did not have any recording for the Bantu farmers, farmers are not included in the analysis for age.

7.2.3 Results

7.2.3.1 Frequency of wage labour and the amount of bride-price paid was higher in the town camp

My analyses of the sums of bride price paid revealed that hunter-gatherers in the town camp paid larger sums of bride price than those in forest camps (permutation test: $p< 0.01$; Figure 7-1A). The range of bride prices was larger in the town camp, indicating accumulation of resources and emerging inequalities (Figure 7-1A). Moreover, hunter-gatherers in the town camp engaged in wage labour much more frequently than those living in forest camps (n= 119, χ^2_1= 17.35, $p< 0.001$; Figure 7-1B).

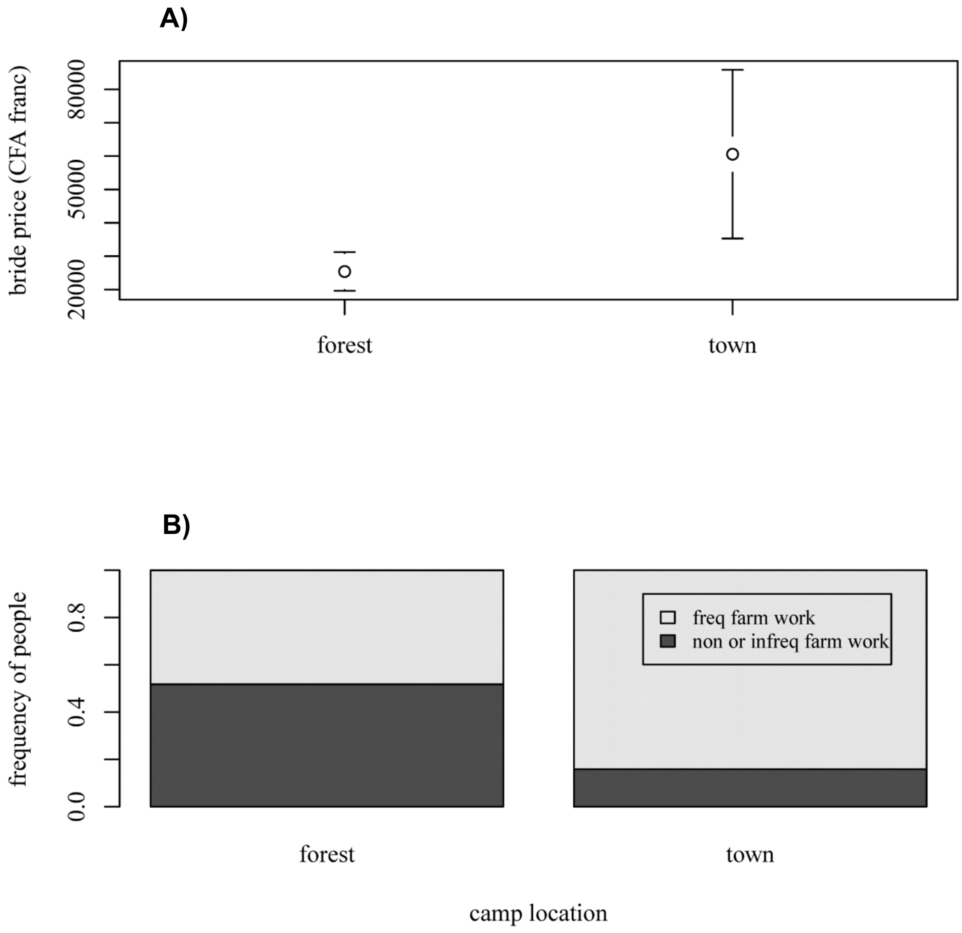


Figure 7-1: Socio-economic differences between hunter-gatherers living in forest camps and a town camp. A) mean and 95% CI of the amount of bride price that men paid, B) the frequency of wage labour in each location.

7.2.3.2 *Mbendjele in forest camps discounted the future more compared to Mbendjele in the town camp and Bantu farmers*

There was no difference between the proportions of participants that chose one cube today in the two hunter-gatherer forest camps (camp 1 and camp 2, *n*= 53, χ^2_1= 0.9, *p*= 0.48; Figure 7-2). Therefore, I pooled the data of camp 1 and camp 2 (forest camps).

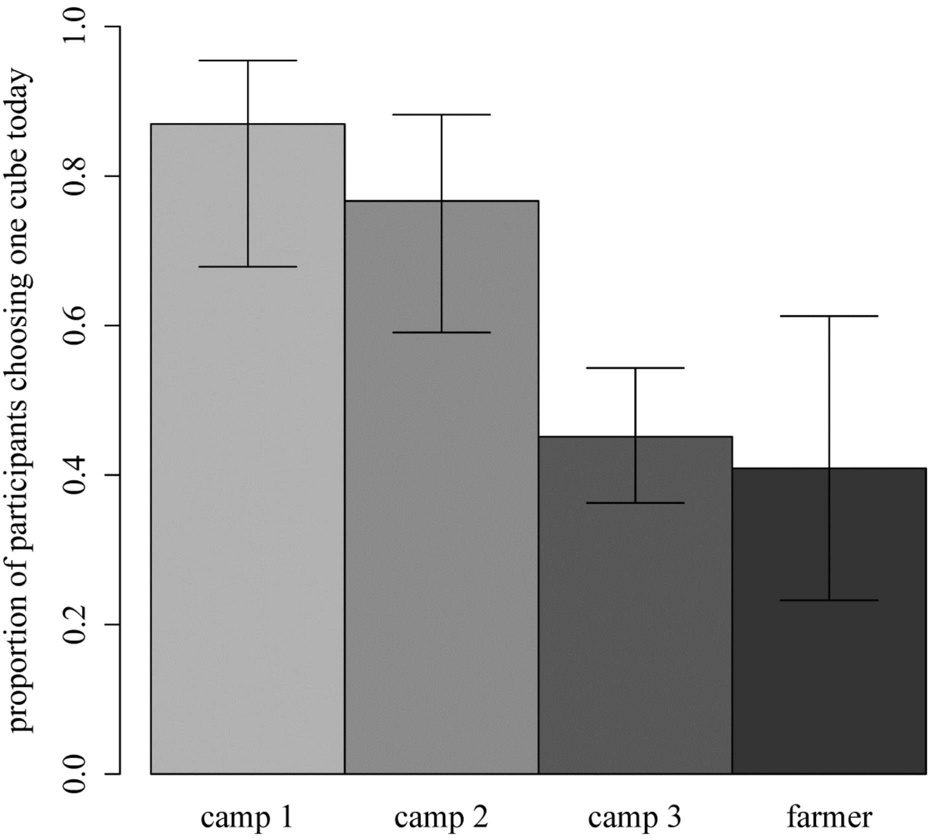


Figure 7-2: Proportion of participants that chose to receive one cube today in 3 Mbendjele camps and one Bantu farmer village. Camp 1 (Masia) and camp 2 (Ibamba) were located in the forest; camp 3 (Sembola) was located in the town. Error bars indicate 95% confidence intervals.

There was a significant difference in the probability of future discounting between the hunter-gatherers from the forest camps and the town camp (Figure 7-2). Table 7-1 shows my initial regression model with all the predictor variables (Model 1), and my optimal model (Model 2). According to Model 2, hunter-gatherers living in the forest discounted the future 5 times more than those in the town (odds ratio (OR)= 0.20, $CI_{.95}$ = [0.09-0.43]). There was also a significant difference between hunter-gatherers living in the forest and Bantu farmers. Accordingly, odds of future discounting were 6 times higher in forest hunter-gatherers (OR= 0.16, $CI_{.95}$= [0.05-0.47]). Interestingly, there was no difference in future discounting between the town-living hunter-gatherers and farmers (n= 133, χ^2_1= 0.13, p= 0.82).

Table 7-1: Logistic regression models for probability of future discounting.

	Model 1		**Model 2**	
Predictor	**Coeff. (SE)**	**P**	**Coeff. (SE)**	**P**
Group type- town camp	-1.61 (0.41)	<0.001	-1.65 (0.40)	<0.001
Group type- Bantu	-1.83 (0.56)	<0.01	-1.83 (0.56)	<0.01
Sex- male	-0.30 (0.32)	0.43		
Intercept	1.58 (0.38)	<0.001	1.46 (0.35)	<0.001
Pseudo-R^2 (Hosmer-Lemeshow)	0.09		0.09	
-2 log likelihood	232.98		233.89	
N	186		186	

Response variable: future discounting (i.e. choosing one stock cube today over 5 stock cubes tomorrow). *Group type* encodes for the group of the participants (forest camps, town camp and Bantu agriculturalist village). *N* is the number of subjects. Omitting *Sex* did not affect the model fit significantly ($P[\chi^2(1) > 0.91] = 0.34$).

For the subsample of the hunter-gatherers where I had information on frequency of wage labour and future discounting at the individual level, I found that those who engaged in frequent wage labour in farms discounted the future about 3 times less than the individuals who never or only infrequently engaged in wage labour (OR= 0.35, $CI_{.95}$= [0.13-0.88]; Table 7-2).

Table 7-2: Logistic regression models for the probability of future discounting with frequency of wage labour as a predictor.

	Model 1		**Model 2**	
Predictor	**Coeff. (SE)**	**P**	**Coeff. (SE)**	**P**
Wage labour frequency- frequent	-1.05 (0.49)	<0.05	-1.04 (0.48)	<0.05
Sex – male	-0.61 (0.43)	0.16		
Intercept	1.39 (0.48)	<0.01	1.10 (0.41)	<0.01
Pseudo-R^2 (Hosmer-Lemeshow)	0.05			0.04
-2 log likelihood	128.10			130.20
N	100			100

Logistic regression coefficients, standard errors and P-values. Response variable: future discounting (i.e. choosing one stock cube today over getting 5 stock cubes tomorrow). *Wage labour frequency* encodes for the frequency of wage labour (non/infrequent or frequent wage labour). *N* is the number of subjects. I used quasi-binomial logistic regression when the residual deviance exceeded the residual degrees of freedom. Omitting *Sex* did not affect the model fit significantly ($P[\chi^2(1) > 2.10] = 0.15$).

To test whether the group type remains a significant predictor after controlling for the frequency of wage labour I performed the above analysis by adding the group type as one of the main predictors. It should be noted that in this analysis, group type included forest camps and town camp, but not the farmer village since I only collected data on frequency of wage labour from the Mbendjele. The model revealed group type as the only significant predictor for future discounting. Accordingly, odds of future discounting were 5.5 times higher in forest hunter-gatherers compared to the ones living in the town (OR= 0.18, $CI_{.95}$= [0.06-0.48]; Table 7-3). The fact that frequency of wage labour lost its significance suggests that the wage labour effects were actually the result of the group type. This is not a surprising result, as wage labour is only one of the factors involved in the transition from an immediate to a delayed-return system. In order to be able to capture the whole effect of group type I would have to have individual measures of food sharing, mobility, trade, wage labour, consumption of agricultural products, frequency of hunting trips etc., since the logging town and the forest camps have very different lifestyles.

Table 7-3: Logistic regression model for the probability of future discounting with frequency of wage labour and group type as the main predictors.

Predictor	Coeff.(SE)	P
Group type- town camp	-1.72 (0.53)	<0.01
Wage labour frequency- frequent	-1.05 (0.49)	0.53
Sex – male	-0.61 (0.43)	0.22
Intercept	1.39 (0.48)	<0.001
Pseudo-R^2 (Hosmer-Lemeshow)	0.15	
-2 log likelihood	115.55	
N	100	

I have conducted additional analyses to test the effect of amount of bride price paid by males on future discounting. Since the information on bride prices was only available for married men, I had data on the amount of bride prices for 18 males in the forest camps, and 26 males in the town camp. Among those 44 males I had data for 38 of them on their future discounting. My logistic regression analysis showed that the amount of bride price paid by a male did not affect his choice in the discount experiment, in this subset of the sample (Table 7-4).

Table 7-4: Logistic regression models for the probability of future discounting with the amount of bride price paid as a predictor.

Predictor	Model 1		Model 2	
	Coeff (SE)	**P**	**Coeff (SE)**	**P**
Bride price (amount)	0 (0)	0.16	0 (0)	0.39
Group type- town camp			-1.51 (0.85)	0.08
Intercept	0.67 (0.54)	0.23	1.41 (0.72)	0.06
Pseudo-R^2 (Hosmer-Lemeshow)	0.06		0.13	
-2 log likelihood	49.34		45.64	
N	38		38	

Finally, my analysis on the effects of age on future discounting in Mbendjele showed no age effect (Table 7-5).

Table 7-5: Logistic regression model for the probability of future discounting with age group, group type and sex as the main predictors.

Predictor	Coeff. (SE)	P
Sex- male	-0.58 (0.36)	0.11
Group type- forest camp 1	0.73 (0.77)	0.35
Group type- town camp	-1.27 (0.49)	0.01
Age group*- adult	-0.23 (0.44)	0.6
Age group*- old adult	-0.04 (0.5)	0.94
(Intercept)	1.58 (0.59)	0.01
Pseudo-R^2 (Hosmer-Lemeshow)	0.11	
-2 log likelihood	195.98	
N	161	

*For age group, the baseline is young adult.

7.2.4 Discussion

Consistent with my predictions, individuals in the town camp engage in more resource accumulation and have more variation in bride price payments, which is indicative of emergent inequalities. Moreover, I show that immediate-return Mbendjele hunter-gatherers that are less market integrated and engage in less resource accumulation activities, discount the future more than Mbendjele living in a logging town. Strikingly, those living in the town do not differ in their inter-temporal choices from Bantu farmers. These results reveal the socioeconomic transitions that Mbendjele experience as they move closer to towns, and get more market integrated.

There are several other indicators that point to the differences between forest versus town-dwelling Mbendjele. For instance, individuals in forest camps use traditional leaf and liana huts that can be easily abandoned and re-made to match their mobile lifestyle (Figure 7-3A); whereas individuals living in towns have permanent houses made of old timbers (Figure 7-3B). In forest camps I observed very few personal possessions (such as pots, machetes, traditional baskets and mats, and some clothing) in households, however in town camps some houses even had furniture (e.g. old chairs) in them. Both the house type and large population densities (> 100 adults) indicate a transition to a sedentary lifestyle in town camps. It has been shown elsewhere that Mbendjele groups living in conservation-forestry towns spend much more time in formal employment, gun-hunting for villagers, wage labour and have become more sedentary (Riddell, 2013).

Figure 7-3: A) Two huts in the Mbendjele forest camp Masia, B) An Mbendjele house in the town camp with a garden of manioc plants and banana trees.

My results point to a group-level phenomenon; that socio-economic transitions affect the levels of future discounting however, I cannot specifically determine what factors play what role. It is possible that decreased mobility, increased population size, reduction in sharing and the change in subsistence mode, egalitarian norms and levelling mechanisms all contribute to the observed phenomenon in an intervening way. More individual-level measures are required to elucidate the effects of these factors.

Ethnographic observations on the effects of cacao cultivations in Baka Pygmies support my results on emerging inequalities in more market-integrated hunter-gatherer groups. Accordingly, many Baka prefer to work as wage-labourers in neighbouring groups' cacao plantations rather than earning larger amounts of income by owning their own cacao plantations (Oishi, 2012). This is because the latter requires patience, but rather than keeping their harvest and waiting for cacao price to increase, many Baka sell their cacao little by little and buy alcohol or goods such as clothes, radios or perfumes immediately. However, there are a few Baka who are more future-oriented and willing to accumulate money. Oishi suggests that because of the variation in levels of patience in the Baka, the monetary economy creates big economic inequalities among these hunter-gatherers, possibly resulting in the breakdown of egalitarian social relationships (Oishi, 2012).

The results that are presented in this section have important consequences on the social structure of the Mbendjele. In the previous chapters I discussed how mobility, cooperative group living, extended interactions among the affinal kin and cooperative breeding might have facilitated the sharing of knowledge and contributed to the evolution of rich plant use repertoire in the Mbendjele. With the presented socioeconomic transitions and emergence of inequalities it is likely that extensive sharing, cooperative breeding and visits between camps will become less frequent. Moreover, with changes in subsistence activities, there will be fewer opportunities for social learning of forest related activities through participation and observations. How these changes affect sharing of knowledge and the levels of plant knowledge and use is the main topic of the next section.

7.3 Plant knowledge and use declines with socioeconomic transitions

Globalization and rapid development make cultural change inevitable even in the most remote places on earth. Traditional ecological knowledge refers to the accumulated knowledge, practices and beliefs of indigenous populations about the relationships of living organisms with each other and with their environment (Berkes, Colding, & Folke, 2000). This form of knowledge is in decline in many parts of the world mainly because of new economic, social and environmental conditions (Benz, Judith Cevallo, Francisco Santana, Jesus Rosales, & Graf, 2000; Gómez-Baggethun & Reyes-García, 2013; Reyes-García, Guèze, et al., 2013). In this section, I examine the change in knowledge of plant uses in the Mbendjele by comparing the number of plants that are known and used by the hunter-gatherers who were born in the logging town with those who were born in other regions. I then investigate the type of plant uses by the Mbendjele from different birth regions, and the factors associated with the change in plant knowledge.

The rate of cultural change depends on the different cultural transmission and innovation processes (Aunger, 2000; L. L. Cavalli-Sforza & Feldman, 1981, 1982; Mesoudi, 2011). For instance, in the case of vertical transmission or face-to-face learning in a small hunter-gatherer community the rates of cultural change are relatively slow (Mesoudi, 2011). On the other hand, cultural evolution is more rapid via horizontal transmission (e.g. transmission through mass media or mass education) (Mesoudi, 2011). Because vertical transmission occurs within single families, it also results in more cultural variation within groups (Aunger, 2000; L. L. Cavalli-Sforza & Feldman, 1981, 1982; Mesoudi, 2011). I showed in Chapter 6 that medicinal plant knowledge in the Mbendjele was shared within families, and this might have contributed to the rich repertoire of medicinal plant uses in hunter-gatherers.

Not only the processes of cultural transmission, but also external factors affect cultural change and variation. Rapid changes in socio-economic, political and environmental conditions may result in the loss of cultural traits within a generation (Godoy & Reyes-García, 2009; Gomez-Baggethun et al., 2010; Reyes-García, Guèze, et al., 2013; Reyes-García, Luz, et al., 2013). For instance, research on traditional plant knowledge in Tsimane forager-horticulturalists have found that, although the knowledge was shared widely among the Tsimane of different villages (Reyes-García et al., 2003), it was in decline for people who were living in villages close to market towns (Reyes-García, Guèze, et al., 2013). Accordingly, Tsimane adults living close to towns experienced a 3% decrease in their report of plant uses per year due to rapidly changing socio-economic, political, and environmental conditions (Reyes-García, Guèze, et al., 2013). In populations like Mbendjele where traditional medicinal knowledge is shared within families through vertical transmission, one can predict that such cultural loss in one generation will lead to the reduction in knowledge repertoire.

In the previous section I examined the socio-economic transition that is experienced by the Mbendjele living in the logging town. My analyses showed that the Mbendjele living in the town engaged in wage-labour more frequently and had greater financial capital (as indicated in the amount of bride-price paid) than the Mbendjele living further away from logging towns (Salali & Migliano, 2015). They were also more future-oriented (Salali & Migliano, 2015). Consistent with my observations, Riddell has shown that the Mbendjele who live in the villages with conservation and forestry, such as the town Pokola, spent more time in doing piece-work for fisher-farmers, formal employment, gun-hunting for villagers or working in farmer's fields (Riddell, 2013). On the other hand, the time spent in hunting with traditional techniques (such as spear hunting) and honey-collecting was reduced (Riddell, 2013). The forest trips were shorter and more commercially-oriented, focused only on products relevant for trading: *koko* leaves, honey and bush meat (Riddell, 2013). Riddell also found that the actual forest space used by the Mbendjele in logging villages was reduced compared to hunter-gatherers living in other villages (Riddell, 2013), most probably due to rapid deforestation in the area (Laporte et al., 2007).

How these changes in socio-economic and environmental conditions affect plant knowledge and use in the Mbendjele is the topic of this section. I assess the cultural change by comparing the plant knowledge and use in Mbendjele who were born in forest regions with those who were born in the logging town. I address the following questions: 1) Does plant knowledge and use decline with market integration and socio-economic transitions? 2) Do Pygmies that move to market towns lose their plant knowledge? 3) Do Pygmies from different regions share knowledge on plant uses when they gather in large town camps? To answer these questions, I investigated the number of plants that are known and used by individuals from different birth regions and camps. In addition, I examined the type of plant uses by different birth regions and tested whether birth region was a significant factor in explaining the similarity of plant uses in the town camp.

7.3.1 Methods

7.3.1.1 Study population

The study sample in this analysis is the same as presented in Chapter 4 (total *n*= 219; forest camp 1- Longa: = 59; forest camp 2- Masia: *n*= 22; forest camp 3- Ibamba: *n*= 31; town camp- Sembola: *n*= 107).

7.3.1.2 Measuring plant knowledge and use

The data contained participants' responses about the knowledge and use of 33 plants (see Chapter 5 for details). I calculated the sum of the number of plants known (i.e. knowledge score) and used (i.e. use score) to measure each participant's plant knowledge and use.

7.3.1.3 Statistical Analyses

To examine the effects of camp residence, sex, age group and birth place on plant knowledge and use score I conducted ANOVAs. The response variable was either the plant knowledge or the use score, and the factorial variables were: current camp residence (forest camp 1, forest camp 2, forest camp 3, town camp), birth place (Minganga, Ibamba, Other, Pokola), sex (female, male) and age group (child, young adult, adult, old adult). I used Tukey's HSD tests to compare the means of knowledge and use scores among different levels of each factorial variable as a post-hoc ANOVA.

I investigated the effects of birth region, as well as current camp residence. This is because one of my aims was to test whether people who were actually born in the town (Pokola) differed in their plant knowledge and use score from those who were born in forest regions, regardless of their current camp residence. I performed separate ANOVAs for the birth region and camp residence, because 1) majority of the participants in forest camps were from the same birth region: 91% of the participants from the forest camps 1-2 was born in Minganga region; 97% of the participants from forest camp 3 was born in Ibamba region (Figure 7-4), 2) there was missing data for the birth region, so the sample size was smaller (*n*= 193).

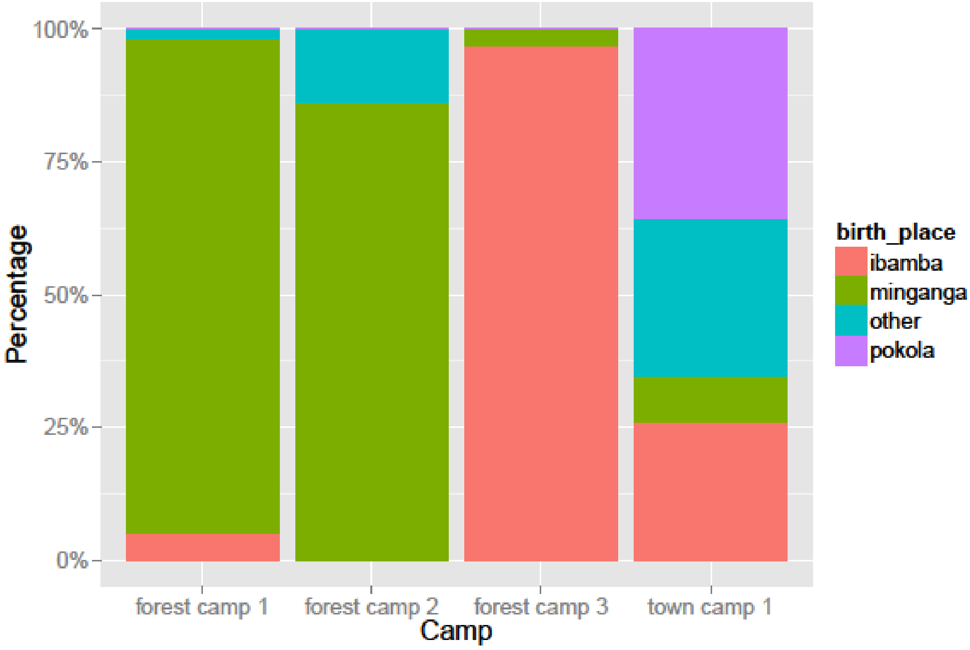


Figure 7-4: Birth place of the participants by their camp residence**.**

I further investigated how birth region affected the use of plants by using multiple correspondence analysis (MCA). MCA is a nonlinear multivariate analysis method that is mainly used to visualize data with categorical variables (Hoffman & Leeuw, 1992). Its principles are the same as principle component analysis (PCA), except that the data consists of factorial variables. I performed MCA to visualize the clustering of individuals based on their uses of 33 plants by using the R package FactoMineR (Le, Josse, & Husson, 2008). This package generates scatter plots of individuals where an individual is seen at the same side as the variables for which it takes high values (e.g. particular plants and their corresponding uses), and at the opposite side of the variables for which it takes low values (Le et al., 2008). It also allows for the addition of supplementary variables on the scatter plots for a better understanding of the data (Le et al., 2008). My supplementary variables in this case were birth region, camp residence, age group and sex of the participants. Specifically, my aim was to investigate whether the plant uses of individuals that were born in the town differed from those that were born in forest regions but moved to town. For this, I used the subset of the data that only included participants from the town camp ($n = 107$).

I also performed mixed effects logistic regressions to this subset of the data consisting town-dwelling Mbendjele. I tested whether birth place was a significant predictor in explaining the reported co-occurrence of plant uses for medicinal and non-medicinal purposes, controlling for relatedness, affinal kin ties, age group and sex of the dyads (see Chapter 6 for details). The analyses contained 3240 dyads, and 80025 data points for medicinal uses and 69151 data points for non-medicinal uses.

7.3.2 Results

7.3.2.1 People who were born in the logging town know and use less plants than people who were born in forest regions

People who were born in the logging town had significantly lower plant knowledge scores (i.e. number of plants reported as known out of 33 plants) compared to people that were born in all other regions (Figure 7-5A; Table 7-6 Model 1; Tukey's HSD, $p < 0.001$). People from the two forest regions, Ibamba and Minganga, did not differ in their plant knowledge (Tukey's HSD: $p = 0.36$), neither people coming from Ibamba or other unvisited regions (Tukey's HSD, $p = 0.58$). Participants from Minganga region had a slightly but significantly lower plant knowledge score compared to participants from other unvisited regions (Figure 7-5A; Tukey's HSD, $p < 0.05$). When I examined effects of current camp residence in another ANOVA, I found that camp residence was a significant predictor (Table 7-6 Model 2). However, the post-hoc analysis revealed that only people from the town camp were significantly lower in their plant knowledge score compared to people from the forest camp 3 (Figure 7-5B, Tukey's HSD, $p < 0.05$). All other camp comparisons were insignificant. Moreover, my further analysis with the subset of the data revealed that birthplace is the significant factor in explaining the variation in plant knowledge score among the Mbendjele living in the town. Accordingly, those who were born in the town had a lower knowledge score compared to those who were born in other regions, and moved to town later (ANOVA followed by post-hoc Tukey HSD, $p<0.001$). In sum, these results suggest that the significant effect of camp residence on plant knowledge score is in fact driven by the effect of birthplace.

Not only the number of plants known but also how many plants a person used was lower for the Mbendjele that were born in the town (Figure 7-5A; Table 7-6 Model 1; Tukey's HSD, $p< 0.001$). Participants that were born in the two forest regions and the other unvisited regions did not differ in their plant use score (Tukey's HSD: $p= 0.17$ for Minganga-Ibamba, $p= 1$ for Ibamba-other, $p= 0.31$ for Minganga-other). The analysis on the current camp residence revealed that people residing in the town camp used less plants compared to people from forest camps 2 and 3 (Figure 7-5B, Table 7-6, Model 2; Tukey's HSD, $p< 0.05$ for town camp and forest camp 2 and $p< 0.01$ for town camp and forest camp 3). Similar to the number of plants known, people who were born in the town used less plants compared to those who were born in other regions, and moved to town later (ANOVA followed by post-hoc Tukey HSD, p< 0.001). Therefore, the effect of camp residence is in fact driven by the effect of birthplace.

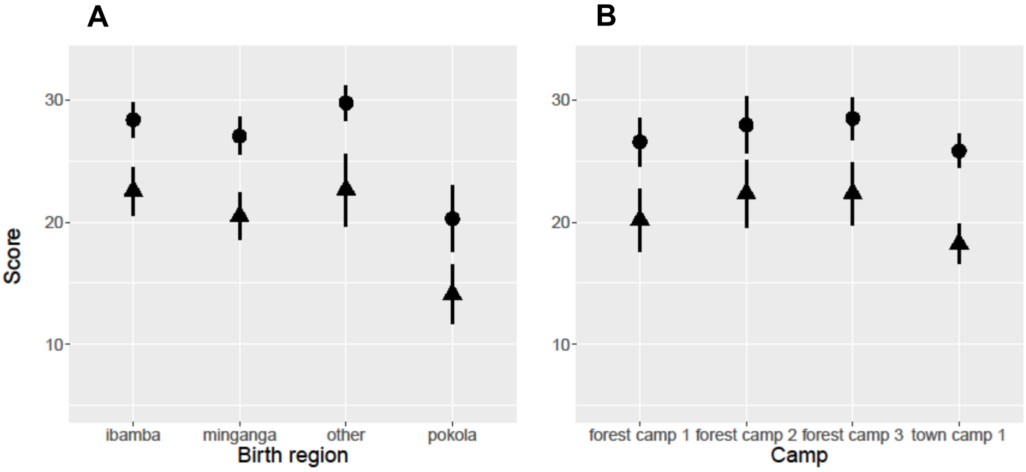


Figure 7-5: Mean plant knowledge and use scores by A) birth place (Pokola is the logging town, and the other places are regions that include camps in the forest), B) current camp residence. Dots indicate plant knowledge score and triangles plant use score. Error bars show 95% confidence intervals.

7.3.2.2 Mbendjele know and use more plants as they get older

The Mbendjele knew and used more plants as they got older (Figure 7-6A, Tables 7-6, 7-7). Post-hoc ANOVA showed that people who belonged to the older age groups knew about and used significantly more number of plants compared to the people with younger age groups.

I also examined birth region x age interaction to test whether the Mbendjele in each age group differed in their plant knowledge and use depending on where they were born. Overall, birth region x age interaction was not a significant factor in explaining the variation in knowledge and use scores (Tables 7-6, 7-7, Model 1). My post-hoc analyses revealed that young adults and adults that were born in the town knew significantly lower number of plants than those that were born in Minganga region (Tukey HSD, $p < 0.001$ for young adults, $p < 0.05$ for adults).

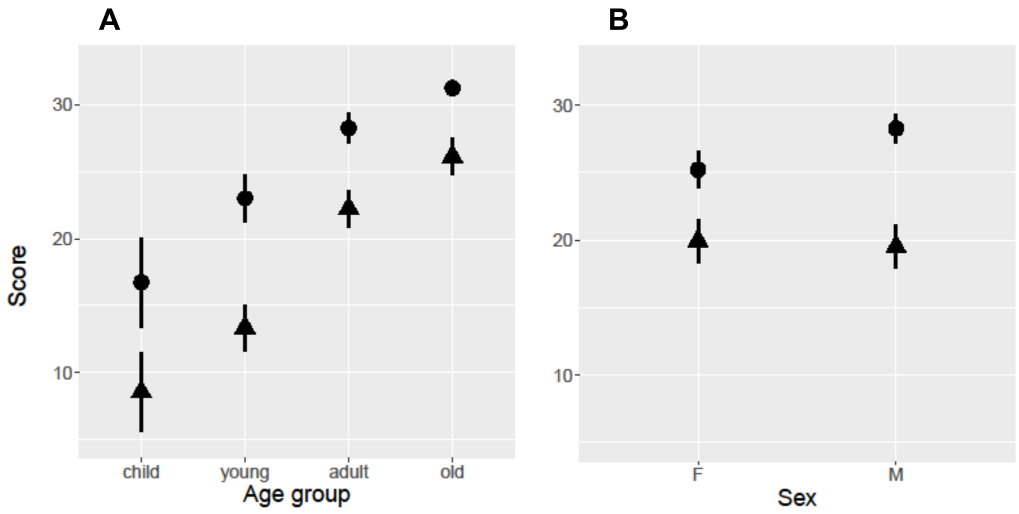


Figure 7-6: Mean plant knowledge and use scores by A) age group (child: 5-15 years, young adult: 15-25 years, adult: 25-45 years, old adult: 45+ years), B) sex. Dots indicate plant knowledge score and triangles plant use score. Error bars show 95% confidence intervals.

7.3.2.3 Number of plants used did not differ between males and females

Although male participants had slightly but significantly higher plant knowledge score than female participants (Figure 7-6B, Table 7-6, mean= 25.2 for females; mean= 28.3 for males), their plant use scores did not differ (Figure 7-6B, Table 7-7, mean= 19.9 for females; mean= 19.5 for males).

Table 7-6: ANOVA results of the effects of birth region, camp residence, sex and age group on the number of plants that are known by participants.

	Model 1			Model 2		
Predictor	**df**	**F-value**	**P**	**df**	**F-value**	**P**
birth region	3	25.04	**<0.001**			
camp				3	3.30	**<0.05**
sex	1	13.53	**<0.001**	1	24.11	**<0.001**
age group	3	44.15	**<0.001**	3	71.84	**<0.001**
birth region x age group	8	0.90	0.52			
camp x age group				9	1.87	0.06
n	193			219		

Table 7-7: ANOVA results of the effects of birth region, camp residence, sex and age group on the number of plants that are used by participants.

	Model 1			Model 2		
Predictor	**df**	**F-value**	**P**	**df**	**F-value**	**P**
birth region	3	15.45	**<0.001**			
camp				3	6.58	**<0.001**
sex	1	0.39	0.53	1	0.35	0.55
age group	3	51.48	**<0.001**	3	87.47	**<0.001**
birth region x age group	8	1.60	0.13			
camp x age group				9	2.44	**<0.05**
n	193			219		

7.3.2.4 The plant uses that are lost by the Mbendjele who were born in the town concerned medicinal purposes

I examined how uses of plants differed among the Mbendjele that were born in different regions. First, I conducted MCA on plant uses to explore the data on a 2-dimensional plane. This analysis showed that individuals clustered on different coordinates depending on their birth region and camp residence (Figure 7-7). The visual representation matched well with the information on the birth places of different camp members: Individuals that were born in Minganga clustered closely with individuals from forest camps 1 and 2 as the majority were born in Minganga region (Figures 7-7 and 7-4). The same was true for birth region Ibamba and forest camp 3 (Figures 7-7 and 7-4). Mbendjele from the town camp clustered somewhere between individuals that were born in Ibamba, the town (Pokola), and other- unvisited places as they were coming from diverse regions (Figures 7-7 and 7-4). Interestingly, uses of plants by adults, on average, resembled closely to the uses of plants by people that were born in Ibamba region (Figure 7-7). Note that there were some missing data on birth regions (*n*= 26, shown as "birth region.NA" on Figure 7-7). Since those individuals formed a close cluster with people who were born in Pokola, it is likely that majority of those individuals were also born in the town (Figure 7-7).

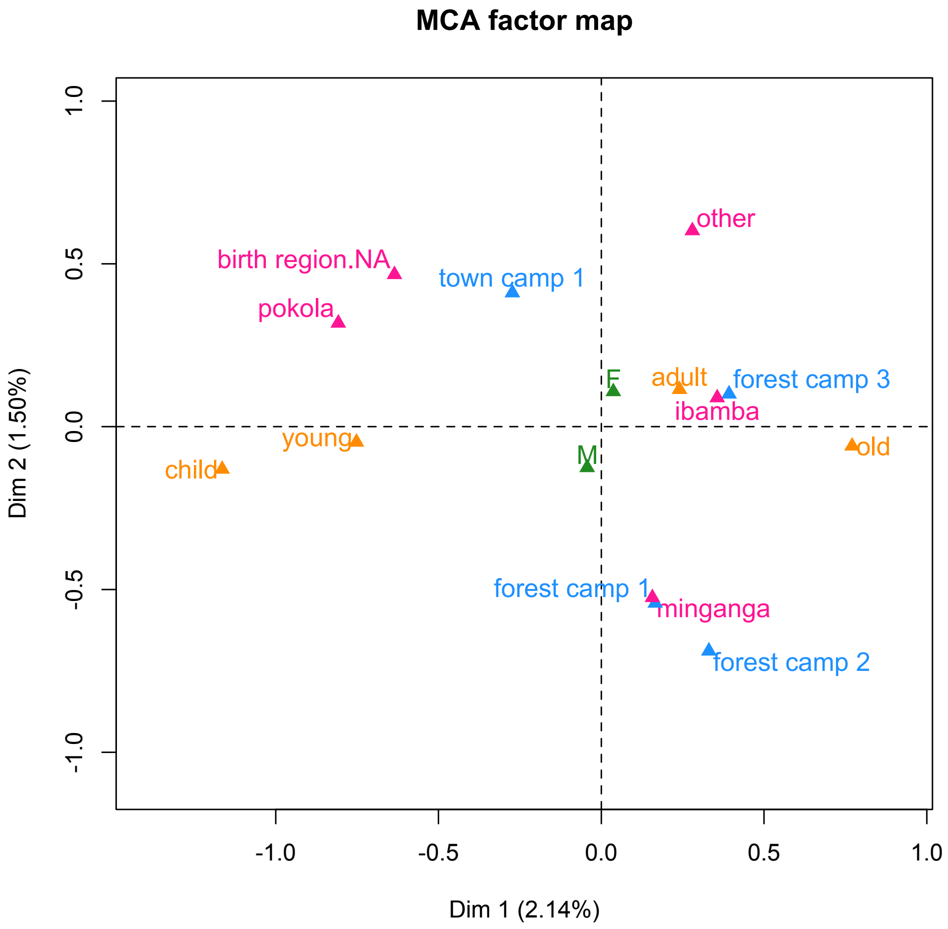


Figure 7-7: MCA map of each factorial variable based on plant uses. Triangles show the mean of the points of individuals who belonged to a particular category. Pink labels show categories of birth region, orange of age groups, blue of current camp residence and green of sex. The further the category is from the origin, the more different it is compared to the average response pattern.

I further investigated the plants that are not frequently used by hunter-gatherers that were born in the town camp. I first identified the plants that were used by only less than half of the people that were born in the town. Among those, I identified the ones that were frequently (more than 50% of the participants) used by the Mbendjele that were born in the forest and other-unvisited regions. This way, I could identify the plants that were not used by the town-born individuals but used by others. All the 8 identified plants were frequently used as medicine by the Mbendjele that came from forest regions (Table 7-8).

Table 7-8: Plants that are not used as frequently by the Mbendjele that were born in the town.

	% People not using by birth region						
Plant	**Ibamba**	**Minganga**	**Other**	**Pokola**	**Most frequent use type**	**% usage for beliefs***	**% usage for foraging**
Bulaki	22.22	32.93	32.14	79.31	pain and injuries (28%)	1	0
Indengo	16.67	7.32	17.86	72.41	respiratory (46%)	0	0
Jongo	31.48	45.12	22.22	72.41	infections (27%)	5	6
Kombo	35.19	32.93	28.57	51.72	respiratory (39%)	1	0
Mopo	37.04	42.68	25.00	79.31	infections (31%)	2	0
Moba	20.37	31.25	25.00	58.62	digestive (29%)	0	0
Mongo	22.22	28.05	28.57	68.97	respiratory (35%)	1	0
Mokula	33.33	34.15	39.29	62.07	digestive, genitourinary, wounds (11% each)	7	0

*maximum percentage of population using a plant for social beliefs is 31; for foraging is 20.

7.3.2.5 *Town-dwelling Mbendjele had increased odds of having the same medicinal use of a plant if they were born in the same region*

If Mbendjele that have built large camps in a logging town shared their knowledge on plant uses with campmates, we expected to observe no effect of birth region on the similarity of plant uses. I first analysed the data on plant uses by using the MCA method to detect underlying patterns concerning the effects of birth region in the town. The analysis showed that participants that were born in the logging town were quite different in how they used a plant compared to participants who were born in forest or other regions and moved to town (Figure 7-8). On the other hand, participants that came from two forest regions made intersecting clusters on a two dimensional plane; indicating that their knowledge on plant uses were similar.

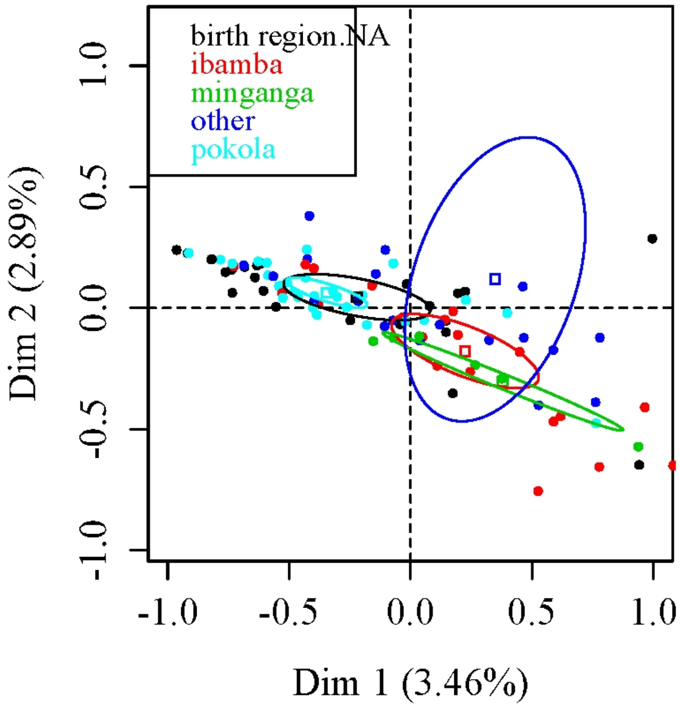


Figure 7-8: Multiple correspondence analysis (MCA) based on the similarity of the uses of 33 plants in Mbendjele living in the town camp. The distance between two points indicates the similarity of two individuals' plant use (*n*= 107). Squares show the mean of the points of individuals who belonged to the same category (e.g. being born in Pokola) and ellipses represent 95% confidence intervals. The plot shows that people who were born in the town, Pokola (light blue circle) constitute a distinct cluster compared to people who were born in the two forest regions, Ibamba (red circle) and Minganga (green circle), and the other unvisited places (dark blue circle). The black circle represents individuals whose birth region was unknown, but likely Pokola.

I further investigated the co-occurrence of plant uses for medicinal purposes (i.e. "shared knowledge of plant uses", see Chapter 6 for details) in the town camp. I found that people that were born in the same region had increased odds of reporting the same medicinal plant use by

9% (Figure 7-9A, odds ratio (OR)= 1.09, 95% CI= 1.04, 1.14, p< 0.001). However, the effect of relatedness was larger. A 0.25 increase in the coefficient of relatedness within a dyad increased the odds of reported co-occurrence of medicinal plant use by 15% (Figure 7-9A, OR= 1.15, 95% CI= 1.08, 1.23, p< 0.001). Breaking down the effects of kinship, dyads including mother and offspring had an increase of 30% in the odds of co-occurrence of medicinal plant use (OR= 1.30, 95% CI= 1.01, 1.67, p< 0.05). The effect was similar in size but not as significant (29%) for father and offspring (OR= 1.29, 95% CI= 0.97, 1.72, p= 0.08). Being siblings increased the odds by 56% (OR= 1.40, 95% CI= 1.22, 1.98, p< 0.001).

Besides the positive effects of birth region and relatedness, dyads that belonged to the same age group (OR= 1.35, 95% CI= 1.29, 1.40, p< 0.001), that were males (OR= 1.10, 95% CI= 1.04, 1.15, p< 0.05, and had a distant affinal kin tie (OR= 1.13, 95% CI= 1.03, 1.25, p< 0.001) had increased odds of reporting the same medicinal use of a plant (Figure 7-9A).

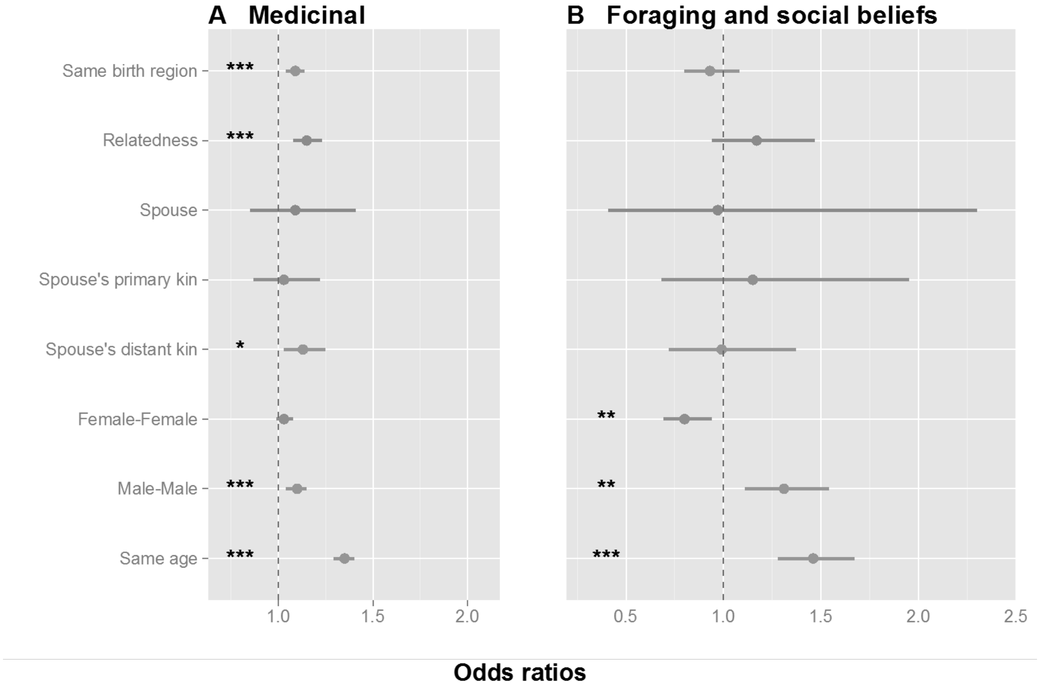


Figure 7-9: Odds ratios for the predictor variables. Response variable is reported co-occurrence of plant use of town-dwelling Mbendjele for A) medicinal purposes (*n*= 80025 data points and 3240 individuals) or B) purposes related to foraging and social beliefs (*n*= 69151 data points and 3240 individuals). The dots show the odds of co-occurrence of plant use when individuals in a dyad were born in the same birth region; are genetically related (odds ratio calculated for a 0.25 increase in coefficient of relatedness); have one of the following affinal kin ties: spouse, spouse's primary kin, or spouse's distant kin; are females; are males; belong to the same age group. Error bars show 95% confidence intervals. ***$p< 0.001$, **$p< 0.01$, *$p< 0.05$.

For non-medicinal use purposes (i.e. foraging and social beliefs, see Chapter 7 for details) neither birth region nor relatedness had a significant effect on the similarity in how two individual in the town camp used a plant (Figure 7-9B). This, however, should be interpreted with caution because of the smaller sample sizes (e.g. there were only 9 cases of spousal dyadic ties, 6 of father-offspring ties, and 16 of mother-offspring ties where the dyad shared knowledge). While dyads that belonged to the same age group (OR= 1.46, 95% CI= 1.28, 1.67, $p < 0.001$) and were males (OR= 1.31, 95% CI= 1.11, 1.54, $p < 0.01$) had increased odds of reporting the same non-medicinal plant use, female-female dyads had decreased odds of sharing knowledge (OR= 0.80, 95% CI= 0.69, 0.94, $p < 0.01$) on non-medicinal plant uses (Figure 7-9B).

7.3.3 Discussion

My results showed that the Mbendjele who were born in the town knew and used fewer plants than the Mbendjele who were born in other, less market-integrated regions. Plant uses that were lost in the town-born Mbendjele concerned uses for medicine. Moreover, among the town-dwelling Mbendjele, those who were born in the town differed in how they used plants compared to those who were born in other regions.

Decline in plant knowledge in the town can be explained by several factors. First, the socioeconomic transitions that are presented above may affect knowledge sharing patterns by changing social interaction patterns. Changes in subsistence activities, for example, result in children being less exposed to forest related activities. I found that adults in the town camp engage in wage labour more frequently than the adults that reside in other camps (Salali & Migliano, 2015). Therefore, Pygmy children that grow up in the town have fewer opportunities to accompany and observe adults during forest-related activities. Moreover, forests around Pokola are degraded by agricultural and logging activities that make the immediate environment less suitable for hunting and gathering (Laporte et al., 2007). Pygmies in town who want to go on hunting or foraging trips have to walk long distances to find food resources. Moreover, unlike children that reside at forest camps, many Mbendjele children attend schools in the town. There is a school in Pokola that is established by a French charity for young Pygmy children that gives education in French with more flexible school hours that match Pygmy life-style (e.g. having holidays during the dry season when Pygmies camp by water resources for fishing). Some Mbendjele students that attend to this school continue on their education at the local schools with Bantu children. Formal schooling means that the Mbendjele children spend less time in the forest and have fewer opportunities to learn skills related to forest life.

As shown in Chapter 6 and this chapter, biological kin is very important in the transmission of medicinal plant knowledge. Interestingly, my results on the sharing of medicinal knowledge in the town camp showed that siblings had a higher similarity in how they used plants for medicine than either mother-offspring or father-offspring pairs. This may also result from the socio-economic shift in the town, where more adults work as day-labourers in agricultural fields (Riddell, 2013; Salali & Migliano, 2015). As adults become less available as models for social-learning, peer-to-peer transmission may replace vertical transmission. Moreover, emerging inequalities mean a shift away from hunter-gatherer egalitarian structure which facilitates sharing of information. I suspect that as the groups in the town get larger and more sedentary, the social interactions within camp members will get more clustered (possibly based on close-kin ties), which will obscure the sharing of knowledge related to group living and cooperative activities.

The importance of family ties in the sharing of medicinal plant knowledge points at a potentially sharp decline in medicinal knowledge with socio-economic transitions. If horizontal transmission among campmates was more prevalent in the sharing of knowledge on medicinal plant uses, migration of Pygmies from different birth regions into larger camps might maintain the richness in medicinal plant uses. However, our results indicate that the future generations of those who were born and reside in the town will know even fewer plants that can be used as medicine, as those traits will be lost in previous generations within families (Cavalli-Sforza & Feldman, 1982, 1981; Mesoudi, 2011).

As shown in Chapter 5, the uses of some medicinal plants have potential health benefits, especially when there is no access to modern medicine. Although there is a well-functioning hospital ran by the logging company in the town, the Mbendjele are often reluctant to go to the hospital. They often prefer to see traditional Pygmy healers. I observed that the town-dwelling Mbendjele still rely on traditional medicine, as they had a traditional healer in the town camp and refused to go to the local hospital in times of sickness. Given that the decline in plant uses concerned medicinal plants, the loss of traditional knowledge may have negative health effects on town-dwelling hunter-gatherers.

It is questionable how much plant knowledge is valued by the young Mbendjele, as often when I ask the Mbendjele about living in the forest as opposed to living by logging roads or towns, I received the following answer: "It (solely living in the forest) was something of the past, something that our ancestors were doing". The Mbendjele are often humiliated by the neighbouring farmer populations because of their forest-oriented way of life and are compared to animals (J. Lewis, 2005, 2014b). I suspect that often, when the Mbendjele make such negative claims about living in the forest, it is driven by the shame or negative feedback that they get from farmers. This effect is much stronger for the young Mbendjele living in towns as they interact with farmers every day. Moreover, the young Mbendjele in town may not consider knowing about wild plants as valuable as learning French which will allow them to better integrate in the society, in ways that they can get jobs and earn money.

Regarding this last point, change in cultural traits can be seen as adaptive responses to changes in socio-economic and ecological conditions, rather than despairing cultural losses (Gómez-Baggethun & Reyes-García, 2013; Reyes-García, Luz, et al., 2013). Although the Mbendjele may be losing the diversity of their traditional plant knowledge, it may be equally important for their resilience to have the necessarily skills to navigate their ways in market economies and become an autonomous group who can successfully defend their rights.

7.4 Conclusion

In this chapter, I examined how socioeconomic transitions and change in social structure in the Mbendjele are associated with cultural change. I found that the Mbendjele that live in the town camp engaged in wage labour more frequently, accumulated more wealth, resulting in emerging inequalities, and became more future oriented compared to Mbendjele that live in forest camps. Associated with those changes, my results showed that the Mbendjele who were born in the town knew and used fewer plants. These results demonstrated how changes in social structure affect cultural transmission patterns, and the way cultural traits evolve in response to changing conditions.

Chapter 8: Conclusion and General Discussion

In this thesis, I have examined the adaptive value, sharing of and change in plant knowledge in the Mbendjele hunter-gatherers of Northern Congo. Specifically, I explored for what reasons the Mbendjele use wild plants (Chapter 4), whether there are adaptive benefits to medicinal plant use (Chapter 5), how the Mbendjele share knowledge on plant uses of different purposes (Chapter 6), the socioeconomic transitions that the Mbendjele experience, and how these transitions affect their knowledge on plants (Chapter 7). In this chapter, I provide an overview of my findings, discuss about their implications on cultural evolution and make suggestions for future directions.

8.1 Overview of findings

I investigated plant knowledge as a case study since it represented a rich cultural repertoire and constitute an important part of life in forest hunter-gatherers. In Chapter 4 I explored the plant uses in the Mbendjele. My findings in this chapter set the stage for my analyses in the following analysis chapters. These findings showed that the plant uses in the Mbendjele are very diverse. The Mbendjele use plants mostly for medicinal purposes, but also for foraging, making materials, consuming as food or regulating the social life and as part of their belief systems. The most common use purposes (treating digestive and respiratory problems) matched the most prevalent diseases that are seen in forest hunter-gatherers. Moreover, some plants were used as medicine more than the others, and had larger consensus on their use purposes. These findings suggested that there may be therapeutic potential to medicinal uses of some wild plants.

In the following chapter I further explored this topic by asking whether there is any adaptive benefit to the medicinal uses of plants. I tested the hypothesis that cultural variation may be subject to natural selection and as a result, adaptive cultural traits may be spread in a population (Boyd & Richerson, 1985). I predicted that medicinal plant knowledge provides adaptive benefits to its bearers as certain medicinal plant uses may increase individuals' chances of survival and reproduction. If this is correct, then knowledge about certain medicinal plants may be discovered independently in multiple places or shared more widely because of their influence on fitness (Saslis-Lagoudakis et al., 2012; Saslis-Lagoudakis, Klitgaard, et al., 2011; Saslis-Lagoudakis, Williamson, et al., 2011). My findings showed that majority of the medicinal plants that are used by the Mbendjele are also used by other Central African Pygmy populations, including the less closely related Eastern Pygmy groups (the Mbuti). Some of those are found to be used as medicine by gorillas and chimpanzees. There was also a large consensus on the use of specific plant species, such as *Alstonia boonei*, for treating similar symptoms among all Pygmy groups. 80% of the plant species that were identified have known bioactive compounds. Finally, I found that mothers' who used *Myrianthus arboreus* to treat respiratory system problems had children with higher BMI. In sum, these findings suggest that there are potential health benefits of using medicinal plants. Nevertheless, these results should be interpreted with caution until more direct associations between plant use and health are discovered.

In Chapter 6, I explored how plant knowledge is shared among the Mbendjele. I found that medicinal plant knowledge is mainly shared between spouses and biological and affinal kin. Together with the results from Chapter 5, these findings suggested that marital ties in hunter-gatherers are crucial in the transmission and accumulation of cultural skills and knowledge that is important for fitness. Previous research on the transmission of medicinal plant knowledge in small-scale populations showed the importance of vertical (parent to offspring) (Hattori, 2006a) and oblique (from older to younger generations) transmissions (Reyes-García et al., 2009). Nevertheless, to my knowledge, none of the previous studies tested the importance of marital relationships in transmission of adaptive knowledge. Given that marital ties are the key links connecting distant families in hunter-gatherers, their importance in information transfer and cultural evolution should be substantial and requires further investigation. My results in this chapter also demonstrated that the content of information affects its transmission pathways in relation to the features of social structure. Accordingly, I found that co-residence of multi-families provided a context for the transmission of plant knowledge that concerned cooperative foraging and social norms and beliefs.

In Chapter 7, I investigated how changes in social structure as a result of socioeconomic transitions affected the sharing and levels of plant knowledge in the Mbendjele. Previous studies have shown that rapid changes in socio-economic, political and environmental conditions result in the loss of traditional knowledge across the world (Godoy & Reyes-García, 2009; Gomez-Baggethun et al., 2010; Reyes-García, Guèze, et al., 2013; Reyes-García, Luz, et al., 2013). My comparisons of subsistence activities, wealth inequalities and future orientation have shown that the Mbendjele who live in the market town (Pokola) engaged in wage labour more frequently, and paid, on average, higher amounts of bride price. Moreover, there was a larger variation in the amount of paid bride prices in the town camp; reflecting the emergence of wealth inequalities among the town-dwelling Pygmies. The Mbendjele living in the town were also more future-oriented (a trait that predicts the emergence of wealth accumulations) compared to the Mbendjele living in the forest regions. In conjunction with these changes in social structure towards a less forest oriented and non-egalitarian system, I found that people who were born in the logging town had significantly lower plant knowledge and use scores (i.e. number of plants reported as known/used out of 33 plants). Among the Mbendjele living in the town, those who were born there differed in how they used plants compared to those who were born in other regions. In general, the lost plant uses in town-born Mbendjele concerned medicinal purposes.

8.2 Implications for cultural evolution

8.2.1 Pair-bonds, affinal kin, life history traits and transmission of adaptive information

This thesis furthers our understanding of how complex cultural traits might have evolved by showing the association between human social structure, life-history traits and cultural transmission. Hunter-gatherer social structure is marked by long-term pair bonds between men and women, exogamy (marriage outside one's own group), multi-locality and multiple families living in groups that are further connected with each other. The importance of marital ties in allowing peaceful interactions between groups and connecting them has long been acknowledged in the anthropological literature (Chapais, 2008; Marlowe, 2004). Nevertheless, their role in cultural transmission has been neglected. This is because previous studies of cultural transmission in hunter-gatherers mainly focused on vertical (parents to offspring), horizontal (peer to peer) and oblique (older to younger generations) transmission and asked which of those is more prevalent (Barry S. Hewlett & Cavalli-Sforza, 1986; Barry S. Hewlett et al., 2011). I argue that investigating knowledge sharing between spouses and among affinal kin is as important as investigating the above transmission pathways. Moreover, researchers of cultural evolution would benefit from considering societies' residence patterns and social structure when exploring cultural transmission. There are only a few studies that explored the importance of residence patterns on the spread of cultural traits within a population (Aunger, 2000; Tehrani & Collard, 2009). As cultural transmission is directly related to interaction patterns, it is necessary to examine the features such as residential mobility, and kinship that facilitate interactions among individuals. Because of strong pair-bonds, human spouses spend much time together and engage in cooperative childcare. This increases the chances for exchange of information. In fact, my results showed that the odds of two individuals sharing medicinal plant knowledge were highest between spouses, even more than mother-offspring dyads. Moreover, not only spouses but also affinal kin (such as in-laws and spouses' second and third degree relatives) exchanged much information that has potential adaptive benefits. The interactions among affinal kin are facilitated in the Mbendjele because of high residential mobility and multi-local residence patterns. My field observations coupled with these results suggest that co-preparation of medicinal plants by people that are connected through marital ties has led to the emergence of new plant combinations and preparation methods, resulting in rich medicinal plant repertoire in this hunter-gatherer population.

My findings have suggested that certain medicinal plant uses may provide fitness benefits and that family ties are especially important in the transmission of such information because of inclusive fitness benefits. Based on these findings, I argue that cooperative breeding provide a context for transmission of such information. Evolutionary anthropologists count humans as cooperative breeders as mothers receive substantial help in childrearing (Burkart et al., 2009; Hrdy, 2009). Our research on childcare in the Mbendjele has shown that nearly 80% of proximate interactions with children under 4 years-old were from non-maternal individuals (Nikhil Chaudhary unpublished data). 70% of non-maternal care came from kin, and 30% non-kin. Siblings were the most important non-maternal caregivers (constituted 32% of offspring-caregiver interactions), followed by uncles and aunts (12%), fathers (10%), grandmothers (8%), other kin (7%) and grandfathers (1%) (Nikhil Chaudhary unpublished data). The importance of siblings in allo-maternal childcare in the Mbendjele is reflected in my findings on the sharing of medicinal plant knowledge. Accordingly, the odds of a dyad sharing knowledge on medicinal plant uses were highest between spouses (61% increased odds), and mothers and their offspring

(57% increased odds), which were followed by siblings (40% increased odds). Given the importance of juvenile help in human cooperative breeding (Kramer, 2011), my findings suggest that siblings are very important in social learning and exchange of medicinal plant uses and other adaptive information.

It has been suggested that cooperative breeding and human life history traits have evolved together (Hill, Barton, & Magdalena Hurtado, 2009). Human life history is characterized by long childhoods, shorter inter-birth intervals and long post-reproductive life-spans. It is likely that because of allo-maternal care human females could afford to look after multiple dependent offspring at the same time. Kaplan et al. (2000) have argued that evolution of extended childhood period in humans has allowed enough time for social learning of skills that are required to obtain high quality, difficult to get resources. Later on when these skills are learnt, the low-productivity during childhood is compensated by higher productivity in adulthood and inter-generational flow of food from older to younger individuals (Kaplan et al., 2000). My results are consistent with this argument that extended childhoods allow for the acquisition of knowledge that have potential adaptive benefits. Moreover, presence of knowledgeable post-reproductive individuals, such as grandmothers, who help in child-care enables human children to acquire knowledge from wide range of social models. Shorter inter-birth intervals results in multiple offspring growing up together and learning from each other. This learning pathway is especially important in the acquisition of medicinal plant knowledge in the Mbendjele, as children aged 0-4 spend much of their time with their older siblings (32% of non-maternal interactions), and engage in social learning mainly through observations (38% of all social learning cases, unpublished video data).

8.2.2 Group living and cultural transmission

Camp membership was a strong predictor in explaining two individuals sharing knowledge on plant uses that concerned foraging and social beliefs. Hunter-gatherer social structure is characterized by small groups of co-resident families. These groups are fluid because of residential mobility and frequent visits between friends, affines and biological kin from different camps. Nevertheless, the frequency of interactions among individuals depends on geographical proximity. For instance, majority of the Mbendjele that I met during fieldwork associated themselves with either Minganga or Ibamba regions and interacted more frequently with individuals that were from the same region (Figure 3-1). Such regional differences may result in cultural drift and formation of new cultural traits that are group specific.

It is not surprising that the content of knowledge that was transmitted among co-residents of a camp, regardless of relatedness, concerned group-living. Foraging related plant uses in the Mbendjele concerned trees that harbor honey and caterpillars and poisonous plants that are used for fishing and hunting animals. Mbendjele engage in these activities in groups, therefore there are ample opportunities for knowledge share. This is also the case for the plant uses that concerned social norms, such as plants that are used for punishing cheaters, or when a sexual taboo is broken.

What do the above results tell about cultural evolution? As documented in laboratory experiments (Derex & Boyd, 2016) and computer simulations (Powell et al., 2009) a population structure with the presence of frequently interacting sub-populations allows for accumulation of cultural traits and leads to rich cultural repertoires. This is because while sub-groups come up with their own cultural traits, interactions among these groups facilitate the combination and generation of new skills, knowledge and technology. The group specificity of certain plant uses in the Mbendjele exemplifies how co-residence leads to the formation of such traits. Nevertheless, as the Mbendjele from different regions have occasional interactions through big ceremonies and marriages; new combinations emerge in those traits.

8.2.3 Cultural change

Almost all Pygmy groups in the Congo Basin work as wage labourers in farmers' field in exchange for alcohol, agricultural food, cigarettes, and other industrial products (Bahuchet & Guillaume, 1982; Oishi, 2012; Turnbull, 1961). Nevertheless, the frequency of such exchanges varies within and among Pygmy groups. My findings showed that a shift in subsistence activities and a less egalitarian and sedentary social structure lead to a loss in forest related knowledge, especially the knowledge on how to use plants for medicine, in the Mbendjele. Although traditional knowledge is crucial and may contribute to fitness in forest dwelling hunter-gatherers, cultural change with changing socio-economic conditions is inevitable. I agree with Gómez-Baggethun & Reyes-García (2013) that rather than seeing this cultural change as a despearing knowledge loss, the researchers should understand the adaptive cultural responses towards such economic, social and political changes. For the Mbendjele who choose to reside in towns permanently, focusing on learning new skills, such as French or mathematics, may be more beneficial in navigating their way through market economies. I believe that the most effective way to support indigenous groups in their interactions with other groups and governmental bodies is to promote education tailored for their life-style and cultural practices. Adaptive cultural change for the Mbendjele will be the one which allows them to be completely autonomous and free in their access to resources, either in the forest or in market towns.

8.3 Future directions:

8.3.1 Extending the research on health effects of medicinal plant use and socioeconomic transitions

In Chapter 5, I examined the potential health effects of using medicinal plants in the Mbendjele. My aim was to understand whether medicinal plant knowledge has adaptive benefits to hunter-gatherers. Most of my measures, however, were indirect. The only health measure I used was children's BMI. BMI in children can be used to assess malnutrition (Cole et al., 2007). For instance, World Health Organization (WHO) uses a growth standard that includes BMI for children aged 0-5 years. Nevertheless, more direct health data will enable us to better understand whether there is any benefit to using plants as medicine. To answer this question, McDade et al. (2007) use the following measures for children's health in Tsimane' forager-horticulturalists: concentrations of C-reactive protein (CRP), skinfold thickness, and stature. CRP is a protein of immune system and its concentration reflects the levels of pathogen infection. The authors used standardized skinfold thickness to measure body fat, and height-for-age z-scores as an indicator of nutritional and health status. These latter two are comparable to my use of BMI as a health proxy. Their findings showed that the children of parents who had lower ethnobotanical knowledge had elevated levels of CRP (McDade et al., 2007).

In another study, our research team at UCL have used blood composition analysis to compare health among different Agta hunter-gatherer camps in the Philippines (Page et al., 2016). White blood cell composition (WBC) analysis is carried out by using a small portable device (HemoCue WBC DIFF system), which gives results within five minutes. Among WBC, neutrophil counts are used to reflect bacterial, and lymphocytes for viral infections. Another key marker for the presence of parasites is eosinophils. In particular, helminths with a tissue migratory phase (e.g. hookworm and *Ascaris spp*. that pass through the lungs) cause elevated levels of eosinophils. Our findings showed that Agta camps that were larger, more sedentary and agricultural showed increased levels of parasitic infections and infant mortality compared to the mobile Agta (Page et al., 2016). On the other hand, women had higher reproductive success in the settled camps, suggesting that there was quantity-quality trade-off associated to the demographic expansion during the Neolithic (Page et al., 2016).

In the future, the similar uses of blood cell composition measures will allow me to test the link between medicinal plant uses in the Mbendjele and their health status. Moreover, similar to the Agta study that is presented above with more direct health measures I will be able to investigate the effects of socioeconomic transitions on hunter-gatherer health and fertility.

8.3.2 Cooperative breeding and knowledge sharing

My findings on the sharing of plant knowledge demonstrated the importance of marital ties in the sharing of adaptive information. Based on these findings, I suggested that cooperative breeding may have been an important medium for knowledge exchange and cultural evolution. I plan to test this hypothesis by examining the relationship between the composition of Mbendjele childcare providers and the similarity in their plant uses. Nikhil Chaudhary examined non-maternal (alloparental) proximate interactions with the Mbendjele children under 4 years-old. I presented some of the results from this data earlier in Section 8.2.1. As a form of cooperative breeding, proximate care allows hunter-gatherer mothers to reallocate time to tasks such as foraging, collecting water, caring for other offspring and domestic jobs while raising multiple dependent offspring simultaneously (Hill & Hurtado, 2009; Kramer, 2010). The results from Chaudhary's analysis showed sibling-care to be especially important in cooperative breeding. Future studies on the cultural transmission in small-scale societies should address whether those individuals who are frequent caregivers of focal children also share much information with each other.

8.3.3 Social networks and socioeconomic transitions

Following my analysis in Chapter 7 where I investigated social and economic changes in the Mbendjele camps that are close to market towns, I plan to compare the social network structure in each camp. The Mbendjele camp located in the town was much larger (>100 residents), with some families permanently residing there, hence being sedentary. Growing groups face the trade-off between resource availability (through the networks of resource exchange) and competition from conspecifics (M. J. Hamilton et al., 2007). Intragroup conflict increases with increasing group size and decline in mobility. Traditionally egalitarian hunter-gatherers use mobility to avoid conflicts by voting with their feet. They may split along similar family lines to maintain cooperation and avoid potential conflicts (M. J. Hamilton et al., 2007; Turnbull, 1961, 1965). In larger and more sedentary groups this option is not available. For example, by analysing the data on the dispute frequency and the camp size in the !Kung, Johnson (1982) found that larger groups had more disputes. Based on this analysis, he has coined the concept of "scalar stress" where population growth results in population-resource imbalance and intragroup conflict.

Scalar stress can be overcome by two processes: 1) the group splits, 2) social norms and institutions (i.e. social complexity) emerge to manage the internal conflict (Johnson, 1982; Salali, Whitehouse, et al., 2015). Moreover, growing populations require the emergence of leaders (Hooper et al., 2010) and hierarchies; where groups have leaders and groups of groups have leaders who process information (Kelly, 2013). Kelly (2013) states that understanding this emergence of hierarchy and inequality is one of the greatest challenges facing students of hunter-gatherers.

Socioeconomic transitions and emerging inequalities can have a large effect on hunter-gatherers' interaction networks. It may be that in larger hunter-gatherer camps social networks are more clustered based on kin groups. In the absence of mobility the camp may be organized in a way that close kin live in close proximity and interact more often to avoid potential conflicts. One measure of social network analysis that can be used to test this hypothesis is *clustering coefficient*. This coefficient measures the tendency of a focal's friends to also be friends with each other. Higher clustering coefficient may indicate population assortment which may reinforce cooperation (Apicella et al., 2012). My prediction is that the social networks of larger, more sedentary hunter-gatherer camps will have a higher clustering coefficient compared to networks of smaller and more mobile camps. Furthermore, I predict these clusters to be formed based on kinship.

8.4 Future of modern day hunter-gatherers

In Chapter 3 I wrote about the problems that the Mbendjele face due to bush meat trade and their land rights, while in Chapter 7 I discussed the changes in the Mbendjele's socioeconomic life due to market integration and globalization. Mbendjele are mobile, except for the ones who live in towns permanently. Majority move between various resource-rich locations in the forest, camps located nearby logging roads, farming villages and logging towns. Their movement depends on the seasons and the distribution of resources as well as opportunities of exchange with traders and farmers. Trading forest products is an integral part of the Mbendjele life. Commonly the money earned from the trade is spent for alcohol, cigarettes, marijuana, agricultural food and other industrial goods. Because Pygmy hunter-gatherers are famous for their hunting and forest skills, they are the favourite employees of bush meat traders. They are also often targeted by conservation NGOs for this reason.

The Mbendjele do not only interact with farmers and traders. Northern Congo is the area where the most rapid extension of road network is occurring in Central Africa (Laporte et al., 2007). There are several large-scale infrastructure projects and acquisitions of large areas of lands for commercial agriculture, forestry, mining, and biofuels throughout Africa (Cotula, Vermeulen, Leonard, & Keeley, 2009; Roe, Nelson, & Sandbrook, 2009). Foreign investment is rapidly entering into the once remote areas. This extension of markets and rapid development has major effects on the Mbendjele (Riddell, 2013). Many Mbendjele around the Minganga region are being forced to relocate from camps like Longa for the purposes of wildlife conservation (J. Lewis, 2005). When the relocation occurs, the Mbendjele and often the accompanied Bantu traders move to camps that are located further inside the forest where the eco-guards and local authorities cannot access easily. Moreover, there is discrimination against Pygmies. For instance, although Pygmies are said to make up about 10% of the workforce of the logging company in Pokola (The Associated Press, 2003), Lewis (2005) writes about how he saw some letters from local government officials ordering the expatriate staff of the logging company not to employ too many BaYaka.

I believe that one way to support the resilience of hunter-gatherers under rapidly globalizing world is enabling their access to information and providing them with education that is tailored for their ways of life. It is important that the indigenous communities can effectively communicate and defend their land rights and are well informed about all the players involved in the management of lands. Moreover, presence of indigenous representatives is important in the successful integration of indigenous communities in modern life. In parts of South America, indigenous populations are effectively defending their land rights, and even establishing parties that are organized around indigenous identity (Rice & Van Cott, 2006).

There are some promising projects that concern Mbendjele well-being and education. One is a school established by a French charity organization, exclusively for the Mbendjele children that live in Pokola. The teachers try to accommodate a schedule that is convenient for the Mbendjele. For example, the vacation times are arranged so that during dry season children can go on fishing trips in the forest with their families. Both of our translators learnt French in this school and were attending a Bantu elementary school to continue their education at the time of our fieldwork. Speaking French would allow the Mbendjele to participate in discussions that concern their land rights and facilitate their access to healthcare and education. Nevertheless, it is important that the education is tailored for their forest oriented life-style. This is possible by developing a schedule that takes Mbendjele’s mobility patterns into account and coincides with seasons where they are more likely to build camps in towns or farmer villages (in which such schools can be established).

Of course, these are ambitious projects, especially in least developed countries where governmental support is almost absent. However, some support comes from NGOs and logging companies that aim for sustainable forestry (although they also target Mbendjele for the same purposes). For example, in 2010 a radio station called *Biso na biso* (meaning Between us in Lingala) is opened in Pokola to broadcast programs to all the BaYaka in the region (Brook, 2010). The programs not only include music and messages from listeners, but also discussions about logging companies, education, health, AIDS, and news on when the local doctor is visiting the village. This is a very promising project that enables the Mbendjele to access to information that is necessary for their resilience in a developing world.

There is also a mobile pharmacy project that is recently launched to help the Mbendjele to access modern medicine ("Project Bwanga: Training hunter-gatherer healers in Congo," 2016). This project is organized by Dr. Jerome Lewis's wife, Ingrid Lewis, in collaboration with a local doctor who works at the hospital in Pokola. The project aims to provide a short and intense health education to the Mbendjele healers and funds establishment of local pharmacies at certain Mbendjele camps. These pharmacies are run by the Mbendjele healers who receive education by the local doctor. The medicines are provided by funds from a Dutch organization. Ingrid also arranges programs at radio Biso na biso, providing information on health and hygiene to the Mbendjele. Health education is a very effective, powerful and simple way to prevent infectious diseases in these communities where most diseases are of parasitic nature and can be avoided by better hygiene practices. As already discussed in the seminal book, African Pygmies (1986) that covered the health research conducted in the area in the 1960s, education programmes on parasites and hygiene can be a more effective and cheaper solution to the use of expensive therapeutic interventions.

8.5 Concluding remarks

In this thesis, I hope to have made some important empirical contributions to the studies of cultural evolution. I argue that the use of certain medicinal plants in hunter-gatherers provide fitness benefits and has evolved through cultural selection. I also advocate the importance of long-term pair bonds, affinal kin and cooperative breeding on the transmission of adaptive knowledge and emergence of rich cultural repertoires. My findings have furthered our understanding of how content of information influences its transmission and how group-living facilitates the emergence of cultural traits that concern cooperative activities and social norms. Finally, I showed that decline in traditional knowledge is inevitable in current day hunter-gatherers who are experiencing socioeconomic transitions and change in their egalitarian social structure. I argue that adapting to new social and political environments through cultural change may help the resilience of extant hunter-gatherers. For this reason, the most important contribution of this thesis is perhaps the documentation of local ecological knowledge that may be lost in a hundred years.

References

Abiodun, O., Gbotosho, G., Ajaiyeoba, E., Happi, T., Falade, M., Wittlin, S., … Oduola, A. (2011). In vitro antiplasmodial activity and toxicity assessment of some plants from Nigerian ethnomedicine. *Pharmaceutical Biology*, *49*(1), 9–14.

AFlora Committee. (2013). AFlora: The database of plant utilization in Africa. Retrieved from http://aflora.africa.kyoto-u.ac.jp/records/top

Aiello, L. C., & Dunbar, R. I. M. (1993). Neocortex Size , Group Size , and the Evolution of Language. *Current Anthropology*, *34*(2), 184–193.

Ainslie, G. W. (1974). Impulse control in pigeons. *Journal of the Experimental Analysis of Behavior*, *21*(3), 485–489.

Alawa, C. B. I., Adamu, A. M., Gefu, J. O., Ajanusi, O. J., Abdu, P. A., Chiezey, N. P., … Bowman, D. D. (2003). In vitro screening of two Nigerian medicinal plants (Vernonia amygdalina and Annona senegalensis) for anthelmintic activity. *Veterinary Parasitology*, *113*(1), 73–81.

Alvard, M. S., & Kuznar, L. (2001). Deferred harvest: the transition from hunting to animal husbandry. *American Anthropologist*, *103*(2), 295–311.

Apicella, C. L., Marlowe, F. W., Fowler, J. H., & Christakis, N. A. (2012). Social networks and cooperation in hunter-gatherers. *Nature*, *481*(7382), 497–501.

Apter, A., Van Praag, H. M., Plutchik, R., Sevy, S., Korn, M., & Brown, S. L. (1990). Interrelationships among anxiety, aggression, impulsivity, and mood: A serotonergically linked cluster? *Psychiatry Research*, *32*(2), 191–199.

Ateufack, G., Domgnim Mokam, E. C., Mbiantcha, M., Dongmo Feudjio, R. B., David, N., & Kamanyi, A. (2015). Gastroprotective and ulcer healing effects of piptadeniastrum Africanum on experimentally induced gastric ulcers in rats. *BMC Complementary and Alternative Medicine*, *15*(1), 214.

Aunger, R. (1994). Are food avoidances maladaptive in the Ituri Forest of Zaire? *Journal of Anthropological Research*, *50*(3), 277–310.

Aunger, R. (2000). The Life History of Culture Learning in a Face-to-Face Society. *Ethos*, *28*(3), 445–481.

Bahuchet, S. (1988). Food supply uncertainity among the Aka Pygmies (Lobaye, Central African Republic). In I. de Garine & G. Harrison (Eds.), *Coping with Uncertainty in Food Supply* (pp. 119–149). Oxford University Press.

Bahuchet, S. (1992). Spatial mobility and access to resources among the African Pygmies. In M. J. Casimir & A. Rao (Eds.), *Mobility and Territoriality. Social and Spatial Boundaries among Foragers, Fishers, Pastoralists and Peripatetics* (pp. 205–257). Oxford: Berg Publishers.

Bahuchet, S. (1999). Aka pygmies. In R. B. Lee & R. Daly (Eds.), *The Cambridge Encyclopedia of Hunter and Gatherers* (2004th ed., pp. 190–194). Cambridge Univ Press, Cambridge, UK.

Bahuchet, S. (2012). Changing language, remaining pygmy. *Human Biology*, *84*(1), 11–43.

Bahuchet, S. (2014). Cultural diversity of African Pygmies. In B. S. Hewlett (Ed.), *Hunter-Gatherers of the Congo Basin* (pp. 1–29). New Brunswick (U.S.A) and London (U.K).

Bahuchet, S., & Guillaume, H. (1982). Aka-farmer relations in the northwest Congo Basin. In E. Leacock & R. B. Lee (Eds.), *Politics and History in Band Societies* (pp. 189–211). Cambridge: Cambridge University Press.

Batini, C., Lopes, J., Behar, D. M., Calafell, F., Jorde, L. B., Van Der Veen, L., … Comas, D. (2011). Insights into the demographic history of African pygmies from complete mitochondrial genomes. *Molecular Biology and Evolution*, *28*(2), 1099–1110.

Becker, G. S., & Mulligan, C. B. (1997). The Endogenous Determination of Time Preference. *Q. J. Econ.*, *112*(3), 729–758.

Benz, B. F., Judith Cevallo, E., Francisco Santana, M., Jesus Rosales, A., & Graf, S. M. (2000).

Losing Knowledge about Plant Use in the Sierra de Manantlan Biosphere Reserve, Mexico. *Economic Botany*, *54*(2), 183–191.

Berkes, F., Colding, J., & Folke, C. (2000). Rediscovery of Traditional Ecological Knowledge as Adaptive Management. *Ecological Applications*, *10*(5), 1251–1262.

Bernhoft, A. (2010). A brief review on bioactive compounds in plants. In A. Bernhoft (Ed.), *Bioactive compounds in plants - benefits and risks for man and animals* (Vol. 50, pp. 11–17). Oslo: The Norwegian Academy of Science and Letters.

Betti, J. L. (2004). An ethnobotanical study of medicinal plants among the Baka pygmies in the Dja biosphere reserve, Cameroon. *African Study Monographs*, *25*(1), 1–27.

Betti, J. L., Yongo, O. D., Mbomio, D. O., Iponga, D. M., & Ngoye, A. (2013). An Ethnobotanical and Floristical Study of Medicinal Plants Among the Baka Pygmies in the Periphery of the Ipassa- Biosphere Reserve , Gabon. *European Journal of Medicinal Plants*, *3*, 174–205.

Bickii, J., Tchouya, G. R. F., Tchouankeu, J. C., & Tsamo, E. (2006). Antimalarial activity in crude extracts of some Cameroonian medicinal plants. *African Journal of Traditional, Complementary, and Alternative Medicines : AJTCAM / African Networks on Ethnomedicines*, *4*(1), 107–11.

Bird, D. W., & Bird, R. B. (2010). Competing to be leaderless. In K. J. Vaughn, J. W. Eerkens, & J. Kantner (Eds.), *The Evolution of Leadership* (pp. 21–49).

Bisong, S., Brown, R., & Osim, E. (2011). Comparative effects of Rauwolfia vomitoria and chlorpromazine on social behaviour and pain. *North American Journal of Medical Sciences*, *3*(1), 48–54.

Blackwell, A. D., Tamayo, M. A., Beheim, B., Trumble, B. C., Stieglitz, J., Hooper, P. L., … Gurven, M. (2015). Helminth infection, fecundity, and age of first pregnancy in women. *Science*, *350*(6263), 6–9.

Boehm, C. (1993). Egalitarian behavior and reverse dominance hierarchy. *Current Anthropology*, *34*(3), 227–254.

Boehm, C. (1999). *Hierarchy in the Forest. The Evolution of Egalitarian Behavior*. Harvard Univ Press, Cambridge, MA.

Bosch, C. H. (2008). Plant Resources of Tropical Africa 11(1). Medicinal plants 1. In G. H. Schmelzer & A. Gurib-Fakim (Eds.). PROTA Foundation, Wageningen, Netherlands/Backhuys Publishers, Leiden, Netherlands/CTA, Wageningen, Netherlands.

Boyd, R., & Richerson, P. J. (1985). *Culture and the Evolutionary Process*. Chicago: University of Chicago Press.

Boyd, R., & Richerson, P. J. (2005). *The origin and evolution of cultures*. *Journal of biology* (Vol. 8). Oxford University Press.

Brook, S. (2010, March 15). Biso na Biso 88FM, a local radio station in the Congo Basin. *Guardian*.

Brusotti, G., Tosi, S., Tava, A., Picco, A. M., Grisoli, P., Cesari, I., & Caccialanza, G. (2013). Antimicrobial and phytochemical properties of stem bark extracts from Piptadeniastrum africanum (Hook f.) Brenan. *Industrial Crops and Products*, *43*(1), 612–616.

Burkart, J. M., Allon, O., Amici, F., Fichtel, C., Finkenwirth, C., Heschl, A., … van Schaik, C. P. (2014). The evolutionary origin of human hyper-cooperation. *Nature Communications*, *5*, 4747.

Burkart, J. M., Hrdy, S. B., & Van Schaik, C. P. (2009). Cooperative breeding and human cognitive evolution. *Evolutionary Anthropology*, *18*(5), 175–186.

Byrne, R. (1996). Machiavellian intelligence. *Evolutionary Anthropology*, *5*(5), 172–180.

Caldwell, C. a, & Millen, A. E. (2010). Human cumulative culture in the laboratory: Effects of (micro) population size. *Learning & Behavior*, *38*(3), 310–318.

Cantor, M., Shoemaker, L. G., Cabral, R. B., Flores, C. O., Varga, M., & Whitehead, H. (2015). Multilevel animal societies can emerge from cultural transmission. *Nature Communications*, *6*, 8091.

Cantor, M., & Whitehead, H. (2013). The interplay between social networks and culture: theoretically and among whales and dolphins. *Philosophical Transactions of the Royal Society B*, *368*, 20120340.

Carvalho, S., Biro, D., Cunha, E., Hockings, K., McGrew, W. C., Richmond, B. G., & Matsuzawa, T. (2012). Chimpanzee carrying behaviour and the origins of human bipedality. *Current Biology*, *22*(6), R180–R181.

Cavalli-Sforza, L. (Ed.). (1986). African Pygmies. Orlando, Florida: Academic Press.

Cavalli-Sforza, L. L. (2001). *Genes, Peoples and Languages*. Penguin.

Cavalli-Sforza, L. L., & Feldman, M. W. (1981). *Cultural Transmission and Evolution: A Quantitative Approach*. Princeton Univ. Press.

Cavalli-Sforza, L. L., & Feldman, M. W. (1982). Theory and observation in cultural transmission. *Science*, *218*(4567), 19–27.

Cavalli-Sforza, L. L., Zonta, L. a, Nuzzo, F., Bernini, L., De Jong, W. W., Meera Khan, P., … Modiano, G. (1969). Studies on African Pygmies. I. A pilot investigation of Babinga Pygmies in the Central African Republic (with an analysis of genetic distances). *American Journal of Human Genetics*, *21*(3), 252–274.

Chapais, B. (2008). *Primeval kinship: how pair-bonding gave birth to human society*. Cambridge, MA: Harvard University Press.

Chapais, B. (2010). The deep structure of human society: primate origins and evolution. In P. M. Kappeler & J. B. Silk (Eds.), *Mind the Gap Tracing the Origins of Human Universals* (Vol. 32, pp. 19–51). Berlin: Springer.

Chapais, B. (2013). Monogamy, strongly bonded groups, and the evolution of human social structure. *Evolutionary Anthropology*, *22*(2), 52–65.

Chaudhary, N., Salali, G. D., Thompson, J., Dyble, M., Page, A., Smith, D., … Migliano, A. B. (2015). Polygyny without wealth: popularity in gift games predicts polygyny in BaYaka Pygmies. *Royal Society Open Science*, *2*(5), 150054.

Chaudhary, N., Salali, G. D., Thompson, J., Rey, A., Gerbault, P., Stevenson, E. G. J., … Gilbert, P. (2016). Competition for Cooperation: variability, benefits and heritability of relational wealth in hunter-gatherers. *Scientific Reports*, *6*, 29120.

Cole, T. J., Flegal, K. M., Nicholls, D., & Jackson, A. a. (2007). Body mass index cut offs to define thinness in children and adolescents: international survey. *BMJ (Clinical Research Ed.)*, *335*, 1–8.

Collard, M., Buchanan, B., O'Brien, M. J., & Scholnick, J. (2013). Risk, mobility or population size? Drivers of technological richness among contact-period western North American hunter-gatherers. *Philosophical Transactions of the Royal Society B*, *368*, 20120412.

Collard, M., Shennan, S. J., & Tehrani, J. J. (2006). Branching, blending, and the evolution of cultural similarities and differences among human populations. *Evolution and Human Behavior*, *27*(3), 169–184.

Cook, F. E. M. (1995). *Economic Botany Data Collection Standard. Prepared for the International Working Group on Taxonomic Databases for Plant Sciences (TDWG).* Kew: Royal Botanic Gardens, Kew.

Coster, A. (2012). Package "pedigree."

Cotula, L., Vermeulen, S., Leonard, R., & Keeley, J. (2009). *Land grab or development opportunity? Agricultural investment and international land deals in Africa*. London/Rome: IIED/FAO/IFAD. https://doi.org/978-1-84369-741-1

Cousins, D., & Huffman, M. A. (2002). Medicinal Properties in the Diet of Gorillas : an Ethno-Pharmacological Evaluation. *African Study Monographs*, *23*(2), 65–89.

Daly, M., & Wilson, M. (2005). Carpe diem: Adaptation and devaluing the future. *The Quarterly Review of Biology*, *80*(1), 55–60.

Davis, S. G., Vale, G. L., Schapiro, S. J., Lambeth, S. P., & Whiten, A. (2016). Foundations of cumulative culture in apes: improved foraging efficiency through relinquishing and combining witnessed behaviors in chimpanzees (Pan troglodytes). *Scientific Reports*, *6*, 35953.

Dean, L. G., Kendal, R. L., Schapiro, S. J., Thierry, B., & Laland, K. N. (2012). Identification of the Social and Cognitive Processes Underlying Human Cumulative Culture. *Science*, *335*(6072), 1114–1118.

Dean, L. G., Vale, G. L., Laland, K. N., Flynn, E., & Kendal, R. L. (2014). Human cumulative culture: A comparative perspective. *Biological Reviews*, *89*(2), 284–301.

Derex, M., Beugin, M. P., Godelle, B., & Raymond, M. (2013). Experimental evidence for the influence of group size on cultural complexity. *Nature*, *503*(7476), 389–391.

Derex, M., & Boyd, R. (2015). The foundations of the human cultural niche. *Nature Communications*, *6*, 1–7.

Derex, M., & Boyd, R. (2016). Partial connectivity increases cultural accumulation within groups. *Proceedings of the National Academy of Sciences*, *113*(11), 2982–2987.

Diamond, J. (1978). The Tasmanians: the longest isolation, the simplest technology. *Nature*, *273*, 185–186.

Díaz-Reviriego, I., González-Segura, L., Fernández-Llamazares, Á., Howard, P. L., Molina, J. L., & Reyes-García, V. (2016). Social organization influences the exchange and species richness of medicinal plants in Amazonian homegardens. *Ecology and Society*, *21*(1), 1.

Dimo, T., Ngueguim, F. T., Kamtchouing, P., Dongo, E., & Tan, P. V. (2006). Glucose lowering efficacy of the aqueous stem bark extract of Trema orientalis (Linn) Blume in normal and streptozotocin diabetic rats. *Die Pharmazie*, *61*(3), 233–6.

Dunbar, R. I. M. (1991). Functional significance of social grooming in primates. *Folia Primatologica*, *57*(3), 121–131.

Dunbar, R. I. M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evolution*, *22*, 469–493.

Dunbar, R. I. M. (1993). Coevolution of neocortical size, group size and language in humans. *Behavioral and Brain Sciences*, *16*, 681–735.

Dunbar, R. I. M. (1998). Theory of mind and the evolution of language. In M. Studdert-Kennedy & C. Knight (Eds.), *Approaches to the Evolution of Language* (pp. 92–110).

Dunbar, R. I. M. (2004). Gossip in Evolutionary Perspective. *Review of General Psychology*, *8*(2), 100–110.

Dunbar, R. I. M. (2016). Group size, vocal grooming and the origins of language. *Psychonomic Bulletin & Review*, 1–4.

Dunn, F. L. (1968). Epidemiological factors: Health and disease in hunter-gatherers. In R. B. Lee & I. DeVore (Eds.), *Man the hunter*. Chicago: Aldine.

Durham, W. H. (1991). *Co-evolution: Genes, Culture and Human Diversity*. Stanford Univ. Press.

Dyble, M., Salali, G. D., Chaudhary, N., Page, A., Smith, D., Thompson, J., … Migliano, A. B. (2015). Sex equality can explain the unique social structure of hunter-gatherer bands. *Science*, *348*(6236), 796–798.

Dyble, M., Thompson, J., Smith, D., Salali, G. D., Chaudhary, N., Page, A. E., … Migliano, A. B. (2016). Networks of Food Sharing Reveal the Functional Significance of Multilevel Sociality in Two Hunter- Gatherer Groups. *Current Biology*, *26*, 1–5.

Erdal, D., & Whiten, A. (1994). On Human Egalitarianism: An Evolutionary Product of Machiavellian Status Escalation? *Current Anthropology*, *35*(2), 175–183.

Erharuyi, O., Falodun, A., & Langer, P. (2014). Medicinal uses, phytochemistry and pharmacology of Picralima nitida (Apocynaceae) in tropical diseases: A review. *Asian Pacific Journal of Tropical Medicine*, *7*(1), 1–8.

Evans, T. A., & Beran, M. J. (2007). Chimpanzees use self-distraction to cope with impulsivity. *Biology Letters*, *3*(6), 599–602.

Fabricant, D. S., & Farnsworth, N. R. (2001). The value of plants used in traditional medicine for drug discovery. *Environmental Health Perspectives*, *109*(SUPPL. 1), 69–75.

Foley, R. A., & Gamble, C. (2009). The ecology of social transitions in human evolution. *Philosophical Transactions of the Royal Society B*, *364*, 3267–3279.

Frederick, S., Loewenstein, G., & O'Donoghue, T. (2002). Time discounting and time preference: a critical review. *Journal of Economic Literature*, *XL*, 351–401.

Froment, A. (2001). Evolutionary biology and health of hunter-gatherer populations. *Hunter-Gatherers: An Interdisciplinary Perspective*, 239–266.

Froment, A. (2014). Human Biology and Helath of African Rainforest Inhabitants. In B. S. Hewlett (Ed.), *Hunter-Gatherers of the Congo Basin* (pp. 117–164). New Brunswick (U.S.A) and London (U.K): Transaction Publishers.

Galef, B. G., & Laland, K. N. (2005). Social Learning in Animals: Empirical Studies and Theoretical Models. *BioScience*, *55*(6), 489.

Gavrilets, S. (2012a). Human origins and the transition from promiscuity to pair-bonding. *Proceedings of the National Academy of Sciences*, *109*(25), 9923–8.

Gavrilets, S. (2012b). On the evolutionary origins of the egalitarian syndrome. *Proceedings of the National Academy of Sciences*, *109*(35), 14069–74.

Gillet, J.-F., & Doucet, J.-L. (2012). A commented checklist of woody plants in the Northern Republic of Congo. *Plant Ecology and Evolution*, *145*(2), 258–271.

Gillet, J. F., & Doucet, J. L. (2012). A commented checklist of woody plants in the Northern Republic of Congo. *Plant Ecology and Evolution*, *145*(2), 258–271.

Godoy, R., Byron, E., Reyes-García, V., Leonard, W. R., Patel, K., Apaza, L., … Wilkie, D. (2004). Patience in a foraging-horticultural society: a test of competing hypotheses. *Journal of Anthropological Archaeology*, *60*(2), 179–202.

Godoy, R., & Jacobson, M. (1999). Covariates of private time preference: a pilot study among the Tsimane'Indians of the Bolivian rain forest. *Evolution and Human Behavior*, *20*, 249–256.

Godoy, R., & Reyes-García, V. (2009). Long-term (secular) change of ethnobotanical knowledge of useful plants: separating cohort and age effects. *Journal of Anthropological Research*, *65*, 51–67.

Godoy, R., Reyes-García, V., Byron, E., Leonard, W., & Vadez, V. (2005). The effect of market economies on the well-being of indigenous peoples and on their use of renewable natural resources. *Annu. Rev. Anthropol.*, *34*, 121–138.

Gomez-Baggethun, E., Mingorria, S., Reyes-García, V., Calvet, L., & Montes, C. (2010). Traditional Ecological Knowledge Trends in the Transition to a Market Economy: Empirical Study in the Donana Natural Areas. *Conservation Biology*, *24*(3), 721–729.

Gómez-Baggethun, E., & Reyes-García, V. (2013). Reinterpreting Change in Traditional Ecological Knowledge. *Human Ecology*, *41*(4), 643–647.

Gowlett, J. A. J. (2008). Deep roots of kin: Developing the evolutionary perspective from prehistory. In N. Allen, H. Callan, R. Dunbar, & W. James (Eds.), *Early Human Kinship: From Sex to Social Reproduction* (pp. 41–57). Wiley-Blackwell, Oxford.

Griskevicius, V., & Tybur, J. (2011). The Influence of Mortality and Socioeconomic Status on Risk and delayed rewards: a life history theory approach. *J Pers Soc Psychol.*, *100*(6), 1015–1026.

Grueter, C. C., Chapais, B., & Zinner, D. (2012). Evolution of Multilevel Social Systems in Nonhuman Primates and Humans. *International Journal of Primatology*, *33*(5), 1002–1037.

Hamilton, M. J., Milne, B. T., Walker, R. S., Burger, O., & Brown, J. H. (2007). The complex structure of hunter-gatherer social networks. *Proceedings of the Royal Society B*, *274*, 2195–202.

Hamilton, W. D. (1964). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, *7*(1), 1–16.

Harari, Y. N. (2011). *Sapiens: A Brief History of Humankind*. Penguin.

Hattori, S. (2006a). Diversity and variability of plant knowledge among adult Baka hunter-gatherers in Cameroonian rainforests. In *Proceeding of Kyoto Symposium* (pp. 229–235).

Hattori, S. (2006b). Utilization of marantaceae plants by the Baka hunter-gatherers in southeastern Cameroon. *African Study Monographs*, (May), 29–48.

Havyarimana, L., Ndendoung, S. T., Tamokou, J. D. D., Atchadé, A. D. T., & Tanyi, J. M. (2012). Chemical constituents of Millettia barteri and their antimicrobial and antioxidant activities. *Pharmaceutical Biology*, *50*(2), 141–6.

Hawkes, K. (2000). Hunting and the evolution of egalitarian societies: lessons from the Hadza. In M. Diehl (Ed.), *Hierarchies in action: cui bono?* (pp. 59–83). Center for Archaeological Investigations Occasional Paper.

Hawkes, K., O'Connell, J. F., Blurton Jones, N. G., Alvarez, H., & Charnov, E. L. (1998). Grandmothering, menopause, and the evolution of human life histories. *Proceedings of the National Academy of Sciences*, *95*(3), 1336–1339.

Henrich, J. (2004). Demography and cultural evolution: how adaptive cultural processes can produce maladaptive losses: the Tasmanian case. *American Antiquity*, *69*(2), 197–214.

Henrich, J., & Boyd, R. (1998). The evolution of conformist transmission and the emergence of between-group differences. *Evolution and Human Behavior*, *19*(4), 215–241.

Henrich, J., Boyd, R., & Richerson, P. J. (2012). The puzzle of monogamous marriage. *Philosophical Transactions of the Royal Society B*, *367*(1589), 657–69.

Henrich, J., & Broesch, J. (2011). On the nature of cultural transmission networks: evidence from Fijian villages for adaptive learning biases. *Philosophical Transactions of the Royal Society B*, *366*(1567), 1139–48.

Henrich, J., & Gil-White, F. J. (2001a). The evolution of prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior*, *22*(3), 165–196.

Henrich, J., & Gil-White, F. J. J. (2001b). The evolution of prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior*, *22*(3), 165–196.

Henrich, J., & Henrich, N. (2010). The evolution of cultural adaptations: Fijian food taboos protect against dangerous marine toxins. *Proceedings of the Royal Society B*, *277*(1701), 3715–24.

Hewlett, B. S. (Ed.). (2014). *Hunter-Gatherers of the Congo Basin*. New Brunswick New jersey: Transaction Publishers.

Hewlett, B. S., & Cavalli-Sforza, L. L. (1986). Cultural transmission among Aka pygmies. *American Anthropologist*, *88*(4), 922–934.

Hewlett, B. S., Fouts, H. N., Boyette, A. H., & Hewlett, B. L. (2011). Social learning among Congo Basin hunter–gatherers. *Philosophical Transactions of the Royal Society B*, *366*(1567), 1168–78.

Hewlett, B. S., Koppel, J. Van De, & Cavalli-Sforza, L. L. (1982). Exploration ranges of Aka pygmies of the Central African Republic. *Man*, *17*(3), 418–430.

Hewlett, B. S., & Roulette, C. J. (2016). Teaching in hunter – gatherer infancy. *Royal Society Open Science*, *3*, 150403.

Hewlett, B. S., van de Koppel, J. M. H., & van de Koppel, M. (1986). Causes of Death among Aka Pygmies of the Central African Republic. In L. Cavalli- Sforza (Ed.), *African Pygmies* (pp. 45–63). New York: Academic Press.

Hill, K., Barton, M., & Magdalena Hurtado, a. (2009). The emergence of human uniqueness: Characters underlying behavioral modernity. *Evolutionary Anthropology*, *18*(5), 187–200.

Hill, K., & Hurtado, A. M. (1996). *Ache Life History: The Ecology and Demography of a Foraging People.* Aldine Press.

Hill, K., & Hurtado, A. M. (2009). Cooperative breeding in South American hunter-gatherers. *Proceedings of the Royal Society B*, *276*(1674), 3863–70.

Hill, K., Walker, R. S., Bozicević, M., Eder, J., Headland, T., Hewlett, B. S., … Wood, B. (2011). Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science*, *331*(6022), 1286–89.

Hill, K., Wood, B. M., Baggio, J., Hurtado, A. M., & Boyd, R. T. (2014). Hunter-gatherer inter-band interaction rates: implications for cumulative culture. *PloS One*, *9*(7), e102806.

Hoffman, D. L., & Leeuw, J. (1992). Interpreting multiple correspondence analysis as a multidimensional scaling method. *Marketing Letters*, *3*, 259–272.

Hohmann, G., Robbins, M., & Boesch, C. (2006). *Feeding ecology in apes and other primates* (Vol. 48). Cambridge University Press.

Holden, C. J., & Mace, R. (2003). Spread of cattle led to the loss of matrilineal descent in Africa: a coevolutionary analysis. *Proceedings of the Royal Society B*, *270*(1532), 2425–33.

Holden, C. J., & Mace, R. (2009). Phylogenetic Analysis of the Evolution of Lactose Digestion in Adults. *Human Biology*, *81*, 597–619.

Hooper, P. L., Kaplan, H. S., & Boone, J. L. (2010). A theory of leadership in human cooperative groups. *Journal of Theoretical Biology*, *265*(4), 633–646.

Horner, V., & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (Pan troglodytes) and children (Homo sapiens). *Animal Cognition*, *8*(3), 164–81.

Hrdy, S. B. (2009). *Mothers and Others: The Evolutionary Origins of Mutual Understanding*. Cambridge, MA: Harvard University Press.

Huffman, M. A. (1997). Current evidence for self- medication in primates: A multidisciplinary perspective. *American Journal of Physical Anthropology*, *104*(S25), 171–200.

Huffman, M. A. (2001). Self-Medicative Behavior in the African Great Apes: An Evolutionary Perspective into the Origins of Human Traditional Medicine. *BioScience*, *51*(8), 651.

Huffman, M. A., Gotoh, S., Izutsu, D., Koshimizu, K., & Kalunde, M. S. (1993). Further observations on the use of the medicinal plant , Vernonia amygdalina (Del) by a wild chimpanzee, its possible effect on parasite load, and its phytochemistry. *African Study Monographs*, *14*, 227–240.

Huffman, M. A., & Hirata, S. (2004). An experimental study of leaf swallowing in captive chimpanzees: Insights into the origin of a self-medicative behavior and the role of social learning. *Primates*, *45*(2), 113–118.

Huffman, M. A., & Wrangham, R. W. (1994). Diversity of medicinal plant use by chimpanzees in the wild. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, & P. G. Heltne (Eds.), *Chimpanzee Cultures* (pp. 129–148). Harvard Univ Press, Cambridge, MA.

Ibrahim, B., Sowemimo, A., Van Rooyen, A., & Van De Venter, M. (2012). Antiinflammatory, analgesic and antioxidant activities of Cyathula prostrata (Linn.) Blume (Amaranthaceae). *Journal of Ethnopharmacology*, *141*(1), 282–289.

Jaeggi, A. V., Dunkel, L. P., van Noordwijk, M. a., Wich, S. a., Sura, A. a L., & van Schaik, C. P. (2010). Social learning of diet and foraging skills by wild immature Bornean orangutans: Implications for culture. *American Journal of Primatology*, *72*(1), 62–71.

Johnson, G. A. (1982). Organizational structure and scalar stress. In C. Renfrew, M. Rowlands, & B. A. Segraves (Eds.), *Theory and explanation in archaeology* (pp. 389–421). Academic Press New York.

Jones, R. (1977). The Tasmanian Paradox. In V. S. Wright (Ed.), *In Stone Tools As Cultural Markers: Change, Evolution and Complexity*. New Jersey: Humanities Press.

Jones, R. (1995). Tasmanian Archaeology: Establishing the Sequences. *Annual Review of Anthropology*, *24*, 423–446.

Kamanzi Atindehou, K., Schmid, C., Brun, R., Koné, M. W., & Traore, D. (2004). Antitrypanosomal and antiplasmodial activity of medicinal plants from Côte d'Ivoire. *Journal of Ethnopharmacology*, *90*(2–3), 221–227.

Kaplan, H. S., Gurven, M. D., & Lancaster, J. B. (2007). Brain evolution and the human adaptive complex: An ecological and social theory. In S. Gangestad & J. A. Simpson (Eds.), *The evolution of mind: Fundamental questions and controversies* (pp. 269–279). New York: Guilford Press.

Kaplan, H. S., Gurven, M., Winking, J., Hooper, P. L., & Stieglitz, J. (2010). Learning, menopause, and the human adaptive complex. *Annals of the New York Academy of Sciences*, *1204*, 30–42.

Kaplan, H. S., Hill, K., Lancaster, J., & Hurtado, A. M. (2000). A theory of human life history evolution: diet, intelligence, and longevity. *Evolutionary Anthropology*, *9*, 156–185.

Kaplan, H. S., & Lancaster, J. B. (2003). An evolutionary and ecological analysis of human fertility, mating patterns, and parental investment. In K. W. Wachter & R. A. Bulatao (Eds.), *Offspring: human fertility behavior in biodemographic perspective* (pp. 223–270).

Kappeler, P. M., & Van Schaik, C. P. (2002). Evolution of primate social systems. *Int. J. Primatol.*, *23*(4), 707–740.

Kelly, R. L. (2013). *The Lifeways of Hunter-Gatherers: The Foraging Spectrum*. Cambridge University Press.

Kempe, M., & Mesoudi, A. (2014). An experimental demonstration of the effect of group size on cultural accumulation. *Evolution and Human Behavior*, *35*(4), 285–290.

Kendal, J., Tehrani, J. J., & Odling-Smee, J. (2011). Human niche construction in interdisciplinary focus. *Philosophical Transactions of the Royal Society B*, *366*(1566), 785–792.

Kimura, D. (2013). Constructing AFlora: A Database of Plant Use In Africa. *African Study Monographs*, *34*(3), 143–159.

Kirby, K. N., Godoy, R., Reyes-García, V., Byron, E., Apaza, L., Leonard, W., … Wilkie, D. (2002). Correlates of delay-discount rates: Evidence from Tsimane’ Amerindians of the Bolivian rain forest. *Journal of Economic Psychology*, *23*, 291–316.

Kitanishi, K. (1995). Seasonal changes in the subsistence activities and food intake of the Aka hunter-gatherers in northeastern Congo. *African Study Monographs*, *16*(2), 73–118.

Kitanishi, K. (2006). The impact of cash and commoditization on the Baka hunter-gatherer society in southeastern Cameroon. *African Study Monographs*, *33*, 121–142.

Kline, M. a, & Boyd, R. (2010). Population size predicts technological complexity in Oceania. *Proceedings of the Royal Society B*, *277*(1693), 2559–2564.

Kohler, A., & Lewis, J. (2002). Putting Hunter-Gatherer and Farmer Relations in Perspective. A Commentary from Central Africa. In S. Kent (Ed.), *Ethnicity, Hunter-Gatherers, and the "Other": Association or Assimilation in Southern Africa?* (pp. 276–306). Smithsonian Institute: Washington.

Kouam, S. F., Kusari, S., Lamshöft, M., Tatuedom, O. K., & Spiteller, M. (2012). Sapelenins G-J, acyclic triterpenoids with strong anti-inflammatory activities from the bark of the Cameroonian medicinal plant Entandrophragma cylindricum. *Phytochemistry*, *83*, 79–86.

Kramer, K. L. (2010). Cooperative Breeding and its Significance to the Demographic Success of Humans. *Annual Review of Anthropology*, *39*(1), 417–436.

Kramer, K. L. (2011). The evolution of human parental care and recruitment of juvenile help. *Trends in Ecology & Evolution*, *26*(10), 533–540.

Krief, S., Hladik, C. M., & Haxaire, C. (2005). Ethnomedicinal and bioactive properties of plants ingested by wild chimpanzees in Uganda. *Journal of Ethnopharmacology*, *101*(1–3), 1–15.

Kumar, R., Sharma, R. J., Bairwa, K., Roy, R. K., & Kumar, A. (2010). Pharmacological review on natural antidiarrhoel agents. *Der Pharma Chemica*, *2*(2), 66–93.

Laland, K. N., & Hoppitt, W. (2003). Do Animals Have Culture? *Evolutionary Anthropology*, *12*(3), 150–159.

Lamidi, M., DiGiorgio, C., Delmas, F., Favel, a, Eyele Mve-Mba, C., Rondi, M. L., … Balansard, G. (2005). In vitro cytotoxic, antileishmanial and antifungal activities of ethnopharmacologically selected Gabonese plants. *Journal of Ethnopharmacology*, *102*(2), 185–90.

Lamidi, M., Ollivier, E., Gasquet, M., Faure, R., Nzé-Ekekang, L., & Balansard, G. (1996). Structural and Antimalarial Studies of Saponins from Nauclea diderrichii Bark. In G. Waller & K. Yamasaki (Eds.), *Saponins Used in Traditional and Modern Medicine* (Vol. 404, pp. 383–399). Springer US.

Langergraber, K. E., Mitani, J. C., & Vigilant, L. (2007). The limited impact of kinship on cooperation in wild chimpanzees. *Proceedings of the National Academy of Sciences*, *104*(19), 7786–7790.

Laporte, N. T., Stabach, J. A., Grosch, R., Lin, T. S., & Goetz, S. J. (2007). Expansion of industrial logging in Central Africa. *Science*, *316*(5830), 1451.

Le, S., Josse, J., & Husson, F. (2008). FactoMineR: an R package for multivariate analysis. *Journal of Statistical Software*, *25*(1), 1–18.

le Roux, A., Beehner, J. C., & Bergman, T. J. (2011). Female philopatry and dominance patterns in wild geladas. *American Journal of Primatology*, *73*(5), 422–430.

Lee, R. B. (1982). Politics, sexual and non-sexual, in an egalitarian society. In *Politics and history in band societies* (pp. 37–59).

Lee, R. B., & Daly, R. (2004). *The Cambridge Encyclopedia of Hunters and Gatherers*. (R. B. Lee & R. Daly, Eds.). Cambridge University Press.

Leeson, P. T., & Coyne, C. J. (2012). Sassywood. *Journal of Comparative Economics*, *40*(4), 608–620.

Lévi-Strauss, C. (1969). *The elementary structures of kinship*. Boston: Beacon Press.

Lewis, H. M., & Laland, K. N. (2012). Transmission fidelity is the key to the build-up of cumulative culture. *Philosophical Transactions of the Royal Society B*, *367*(1599), 2171–2180.

Lewis, H. M., Vinicius, L., Strods, J., Mace, R., & Migliano, A. B. (2014). High mobility explains demand sharing and enforced cooperation in egalitarian hunter-gatherers. *Nature Communications*, *5*, 5789.

Lewis, J. (2002). *PhD Thesis. Forest hunter-gatherers and their world: A Study of the Mbendjele Yaka Pygmies of Congo-Brazzaville and Their Secular and Religious Activities and Representations*. London School of Economics and Political Science.

Lewis, J. (2005). Whose forest is it anyway? Mbendjele Yaka pygmies, the Ndoki Forest and the wider world. In T. Widlok & W. Tadesse (Eds.), *Property and Equality, Vol. 2 Encapsulation, Commercialisation, Discrimination* (pp. 56–78). Berghahn Books.

Lewis, J. (2008a). Ekila: blood, bodies, and egalitarian societies. *Journal of the Royal Anthropological Institute*, (1989), 297–315.

Lewis, J. (2008b). Maintaining abundance, not chasing scarcity: the big challenge for the twenty-first century. *Radical Anthropology Group Journal*, *2*, 7–18.

Lewis, J. (2014a). BaYaka Pygmy multi-modal and mimetic communication traditions as suggestive of the social origins of language. In D. Dor, C. Knight, & J. Lewis (Eds.), *Social origins of language*. Oxford Studies in the Evolution of Language.

Lewis, J. (2014b). Egalitarian social organization: the case of the Mbendjele BaYaka. In B. S. Hewlett (Ed.), *Hunter-Gatherers of the Congo Basin* (pp. 219–243). New Brunswick (U.S.A) and London (U.K): Transaction Publishers.

Lewis, J. (2015). Where goods are free but knowledge costs: the economics of ritual among forest hunter-gatherers in Western Central Africa. *Hunter Gatherer Research*, *1*(1), 1–27.

Lovejoy, C. O. (1981). The Origin of Man. *Science*, *211*(4480), 341–350.

Lukas, D., & Clutton-Brock, T. H. (2013). The evolution of social monogamy in mammals. *Science*, *341*(6145), 526–30.

Lyons, D. E., Damrosch, D. H., Lin, J. K., Macris, D. M., & Keil, F. C. (2011). The scope and limits of overimitation in the transmission of artefact culture. *Philosophical Transactions of the Royal Society B*, *366*(1567), 1158–67.

Lyons, D. E., Young, A. G., & Keil, F. C. (2007). The hidden structure of overimitation. *Proceedings of the National Academy of Sciences*, *104*(50), 19751–6.

Mace, R. (2000). Evolutionary ecology of human life history. *Animal Behaviour*, *59*(1), 1–10.

Marlowe, F. W. (2000). Paternal investment and the human mating system. *Behavioural Processes*, *51*(1–3), 45–61.

Marlowe, F. W. (2004). Marital residence among foragers. *Current Anthropology*, *45*(2), 277–284.

Marlowe, F. W. (2005). Hunter-gatherers and human evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, *14*(2), 54–67.

Marlowe, F. W. (2010). *The Hadza: Hunter-gatherers of Tanzania*. University of California Press.

Masi, S., Gustafsson, E., Saint Jalme, M., Narat, V., Todd, A., Bomsel, M. C., & Krief, S. (2012). Unusual feeding behavior in wild great apes, a window to understand origins of self-medication in humans: Role of sociality and physiology on learning process. *Physiology and Behavior*, *105*(2), 337–349.

Mbaze, L. M. a, Poumale, H. M. P., Wansi, J. D., Lado, J. A., Khan, S. N., Iqbal, M. C., … Laatsch, H. (2007). a-Glucosidase inhibitory pentacyclic triterpenes from the stem bark of Fagara tessmannii (Rutaceae). *Phytochemistry*, *68*(5), 591–595.

McDade, T. W., Reyes-García, V., Blackinton, P., Tanner, S., Huanca, T., & Leonard, W. R. (2007). Ethnobotanical knowledge is associated with indices of child health in the Bolivian Amazon. *Proceedings of the National Academy of Sciences*, *104*(15), 6134–9.

Meehan, C. L., Helfrecht, C., & Quinlan, R. J. (2014). Cooperative breeding and Aka children's nutritional status: Is flexibility key? *American Journal of Physical Anthropology*, *153*, 513–525.

Meehan, C. L., Quinlan, R., & Malcom, C. D. (2013). Cooperative breeding and maternal energy expenditure among aka foragers. *American Journal of Human Biology*, *25*(1), 42–

57.

Mellars, P. (2005). The impossible coincidence. A single-species model for the origins of modern human behavior in Europe. *Evolutionary Anthropology: Issues, News, and Reviews*, *14*(1), 12–27.

Memvanga, P. B., Tona, G. L., Mesia, G. K., Lusakibanza, M. M., & Cimanga, R. K. (2015). Antimalarial activity of medicinal plants from the democratic republic of Congo: A review. *Journal of Ethnopharmacology*, *169*, 76–98.

Mesia, G. K., Tona, G. L., Nanga, T. H., Cimanga, R. K., Apers, S., Cos, P., … Vlietinck, a. J. (2007). Antiprotozoal and cytotoxic screening of 45 plant extracts from Democratic Republic of Congo. *Journal of Ethnopharmacology*, *115*(3), 409–415.

Mesman, J., Minter, T., Angnged, A., Cissé, I. A. H., Salali, G. D., & Migliano, A. B. (2017). Universality without Uniformity: A Culturally Inclusive Approach to Sensitive Responsiveness in Infant Caregiving. *Child Development*, *in press*.

Mesoudi, A. (2011). *Cultural Evolution*. University of Chicago Press, Chicago.

Mesoudi, A. (2016). Cultural Evolution: A Review of Theory, Findings and Controversies. *Evolutionary Biology*, *43*, 481.

Mesoudi, A., Whiten, A., & Dunbar, R. I. M. (2006). A bias for social information in human cultural transmission. *British Journal of Psychology*, *97*, 405–23.

Mesoudi, A., Whiten, A., & Laland, K. N. (2004). Perspective: Is Human Cultural Evolution Darwinian? Evidence Reviewed From The Perspective Of The Origin Of Species. *Evolution*, *58*(1), 1–11.

Mesoudi, A., Whiten, A., & Laland, K. N. N. (2006). Towards a unified science of cultural evolution. *Behavioral and Brain Sciences*, *29*(4), 329–347.

Migliano, A. B., Page, A., Gomez-Gardenes, J., Salali, G. D., Viguier, S., Dyble, M., … V., L. (2017). Characterisation of hunter-gatherer networks and implications for cumulative culture. *Nature Human Behaviour*, *1*, 43.

Migliano, A. B., Vinicius, L., & Lahr, M. M. (2007). Life history trade-offs explain the evolution of human pygmies. *Proceedings of the National Academy of Sciences*, *104*(51), 20216–9.

Mühlhoff, N., Stevens, J. R., & Reader, S. M. (2011). Spatial discounting of food and social rewards in guppies (poecilia reticulata). *Frontiers in Psychology*, *2*(April), 68.

Musuyu Muganza, D., Fruth, B. I., Nzunzu Lami, J., Mesia, G. K., Kambu, O. K., Tona, G. L., … Pieters, L. (2012). In vitro antiprotozoal and cytotoxic activity of 33 ethonopharmacologically selected medicinal plants from Democratic Republic of Congo. *Journal of Ethnopharmacology*, *141*(1), 301–308.

Neuwinger, H. D. (2004). Plants used for poison fishing in tropical Africa. *Toxicon*, *44*(4), 417–430.

Ngamga, D., Fanso Free, S. N. Y., Tane, P., & Fomum, Z. T. (2007). Millaurine A, a new guanidine alkaloid from seeds of Millettia laurentii. *Fitoterapia*, *78*(3), 276–7.

Oishi, T. (2012). Cash crop cultivation and interethnic relations of the Baka hunter-gatherers in Southeastern Cameroon. *African Study Monographs*, *43*, 115–136.

Okany, C. C., Ishola, I. O., & Ashorobi, R. B. (2012). Evaluation of analgesic and antistress potential of methanolic stem wood extract of Microdesmis puberula Hook.f. Ex Planch (Pandaceae) in mice. *International Journal of Applied Research in Natural Products*, *5*(3), 30–36.

Olatokunboh, A. O., Kayode, Y. O., & Adeola, O. K. (2009). Anticonvulsant Activity of Rauvolfia vomitoria (Afzel). *African Journal of Pharmacy and Pharmacology*, *3*(6), 319–322.

Olivero, J., Fa, J. E., Farfán, M. A., Lewis, J., Hewlett, B., Breuer, T., … Nasi, R. (2016). Distribution and numbers of Pygmies in Central African forests. *PLoS ONE*, *11*(1), 1–16.

Onguéné, P. A., Ntie-Kang, F., Lifongo, L. L., Ndom, J. C., Sippl, W., & Mbaze, L. M. (2014). The potential of anti-malarial compounds derived from African medicinal plants, part II: a pharmacological evaluation of non-alkaloids and non-terpenoids. *Malaria Journal*, *13*(1), 81.

Opie, C., Atkinson, Q. D., Dunbar, R. I. M., & Shultz, S. (2013). Male infanticide leads to social monogamy in primates. *Proceedings of the National Academy of Sciences*, *110*(33), 13328–32.

Opie, C., Atkinson, Q. D., & Shultz, S. (2012). The evolutionary history of primate mating systems. *Communicative and Integrative Biology*, *5*(5), 458–461.

Page, A. E., Viguier, S., Dyble, M., Smith, D., Chaudhary, N., Salali, G. D., … Migliano, A. B. (2016). Reproductive trade-offs in extant hunter-gatherers suggest adaptive mechanism for the Neolithic expansion. *Proceedings of the National Academy of Sciences*, *113*(17), 201524031.

Pampiglione, S., & Ricciardi, M. L. (1986). Parasitological surveys of Pygmy groups. In L. Cavalli- Sforza (Ed.), *African Pygmies* (pp. 153–167). New York: Academic Press.

Patin, E., Katherine, J. S., Guillaume, L., Hélène, Q., Harmant, C., Becker, N., … Quintana-Murci, L. (2014). The impact of agricultural emergence on the genetic history of African rainforest hunter-gatherers and agriculturalists. *Nature Communications*, *5*, 3163.

Patin, E., Laval, G., Barreiro, L. B., Salas, A., Semino, O., Santachiara-Benerecetti, S., … Quintana-Murci, L. (2009). Inferring the demographic history of African farmers and Pygmy hunter-gatherers using a multilocus resequencing data set. *PLoS Genetics*, *5*(4).

Pebsworth, P., Krief, S., & Huffman, M. A. (2006). The role of diet in self-medication among chimpanzees in the Sonso and Kanyawara Communities, Uganda. In N. E. Newton-Fisher, H. Notman, J. D. Paterson, & V. Reynolds (Eds.), *Primates of Western Uganda* (pp. 105–133). New York: Springer.

Perry, S. (2011). Social traditions and social learning in capuchin monkeys (Cebus). *Philosophical Transactions of the Royal Society B*, *366*(1567), 988–996.

Perry, S., Baker, M., Fedigan, L., Gros- Louis, J., Jack, K., MacKinnon, K. C., … Rose, L. (2003). Social Conventions in Wild White- faced Capuchin Monkeys: Evidence for Traditions in a Neotropical Primate. *Current Anthropology*, *44*(2), 241–268.

Pinker, S. (1994). *The language instinct. The new science of language and mind*. Penguin.

Pinker, S. (2010). Colloquium paper: the cognitive niche: coevolution of intelligence, sociality, and language. *Proceedings of the National Academy of Sciences*, *107 Suppl*, 8993–8999.

Pinker, S., & Bloom, P. (1992). Natural language and natural selection. *Behavioral and Brain Sciences*, *13*, 1–50.

Powell, A., Shennan, S., & Thomas, M. G. (2009). Late Pleistocene demography and the appearance of modern human behavior. *Science*, *324*(5932), 1298–301.

Project Bwanga: Training hunter-gatherer healers in Congo. (2016). Retrieved from http://www.bwanga.org/

Ramachandran, V. S. (2011). *The tell-tale brain. Unlocking the mystery of human nature*. Windmill Books.

Read, D. (2012). Population Size Does Not Predict Artifact Complexity: Analysis of Data from Tasmania, Arctic Hunter-Gatherers, and Oceania. *UCLA: Human Complex Systems*.

Reyes-García, V., Broesch, J., Calvet-Mir, L., Fuentes-Peláez, N., McDade, T. W., Parsa, S., … Martínez-Rodríguez, M. R. (2009). Cultural transmission of ethnobotanical knowledge and skills: an empirical analysis from an Amerindian society. *Evolution and Human Behavior*, *30*(4), 274–285.

Reyes-García, V., Godoy, R., Huanca, T., Leonard, W. R., McDade, T. W., Tanner, S., & Vadez, V. (2007). The origins of monetary income inequality Patience, human capital, and division of labor. *Evolution and Human Behavior*, *28*(1), 37–47.

Reyes-García, V., Godoy, R., Vadez, V., & Apaza, L. (2003). Ethnobotanical knowledge shared widely among Tsimane'Amerindians, Bolivia. *Science*, *299*, 2451.

Reyes-García, V., Guèze, M., Luz, A. C., Paneque-Gálvez, J., Macía, M. J., Orta-Martínez, M., … Rubio-Campillo, X. (2013). Evidence of traditional knowledge loss among a contemporary indigenous society. *Evolution and Human Behavior*, *34*(4), 249–257.

Reyes-García, V., Luz, A. C., Gueze, M., Paneque-Gálvez, J., Macía, M. J., Orta-martínez, M., … Team, T. B. S. (2013). Secular trends on traditional ecological knowledge: An analysis of changes in different domains of knowledge among Tsimané men. *Learning and Individual Differences*, *34*(93), 206–212.

Rice, R., & Van Cott, D. L. (2006). The emergence and performance of indigenous peoples' parties in South America: A subnational statistical analysis. *Comparative Political Studies*, *39*(6), 709–732.

Richerson, P. J., & Boyd, R. (1998). The evolution of human ultra-sociality. In I. Eibl-Eibesfeldt & F. K. Salter (Eds.), *Ideology, warfare, and indoctrinability* (pp. 71–96). New York: Berghahn Books.

Richerson, P. J., & Boyd, R. (2005). *Not By Genes Alone: How Culture Transformed Human Evolution*. Univ. of Chicago Press.

Richerson, P. J., Boyd, R., & Bettinger, R. L. (2009). Cultural innovations and demographic change. *Human Biology*, *81*(2–3), 211–235.

Riddell, M. (2013). Assessing the Impacts of Conservation and Commercial Forestry on Livelihoods in Northern Republic of Congo. *Conservation and Society*, *11*(3), 199–217.

Roe, D., Nelson, F., & Sandbrook, C. (Eds.). (2009). *Community management of natural resources in Africa: Impacts , experiences and future directions*. Natural Resource Issues No. 18.

Salali, G. D. (2014). Faces from the Mbendjele camps. Retrieved from https://congokongo.wordpress.com/2014/03/12/faces-from-the-mbendjele-camps/

Salali, G. D., Chaudhary, N., Thompson, J., Grace, O. M., Burgt, X. M. van der, Dyble, M., … Migliano, A. B. (2016). Knowledge-sharing networks in hunter-gatherers and the evolution of cumulative culture. *Current Biology*, *26*, 1–6.

Salali, G. D., Juda, M., & Henrich, J. (2015). Transmission and development of costly punishment in children. *Evolution and Human Behavior*, *36*(2), 86–94.

Salali, G. D., & Migliano, A. B. (2015). Future Discounting in Congo Basin Hunter-Gatherers Declines with Socio-Economic Transitions. *Plos One*, *10*(9), e0137806.

Salali, G. D., Whitehouse, H., & Hochberg, M. E. (2015). A Life-Cycle Model of Human Social Groups Produces a U-Shaped Distribution in Group Size. *Plos One*, *10*(9), e0138496.

Saslis-Lagoudakis, C. H., Klitgaard, B. B., Forest, F., Francis, L., Savolainen, V., Williamson, E. M., & Hawkins, J. A. (2011). The Use of Phylogeny to Interpret Cross-Cultural Patterns in Plant Use and Guide Medicinal Plant Discovery: An Example from Pterocarpus (Leguminosae). *PLoS ONE*, *6*(7), e22275.

Saslis-Lagoudakis, C. H., Savolainen, V., Williamson, E. M., Forest, F., Wagstaff, S. J., Baral, S. R., … Hawkins, J. A. (2012). Phylogenies reveal predictive power of traditional medicine in bioprospecting. *Proceedings of the National Academy of Sciences*, *109*(39), 15835–40.

Saslis-Lagoudakis, C. H., Williamson, E. M., Savolainen, V., & Hawkins, J. a. (2011). Cross-cultural comparison of three medicinal floras and implications for bioprospecting strategies. *Journal of Ethnopharmacology*, *135*(2), 476–487.

Sear, R., & Mace, R. (2008). Who keeps children alive? A review of the effects of kin on child survival. *Evolution and Human Behavior*, *29*(1), 1–18.

Shennan, S. (2001). Demography and Cultural Innovation: a Model and its Implications for the Emergence of Modern Human Culture. *Cambridge Archaeological Journal*, *11*(September 2001), 5–16.

Shultz, S., Opie, C., & Atkinson, Q. D. (2011). Stepwise evolution of stable sociality in primates. *Nature*, *479*(7372), 219–22.

Silk, J. B. (2002). Kin selection in primate groups. *International Journal of Primatology*, *23*(4), 849–875.

Snopkowski, K., & Sear, R. (2013). Kin influences on fertility in Thailand: Effects and mechanisms. *Evolution and Human Behavior*, *34*(2), 130–138.

Strier, K. B. (2000). *Primate Behavioral Ecology*. Boston: Allyn and Bacon.

Swedell, L., & Plummer, T. (2012). A Papionin Multilevel Society as a Model for Hominin Social Evolution. *International Journal of Primatology*, *33*(5), 1165–1193.

Takeuchi, K. (2012). Food Restriction and Social Identity of Aka Forager Adolescents in the Republic of Congo. In B. L. Hewlett (Ed.), *Adolescent Identity: Evolutionary, Cultural and and Developmental Perspectives* (pp. 165–185). New York: Routledge.

Tanaka, T., Camerer, C. F., & Nguyen, Q. (2010). Risk and time preferences: Experimental and household survey data from Vietnam. *The American Economic Review*, *100*(1), 557–571.

Tehrani, J. J. (2011). Patterns of Evolution in Iranian Tribal Textiles. *Evolution: Education and Outreach*, *4*(3), 390–396.

Tehrani, J. J., & Collard, M. (2009). On the relationship between interindividual cultural transmission and population-level cultural diversity: a case study of weaving in Iranian tribal populations. *Evolution and Human Behavior*, *30*(4), 286–300.e2.

Tekwu, E. M., Pieme, A. C., & Beng, V. P. (2012). Investigations of antimicrobial activity of some Cameroonian medicinal plant extracts against bacteria and yeast with gastrointestinal relevance. *Journal of Ethnopharmacology*, *142*(1), 265–273.

Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: on the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B*, *364*(1528), 2405–2415.

Terashima, H. (2001). The relationships among plants, animals, and man in the African tropical rainforest. *African Study Monographs*, *27*(October), 43–60.

Terashima, H. (2003). Names , Use and Attributes of Plants and Animals Among the Ituri Forest Foragers: a Comparative Ethnobotanical and Ethnozoological Study. *African Study Monographs*, *Suppl. 28*(November), 7–24.

Terashima, H., & Ichikawa, M. (2003). A comparative ethnobotany of the Mbuti and Efe Hunter-Gatherers in the Ituri Forest, Democratic Republic of Congo. *African Study*

Monographs, *24*(March), 1–168.

Terashima, H., Ichikawa, M., & Sawada, M. (1988). Wild Plant Utilization of the Balese and the Efe of the Ituri Forest, The Republic of Zaire. *African Study Monographs*, *8*(March), 1–78.

The Associated Press. (2003). Logging Jobs Benefit Pygmies, But Imperil Their Forest Home.

Therneau, T., Atkinson, E., Sinnwell, J., Schaid, D., & McDonnell, S. (2013). kinship2: Pedigree functions.

Tishkoff, S. a, Reed, F. a, Friedlaender, F. R., Ehret, C., Ranciaro, A., Froment, A., … Williams, S. M. (2009). The genetic structure and history of Africans and African Americans. *Science*, *324*(5930), 1035–44.

Tobin, H., & Logue, A. W. (1994). Self-Control Across Species. *Journal of Comparative Psychology*, *108*(2), 126–133.

Tomasello, M. (1999). *The Cultural Origins of Human Cognition*. Harvard University Press, Cambridge Massachusetts.

Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: the origins of cultural cognition. *The Behavioral and Brain Sciences*, *28*(5), 675-91-735.

Tomasello, M., Kruger, A. C., & Ratner, H. H. (1993). Cultural learning. *Behavioral and Brain Sciences*, *16*, 495–552.

Tomasello, M., & Rakoczy, H. (2003). What Makes Human Cognition Unique? From Individual to Shared to Collective Intentionality. *Mind & Language*, *18*(2), 121–147.

Tshibangu, J. N., Chifundera, K., Kaminsky, R., Wright, A. D., & König, G. M. (2002). Screening of African medicinal plants for antimicrobial and enzyme inhibitory activity. *Journal of Ethnopharmacology*, *80*(1), 25–35.

Tucker, B. (2006). A future discounting explanation for the persistence of a mixed foraging-horticulture strategy among the Mikea of Madagascar. In D. Kennett & B. Winterhalder

(Eds.), *Behavioral ecology and the transition to agriculture* (pp. 22–40). Berkeley: University of California Press.

Tucker, B. (2012). Do Risk and Time Experimental Choices Represent Individual Strategies for Coping with Poverty or Conformity to Social Norms? Evidence from Rural Southwestern Madagascar. *Current Anthropology*, *53*(2), 149–180.

Turnbull, C. (1961). *The Forest People*. Pimlico.

Turnbull, C. (1965). *Wayward servants: the two Worlds of the African Pygmies*. Garden City, NY: Natural History Press.

van Schaik, C. P., & Kappeler, P. M. (2003). The evolution of social monogamy in primates. *Monogamy: Mating Strategies and Partnerships in Birds, Humans, and Other Mammals*, (January), 59–80.

Verdu, P. (2014). Population genetics of Central African Pygmies. In B. S. Hewlett (Ed.), *Hunter-Gatherers of the Congo Basin* (pp. 31–59). New Brunswick New jersey: Transaction Publishers.

Verdu, P., Austerlitz, F., Estoup, A., Vitalis, R., Georges, M., Théry, S., … Heyer, E. (2009). Origins and Genetic Diversity of Pygmy Hunter-Gatherers from Western Central Africa. *Current Biology*, *19*(4), 312–318.

Verdu, P., Becker, N. S. a, Froment, A., Georges, M., Grugni, V., Quintana-Murci, L., … Austerlitz, F. (2013). Sociocultural behavior, sex-biased admixture, and effective population sizes in Central African Pygmies and non-Pygmies. *Molecular Biology and Evolution*, *30*(4), 918–37.

Vinicius, L., & Migliano, A. B. (2016). Reproductive Market Values Explain Post-reproductive Lifespans in Men. *Trends in Ecology & Evolution*, *31*(3), 172–175.

Walker, R. S., Flinn, M. V, & Hill, K. (2010). Evolutionary history of partible paternity in lowland South America. *Proceedings of the National Academy of Sciences*, *107*(45), 19195–19200.

Whitehead, H., & Rendell, L. (2014). *The Cultural Lives of Whales and Dolphins*. Chicago University Press.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., … Boesch, C. (1999). Cultures in chimpanzees. *Nature*, *399*(6737), 682–685.

Whiten, A., Horner, V., & de Waal, F. B. M. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature*, *437*(7059), 737–40.

Wiessner, P. (2002). The Vines of Complexity: Egalitarian Structures and the Institutionalization of Inequality among the Enga. *Current Anthropology*, *43*(2), 233–269.

Wiessner, P. (2005). Norm Enforcement among the Ju /' hoansi Bushmen. *Human Nature*, *16*(2), 115–145.

Wilson, M., & Daly, M. (2004). Do pretty women inspire men to discount the future? *Proceedings of the Royal Society B*, *271*(Suppl. 4), S177-9.

Winterhalder, B. (1986). Diet choice, risk, and food sharing in a stochastic environment. *Journal of Anthropological Archaeology*, *5*, 369–392.

Woodburn, J. (1982). Egalitarian societies. *Man*, *17*(3), 431–451.

Wrangham, R. W. (1995). Relationship of Chimpanzee Leaf-Swallowing to a Tapeworm Infection. *American Journal of Primatology*, *37*(4), 297–303.

Zirihi, G. N., Mambu, L., Guédé-Guina, F., Bodo, B., & Grellier, P. (2005). In vitro antiplasmodial activity and cytotoxicity of 33 West African plants used for treatment of malaria. *Journal of Ethnopharmacology*, *98*(3), 281–285.

Appendix A: Supplementary Videos

Video 1: Mbendjele women and girls gathering wild tubers (mea) in the forest.

https://congokongo.wordpress.com/2015/03/17/searching-for-mea/

Video 2: Fishing trip using a plant-based poison. Multiple families from the forest camp, Ibamba, go on a fishing trip. They use the nuts of *Brenania brieyi* (they call it "mo.lunju" or "mo.unju"; prefix "mo" is for the singular of a noun, and "ba" is for the plural) and mix them with ashes to use as a poison for killing fish. After making dams in the river, women put the mixture in the water and use traps. Unfortunately, no fish were caught on this fishing trip.

https://congokongo.wordpress.com/2016/05/06/fishing-trip/

Video 3: Baby Eteni. A 13-month old hunter-gatherer girl imitating various activities: carrying a machete, helping with finding seeds of *Treculia Africana*, holding a sharp knife to cut a pangolin, and using a machete to make a basket.

https://congokongo.wordpress.com/2015/03/22/baby-eteni/

Video 4: Medicinal plant used by BaYaka parents for their sick children. The couple in the video boil the bark of different trees in front of their hut to use as a remedy for their child who is suffering from stomach pain.

https://congokongo.wordpress.com/2016/09/09/how-do-pygmies-accumulate-medicinal-plant-knowledge/

Appendix B: Research permit from the Congolese Ministry of Scientific Research and Technology

MINISTERE DE LA RECHERCHE SCIENTIFIQUE
ET DE L'INNOVATION TECHNIQUE

DELEGATION GENERALE A LA RECHERCHE
SCIENTIFIQUE ET TECHNOLOGIQUE

Avenue des Premiers Jeux Africains
Face Stade Alphonse MASSAMBA -DEBAT
B.P : 2499
e-mail:dgrst@yahoo.fr

REPUBLIQUE DU CONGO
Unité *Travail* Progrès

N° 006 /MRSIT/DGRST/DMAST.-

AUTORISATION DE RECHERCHE

LA DELEGUE GENERAL A LA RECHERCHE SCIENTIFIQUE ET TECHNOLOGIQUE,

- Vu la loi n° 15/95 du 7 septembre 1995, portant orientation et programmation du développement scientifique et technologique ;
- Vu le décret n° 97/252 du 5 Août 1997, portant organisation et fonctionnement de la Délégation Générale à la Recherche Scientifique et Technologique en République du Congo ;
- Vu, le décret n° 98-475 du 31 décembre 1998, portant détachement et nomination du Délégué Général, à la Recherche Scientifique et Technologique ;
- Vu les lettres de demande d'autorisation de recherche du 1er mars 2013 et 22 mars 2013 adressées par le Professeur Jérôme LEWIS au Ministre de la Recherche Scientifique ;
- Vu la réponse positive du Ministre de la Recherche Scientifique ;
- Vu l'avis de la Direction du Management des Activités Scientifiques et Technologiques ;

Décide :

1. Une autorisation de recherche est accordée à l'équipe de recherche composée ainsi qu'il suit :
    - Chef d'équipe : Pr. Jérôme LEWIS, professeur d'anthropologie, University college London, de nationalité anglaise ;

    - membres :
    Dr. Edward STEVENSON, docteur en anthropologie, de nationalité anglaise;

Dr. Gûl DENIZ SALALI, docteur en anthropologie, de nationalité turque ;
Mme Camille OLOA-BILOA, doctorant en anthropologie, de nationalité française ;
Mr. Charan CHAUDHARY, doctorant en anthropologie, de nationalité anglaise ;
Mr. James THOMPSON, doctorant en anthropologie, de nationalité anglaise.

2. Le projet de recherche porte sur la résilience des peuples autochtones de la République du Congo.

3. La recherche se déroulera dans les départements de la Sangha et de la Likouala.

4. Cette étude s'étalera du 1er avril 2013 au 31 décembre 2014.

5. Un rapport scientifique et technique de cette étude devra être déposé à la Délégation Générale à la Recherche Scientifique et Technologique (DGRST). Sur papier et sous forme électronique (sur support CD-Rom ou DVD).

Fait à Brazzaville, le 30 mars 2013

Le Délégué Général,

[redacted]

Pr. A. ITOUA-NGAPORO

AMPLIATIONS :

MRSIT-CAB…..	1
MID-CAB…….	1
MDDEFE-CAB…	1
MAE-CAB………	1
DGRST………….	1
DMAST…………	1
Département Likouala	1
Département Sangha	1
INTERESSES……	6
ARCHIVES…………	1/15

Appendix C: Information sheet for the participant

Feuille d'informations pour le Participant

Résilience des chasseurs-cueilleurs: Un projet mené par University College London, Londres, U.K.

Ce projet sera développé à **University College London**, par Dr Andrea Bamberg Migliano ainsi que les participants du projet "Résilience des chasseurs-cueilleurs", incluant des doctorants et post-doctorants.

Ce projet a pour but de nous aider à comprendre le mode de vie des chasseurs-cueilleurs et dans quelles mesures ils diffèrent des populations d'agriculteurs. Pour comprendre ces différences nous allons:

- **Mesurer et peser les participants** pour comprendre comment les personnes grandissent et changent avec l'âge;
- **Prendre des échantillons de salive pour obtenir l'ADN des participants pour des etudes génomiques.** L'ADN peut nous dire de quelle facon vous êtes apparentés à d'autres populations de chasseurs-cueilleurs, pourquoi vous êtes différents des agriculteurs et pourquoi certaines personnes sont plus souvent atteintes de malaria que d'autres.
- **Poser des questions au sujet de votre famille** pour comprendre de quelle **façon** vous êtes apparentés les uns aux autres.
- **Utiliser des appareils électroniques** afin de comprendre avec qui vous passez du temps.
- **Vous poser des questions sur différents aspects de la vie en forêt** comme la chasse, le partage, la garde d'enfants et l'utilisation des plantes.
- **Vous demander de participer à des tâches** durant lesquelles vous 1) choisirez de gagner différentes sommes d'argent maintenant ou dans le futur, et 2) partagez du miel avec les gens de votre choix dans le camp.
- **Utiliser le GPS enregistreur de données** afin de mesurer comment les gens utilisent la forêt.
- **Mener des observations** pour identifier quelles activités les gens font ensemble, comme manger, garder les enfants, cuisiner, etc.

Obtenir un **échantillon de salive est simple et sûr**. Si vous acceptez de nous aider, et après avoir signé le formulaire de consentement, nous vous donnerons un contenant en plastique pour recueillir votre salive. Vous aurez besoin de le remplir de votre salive jusqu'à ce qu'il soit à moitié plein, le refermer et le rendre au chercheur. Le chercheur attribuera un numéro à ce contenant, accompagné de la date du jour, votre sexe et le nom de votre village.

Ce projet est mené au sein de l'University College London, Angleterre, et il répond par conséquent aux lois britanniques. Les données et toutes les informations seront traitées de façon strictement confidentielles et manipulées selon le code de la protection des données de 1998 (**the provisions of the Data Protection Act, UK, 1998).**

Appendix D: Plant uses that are reported by participants and their corresponding categorization

Master use type	Main use category	Sub use category
abortion	medicine	pregnancy
abortion with string	medicine	pregnancy
ache	medicine	pain injuries
ache fever	medicine	pain injuries
after birth decrease size vagina	medicine	pregnancy
aids	medicine	infections
animals eat	animal food	animal food
animals eat seed	animal food	animal food
animals porcupine eat	animal food	animal food
antelopes eat seed	animal food	animal food
anus	medicine	digestive
anus wounds	medicine	wounds
arbalet	foraging	poison for monkeys
arbalet poison for monkey	foraging	poison for monkeys
arbalet poison for monkey and birds	foraging	poison for monkeys
arm pain	medicine	pain injuries
attach *ngongo* leaves with fire string	uncategorised	uncategorised
attach to ribs with palm oil	medicine	pain injuries
avoid gorilla attacks	avoid attacks	avoid attacks
avoid sickness bad spirits	beliefs	spirit
ax	materials	ax
baby cries a lot	beliefs	baby
baby fever	medicine	infections
baby to have strong head	beliefs	baby
baby if had sex	beliefs	baby
baby may get sick	beliefs	baby
baby to be white	beliefs	baby
baby to walk	beliefs	baby

baby vomits	medicine	digestive
backache	medicine	pain injuries
if you washed in dirty water	uncategorised	uncategorised
basket for honey	materials	basket
basket string	materials	basket
better sing	beliefs	sing
skin lump	medicine	skin
lumps next to chest respiration	medicine	respiratory
skin lumps	medicine	skin
birth facilitation	medicine	pregnancy
blood diminish	medicine	circulatory
blood increase	medicine	circulatory
breast ache	medicine	pain injuries
broken parts	medicine	pain injuries
burry baby who died at birth leaf	beliefs	baby
caterpillar	foraging	invertebrate food
change colour of piss sickness	medicine	infections
children vertigo	medicine	ill defined
circumcision	medicine	wounds
circumcision wound healing	medicine	wounds
circumcision penis wounds	medicine	wounds
core pain	medicine	pain injuries
core pain small buttons	medicine	pain injuries
core pain *sue sue*	medicine	pain injuries
core pain works like Vicks	medicine	pain injuries
cough	medicine	respiratory
cough works like Vicks	medicine	respiratory
diarrhoea	medicine	digestive
diarrhoea put in anus can’t drink	medicine	digestive
diarrhoea string attached to baby	medicine	digestive
digestion	medicine	digestive
digestion get microbes out	medicine	digestive
digestion if can’t defecate	medicine	digestive

digestion if someone drinks vomits it	medicine	digestive
digestion mix with honey from *koma* bees vomit to get microbes out	medicine	digestive
digestion string	medicine	digestive
digestion vomit after drink	medicine	digestive
digestion when eating honey	medicine	digestive
digestion worms	medicine	digestive
digestion worms but you can't drink much because it's bad	medicine	digestive
drink like coffee	food	food additives
drink like water	food	food additives
dysentery	medicine	digestive
ear pain infection	medicine	infections
elephant eats	animal food	animal food
escape from elephants	avoid attacks	avoid attacks
eyes	medicine	infections
eyes flu	medicine	infections
eyes get bad	medicine	infections
eyes infection	medicine	infections
eyes vertigo	medicine	ill defined
face wash	medicine	skin
facilitate eating	medicine	digestive
facilitate walk baby string	beliefs	baby
facilitating birth	medicine	pregnancy
feet pain	medicine	pain injuries
something that enters from feet	medicine	infections
females after birth	medicine	pregnancy
fever	medicine	infections
fever baby	medicine	infections
fever - malaria	medicine	infections
find honey better	foraging	bee plants
finding path in forest	uncategorised	uncategorised
firewood	materials	firewood
***flam de pluie* (unknown)**	uncategorised	uncategorised
flu	medicine	infections

food	food	food
for itching	medicine	skin
for twins not to get sick	beliefs	baby
force penis	medicine	genitourinary
fruit	food	food
get husband back	beliefs	partner
get microbes out by vomiting	medicine	digestive
get microbes out coughing	medicine	respiratory
get microbes out if smoked lot	medicine	respiratory
get rid of bad spirits string baby	beliefs	baby
grave mat for lying dead	uncategorised	uncategorised
have a clean baby	beliefs	baby
have a strong baby	beliefs	baby
have healthy baby	beliefs	baby
head lice	medicine	infections
head not good like crazy	medicine	ill defined
head vertigo	medicine	ill defined
headache	medicine	pain injuries
headache cut blood out	medicine	pain injuries
headache string	medicine	pain injuries
heart if it beats hard	medicine	circulatory
haemorrhoid	medicine	digestive
hernia	medicine	digestive
hernia around penis	medicine	digestive
hernia of men	medicine	digestive
hernia of penis	medicine	digestive
honey collecting	foraging	bee plants
honey collecting *koma* bees	foraging	bee plants
honey shouldn't be eaten if had twins	beliefs	baby
honey taste	foraging	bee plants
house	uncategorised	uncategorised
hut	materials	hut
if baby bites	beliefs	baby
if baby cries a lot	beliefs	baby
if baby cries lot	beliefs	baby

if baby cries a lot hit mouth with leaf	beliefs	baby
if baby doesn't talk hit mouth with leaf	beliefs	baby
if baby doesn't breastfeed	medicine	digestive
if drink a lot put leaf on ears to avoid poisonous drinks	beliefs	spirit
if Ekila (tabooed) food eaten when having twins	beliefs	baby
if a female can't have baby eat seed	medicine	pregnancy
if hands get bigger because of work	beliefs	spirit
if husband search for lots of women	beliefs	partner
if no breastmilk	medicine	pregnancy
if pregnant had sex two men	beliefs	baby
if pregnant had sex two men put in eyes to get microbes out	beliefs	baby
if tongue of baby gets black	beliefs	baby
if want to get pregnant	medicine	pregnancy
if you have extra partner to get microbes out	beliefs	partner
if you hurt someone	beliefs	spirit
if you vomit	medicine	digestive
invite dead people	beliefs	spirit
***kanja* (type of parasite)**	medicine	infections
killing fish	foraging	poison fish
knee pain	medicine	pain injuries
***kole* (type of parasite) limb**	medicine	infections
lamp	uncategorised	uncategorised
limb pain	medicine	pain injuries
limb pain like Vicks	medicine	pain injuries
limb pain lower back	medicine	pain injuries
lost baby when pregnant again want	medicine	pregnancy
lower back pain	medicine	pain injuries
luck in finding crocodiles	beliefs	luck in hunting

luck in finding fish	beliefs	luck in fishing
luck in finding food	beliefs	luck in hunting
luck in finding partner	beliefs	partner
luck in fishing	beliefs	luck in fishing
luck in getting others share	beliefs	share
luck in hunting	beliefs	luck in hunting
luck in hunting antelope	beliefs	luck in hunting
luck in hunting crocodiles	beliefs	luck in hunting
luck in hunting elephant	beliefs	luck in hunting
luck in hunting elephants	beliefs	luck in hunting
luck in hunting pig	beliefs	luck in hunting
luck in partner finding	beliefs	partner
luck in work	beliefs	work
make traps	uncategorised	uncategorised
make women like him	beliefs	partner
make your husband like you	beliefs	partner
malaria	medicine	infections
mat	materials	mat
men genitals	medicine	genitourinary
mouth wounds	medicine	digestive
nails infected	medicine	infections
neck pain	medicine	pain injuries
not to think of lost husband	beliefs	partner
pain	medicine	pain injuries
penis sickness	medicine	genitourinary
pigs and antelopes eat grain	animal food	animal food
piroque	materials	piroque
***piyan* (type of parasite)**	medicine	infections
poison	uncategorised	uncategorised
poison fish	foraging	poison fish
poison for monkeys	foraging	poison for monkeys
***potu potu* (fontanel)**	beliefs	baby
pregnant when having breastfeeding baby	beliefs	baby
problem with others- drink	beliefs	spirit
problem with others- eyes	beliefs	spirit
protect spirit from bad spirits	beliefs	spirit
put in anus for cold	medicine	digestive

put into men’s food	beliefs	partner
put it in babies nose doesn't know why	beliefs	baby
respiration	medicine	respiratory
respiration attach potato	medicine	respiratory
respiration attach string	medicine	respiratory
respiration for vomiting	medicine	respiratory
respiration string attached	medicine	respiratory
respiration strong attached	medicine	respiratory
ribs ache	medicine	pain injuries
salt	food	food additives
seed	food	food
sign for graveyard	uncategorised	uncategorised
small buttons	medicine	infections
snake bite	medicine	poisonings
sore throat	medicine	infections
stomach pain	medicine	digestive
stopping rain	beliefs	rain
strength for fighting string	beliefs	fight
strength in fights	beliefs	fight
tamtam	materials	tamtam
teeth	medicine	digestive
teeth after eating *mobey* (fruit) for brush	medicine	digestive
teeth attach string	medicine	digestive
teeth brush	medicine	digestive
teeth brush can't eat with pepper	medicine	digestive
teeth brush if sick with pepper salt	medicine	digestive
teeth brush mouth wounds	medicine	digestive
teeth if eat lots of pineapple brush	medicine	digestive
teeth serious illness	medicine	digestive
teeth serious illness can’t eat	medicine	digestive
teeth you can’t eat- mouth ulcers	medicine	digestive
tiredness	medicine	ill defined

to avoid animals attacking when wife pregnant	avoid attacks	avoid attacks
to be good at school	beliefs	work
to call woman to your house	beliefs	partner
to have baby for women	medicine	pregnancy
to have baby get microbes out	medicine	pregnancy
to make husband get excited	beliefs	partner
to sing well	beliefs	sing
to vomit if smoke a lot	medicine	respiratory
underarm pain	medicine	pain injuries
vagina	medicine	genitourinary
vagina because of backache	medicine	genitourinary
vagina gets bigger	medicine	genitourinary
vagina gets swollen	medicine	genitourinary
vagina if white water comes out	medicine	genitourinary
vagina pump	medicine	genitourinary
vertigo	medicine	ill defined
vertigo vomit	medicine	ill defined
vomit respiration problems	medicine	respiratory
vomit serious sickness	medicine	digestive
wash baby	medicine	skin
water	food	food additives
when passing from cemetery to avoid sickness	beliefs	spirit
wounds	medicine	wounds
wrist pain	medicine	pain injuries
yellow fever	medicine	infections
yellow fever eyes	medicine	infections
you have a problem eat leaf	beliefs	spirit

Appendix E: Salali et al. 2016 Current Biology

Salali GD, Chaudhary N, Thompson J, Grace OM, van der Burgt XM, Dyble M, Page AE, Smith D, Lewis J, Mace R, Vinicius L. Knowledge-Sharing Networks in Hunter-Gatherers and the Evolution of Cumulative Culture. *Current Biology*, *26*(18), 2516-2521.

Current Biology, Volume *26*

Supplemental Information

Knowledge-Sharing Networks in Hunter-Gatherers and the Evolution of Cumulative Culture

Gul Deniz Salali, Nikhil Chaudhary, James Thompson, Olwen Megan Grace, Xander M. van der Burgt, Mark Dyble, Abigail E. Page, Daniel Smith, Jerome Lewis, Ruth Mace, Lucio Vinicius, and Andrea Bamberg Migliano

Appendix F: Salali and Migliano 2015 PLOS ONE

Salali, G. D., & Migliano, A. B. (2015). Future Discounting in Congo Basin Hunter-Gatherers Declines with Socio-Economic Transitions. *PloS one*, *10*(9), e0137806

RESEARCH ARTICLE

Future Discounting in Congo Basin Hunter-Gatherers Declines with Socio-Economic Transitions

Gul Deniz Salali*, **Andrea Bamberg Migliano**

Department of Anthropology, University College London, London, United Kingdom

* guldeniz.salali.12@ucl.ac.uk

Abstract

Humans have a tendency to discount the future; that is we value small, short-term rewards over larger, long-term rewards. The degree of future discounting, however, changes in response to socio-ecological factors. Here, we study Mbendjele BaYaka hunter-gatherers of northern Congo and their farmer neighbours to investigate adaptations in inter-temporal preferences in humans. We argue that in immediate-return systems, where food storage is absent and egalitarianism is enforced through levelling mechanisms, future discounting is an adaptive strategy to prevent wealth accumulation and the emergence of hierarchies. This ensures food sharing and allows for survival in unpredictable environments where there is risk of an energy shortfall. On the other hand, when food storage is made possible by the emergence of agriculture or as seen in some delayed-return hunter-gatherer populations, wealth accumulation, hierarchies and lower discount rates become the adaptive strategy. Therefore, individuals in immediate-return, egalitarian societies will discount the future more than those in non-egalitarian, delayed-return societies. Consistent with the predictions we found that market integration and socio-economic transitions decrease the future discounting in Mbendjele hunter-gatherers. Our measures of socio-economic differences marked this transition in hunter-gatherers living in a logging town. The degree of future-discounting was the same between more market-integrated hunter-gatherers and their farmer neighbours.

Citation: Salali GD, Migliano AB (2015) Future Discounting in Congo Basin Hunter-Gatherers Declines with Socio-Economic Transitions. PLoS ONE 10(9): e0137806. doi:10.1371/journal.pone.0137806

Editor: Cédric Sueur, Institut Pluridisciplinaire Hubert Curien, FRANCE

Received: March 16, 2015

Accepted: August 21, 2015

Published: September 18, 2015

Data Availability Statement: All relevant data are within the paper's Supporting Information files.

Funding: This work was funded by the Leverhulme Trust Foundation Grant RP2011-R-045 to ABM.

Competing Interests: The authors have declared that no competing interests exist.

Introduction

Organisms often prefer immediate rewards over future ones, a preference that is known as "future discounting" [1]. A person with a higher discount rate (or higher impulsivity or lower patience) might choose 5 monetary units now, over 10 monetary units in a week. Although, the ability to fight impulsivity has been observed in non-human animals such as chimpanzees [2], pigeons [3] and guppies [4], humans appear to have evolved greater capacities for patience [5]. Some studies indicate that levels of future discounting are deep psychological attributes, linking early childhood time preferences with phenotypes developed later in life [6,7]. Others support the idea that choice of immediate versus delayed rewards varies more plastically in response to socio-ecological factors in both non-human primates [8,9] and humans [10,11].

Although there is a large body of literature investigating the determinants of future discounting in Western populations [7,11–14], there are only a handful of studies examining the level of future discounting in small-scale societies [15–21]. For example, Tucker [15] tested whether individual-level wealth and income variables or conformity to social norms better predicted time preferences in Mikea forest forager-farmers and their fisher and farmer neighbours. Godoy et al. [17] investigated whether the effects of years of schooling, age or income affected the levels of patience in Tsimane' forager-horticulturalists. They also compared rates of discounting in Tsimane' with those from two samples from the United States. While both studies found higher discount rates in forager-horticulturalist groups, they did not directly test whether a shift in social structure from an egalitarian one to a hierarchical one affects levels of future discounting. We believe investigating temporal preferences in foraging populations with egalitarian social structure may help us to understand when and how humans have developed greater patience.

Current-day hunter-gatherers present ideal populations to understand the trajectory of inter-temporal preferences in humans, since the decisions that extant hunter-gatherers make relative to their environment have a resemblance to the decisions that were made by pre-historic hunter-gatherers [22,23]. Some hunter-gatherer societies are immediate-return, where the obtained food is consumed in a short time. Immediate return hunter-gatherers are marked by high mobility and egalitarian political organization, which is believed to facilitate extensive food sharing as opposed to resource accumulation [24]. In delayed return systems (most farmers, herders and western systems) on the other hand, the food yield is obtained over long periods and stored; individuals accumulate wealth; and the political structure is less egalitarian and more hierarchical [24]. Immediate return societies sustain their egalitarian structure through levelling mechanisms that prohibit saving, accumulation and dominance [25–28]. These levelling mechanisms are believed to be important adaptations to ensure food sharing and in turn survival in unpredictable environments [27,29–31]. Transitions from immediate- to delayed-return systems are most likely triggered by new storage systems and domestication [23,32]. Changes in subsistence mode and food surpluses break down social systems of sharing, resulting in inequalities [29]. In a similar way, market integration, sedentism and high population density push immediate return hunter-gatherers towards a delayed-return system [23].

We suggest that future discounting in humans is a flexible behavioural adaptation associated with immediate-return systems and is subject to change in different socio-ecological conditions. The preference for immediate over delayed rewards will be adaptive in an immediate-return system where food is shared widely and consumed immediately without storage. In a society where individuals are obliged to share upon demand [33] and accumulation is prevented via norms, it will be risky to wait for larger rewards. With the dawn of agriculture and the possibility of food storage, which brought about the reduction of food sharing and the emergence of delayed-return economies, humans may have also developed delayed-return ways of thinking (i.e. patience) and adapted their behavioural strategies towards longer-term, higher-yield rewards. A shift away from immediate- towards a delayed-return system should therefore decrease individuals' future discounting rates. Here we test whether: i) hunter-gatherers living in larger, more sedentary and market integrated groups will have more resource accumulation and less future discounting compared to mobile and forest-dwelling hunter-gatherers; ii) farmers will discount the future less than the hunter-gatherers. To test these predictions, we investigate the extent of future discounting and resource accumulation activities in Mbendjele BaYaka hunter-gatherers of the Republic of Congo who are characterized by their egalitarian social organization [34–37]. We compare inter-temporal decisions in hunter-gatherer camps living further away from a town with those who live in a town, and with Bantu farmers.

Methods

Study Population

There were 186 adult (> 15 years old) participants (91 females). Two Mbendjele camps (camp 1: $n = 23$, 14 females; and camp 2: $n = 30$, 18 females) were located in the forest, but close to mud roads opened by a logging company. In these camps subsistence was based on hunted and gathered products, although parts of hunted game were sold to bush meat traders. One Mbendjele camp (camp 3: $n = 111$, 46 females) was located in a logging town where most of the consumed products were bought in local markets. The last location was a Bantu farmer village ($n = 22$, 13 females; see S1 Supporting Information for further details).

Mbendjele BaYaka hunter-gatherers present an ideal population to study the adaptations in inter-temporal preferences in humans. They have an egalitarian social organization [35,37], however their way of life is changing because of increasing pressure from logging activities [38], commercial hunting, and protected forest areas for conservation [39,40]. Because camps vary in their proximity to logging towns, groups differ in their market integration and livelihood activities [39,40]. For example, during our field trip we observed frequent movement among hunter-gatherers living in the forest. Bush meat trade is common (the reason why many camps are located close to mud roads rather than deep in the forest), and sometimes individuals travel to the nearest farmer village to engage in wage labour [40]. Nevertheless, the main subsistence is hunting and gathering, and the money that is earned by selling meat is often spent immediately on goods such as alcohol, cigarettes, clothing and agricultural products. On the other hand, hunter-gatherers living in the logging towns engage in wage labour much more frequently [39], and they often buy their food from the local market with the money they earn via employment from farmers or the logging company. Individuals in forest camps use traditional round leaf and liana huts that can be easily abandoned and re-made to match their mobile lifestyle; whereas individuals living in towns have permanent houses made of old timbers (see S1 Supporting Information). In forest camps we observed very few personal possessions (such as pots, machetes, traditional baskets and mats, and some clothing) in households, however in town camps some houses even had furniture (e.g. old chairs) in them. Both the house type and large population densities (> 100 adults) indicate a transition to a sedentary lifestyle in town camps. It has been shown elsewhere that Mbendjele groups living in conservation-forestry towns spend much more time in formal employment, gun-hunting for villagers, wage labour and have become more sedentary [39].

Experiment

The participants were informed that they were going to receive stock cubes (also known as bouillon cubes that are used widely in West and Central Africa as a food flavouring agent) for their participation in another study. Stock cubes are highly valued by Mbendjele to spice up food and obtained from traders, or local markets. At the end of the study, participants were asked whether they would prefer to receive one stock cube today or five tomorrow, and were given the stock cube(s) accordingly. This research was approved by UCL Ethics Committee, and carried out with permission from the Ministry of Scientific Research, Congo. Consent forms were verbally translated by a local translator, and questions from the participant were answered by researchers via the translator. Each participant, who agreed to take part, signed the informed consent form. The data supporting this article are available as part of the Supporting Information (S1 and S2 Datasets).

Data were analysed using R 3.2.0. To test whether people's choices differed between locations, we performed logistic regression analyses. Our response variable was future discounting: the choice of one cube today was coded as 1; the choice of five cubes tomorrow was coded as 0. Our predictor variables were *Group type* (forest camps, town camp and Bantu village) and *Sex*. To obtain the optimal model, we removed non-significant variables based on the likelihood ratio test statistic and its associated p-value.

In the current study, we had two measures to examine the socio-economic differences between forest and town camps: 1-) sums paid as bride prices ($n = 18$ for forest camps, $n = 26$ for the town camp) as a proxy for resource accumulation, since bride price has to be accumulated and planned ahead [41]; 2-) frequency of farming work ($n = 56$ for forest camps, $n = 63$ for the town camp) as a proxy for integration in a delayed-return system [41]. We used a one-way permutation test based on Monte-Carlo simulations to compare the means of bride prices across locations. For the frequency of wage labour, we asked individuals how frequently they work for farmers, coding responses as 1) no/infrequent farm work, and 2) frequent farm work. We compared these responses using the Chi-square test of independence with Monte-Carlo re-samplings.

Results

We first analysed the indicators of socio-economic differences between forest and town camps. These analyses revealed that hunter-gatherers in the town camp paid larger sums of bride price than those in forest camps (permutation test: $p < 0.01$; Fig 1a). The range of bride prices was larger in the town camp, indicating accumulation of resources and emerging inequalities (Fig 1a). Moreover, hunter-gatherers in the town camp engaged in wage labour much more frequently than those living in forest camps ($n = 119$, $\chi^2{}_1 = 17.35$, $p < 0.001$; Fig 1b).

There was no difference between the proportions of participants that chose one cube today in the two hunter-gatherer forest camps (camp 1 and camp 2, $n = 53$, $\chi^2{}_1 = 0.9$, $p = 0.48$; Fig 2). Therefore, we pooled the data of camp 1 and camp 2 and refer to them as "forest camps" hereafter.

There was a significant difference in the probability of future discounting between the hunter-gatherers from the forest camps and the town camp (Fig 2). Table 1 shows our initial regression model with all the predictor variables (Model 1), and our optimal model (Model 2). According to Model 2, hunter-gatherers living in the forest discounted the future 5 times more than those in the town (odds ratio (OR) = 0.20, $CI_{.95}$ = [0.09–0.43]). There was also a significant difference between hunter-gatherers living in the forest and Bantu farmers. Accordingly, odds of future discounting were 6 times higher in forest hunter-gatherers (OR = 0.16, $CI_{.95}$ = [0.05–0.47]). Interestingly, there was no difference in future discounting between the town-living hunter-gatherers and farmers ($n = 133$, $\chi^2{}_1 = 0.13$, $p = 0.82$).

For the subsample of the hunter-gatherers where we had information on frequency of wage labour and future discounting at the individual level, we found that those who engaged in frequent wage labour discounted the future less (Tables B-C in S1 Supporting Information). However, for the subsample of hunter-gather males ($N = 38$) the amount of bride price an individual paid did not have a significant effect on his future-discounting (Table D in S1 Supporting Information). In addition, our analysis on the effects of age on future discounting in Mbendjele showed no age effect (Tables E-H in S1 Supporting Information).

Discussion

Consistent with our predictions, individuals in the town camp engage in more resource accumulation and have more variation in bride price payments, which is indicative of emergent

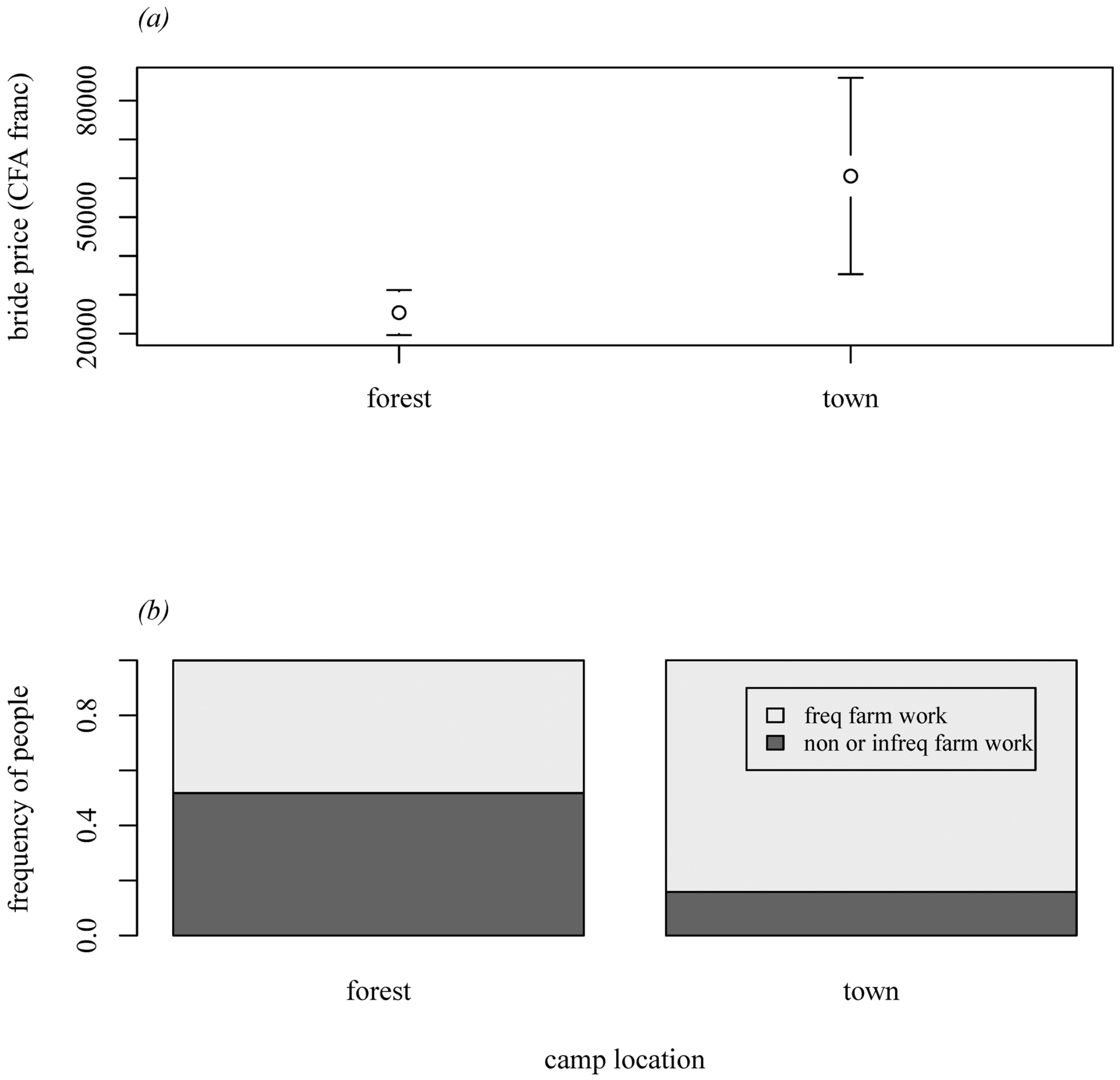


Fig 1. Socio-economic differences between hunter-gatherers living in forest camps and a town camp. *(a)* mean and 95% CI of the amount of bride price that men paid, *(b)* the frequency of wage labour in each location.

doi:10.1371/journal.pone.0137806.g001

inequalities. We show that immediate-return Mbendjele hunter-gatherers, that are less market integrated and engage in less resource accumulation activities, discount the future more than Mbendjele living in a logging town. Strikingly, those living in the town do not differ in their inter-temporal choices from Bantu farmers. Our results point to a group-level phenomenon; that socio-economic transitions affect the levels of future discounting; however we cannot specifically determine what factors play what role. It is possible that decreased mobility, increased population size, reduction in sharing and the change in subsistence mode, egalitarian norms and levelling mechanisms all contribute to the observed phenomenon in an intervening way. More individual-level measures are required to elucidate the effects of these factors.

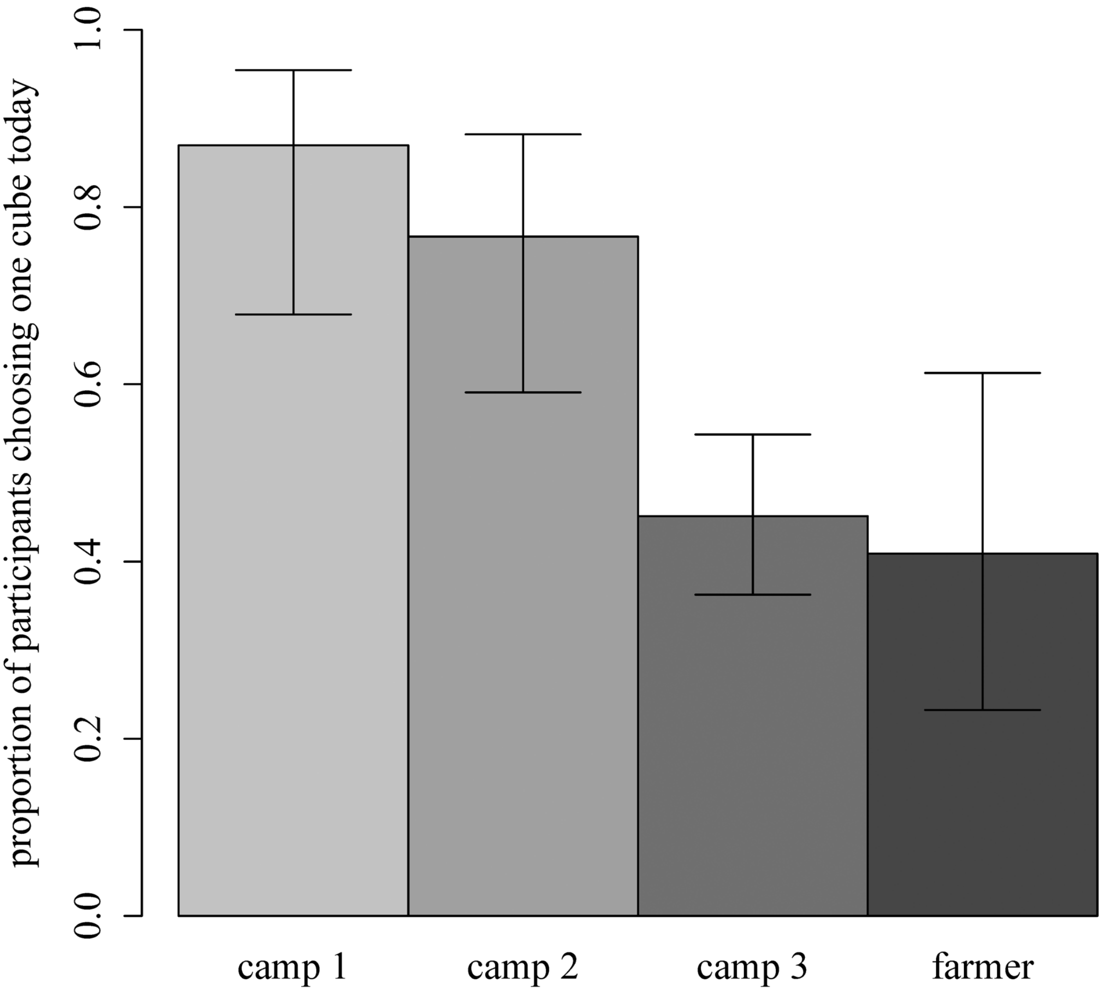


Fig 2. Proportion of participants that chose to receive one cube today in 3 Mbendjele camps and one Bantu farmer village. Camp 1 and camp 2 were located in the forest; camp 3 was located in the town. Error bars indicate 95% confidence intervals.

doi:10.1371/journal.pone.0137806.g002

The currency value matters in temporal choice experiments and resulting preferences may be study specific [15,17]. Although currency may matter, similar results in temporal discounting were found with different currencies, in different populations of foragers when compared to their neighbouring farmers, fishers or Western populations. For example, Mikea forest forager-farmers from Madagascar chose more immediate and low-risk options compared to their farmer and fisher neighbours [15]; and Tsimane' forager-horticulturalists were on average more impatient compared to Western populations [17]. It requires further examination to establish whether the same decline in future discounting in the town camp would be observed by using a different currency (such as rice or money). Although discount rates may differ across different currencies, on average individuals living in a more delayed-return system will likely discount the future less regardless of the currency of choice.

An alternative interpretation is that time preference is a deep psychological attribute and not a flexible context-specific behavioural adaptation [17]. In this case the difference between

Table 1. Logistic regression models for probability of future discounting.

Predictor	Model 1 Coeff. (SE)	Model 1 P	Model 2 Coeff. (SE)	Model 2 P
Group type- town camp	-1.61 (0.41)	<0.001	-1.65 (0.40)	<0.001
Group type- Bantu	-1.83 (0.56)	<0.01	-1.83 (0.56)	<0.01
Sex- male	-0.30 (0.32)	0.43		
Intercept	1.58 (0.38)	<0.001	1.46 (0.35)	<0.001
Pseudo-R^2 (Hosmer-Lemeshow)	0.09		0.09	
-2 log likelihood	232.98		233.89	
N	186		186	

Response variable: future discounting (i.e. choosing one stock cube today over 5 stock cubes tomorrow). *Group type* encodes for the group of the participants (forest camps, town camp and Bantu agriculturalist village). *N* is the number of subjects. Omitting *Sex* did not affect the model fit significantly ($P[\chi^2(1) > 0.91] = 0.34$).

doi:10.1371/journal.pone.0137806.t001

forest camps and the logging town would be explained by assortment of individuals who are more future-oriented in logging towns [19]. If this is correct, then individual preferences would precede group effects. However, this interpretation does not explain the higher prevalence of preference for immediate rewards in forager societies compared to fisher, farmer or industrial populations found in this study, and others [15–17]. Thus these results suggest that the capacity for patience in humans is a plastic trait [42–44] that is expressed in response to socio-ecological conditions. Higher prevalence of patience in humans only became adaptive when food storage was possible. Nevertheless, an individual-level investigation analysing the change in time preferences in individuals moving from forest camps to towns may help us to further test behavioural flexibility in levels of patience.

Decisions on future discounting can also be analysed in light of life-history trade-offs [10]. According to life history theory, individuals adopt fast or slow reproductive strategies depending on resource availability and the stability of their environment [45], thus preference for immediate returns would be favoured in risky environments [46,47]. Accordingly, effects such as age and age specific mortality rates on life history strategies could also affect future discounting. In our study we did not find any effects of age estimates on inter-temporal preferences of the Mbendjele. Calculating mortality rates require adequate data on age estimates of both living and dead people (i.e. age at death and the year of birth) [48,49] and this data is not currently available for the Mbendjele. Therefore, it is not possible to confirm whether the mortality rates of the Mbendjele affect their levels of patience. Nevertheless, since hunter-gatherers live in unpredictable environments and thus depend more on immediate adaptive strategies such as fast life histories [50,51] and reliance on sharing rather than storage [30], it is expected that high mortality rates, and fast life history strategies may result in higher discount rates. More data is required to test these associations.

Our study corroborates the idea that in a society where sharing is enforced and accumulation is prevented via norms, it will be a risky strategy to wait for larger rewards. The sharing system, levelling mechanisms and future discounting can all be seen as social adaptations that ensure that immediate-return, egalitarian hunter-gatherers can buffer the pressures that result from unpredictable environments [29,30]. On the other hand, a change in the subsistence mode, possibility of food storage, sedentism, and increasing population size may all contribute to the emergence of wealth accumulation and inequalities [23]. As these changes occur humans may have adapted their behavioural strategies towards longer-term, higher-yield rewards. Nevertheless, there is only a handful of studies that focus on future-discounting in forager populations [15–17,21]. More comparative studies of immediate-return foragers versus delayed-return systems are necessary to shed light on the origins and flexibility of inter-temporal choices in humans.

Supporting Information

S1 Supporting Information. Detailed description of the methods and the results on the frequency of wage labour.
(DOCX)

S1 Dataset. Discount. Data on each participant's discount choice (1 versus 5 stock cubes), sex, camp membership, age estimate, farming frequency and amount of bride price.
(XLSX)

S2 Dataset. Socioeconomic indicators. Data on each participant's amount of bride price paid, farming frequency, camp membership and sex.
(XLSX)

Acknowledgments

We thank all the Mbendjele and Bantu participants for their hospitality; Aude Rey and our Mbendjele translators Nicolas, and Gifhanou for their help in data collection; Jerome Lewis for his help in logistics; the HEEG group for their comments on the manuscript and Nikhil Chaudhary for proof-reading.

Author Contributions

Conceived and designed the experiments: GDS ABM. Performed the experiments: GDS. Analyzed the data: GDS. Contributed reagents/materials/analysis tools: GDS ABM. Wrote the paper: GDS ABM.

References

1. Daly M, Wilson M. Carpe diem: Adaptation and devaluing the future. Q Rev Biol. 2005; 80: 55–60. PMID: 15884736
2. Evans TA, Beran MJ. Chimpanzees use self-distraction to cope with impulsivity. Biol Lett. 2007; 3: 599–602. doi: 10.1098/rsbl.2007.0399 PMID: 17716966
3. Ainslie GW. Impulse control in pigeons. J Exp Anal Behav. 1974; 21: 485–489. PMID: 16811760
4. Mühlhoff N, Stevens JR, Reader SM. Spatial discounting of food and social rewards in guppies (poecilia reticulata). Front Psychol. 2011; 2: 68. doi: 10.3389/fpsyg.2011.00068 PMID: 21738517
5. Tobin H, Logue AW. Self-Control Across Species. J Comp Psychol. 1994; 108: 126–133. PMID: 8026163
6. Shoda Y, Mischel W, Peake PK. Predicting adolescent cognitive and self-regulatory competencies from preschool delay of gratification: Identifying diagnostic conditions. Dev Psychol. 1990; 26: 978–986. doi: 10.1037//0012-1649.26.6.978
7. Apter A, Van Praag HM, Plutchik R, Sevy S, Korn M, Brown SL. Interrelationships among anxiety, aggression, impulsivity, and mood: A serotonergically linked cluster? Psychiatry Res. 1990; 32: 191–199. doi: 10.1016/0165-1781(90)90086-K PMID: 2367604
8. Stevens JR. Intertemporal Choice. Encycl Anim Behav. 2010; 2: 203–208.
9. Stevens JR, Mühlhoff N. Intertemporal choice in lemurs. Behav Processes. 2012; 89: 121–7. doi: 10.1016/j.beproc.2011.10.002 PMID: 22024661
10. Van der Wal A, Schade HM, Krabbendam L, van Vugt M. Do natural landscapes reduce future discounting in humans? Proc R Soc B Biol Sci. 2013; 280: 20132295.
11. Wilson M, Daly M. Do pretty women inspire men to discount the future? Proc R Soc B Biol Sci. 2004; 271: S177–9. doi: 10.1098/rsbl.2003.0134

12. Frederick S, Loewenstein G, O'Donoghue T. Time discounting and time preference: a critical review. J Econ Lit. 2002; XL: 351–401.

13. Griskevicius V, Tybur J. The Influence of Mortality and Socioeconomic Status on Risk and delayed rewards: a life history theory approach. J Pers Soc Psychol. 2011; 100: 1015–1026. doi: 10.1037/a0022403 PMID: 21299312

14. Becker GS, Mulligan CB. The Endogenous Determination of Time Preference. Q J Econ. 1997; 112: 729–758. doi: 10.1162/003355397555334

15. Tucker B. Do Risk and Time Experimental Choices Represent Individual Strategies for Coping with Poverty or Conformity to Social Norms? Evidence from Rural Southwestern Madagascar. Curr Anthropol. 2012; 53: 149–180.

16. Tucker B. A future discounting explanation for the persistence of a mixed foraging-horticulture strategy among the Mikea of Madagascar. In: Kennett D, Winterhalder B, editors. Behavioral ecology and the transition to agriculture. Berkeley: University of California Press; 2006. pp. 22–40.

17. Godoy R, Byron E, Reyes-García V, Leonard WR, Patel K, Apaza L, et al. Patience in a foraging-horticultural society: a test of competing hypotheses. J Anthropol Archaeol. 2004; 60: 179–202.

18. Kirby KN, Godoy R, Reyes-García V, Byron E, Apaza L, Leonard W, et al. Correlates of delay-discount rates: Evidence from Tsimane' Amerindians of the Bolivian rain forest. J Econ Psychol. 2002; 23: 291–316.

19. Reyes-García V, Godoy R, Huanca T, Leonard WR, McDade T, Tanner S, et al. The origins of monetary income inequality Patience, human capital, and division of labor. Evol Hum Behav. 2007; 28: 37–47. doi: 10.1016/j.evolhumbehav.2006.07.001

20. Tanaka T, Camerer CF, Nguyen Q. Risk and time preferences: Experimental and household survey data from Vietnam. Am Econ Rev. 2010; 100: 557–571. doi: 10.1257/aer.100.1.557

21. Godoy R, Jacobson M. Covariates of private time preference: a pilot study among the Tsimane'Indians of the Bolivian rain forest. Evol Hum Behav. 1999; 20: 249–256.

22. Lee RB, Daly R. The Cambridge Encyclopedia of Hunters and Gatherers. Lee RB, Daly R, editors. Cambridge University Press; 2004.

23. Kelly RL. The Lifeways of Hunter-Gatherers: The Foraging Spectrum. Cambridge University Press; 2013.

24. Woodburn J. Egalitarian societies. Man. 1982; 17: 431–451.

25. Boehm C. Hierarchy in the Forest. The Evolution of Egalitarian Behavior. Harvard Univ Press, Cambridge, MA; 1999.

26. Boehm C. Egalitarian behavior and reverse dominance hierarchy. Curr Anthropol. 1993; 34: 227–254.

27. Gavrilets S. On the evolutionary origins of the egalitarian syndrome. Proc Natl Acad Sci U S A. 2012; 109: 14069–74. doi: 10.1073/pnas.1201718109 PMID: 22891349

28. Wiessner P. Norm Enforcement among the Ju /' hoansi Bushmen. Hum Nat. 2005; 16: 115–145. doi: 10.1007/s12110-005-1000-9 PMID: 26189619

29. Erdal D, Whiten A. On Human Egalitarianism: An Evolutionary Product of Machiavellian Status Escalation? Curr Anthropol. 1994; 35: 175–183. doi: 10.1086/204255

30. Lewis HM, Vinicius L, Strods J, Mace R, Migliano AB. High mobility explains demand sharing and enforced cooperation in egalitarian hunter-gatherers. Nat Commun. 2014; 5: 5789. doi: 10.1038/ncomms6789 PMID: 25511874

31. Winterhalder B. Diet choice, risk, and food sharing in a stochastic environment. J Anthropol Archaeol. 1986; 5: 369–392. doi: 10.1016/0278-4165(86)90017-6

32. Alvard MS, Kuznar L. Deferred harvest: the transition from hunting to animal husbandry. Am Anthropol. 2001; 103: 295–311.

33. Peterson N. Demand Sharing: Reciprocity and the Pressure for Generosity among Foragers. Am Anthropol. 1993; 95: 860–874.

34. Lewis J. Ekila: blood, bodies, and egalitarian societies. J R Anthropol Inst. 2008; 297–315.

35. Lewis J. Egalitarian social organization: the case of the Mbendjele BaYaka. In: Hewlett BS, editor. Hunter-Gatherers of the Congo Basin. New Brunswick (U.S.A) and London (U.K): Transaction Publishers; 2014. pp. 219–243.

36. Chaudhary N, Salali GD, Thompson J, Dyble M, Page A, Smith D, et al. Polygyny without wealth: popularity in gift games predicts polygyny in BaYaka Pygmies. R Soc Open Sci. 2015; 2: 150054. doi: 10.1098/rsos.150054 PMID: 26064662

37. Dyble M, Salali GD, Chaudhary N, Page A, Smith D, Thompson J, et al. Sex equality can explain the unique social structure of hunter-gatherer bands. Science. 2015; 348: 796–798. doi: 10.1126/science.aaa5139 PMID: 25977551

38. Laporte NT, Stabach JA, Grosch R, Lin TS, Goetz SJ. Expansion of industrial logging in Central Africa. Science. 2007; 316: 1451. PMID: 17556578

39. Riddell M. Assessing the Impacts of Conservation and Commercial Forestry on Livelihoods in Northern Republic of Congo. Conserv Soc. 2013; 11: 199–217. doi: 10.4103/0972-4923.121002

40. Lewis J. Whose forest is it anyway? Mbendjele Yaka pygmies, the Ndoki Forest and the wider world. In: Widlok T, Tadesse W, editors. Property and Equality, Vol 2 Encapsulation, Commercialisation, Discrimination. Berghahn Books; 2005. pp. 56–78.

41. Kitanishi K. The impact of cash and commoditization on the Baka hunter-gatherer society in southeastern Cameroon. African study Monogr Suppl. 2006; 33: 121–142.

42. Bickel WK, Miller ML, Yi R, Kowal BP, Lindquist DM, Pitcock JA. Behavioral and Neuroeconomics of Drug Addiction: Competing Neural Systems and Temporal Discounting Processes. Drug Alcohol Depend. 2007; 90: S85–S91. doi: 10.1016/j.drugalcdep.2006.09.016 PMID: 17101239

43. McClure SM, Laibson DI, Loewenstein G, Cohen JD. Separate neural systems value immediate and delayed monetary rewards. Science. 2004; 306: 503–507. doi: 10.1126/science.1100907 PMID: 15486304

44. McClure SM, Ericson KM, Laibson DI, Loewenstein G, Cohen JD. Time discounting for primary rewards. J Neurosci. 2007; 27: 5796–5804. doi: 10.1523/JNEUROSCI.4246-06.2007 PMID: 17522323

45. Migliano AB, Guillon M. The effects of mortality, subsistence, and ecology on human adult height and implications for Homo evolution. Curr Anthropol. 2012; 53: S359–S368. doi: 10.1086/667694

46. Kaplan H, Gangestad S. Life history theory and evolutionary psychology. In: Buss D, editor. The handbook of evolutionary psychology. Hoboken, NJ: John Wiley and Sons.; 2005. pp. 68–95.

47. Winterhalder B, Lu F, Tucker B. Risk-senstive adaptive tactics: Models and evidence from subsistence studies in biology and anthropology. J Archaeol Res. 1999; 7: 301–348. doi: 10.1007/BF02446047

48. Hill K, Hurtado AM. Ache Life History: The Ecology and Demography of a Foraging People. Aldine Press; 1996.

49. Hill K, Hurtado a. M, Walker RS. High adult mortality among Hiwi hunter-gatherers: Implications for human evolution. J Hum Evol. 2007; 52: 443–454. doi: 10.1016/j.jhevol.2006.11.003 PMID: 17289113

50. Migliano AB, Vinicius L, Lahr MM. Life history trade-offs explain the evolution of human pygmies. Proc Natl Acad Sci U S A. 2007; 104: 20216–9. doi: 10.1073/pnas.0708024105 PMID: 18077366

51. Stock J, Migliano A. Stature, Mortality, and Life History among Indigenous Populations of the Andaman Islands, 1871–1986. Curr Anthropol. 2009; 50: 713–725. doi: 10.1086/605429