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The foraging ecology of two neighbouring chimpanzee communities from Budongo Forest

A Dissertation Presented

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Abstract of the Dissertation

The foraging ecology of two neighbouring chimpanzee communities from Budongo Forest

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Chimpanzees (*Pan troglodytes*) often serve as a model species to test socio-ecological theories of foraging behaviour. Due to a high degree of fission-fusion dynamics, essential foraging variables, such as group size, patch size and travel distance, are expected to be more closely linked in chimpanzees than in animals that forage in cohesive groups. While it has been clearly established that the relationship between party size and patch size follows theoretical predictions, the importance of other foraging variables, such as travel distance, and sex differences in foraging strategies are less well understood. Also, the picture of chimpanzee feeding ecology is informed by a large number of individual chimpanzee communities from all across Africa, but foraging behaviour in chimpanzees of the same population has rarely been studied in detail.

Here I present the feeding ecology of two neighbouring, interbreeding chimpanzee communities from the Budongo Forest Reserve in Uganda, Sonso and Waibira, that occupy home ranges of different vegetation composition and differ in overall size. From October 2015 to June 2017 I followed adult male and female chimpanzees in each study community for a period of 8 months, collecting data on individual food patches and inter-patch distances by specific focals. These were combined with measurements of food availability and data on forest composition within the home ranges of each community.

A first assessment of forest composition across home ranges showed that two important non-fig food species might be more abundant within the Waibira home range. During this study, the diet of the Sonso community was characterized by a low diversity and considerable variation in quality. Food availability for this community varied and chimpanzees, especially males, supplemented their diet with field-crops. Food availability and diet quality for the Waibira community was more stable, resulting in overall more balanced activity budgets. Waibira chimpanzees do not forage on field crops and, possibly as a result of this, diet composition of this community was more variable and diet diversity was higher. Young leaves were an integral part of the diet in both communities, a result which underlines the importance of protein in chimpanzee diet and the need to reassess chimpanzee foraging strategies with regard to a balanced intake of macronutrients.

The Waibira community foraged on average in smaller parties and smaller food patches, travelling shorter inter-patch distances when all travel was considered. However, the general foraging strategy of using fission-fusion dynamics to minimize feeding competition appeared to be very similar in both communities: Larger parties foraged in larger food patches and party size increased with travel distance and feeding bout length. Chimpanzees in both communities chose food patches in a similar way: Across sexes and communities, chimpanzees exhibited a clear preference for closer as well as novel food patches, whereas the predictive power of patch size was generally low. Overall, sex differences in activity budgets and foraging behaviour were insignificant, questioning the general assumption that female chimpanzees need to forage in a fundamentally different way compared to male chimpanzees.

Findings of this study demonstrate that, in order to judge the utility of socio-ecological models and advance our understanding of factors that shape foraging strategies, comprehensive models of foraging behaviour are needed, that incorporate several important variables simultaneously. The extent to which chimpanzees were able to adjust activity patterns and dietary composition as well as diversity to different forest environments, while maintaining a general strategy to maximize foraging success, suggest that they are more generalist foragers than currently acknowledged.

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This thesis is dedicated to my parents, Sabine and Karl-Heinz.

Table of contents

Chapter 1 Introduction

Chapter 2 Diet composition and activity patterns in two neighbouring chimpanzee communities

Chapter 3 Adjusting the ecological constraints model to fission-fusion dynamics in chimpanzees (*Pan troglodytes*)

Chapter 4 Introducing discrete-choice models to chimpanzee feeding ecology

Chapter 5 Conclusion

Chapter 1 Introduction

To survive, any animal must acquire food. The necessity of finding sufficient food, and food that meets nutritional requirements, is one of the most significant selective pressures that acts on animals (Chapman et al., 2012). How well an animal achieves the task of securing food will determine its survival and also its reproductive success (Altmann, 1991, 1998). In his landmark study, Altmann (1991, 1998) demonstrated that the survival and reproductive success of young female baboons could be accurately predicted from the amounts of protein and energy in their diets as immatures. Due to its crucial role, foraging behaviour and how animals compete over food has attracted considerable attention, most notably through models of optimal foraging (OFT: Emlen, 1966; MacArthur and Pianka, 1966).

Animals that forage in groups face an additional challenge as they have to compete with group members over limited food resources (Alexander, 1974; Krause and Ruxton, 2002). Such feeding competition can occur in two ways: scramble competition and contest competition (Nicholson, 1954). Scramble competition occurs when individuals cannot effectively monopolize access to resources. Under such circumstances, all foragers of a group share the food supply and competition only takes place in an indirect manner, for example through an increase in patch depletion rate (van Schaik, 1989). Contest competition, on the other hand, can arise when some individuals of the group are able to monopolize resources to some extent and restrict other individuals' access to food by means of direct confrontations, such as aggressive interactions (Janson and van Schaik, 1988; van Schaik, 1989). In this case some foragers will obtain more from food sources than others. Under most natural conditions both of these types of feeding competition occur simultaneously (van Schaik and van Noordwijk, 1988). Based on this distinction, behavioural ecologists have developed models which predict under which circumstances scramble and contest competition are more likely to occur. According to these models (e.g. Wrangham, 1980; Janson and van Schaik 1988), scramble competition is more likely when food resources are highly dispersed, or very large relative to the size of the group. Contest competition, in contrast, is expected to occur when food patches are clumped and of intermediate size, so that the amount of food available to a group within feeding patches is clearly limited. Wrangham (1980) further postulated that these different types of feeding competition would then have a strong effect on social relationships among group members; while strong contest competition should lead to clearly defined dominance relationships and individuals should form long-term alliances with relatives, there is no need for overt aggressive interactions over food in scramble competition and consequently differentiated dominance relationships will be absent.

Another important insight during the early phase of these foraging models was that in female mammals, reproductive success is ultimately limited by access to resources whereas male reproductive success is more strongly limited by access to receptive females (Trivers, 1972; Emlen and Oring, 1977). This follows from the observation that in mammals, females typically have to invest much more parental effort, through gestation, lactation and infant rearing, and can only reproduce comparatively few times. Parental investment by male mammals, in contrast, is usually low, but reproductive success, as measured in terms of sired offspring, can be many times higher than that of females (Clutton-Brock and Parker, 1992). Female fitness thus depends strongly on their nutritional status and consequently females benefit more from acquiring high quality food resources than males, who benefit instead more from acquiring additional mates (Schoener, 1971).

These considerations led Wrangham (1980) to propose that group living in primates might have evolved as a result from the advantages that female relatives gain when together defending discrete food patches. He reasoned that, not only does regular contest competition favour the formation of dominance hierarchies, but also the formation of stable kin groups.

Since kin share a common genetic interest (Hamilton, 1964), coalitionary alliances can form under conditions when competition between groups of foragers is intense. Thus, in contest competition over discrete food patches, selective pressure favours female philopatry and strong female bonds. van Schaik (1983) instead argued that grouping evolved as a defence against predators and that the benefits of female grouping in competition with other groups was not sufficient to explain the evolution of sociality. Research that followed the development of these two theories found some support for both of them (Janson, 2000, 1992) and subsequently, further models were developed that incorporated both, the selective pressure of contest competition and those of predation risk, along with a large number of other costs and benefits of grouping (Sterck et al., 1997), such as an increased risk of disease transmission (Freeland, 1976; Côté and Poulinb, 1995) and infanticide (van Schaik, 2000). Although none of these models included any formal modelling, they are now referred to as ‘‘socio-ecological models’’ (Janson, 2000; Clutton-Brock and Janson, 2012). Since their initial development, socio-ecological models have become increasingly complex and more detailed; at their core, these models suggest that the intensity of feeding competition, as based on the distribution and abundance of resources, has clear and predictable effects on the social organization of animal groups.

A socio-ecological model that was developed more recently and that focuses predominantly on ecological costs of grouping is the ecological constraints (EC) model (Chapman and Chapman, 2000). This model posits that each individual within a group has to fulfil its energetic and nutritional requirements (Chapman et al., 1995; Chapman, 1990; Chapman and Chapman, 2000). Larger groups deplete food resources within a given area faster than smaller groups, either directly through overt contest competition or indirectly through an increase in patch depletion rate (Janson and Goldsmith, 1995; Janson and Van Schaik, 1988). As a result, a larger group will have to search for new food resources more often or look for larger feeding patches so that all individuals can meet their energetic and nutritional requirements (White and Wrangham, 1988). Groups which travel further distances are expected to reach a point where the energy spent on travelling will exceed energy obtained from resources that can be acquired in this manner. At this point it becomes advantageous to instead forage in smaller groups - and thus the maximum group size is reached (Chapman and Chapman, 2000).

Central to the EC model is the abundance, distribution and quality of resources. While abundant food patches allow foraging animals more easily to form larger groups, more widely dispersed resources should force foragers into smaller groups (Chapman, 1990; Chapman and Chapman, 2000; Janson, 1988). For example, feeding competition, and thus the proposed relationship between group size and travel distances, is assumed to be weaker or absent in folivorous animals because food patches of leaves and grass are usually abundant and rather evenly distributed (Isbell, 1991; Sterck et al., 1997; Isbell and Young, 2002; but see: Gillespie and Chapman, 2001; Snaith and Chapman, 2005).

Investigations which took a comparative approach and compared average group size and day-ranges across a large number of primate species supported the hypothesis that species which on average forage in larger groups have to travel further distances (Isbell, 1991; Janson and Goldsmith, 1995). Results from a number of single-species studies support the predictions of the EC model as well: in five groups of long-tailed macaques (*Macaca fascicularis*), daily travel distance and time spent travelling increased with group size (van Schaik et al., 1983). Similarly, in both spider monkeys (*Ateles geoffroyi)* and howler monkeys (*Alouatta palliata*), subgroup size was positively correlated with time spent travelling (Chapman, 1990). Several studies have found an increase in the size of chimpanzee subgroups (parties: Sugiyama, 1968) within larger food patches (Ghiglieri, 1984; Isabirye-Basuta, 1993; Newton-Fisher et al., 2000; White and Wrangham, 1988), and travel costs seem to constrain party size in chimpanzees as well (Chapman et al., 1995).

Such a positive relationship between group size and travel costs can, however, not always be found: in redtail monkeys (*Cercopithecus ascanius*), a large group of 32 individuals travelled a similar daily range than a much smaller group of 15 individuals

(Struhsaker and Leland, 1988). Bronikowski and Altmann (1996) compared daily travel distances of baboon (*Papio cynocephalus*) groups across a ten-year period and found that groups travelled farther in years when group size was smaller. Mean daily path length was also not correlated with group size in five groups of black-and-white colobus (*Colobus guereza*), although the largest group exhibited the longest mean daily path length (Fashing, 2001). More recently, Pengfei et al., (2015) reported that daily path length in Indo-Chinese grey langurs (*Trachypithecus crepusculus*) did not increase with group size but remained relatively constant even when explicit monthly changes in dietary pattern occurred. Similarly, the proposed relationship between group size and patch size has been challenged: Busia et al., (2016) found no association between daily party size of spider monkeys (*Ateles geoffroyi)* and daily fruit abundance as measured by the biomass of the food patches visited during the day. Studies which apply habitat-wide measures of food availability to group size fail to find the predicted relationship even more often (Anderson et al., 2002; Ramos-Fernandez, 2001; Stevenson et al., 1998; Weghorst, 2007).

Several possible reasons for the lack of distinct relationships between group size, patch size and travel distance have been proposed. Resource distribution and availability are usually quantified by botanical measures, such as densities of available feeding trees or/and monthly phenology scores (Anderson et al., 2002; Chapman et al., 1995, 1994; Doran et al., 2002; Hashimoto et al., 2001; Richter and Cumming, 2006; Stevenson et al., 1998). These measures, however, might be very different from how foraging animals themselves perceive distribution and availability of relevant resources (Wiens, 1976; Isbell et al., 1998; Koenig and Borries, 2006; Vogel and Janson, 2011, 2007) and consequently group sizes do not always increase with such measures of food abundance. Isbell et al. (1998) and Vogel and Janson (2007) argue that instead it is more meaningful to use movements of the foraging animals themselves to derive a measure of food distribution and/or abundance: actual travel distances between food patches should be a better reflection of how animals view the dispersion of food resources. Applying this rational, the former study demonstrated that habitat characteristics, in this case food tree species, can be important factors in the interaction between group size and travel distance as well (Isbell et al. 1998).

Further, the temporal scale on which foraging decisions are usually analysed might be too large (see Asensio et al., 2009). The majority of studies use daily averages from primates foraging in cohesive groups and whose group size and/or daily path length is expected to only vary with seasonal changes in food abundance and/or the size of feeding patches (Bronikowski and Altmann, 1996; Busia et al., 2016; Fashing, 2001; Pengfei et al., 2015; Struhsaker and Leland, 1988; Wrangham et al., 1993). Daily averages, however, are unlikely to capture adjustments that foragers make throughout the day, especially not in species that live in more flexible social units such as fission-fusion species. Furthermore, foraging in social groups is not only influenced by ecological variables but also by a range of social factors (Isbell and Young, 2002; Marshall et al., 2012; Sterck et al., 1997). The influence of such social factors is usually more fluid than those of ecological ones and might change within foraging groups several times during the day (Aureli et al., 2008). Using average daily values of group size, path length and patch size thus potentially eliminates precisely the variation that one is interested in, i.e. the dynamic response of behaviour to environment is lost and relationships between foraging variables can not be established.

In order to verify the applicability of the EC model it is thus necessary to test its predictive power in a way that addresses these potential shortcomings. In this thesis I will therefore use an appropriately shorter temporal scale and individual travel distances between food patches to build a comprehensive model comprising several important foraging variables (Chapter 3). Applying the EC model in this manner will allow us to evaluate how useful it remains as a tool to investigate the relationships between group site, travel costs and patch size in socially foraging animals.

This study further intentionally adapts a comparative approach of male and female foraging behaviour to determine if predicted sex differences in foraging effort (Trivers, 1972; Emlen and Oring, 1977) can indeed be verified through observational data. The majority of studies investigating foraging behaviour focus solely on female strategies, following the rationale that female foraging is more likely to reflect optimality and thus more relevant for tests of optimal foraging (Hopkins, 2008, 2016; Normand and Boesch, 2009; Normand et al., 2009; Suarez, 2014). However, by ignoring the foraging that is deemed suboptimal (that of male foragers), little can be learned about what optimal foraging really is to the foragers under investigation and how good our understanding of optimality is (Altmann, 1998). Only by comparing both sexes, can we come to understand if and how females may try to optimize their foraging behaviour.

Optimal foraging theory (OFT) is based on the assumption that natural selection favours animals that optimize their foraging efficiency; foragers in these models aim to maximize a certain predefined “currency”, such as the amount of food per unit time, usually measured as energy intake (Emlen 1966; MacArthur and Pianka, 1966). This can either be achieved by minimizing the time needed to obtain a certain amount of energy or by maximizing the amount of energy gained within a certain time (Schoener, 1971). OFT has guided much of the research on foraging behaviour in the past five decades (Giraldeau and Caraco, 2000; Krebs and Davies, 2009), and despite ample criticism (Pyke, 1984; Mangel, 1990; Altmann, 1998) the notion of optimal foraging is deeply embedded in most models of foraging today.

An assumption that has been questioned soon after the development of initial optimality models, is that foraging organisms are supposed to have complete spatial and temporal knowledge of available resources which allows them to optimize net intake rates (Giraldeau and Caraco, 2000; Krebs and Davies, 2009). While optimal foraging theory (OFT) does not exclude the possibility of improving foraging performance through learning about the environment or flexibly employing multiple foraging strategies (McNamara and Houston, 1985), this basic assumption of optimality has been challenged on several grounds. It seems highly unlikely that foraging animals have complete knowledge of their current environment; a much more plausible premise is that individuals are, to some extent, uncertain about foraging conditions (Houston et al., 2007; Mangel, 1990; Pyke, 1984). For example, spatial memory allows to remember places and distances between places, but properties of such places (e.g. food amounts) can change unpredictably, resulting in imperfect expectancies even in animals capable of integrating spatial and temporal information (Spencer, 2012). Many social foragers further live in highly complex environments in which animals may not be able to simultaneously take into account all foraging parameters so that even experienced foragers cannot be expected to constantly make optimal decisions (Fawcett et al., 2014).

Furthermore, natural selection can only be expected to lead to an evolutionary stable or optimal strategy in environments which remain constant for longer periods of time (Houston et al., 2007). In changing environments foragers may thus still be adjusting their foraging strategies to recent conditions so that observed behaviours do not meet the assumption of optimality (McNamara and Houston, 1987). An increasing number of animal populations are now living under conditions which are changing rapidly, due to habitat degradation and other human impacts (Fischer and Lindenmayer, 2007; Hockings et al., 2015) so that evolved foraging strategies may no longer match current ecological contexts (Sih, 2013). Thus, while the simplified models of OFT have provided a natural starting point for the study of foraging behaviour, novel research needs to advance beyond its overly restrictive assumptions.

In this thesis I will use discrete-choice models to investigate how chimpanzees choose food patches (Chapter 4). Discrete-choice models are based on the concept of utility and allow for an approach that does not assume an optimal strategy as the starting point (Cooper and Millspaugh, 1999; Manly et al., 2002). They study the foraging decisions themselves, thereby allowing us to understand which factors truly influence decisions and how individual foragers attempt to meet energy or other nutritional goals across different habitats (Marshall et al., 2012). Such models also more easily allow for the optimised currency to shift or to accommodate multiple currencies at the same time, for example if an animal is both trying to maximise its energy intake and meet particular nutritional requirements (Felton et al., 2009).

Chimpanzees as a model of foraging behavior

The current study investigated the foraging behaviour of two neighbouring chimpanzee communities in the Budongo Forest Reserve. Chimpanzees (*Pan troglodytes*) provide an excellent opportunity to test socio-ecological theories, for two reasons. First, within-species variation in chimpanzee foraging behaviour is vast, as they inhabit a range of different forest environments across Africa, from evergreen lowland rainforest (e.g. Taï National Park, Côte d'Ivoire, Boesch and Boesch-Achermann, 2000) to semi-arid savanna grassland (e.g. Fongoli, Senegal: Pruetz, 2006). Understanding mechanisms that lead to within-species variation has been proposed to be a promising way forward in developing more realistic socio-ecological models (Strier, 2009, 2003, Struhsaker, 2000, 2008). By comparing foraging groups of the same interbreeding population that live under different ecological conditions, it is possible to exclude phylogenetic reasons for any observed differences in foraging strategies or social organization (Chapman and Rothman, 2009).

Within-species variation in chimpanzee foraging behaviour has mostly been explored as a consequence of differences in habitat type (Bogart and Pruetz, 2008) or the extent of seasonality that different chimpanzee populations experience (Boesch and Boesch-Achermann, 2000), while variation within interbreeding populations has rarely been studied (Potts et al., 2015, 2011). Only two research sites exist at which several chimpanzee communities of the same population have been studied in detail (Taï National Park, Côte d'Ivoire, Boesch and Boesch-Achermann,2000; Kibale National Park, Uganda, Ghiglieri, 1984) and only in Kibale National Park has foraging behaviour been compared in more detail within the same population (Potts et al., 2011, 2015, 2016). In the Budongo Forest Reserve, a second community of chimpanzees has recently been habituated to the presence of human observers (Samuni et al., 2014; see below), and, in contrast to communities in Kibale, these are not merely communities of the same population but neighbouring and thus truly interbreeding communities. The two study communities at Budongo therefore offer a unique possibility to gain a better understanding of the extent of within-species variation in chimpanzees (Chapter 2).

Second, chimpanzees are characterized by a high degree of fission-fusion dynamics (Aureli et al., 2008). In contrast to animals which forage in cohesive groups, group membership in species with pronounced fission-fusion dynamics is more fluid and members of a community travel and forage in small subgroups which frequently change in size and composition throughout the day (parties: Sugiyama, 1968). Fission-fusion grouping patterns can be found in several other large bodied primates, such as bonobos (*Pan paniscus*: Nishida and Hiraiwa-Hasegawa, 1987), spider monkeys (*Ateles spp.*: Klein, 1972; Symington, 1990), some populations of muriquis (*Brachyteles spp*.: Milton, 1984; Strier et al., 1993) and hamadryas baboons (*Papio hamadryas*: Kummer, 1971). This type of grouping and foraging behaviour allows individuals to adjust to short-term variation in the distribution/availability of resources and corresponding levels of feeding competition more readily than the collective ranging and feeding patterns of animals that forage in cohesive groups (Chapman et al., 1995; Lehmann and Boesch, 2004). As foragers are free to flexibly adjust to prevailing ecological, social and their nutritional conditions, essential foraging variables, such as group size, patch size and travel distance, are expected to be more closely linked in species with a high degree of fission-fusion dynamics. Therefore, chimpanzees offer an ideal model to explore the effect of different levels of feeding competition on relationships between such foraging variables. And yet, other primates, especially spider monkeys, have in recent years been the focus of many tests of socio-ecological models (Ramos-Fernandez, 2001; Shimooka, 2003; Ospina 2011; Weghorst, 2007; Wallace 2008; Asensio et al., 2009), while in chimpanzees studies of foraging behaviour have received far less attention than those of culture and cognition (McGrew, 1992; Whiten et al., 1999; Call and Tomasello, 2008). Statistical means to analyse data from individual foragers within their groups are now available (Bolker et al., 2009) and one aim of this thesis is to apply these novel instruments in order to explore chimpanzees’ dynamic foraging behaviour in more detail than previous studies.

Budongo forest and study communities

Research was conducted within the Budongo Forest Reserve (1°35’ - 1°55’ N, 31°08’ - 31°42’ E), over a period of 16 months. The forest is located in Western Uganda (Figure 1.1) and comprises 428km² of medium-altitude, moist, semi-deciduous tropical forest. Prior to commercial timber extraction, which was initiated by the British Colonial Administration around 1920, hardwood such as *Cynometra alexandri* was the dominant canopy species. During the 1950's and 1960's arborocide treatment was applied to several tree species, with a focus on climax vegetation, in particular Cynometra forest, to promote the spread of mixed forest and regeneration of mahogonies (Babweteera et al., 2012; Plumptre, 1996). Illegal extraction of timber by hand still persist (Plumptre et al., 2001) and as a result of these two activities today the forest consists of a mosaic of different vegetation types. Mixed forest covers about one-half of the forest area (Plumptre, 1996) and, compared to unlogged Nature Reserves, these areas record a higher density of trees producing fleshy fruits (Tweheyo, 2000). Possibly due to this increase in fruiting trees, densities of multiple monkey species (*Colobus guereza, Cercopithecus mitis* and *Cercopithecus ascanius*) were found to be higher in logged compartments of mixed forest (Plumptre and Reynolds, 1994) and chimpanzees might have similarly benefited from the spread of mixed forest (Reynolds, 2005).

The two study communities in the Budongo Forest Reserve, Sonso and Waibira, differ in overall size and occupy home ranges of different logging history. During the past 20 years community size of the Sonso community has ranged from 50-70 members (Reynolds, 2005); during this study it contained 71 individuals in total. Community size for the more recently habituated Waibira community has been estimated to be 100-120 individuals (Hobaiter et al., 2017). Logging operations within the home ranges of Sonso and Waibira chimpanzees were carried out at different times and followed separate guidelines. While chimpanzee home ranges do not exactly match forest compartments, core ranges of each community can generally be associated with a specific forest compartment. The core home range of the Sonso community corresponds to compartment N3 (Figure 1.2), which was selectively logged between 1947 and 1952, when trees above a DBH of 130cm were removed. The Waibira compartment (W21) was logged more recently, from 1963- 64, during a period when felling limits of timber trees were reduced to 85cm DBH (Plumptre, 1996). As a result of the more recent and heavier logging activity within the Waibira home range, tree species composition and food resource distribution were expected to differ considerably across habitats of the two communities.

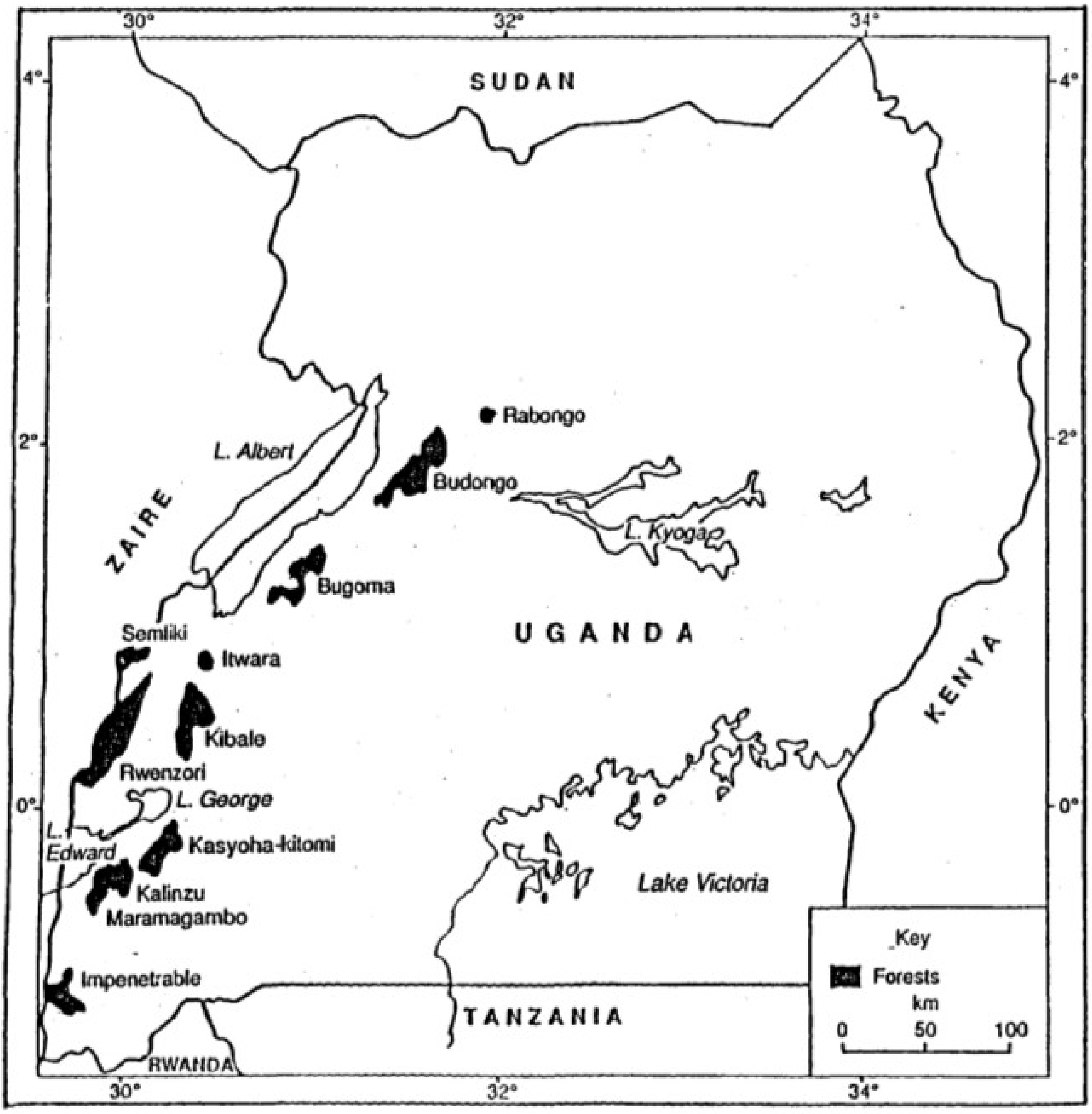

Figure 1.1 Location of the Budongo Forest Reserve and other Forest Reserves containing chimpanzees in Uganda (from Reynolds, 1992)

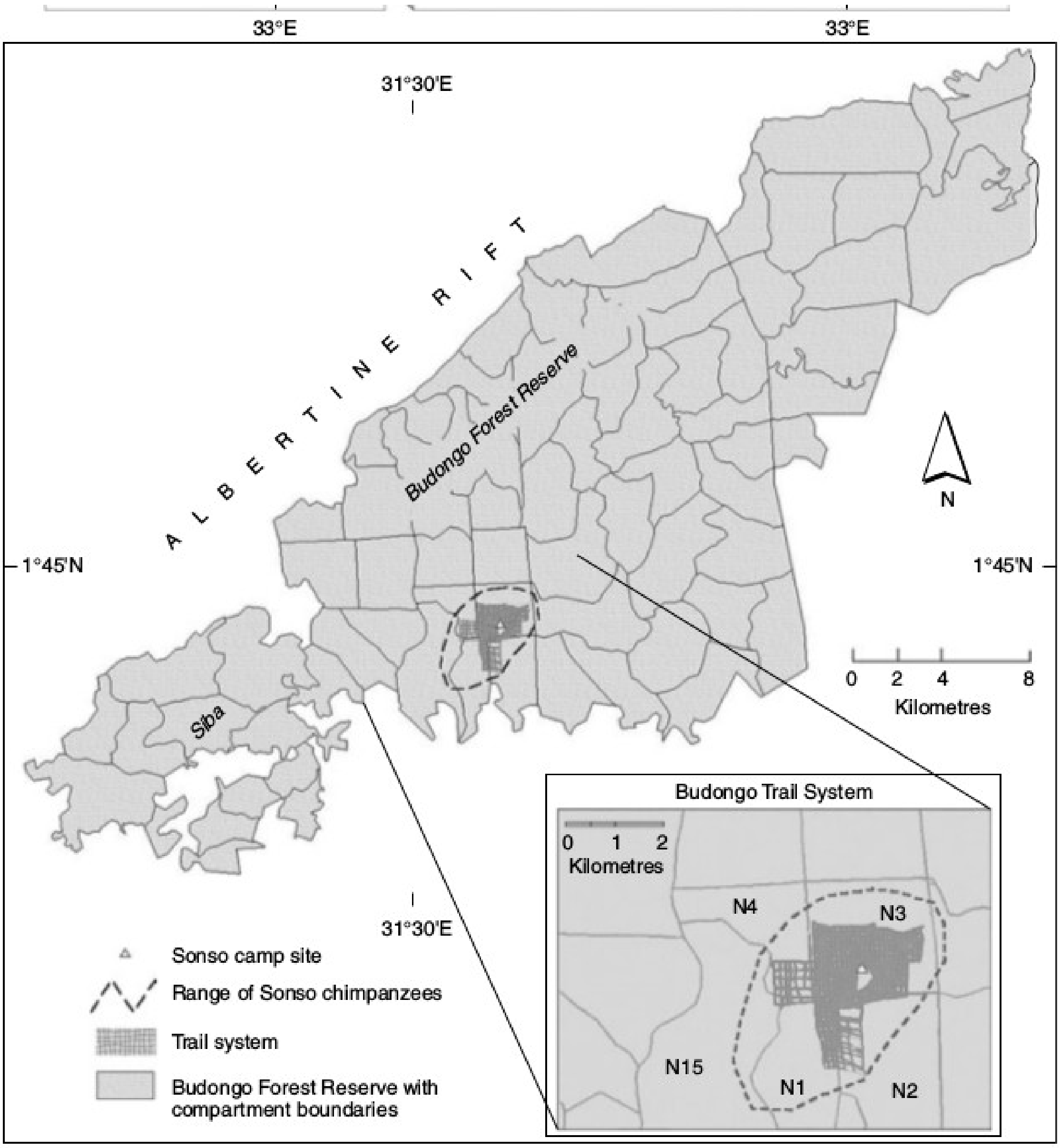

Figure 1.2 Location of the Sonso home range and forest compartments within the Budongo Forest Reserve (from Reynolds, 2005). The home range of the Waibira community lies just to the east of the Sonso community.

Research on chimpanzees at Budongo started with the study by Reynolds and Reynolds (1965) and Sugiyama (1968), who provided a first description of the diet and social organisation of chimpanzees in this area. Work resumed in the 1990s to study the impact of logging on chimpanzee ecology; in 1991 the Budongo Forest Project was officially initiated with funding from the National Geographic Society and Overseas Development Administration (ODA). The Sonso community was habituated between 1990 and 1995 by Budongo Forest Project staff and Newton-Fisher (1997) as part of his PhD thesis on tactical behaviour and decision making in wild chimpanzees. Since then, a large range of ecological, observational and experimental studies have been carried out at Budongo, involving the Sonso community and, since 2011, also the Waibira community. Newton-Fisher (2002, 2003) has calculated home range size of adult male Sonso chimpanzees. Using three methods of analysis (minimum polygon, fixed kernel and adaptive kernel), he estimated it to be between 6.78 and 14.51 km^2; for a community size of 46 individuals at that time, this corresponded to 6.8 to 3.2 individuals/km^2. Investigations of feeding ecology include, most notably, Newton-Fisher's (1999a) detailed assessment of diet composition and Fawcett's thesis (2000) on female relationships and food availability, both in Sonso. These two studies examined the diet of the Sonso community for the periods of 1994 – 1995 (Newton-Fisher, 1999a) and 1997 - 1998 (Fawcett, 2000). Both found *Ficus sur*, *Broussonetia papyrifera* and *Ficus mucoso* to be the top three food species. Feeding on ripe fruit accounted for the majority of feeding time (Newton-Fisher, 1999a: 49%; Fawcett, 2000: 44%) and figs were eaten in most months of the year. *B. papyrifera* (the paper mulberry tree) is an exotic species that was introduced by the British in the 1950s around the Sonso Sawmill (Reynolds, 2005). It grows outwards from the forest edge into the grassland and chimpanzees of the Sonso community have discovered it as a food resource, foraging upon the young leaves, flowers and fruits of this species. Both studies also identified young leaves of *C. mildbraedii* as an important food item in the diet of Sonso chimpanzees, as it potentially serves as a source of protein (Kuroda et al., 1996), whereas the proportion of terrestrial herbaceous vegetation (THV) within the diet was low compared to other chimpanzee populations. Since these two studies were conducted, Sonso chimpanzees have engaged increasingly in crop-foraging behaviour (BCFS, unpublished data) and an evaluation of the impact of this shift in diet on foraging behaviour and activity patterns formed part of the current study (Chapter 2). The diet composition, activity budgets and food availability of the Waibira community have not been described previously and were investigated here for the first time.

Thesis aims

The overall goal of this thesis was to further our understanding of the significance of certain ecological and social parameters for foraging behaviour, as well as their importance to chimpanzee feeding ecology specifically. By applying new methodological approaches to the study of foraging decisions and analysing foraging events in individual food patches across two neighbouring communities, I aimed to provide a rigorous test of socio-ecological models for chimpanzee foraging behaviour.

I begin by a description of the forest composition, diet composition and activity patterns of the two communities in Chapter 2. I conducted a first assessment of forest composition across home ranges, by identifying tree species in 10 randomly stratified plots in each community and calculating densities and productivity of important food species. Based on over 590 hours (Sonso) and 490 hours (Waibira) of observational data I investigated the diet composition, diet diversity and activity budgets of male and female chimpanzees in each community. Differences and similarities in forest composition, diet and activity patterns described in this chapter also provide the relevant basis for more detailed analysis and discussions of patch use and foraging decisions in the following chapters.

In Chapter 3, I tested predictions of the ecological constraints (EC) model in male and female foragers in each community. I used generalized linear mixed-effects models (GLMMs) to explore the relationship between party size, patch size and travel distance, and, in a separate model, the effect of party size and patch size on the occurrence of direct contest competition in food patches. Instead of using daily averages of these foraging variables, I analysed measurements of individual food patches and inter-patch movements of specific focal animals.

Finally, in Chapter 4, I applied discrete-choice models to the study of foraging decisions in chimpanzees. From observations of foraging behaviour and ecological variables of food patches, I created a set of 422 foraging decisions (Sonso: 205, Waibira: 217). This set was used to investigate the relative importance of travel distance, patch size (DBH), novelty of the food patch, food type and feeding bout length on patch choice in chimpanzees of both sexes in each community.

The chapters in this dissertation are presented as independent papers, yet, following one another in the order presented here, also explore foraging behaviour with an increasing level of detail. The concluding Chapter 5 provides a synthesis of the results from Chapters 2 to 4 and discusses the broader implications of these for our general notion of chimpanzee feeding ecology and the applicability of socio-ecological models.

Chapter 2

Diet composition and activity patterns in two neighbouring chimpanzee communities

Abstract

Understanding mechanisms that lead to within-species variation has been proposed to be a promising way forward in developing more realistic socio-ecological models. Chimpanzees (*Pan troglodytes*) represent an excellent candidate species to investigate within-species variation in feeding ecology - variation within interbreeding populations has, however, rarely been studied. Here I describe the feeding ecology of two neighbouring chimpanzee communities in the Budongo Forest Reserve, Sonso and Waibira. Over 590h of observational data were collected on the Sonso community from October 2015 to June 2016 and over 490h of data on the Waibira community from October 2016 to June 2017; these were combined with measurements of food availability and data on forest composition within the home ranges of each community.

As it was not possible to collect data from both communities simultaneous and climatic conditions during the two periods of data collection differed substantially, a direct comparison of diets and activity budgets was not meaningful. Instead the data sets from each community were analysed and discussed separately and I generated new, testable predictions for future work. For the Sonso community, food availability within the forest and diet quality varied considerably, as did monthly activity budgets. During times of low food availability within the forest, this community supplemented its diet with field-crops. Food availability and diet quality for the Waibira community was more stable, resulting in overall more

balanced activity budgets. This community does not forage on field crops and, possibly as a result of this, diet composition was more variable and diet diversity was higher. In both communities, activity budgets of male and female chimpanzees differed very little, suggesting that male and female foraging efforts might not be as divergent as current theories of sex differences in foraging assume. Young leaves were an integral part of the diet in both communities, which underlines the importance of protein in chimpanzee diet and the need to reassess chimpanzee foraging strategies with regard to a balanced intake of macronutrients. A first assessment of forest composition across home ranges showed that two important non-fig food species might be more abundant within the Waibira home range. Future comparisons of the two chimpanzee communities at Budongo should be guided by results from more detailed botanical surveys and the results and hypotheses presented in this study.

Introduction

Socio-ecological models aim to find meaningful relationships between the social organization of animal groups and their ecology (see Chapter 1). The intensity of feeding competition, as caused by differences in resource distribution, is a central aspect of models which examine variation in the size and structure of primate groups (reviewed in: Janson, 2000; Clutton-Brock and Janson, 2012).One way to test predictions of socio-ecological models is to compare closely related species that only differ in certain quantifiable features of their ecology (Isbell et al., 1998, 1999; Mitchell et al., 1991) or populations of the same species that live in different habitats (Barton et al., 1996; Koenig et al., 1998; Sinha et al., 2005; Potts et al., 2011). For example, Barton et al. (1996) compared within-group competition for food, predation pressures and female bonds of baboons at two sites. At one site, within-group competition for food and predation pressures were high, while at the other site food was more evenly distributed and predation pressure lower. In accordance with predictions, in groups from the site of high within-group competition females formed strong bonds with one another, whereas at the site of low-group competition bonds among females were weaker.

Another possibility is to take a broader comparative approach and test whether the variables of socio-ecological models vary in the predicted manner when comparing patterns across a large number of primate taxa (Clutton-Brock and Harvey, 1977; Isbell, 1991; Janson and Goldsmith, 1995; Majolo et al., 2008; Nunn, 1999; Sterck et al., 1997; Wheeler et al., 2013). Wheeler et al. (2013), for example, tested whether dietary categories do indeed predict rates of female-female agonism across 44 primate groups from 23 species. Species that forage predominantly on fruits and other high-quality resources that occur in discrete patches are expected to compete more openly over food resources than species that feed on evenly distributed foods, such as leaves and grass. Wheeler et al. (2013) found instead group size and the degree of terrestriality to be positively associated with rates of female-female agonism, whereas the effect of dietary variables pointed in the opposite direction than predicted for almost all taxa.

For such a broader comparative approach, species or entire taxa need to be categorized into distinct groups for each of the variables that are included in the model (Strier, 2009, 2003; Struhsaker, 2008); for example, diet (frugivorous, folivorous, omnivorous etc.) or substrate use (i.e., degree of arboreality) of each species or taxa have to be classified. For count data (e.g. group size) and continuous variables (e.g. body weight, daily path length, home range size, rates of agonism) values for each species or group are calculated by averaging across species or groups, from all populations that have been studied in sufficient detail (Clutton-Brock and Harvey, 1981; Mitani and Rodman, 1979; Wheeler et al., 2013; Wich and Nunn, 2002). Comparative studies that use single values to represent model variables, such as diet, ranging or group size, for an entire species or population are, however, problematic (Strier, 2003; Struhsaker, 2008). In wild non-human primates an increasing number of studies document that foraging behaviour and diet not only vary across species, but that substantial within-species variation exists in this regard as well (Chapman and Chapman, 1999; Fashing, 2001; Ganas et al., 2004; Harris and Chapman, 2007). Such intra-specific variation has important implications for comparative models that attempt to place species into distinct categories: primate species that exhibit considerable variation in, for example, diet composition, either between populations, or between groups within a population, cannot easily be categorized. For example, African colobines, such as guerezas (*Colobus guereza*), are usually highly folivorous, yet they also consume fruit and the percentage of fruit in their diet can range from 2 to 40% (summarized in: Fashing, 2007). Using averages of a species or populations therefore runs the risk of overgeneralization and severely limits the validity of any comparative model (Strier, 2009). The potential range of variation within populations thus deserves more attention and needs to be taken into account in interpretations of species- and population-level characteristics in primates (Chapman and Rothman, 2009; Harris and Chapman, 2007; Potts et al., 2011).

Species that live across a wide range of different habitat types, or experience strong seasonality in food supply, are expected to display higher levels of within-species variation in foraging behaviour and are therefore particularly suitable for exploring mechanisms that lead to intra-specific variation. Chimpanzees (*Pan troglodytes*) inhabit a range of different forest environments across Africa, from evergreen lowland rainforest (e.g. Taï National Park, Côte d’Ivoire, Boesch and Boesch-Achermann, 2000) to grassland–woodland–forest mosaics (e.g. Gombe National Park, Tanzania: Goodall, 1986) and semi-arid savanna grassland (e.g. Fongoli, Senegal: Pruetz, 2006). Accordingly, substantial differences in feeding ecology across different chimpanzee sub-species and populations exist. While chimpanzees are generally described as ripe fruit specialists (Ghiglieri, 1984; Watts et al., 2012; Wrangham et al., 1998), research across these different habitat types has demonstrated that chimpanzees can include a large variety of food types into their diet: At Taï National Park chimpanzee supplement their diet by nut-cracking during the dry season (Boesch and Boesch-Achermann, 2000). Chimpanzees at Bossou in West-Africa feed on oil-palm kernel and oil-palm pith in farmlands when little ripe fruit available in the forest (Yamakoshi, 1998). And in a semi-arid, open environment in south-eastern Senegal, the Fongoli community feeds on termites continuously throughout the year (Bogart and Pruetz, 2008).

Besides habitat type, habitat productivity and the extent of seasonality experienced by foragers have an impact on diet diversity as well. According to optimal foraging theory (OFT), dietary diversity should be lower in highly productive habitats or during times of high food abundance (Schoener, 1971; Pyke et al., 1977). If high-quality resources are abundant throughout the year, frugivores may not need to forage on a diverse number of food species but instead focus on fewer preferred ones (Terborgh, 1983). In the moist lowland equatorial rain forest of Taï National Park, ripe fruits are abundant during most months of the year and chimpanzees seem to experience less seasonality in resource availability compared to other chimpanzee communities (Anderson et al., 2005; Doran, 1997; Wittiger and Boesch, 2013). Diet diversity of this population has not been examined in a manner comparable to other chimpanzee communities, but the proportion of fruit in the diet was lowest in the minor dry season of July and August (Doran, 1997). If chimpanzee foraging in more productive habitats follows predictions of OFT, diet diversity should, at most times, be lower in these West African populations.

Investigations of other chimpanzee populations have compared diet diversity at times of high and low food abundance: In habitats of more pronounced seasonality, such as the semi-deciduous forest of the Budongo Forest Reserve and Kibale National Park, with a bimodal pattern of rainfall (Chapman et al., 1999; Newton-Fisher, 1999a), chimpanzees can experience months of fruit scarcity (Fawcett, 2000; Wrangham et al., 1998, 1991). In accordance with OFT, chimpanzees of the Kanyarara community at Kibale National Park displayed higher levels of monthly dietary diversity when preferred food was scarce (Wrangham et al., 1998). Fawcett (2000), too, found dietary diversity of the Sonso community at Budongo to be negatively correlated with the availability of ripe fruit. During times of food scarcity males of the Kanyawara community increased the amount of terrestrial herbaceous vegetation (THV) in their diet (Wrangham et al., 1991) and chimpanzees of the

Sonso community relied heavily on young leaves and flowers of *B. papyrifera* (Newton-Fisher, 1999a; Fawcett 2000). Thus, fibrous piths (Wrangham et al., 1991) and young leaves (Newton-Fisher, 1999a; Fawcett, 2000) appear to be a vital component in the diet of some chimpanzee communities as well. Fibrous piths and stems can offer an additional source of carbohydrate energy (Matsumoto-Oda and Hayashi, 1999; Wrangham et al., 1991) and young leaves provide relatively high levels of protein (Carlson et al., 2013; Takemoto, 2003).

More recently, Potts and colleagues (Potts 2009; Potts et al., 2011, 2015, 2016) have shown that habitat productivity can also vary considerably on a much smaller spatial scale and that such variation has a profound impact on diet diversity, activity patterns and foraging efficiency in chimpanzees. Their studies explored habitat heterogeneity and chimpanzee densities across two neighbouring communities at Kibale National Park. The Kanyawara and Ngogo communities inhabit home ranges which are separated by only 12km, yet the two communities differ substantially in overall size and density: while for the smaller Kanyawara community (ca. 45-55 individuals) chimpanzee densities are relatively low (1.5 individuals/km^2), the Ngogo community is the largest and most densely populated chimpanzee community currently known, with over 155 members (5.1 individuals/km^2; Bortolamiol et al., 2014). Potts et al. (2011, 2015) were able to relate this difference in chimpanzee density to productivity of their respective home ranges and corresponding differences in foraging efficiency. One highly valuable food resource, *Ficus mucuso,* was only available within the home range of the Ngogo community, and the Ngogo home range supported a higher abundance of plant species which produced fruit during times of low overall food abundance (Potts et al., 2009). In the smaller Kanyawara community chimpanzees spent more time resting, which was interpreted as a cost-minimization strategy, whereas Ngogo chimpanzees incorporated more ripe fruit in their diet and had an overall lower diet diversity (Potts et al., 2011). Ngogo chimpanzees consequently exhibited higher mean net caloric gain rates than did Kanyawara chimpanzees (Potts et al., 2015). It remains unclear however, whether the relationships between chimpanzee densities, habitat productivity and foraging efficiency described by Potts et al. (Potts 2009; Potts et al., 2011, 2015, 2016) apply to other chimpanzee communities as well or instead are specific to conditions in Kibale forest.

As described previously (Chapter 1), the Sonso and Waibira communities differ in several important ecological and demographic factors as well. Some of these differences, such as overall community size and, possibly, density, are less pronounced between the two study communities at Budongo than between the Kanyawara and Ngogo communities in Kibale National Park. Further factors, such as the presence of *F. mucuso* in both home ranges and the possibility for the Sonso community to rely on exotic tree species and field crops, are novel parameters that distinguish this study from investigations at Kibale. The conditions at Budongo thus offer a possibility to investigate the foraging ecology of two chimpanzee communities which more similar in size and habitat quality.

This thesis was, however, initially not designed to be a comparative study of the Sonso and Waibira communities. I hoped to evaluate the universality of Pott’s findings (Potts 2009; Potts et al., 2011, 2015, 2016) by exploring the interaction between community size, forest composition, chimpanzee diets and activity budgets across the two study communities at Budongo. I planned to test, for example, whether the diet of the larger Waibira community would contain more ripe fruit and would be less diverse than that of the Sonso community; or whether activity budgets of the two chimpanzee communities at Budongo reflect forest productivity as for the community at Kibale ; i.e. do more abundant and high quality resources result in less time spend on resting?

Yet, due to concomitant circumstances at the research site, it was later on not possible to collect data from both communities at the same time. Fundamentally different climatic conditions during the two periods of data collection then largely rendered a comparison impossible. A comparison was not meaningful, since it would have been very speculative to say which differences reflect actual differences between communities and which differences were due to climatic conditions or a mixture of both. The results presented from both communities should consequently be viewed as separate data sets and are here only discussed in the context of their respective climatic conditions. Instead of a comparison, I will be presenting mostly descriptive data and use these to generate new, testable predictions.

Comparing the two chimpanzee communities at Budongo allows for further insights into the mechanisms that lead to intra-specific variation in dietary patterns and into the overall feeding ecology in this species. A more detailed understanding of within-species variation from interbreeding populations will help to inform comparative socio-ecological models as it enables researchers to distinguish elements of primate social structure that are adaptations to current environments from ones that may result from phylogenetic inertia (Chapman and Rothman, 2009; Strier, 2009). Differences and similarities in forest composition, dietary quality and activity patterns described in this chapter will also provide the basis for more detailed analysis and discussions of patch use and foraging decisions in the following chapters.

Methods

Study communities

This study focused on two neighbouring chimpanzee communities, Sonso and Waibira. Each community was observed for a period of eight months in consecutive years. Data collection on the Sonso community took place between October 2015 and June 2016. The second field season, during which data on the Waibira community was collected, lasted from October 2016 to June 2017. The Sonso community has been observed continuously since 1990 (Newton-Fisher, 1997; Reynolds, 2005), whilst habituation of the Waibira chimpanzees started in 2011 and is still ongoing (Samuni et al., 2014). During the study period, the Sonso community contained 71 individuals in total and, following age classifications by Goodall (1986), included 12 adult males (≥16 years old) and 24 adult females (≥14 years old). The Waibira community consisted of at least 88 known individuals, including 17 adult males and

29 adult females. All members of the Sonso community were individually recognized and could be observed at close quarters on the ground. For the Waibira community almost all adult members could be individually recognized as well at the time of this study, and observation distances permitted to study foraging behaviour at a sufficiently close range (see for example also, Hobaiter et al., 2017).

The Sonso community engages in crop-foraging (Tweheyo et al., 2005) and in recent years males of the community increasingly feed on field crops. During this study crop-foraging was inferred to take place mainly in November, October, April and May. Direct observations of chimpanzees foraging on field crops was not possible as research permits from forestry authorities (UWA and UNCST) did not include permission to study human-wildlife interactions. Therefore, all data that is presented in this chapter (diet composition, diet diversity, activity budgets) only refers to observations within the forest boundaries. The diet, activity budgets and food availability of the Waibira community have not been described previously. Data from this eight-month study period thus provide a first description of these foraging parameters from the Waibira community.

Behavioural data collection

I aimed to conduct full-day nest-to-nest follows of individual chimpanzees in both communities to obtain a complete record of the individual's foraging behaviour and activity patterns. Focal follows started at the morning nest and continued for as long as conditions allowed. Within the Sonso community, focal follows had to be interrupted when the designated focal left the forest to forage on field crops or during inter-community encounters (mean duration of Sonso follows: 5.6h SD 3.1h, range: 1-12h median: 5h). The ongoing habituation of the Waibira community and their denser habitat made continuous follows of individual chimpanzees more challenging than for the Sonso community (mean duration of Waibira follows: 4.1h SD 2.6h, range: 1-12h median: 4h). At the beginning of each day I selected one focal from a randomised list. When the initial focal individual was lost, I attempted to increase the number of focal samples from individuals that were still underrepresented in the overall sample in order to maintain a balanced sampling regime.

I followed male and female chimpanzees in each community: Six adult males and five adult females were selected as focal individuals from the Sonso community, while ten adult males and nine adult females were chosen from the Waibira community. I sampled a larger number of individuals from the Waibira community since this community is also larger in size and it was not always possible to find a predetermined focal individual within the party that was located in the morning. Males from both communities varied in age and represented different rank categories (high-, mid- and low-ranking). Four of the five females from the Sonso were lactating and travelled with at least one infant and one juvenile during the study. The fifth female was not lactating and only travelled with her juvenile offspring. From the Waibira community seven females were lactating while the other two females were not lactating and only travelled with one juvenile offspring.

During focal follows, the behavioural state of the focal individual was recorded continuously (Altmann, 1974) and categorized as either feeding (which included all behaviours related to food handling – the entire process of picking and ingesting food items), traveling (defined as terrestrial quadrupedal walking as well as arboreal climbing), grooming (giving or receiving grooming), resting (defined as any sustained period (>1 min) in which the individual was sitting or lying and not engaging in any other behaviour) or other (accounting for all other behaviours, e.g. vocalisations, copulations, play, drinking).

For each food item, the type (fruit, leaves, flowers, seeds, bark, soil, meat), species, and phytophase (ripe, unripe, young, mature), of the item was identified and recorded. To investigate differences in food item quality across communities, food items were classified as either high- or low-quality food. Chimpanzees show a strong preference for ripe fruit which offer a high content of easily digestible macronutrients, such as non-structural carbohydrates and lipids, and try to maintain a frugivorous diet even when fruit availability is low (Remis, 2002; Wrangham et al., 1998). At Budongo, seeds of *C. alexandrii* seem to be nutritionally valuable to chimpanzees, as they are rich in lipids (Reynolds, 2005). Thus, all ripe fruit and seeds of *C. alexandrii* were classified as high quality foods, whereas young leaves, flowers and unripe fruit, which usually contain less sugars but higher levels of fibre and antifeedants (Houle et al., 2014; McLennan and Ganzhorn, 2017) were classified as low quality food.

The results of this chapter are based on 594h and 491h of focal animal sampling for Sonso and Waibira, respectively.

Diet diversity

To enable comparisons to investigations of other chimpanzee populations (Potts et al., 2011; Watts et al., 2012; Wrangham et al., 1998, 1991) and previous studies at Budongo (Newton-Fisher, 1999a; Fawcett, 2000), the Shannon-Wiener diversity index (Pielou, 1974) was used to calculate diet diversity and the standardized Shannon-Wiener index (Hill's (1973) equitability index) to estimate dietary evenness. The standardized index measures diversity on a 0–1 scale, with a score of 1 indicating that the chimpanzees spent completely equal amounts of time feeding on each item in their diet.

The Shannon-Wiener index (H') was calculated by:

$$H' = -\sum[P_i \log P_i]$$

where P_i is the proportion of species i in the monthly sample.

The standardized Shannon-Wiener index (J') was calculated by:

$$J' = H'/\log(x)$$

where x is the total number of species sampled.

Measures of food availability

Measuring food availability in tropical rain forests in a manner that is comparable across field sites and study species is notoriously difficult (Chapman et al., 1994). For this study, I chose a method which specifically monitors fruit production of important arboreal food sources in each community. As both communities have already been studied for several years and important food sources of each were known, such a method was assumed to best capture the availability of exploitable food resources within the home range of each community.

For each community, a phenology trail was established that consisted of 237 (Sonso) or 185 (Waibira) individual fruit trees, representing 17 (Sonso) or 15 (Waibira) important food species of each community. Species for each community were selected based on previous studies at Budongo (Newton-Fisher, 1999a; Fawcett, 2000) and discussion with long-term field assistants. The Sonso trail included six species of figs (*F. mucuso*, *F. sur*, *F. exasperata*, *F. natalensis*, *F. variifolia* and *F. barteri*) and nine nonfig species. The Waibira trail included four species of figs (*F. mucuso, F. sur*, *F. exasperata*, *F. variifolia)* and eleven nonfig species (see Appendix III for full list of species monitored and number of individual trees for each species). For each phenology tree, the presence of fruit (ripe and unripe), young leaves, flowers and seeds was noted (Chapman et al., 1994). Trails of each community were monitored on a monthly basis, yielding eight phenology samples per community.

From these phenology samples, two monthly food availability indices (FAI) were calculated. Index one (FAI-1) followed the conventional approach of considering only presence/absence of ripe fruit within each phenology tree (Blake et al 1990, Wrangham et al. 1998, for review see Chapman et al., 1994). In addition to ripe fruit, index two (FAI-2) also took into account unripe fruit that was available in all four monitored fig species and young leaves and flowers of any phenology tree species that chimpanzees were observed to feed on during each particular month. Chimpanzees of both communities rely heavily on a number of non-fruit food items during some times of the year: Young leaves and flowers of

Broussonetia papyrifera made up a substantial part of the Sonso community's diet during October and November 2015 and young leaves of *Celtis mildbraedii* were the most important food item of the Waibira community. Individuals of both communities also consumed young leaves of two fig species (*F. exasperata*, *F. variifolia*) and unripe fruit of four fig species (*F. mucuso*, *F. sur*, *F. exasperata*, *F. variifolia*). Therefore, availability of these food resources was included into FAI-2, which served as an alternative measure of food availability and was compared to FAI-1. I calculated the percentage of trees within the phenology sample that provided food resources by dividing the number of trees containing ripe fruit (FAI-1) or ripe fruit and other potential foods (FAI-2) by the total number of surveyed trees.

Botanical plots

Detailed records exist of the logging history and the effect of logging on forest structure and vegetation composition across forest compartments in Budongo (Plumptre, 1996). Yet, to date no study has investigated the extent of floristic heterogeneity at the level of chimpanzee home ranges within Budongo forest. In order to establish a first, preliminary assessment of the differences in abundance of tree species and forest composition between home ranges of both communities, 20 botanical plots covering an equal area at both sites were established. The location of plots was determined using a stratified random placement technique (Greig-Smith, 1983), such that all habitat subtypes (primary forest, early- to mid-stage regenerating forest, wet (valley bottom) forest, swamp forest) within the core area of each home range were included (see Table 2.1 and 2.2). Habitat types were adapted from Plumptre et al. (1996) and Newton-Fisher (1997) and defined as follows:

1) Primary forest

Old growth, mature forest, with little to no signs of human disturbance. Dominated by mature *Cynometra alexandrii* and *Celtis mildbraedii.*

2) Early- to mid-stage regenerating forest

Forest that was selectively logged (Sonso: between 1947 and 1952; Waibira: from 1963- 64) and is still regenerating. Not dominated by a single species; mostly small, young regenerating tree species. Canopy partly open.

3) Wet forest (valley bottom)

Seasonally flooded forest.

4) Swamp forest

Permanently flooded forest. Swamp species, such as *Raphia farinifera*, present in the sample.

Plots were constructed along pre-existing trails and ran 200m along the trail (see Figure 2.1 and 2.2). On 10m to each side of the trail, all trees above a diameter at breast height (DBH) of 20cm were identified and measured. Each plot was thus 200m by 20m in size, resulting in a total area of 4 ha per community. I calculated the density (trees/ha) of all tree species that were identified within plots and the basal area (m^2/ha) for the top 15 food species of each community to assess the availability and productivity of these important species (Chapman et al, 1994; Rode et al, 2006; Bryson-Morrison, 2017).

Table 2.1 Number of plots per habitat type within the Sonso home range. For definitions of habitat types, see text.

Habitat type	Number of plots	Plot names
Primary forest	4	Plot 1 (AD-1D), Plot 6 (7D-9D), Plot 7 (70-90), Plot 8 (76-96)
Early- to mid-stage regenerating forest	4	Plot 2 (BPY), Plot 3 (A6-16), Plot 9 (7-12), Plot 10 (7-16)
Wet forest (valley bottom)	1	Plot 4 (1-12)
Swamp forest	1	Plot 5 (1-16)

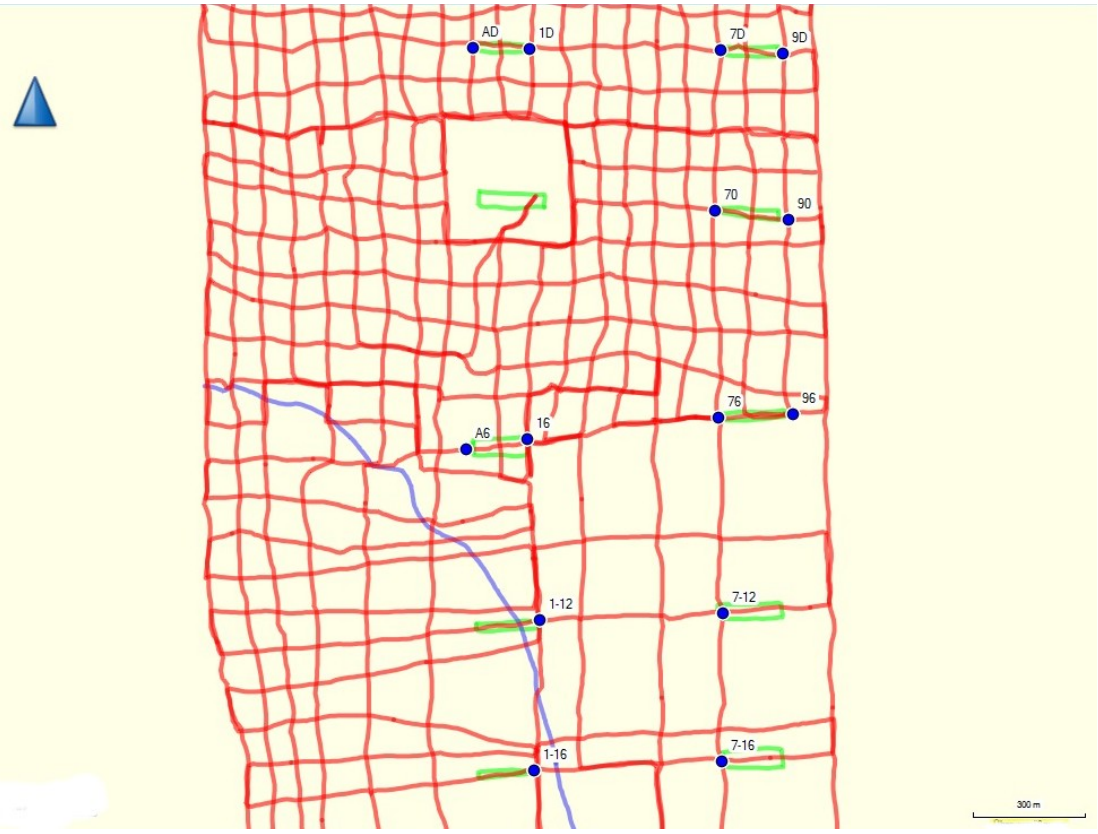

Figure 2.1 Location of the 10 botanical plots within the Sonso grid system.

Table 2.2 Number of plots per habitat type within the Waibira home range. For definitions of habitat types, see text.

Habitat type	Number of plots	Plot names
Primary forest	4	Plot 6 (32-R-34), Plot 8 (32-F), Plot 9 (32-B), Plot 10 (32-4)
Early- to mid-stage regenerating forest	4	Plot 3 (20F-22F), Plot 4 (20B-22B), Plot 5 (20-4), Plot 7 (32-L)
Wet forest (valley bottom)	1	Plot 1 (20R-22R)
Swamp forest	1	Plot 2 (20L-22L)

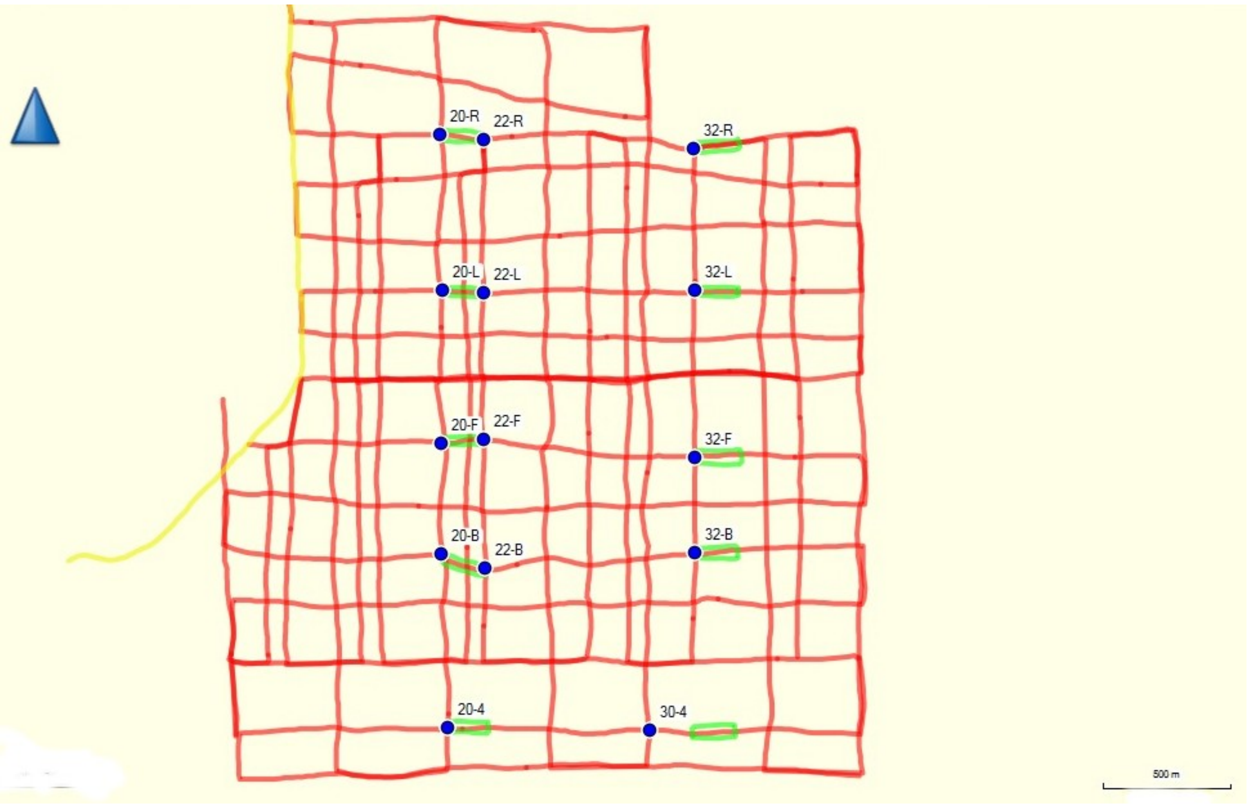

Figure 2.2 Location of the 10 botanical plots within the Waibira grid system.

Climatic variables

Previous studies at Budongo have documented a bimodal distribution of rain with a mean annual rainfall of around 1600mm (Newton-Fisher, 1999a; Reynolds, 2005). Across years, most rain falls between September and November and during a smaller rainy season between March and May. The major dry season occurs between mid-December and mid-February (Newton-Fisher, 1999a). Temperatures vary little across months, with monthly maximum and minimum temperatures between 32C and 19C. For this study the amount of rainfall and its distribution across months was documented, in order to take into account the potential influence of rainfall on fruiting patterns and fruit production (van Schaik et al., 1993) during the two study periods.

Statistical analysis

All statistical analyses were conducted in R 3.4.3 (R Development Core Team 2017). To calculate diversity indices, the vegan package was used (Oksanen et al., 2013).

Results

Rainfall

Amount and patterns of rainfall showed considerable variation across the two field seasons of data collection (Figure 2.3). During data collection at Sonso, the extent of seasonality was distinct, with a 3-months dry season (Jan-Mar) and a period of heavy rainfall from October to November 2015, which is similar to rainfall patterns at Budongo described in former studies (Newton-Fisher, 1999a; Tweheyo and Lye, 2003). During the second field season, in contrast, differences in rainfall across months were less pronounced. Monthly rainfall never exceeded 200mm, so that even during usually very wet months the amount of rainfall was more similar to months of 'inter-rains'. These differences in rainfall had clear effects on fruiting patterns of chimpanzee food species (see below). Different tree species were producing fruit during the second field season, rendering a direct comparison of foraging behaviour across the two study communities impossible.

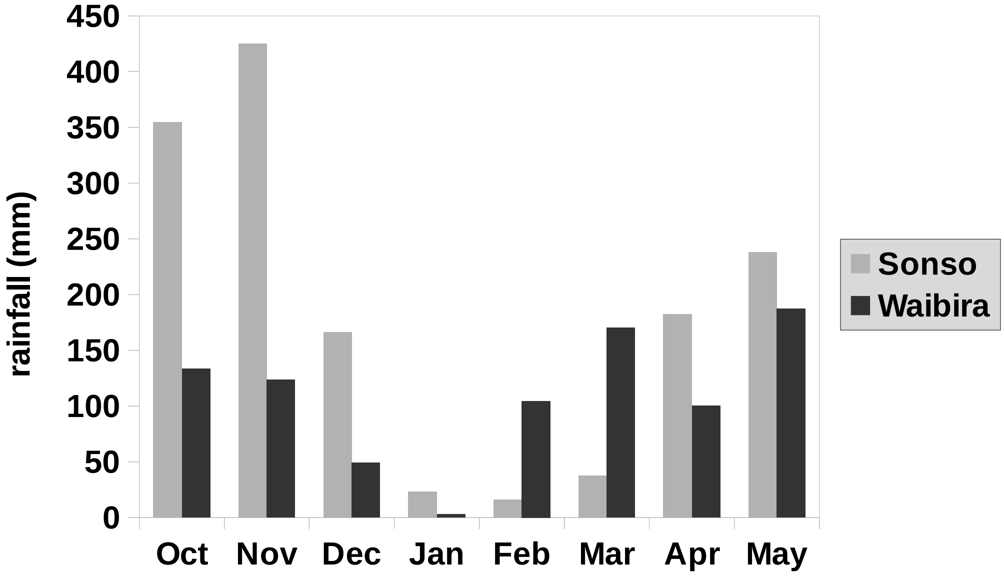

Figure 2.3 Amount of rainfall (mm) during the eight months study period in each community.

Botanical plots

The mean number of trees per plot did not differ significantly across the two communities; yet, within the home range of the Sonso community, most plots contained more trees (range: 113 to 43 trees, mean = 86.6, standard error: 7.27) than within that of the Waibira community (range: 88 to 50 trees, mean = 75.9, standard error: 3.88). The total number of trees (Sonso: 865, Waibira: 750) and tree species (Sonso: 75, Waibira: 70) was larger within Sonso plots as well.

Species composition differed markedly across the two communities: the most frequent species within Waibira plots was *C. midlbraedii* (n = 167, 22%), a major food resource of young leaves for chimpanzees, followed by *C. alexandrii*, which is an important food resource during the dry season of December to February (Table 2.4 and Table 2.6, for full list, see Appendix I and II). Trees of these two species were often mature trees, with a mean DBH of 40-50cm. Within plots of the Sonso community, in contrast, small trees of *F. elastica* were the most frequent type of tree (n = 139, 16%). This species does not produce any food resources that chimpanzees feed upon. *C. midlbraedii* and *C. alexandrii* were among the most common tree species, albeit at much lower density than at Waibira (Table 2.3 and Table 2.5). Consequently, the botanical plots within the Waibira home range contained overall more food tree species than those of the Sonso home range: a comparison of the top 15 food species of each community, as recorded during this study, showed that a total of 333 feeding trees were found within the 10 Waibira plots, but only 197 within Sonso plots (Table 2.3 and Table 2.4). Especially the density (individuals/ha), as well as the total basal area (m^2/ha), of *C. midlbraedii* and *C. alexandrii* were higher within the Waibira home range. While there were differences in densities and basal area of common tree species, the average size (DBH) of tree species did not differ significantly across communities. *Fig species,* such as *F. mucuso, F. sur* or *F. exasperata*, were important food species for both communities, but were not well represented in the randomly stratified plots of this study.

To further investigate differences in densities of food species, tree species were categorized as either regular or rare feeding tree species, based on foraging behaviour recorded during this study. Regular feeding trees made up a larger proportion of surveyed trees within the Waibira home range (Sonso: 47% of all trees, Waibira: 62%) and non-feeding trees were more common within Sonso plots (Sonso: 36%, Waibira: 23%). A similar number of feeding trees were of species that provided ripe fruit and seeds (Sonso: 24%, Waibira: 28%), but within Waibira plots more trees provided young leaves and flowers (Sonso: 17%, Waibira: 34%). This result was largely driven by the high frequency of *C.midlbraedii* within Waibira plots.

Table 2.3 Total number of trees, density (individuals ha^{-1}), mean tree size (cm DBH for trees ≥ 20cm) and the standard error (SE) of tree size for the top 15 tree species within Sonso plots

Species	parts(s) consumed	Total trees	% of total trees	Density	Mean DBH	SE
Funtumia elastica	----	139	16.05	34.75	26.43	0.56
Celtis zenkeri	URF, YL	62	7.16	15.5	30.17	1.58
Khaya anthoteca	raisin	53	6.12	13.25	50.04	3.35
Celtis mildbraedii	YL, flower	39	4.50	9.75	36.23	2.93
Celtis durandii	RF	38	4.39	9.5	40.26	2.13
Broussonetia papyrifera	YL, flower	35	4.04	8.75	28.83	1.33
Cynometra alexandrii	seed	34	3.93	8.5	64.12	6.73
Caloncoba schweinfurthii	----	30	3.46	7.5	30.87	1.84
Trichilia prieuriana	----	29	3.35	7.25	26.03	1.02
Myrianthus holstii	RF	28	3.23	7	31.64	2.08
Antiaris toxicaria	RF, flower	26	3.00	6.5	31.12	2.51
Croton sylvaticus	RF	25	2.89	6.25	40.48	2.53
Margaritaria discoideus	----	20	2.31	5	53.50	3.18
Trichilia rubescens	YL	18	2.08	4.5	25.00	1.35
Bosquea phoberos	----	17	1.96	4.25	33.16	5.91

Note: *Broussonetia papyrifera* (the paper mulberry tree) was only found in one plot at the forest edge. It is an exotic species that was introduced by the British in the 1950s around the Sonso Sawmill (see: Reynolds, 2005).

Table 2.4 Total number of trees, density (individuals ha^{-1}), mean tree size (cm DBH for trees ≥ 20cm) and the standard error (SE) of tree size for the top 15 tree species within Waibira plots

Species	part(s) consumed	Total trees	% of total trees	Density	Mean DBH	SE
Celtis mildbraedii	YL, flower	167	22.27	41.75	39.21	1.4
Cynometra alexandrii	seed	93	12.40	23.25	49.04	2.27
Lasiodiscus mildbraedii	YL, flower	63	8.40	15.75	22.36	0.45
Funtumia elastica	----	53	7.07	13.25	24.91	0.58
Celtis durandii	RF	36	4.80	9	36.97	2.2
Croton sylvaticus	RF	33	4.40	8.25	34.91	2.02
Strychnos mitis	RF	33	4.40	8.25	45.93	3.77
Celtis zenkeri	URF, YL	25	3.33	6.25	31.45	2.15
Margaritaria discoideus	----	19	2.53	4.75	45.32	3.5
Macaranga monandra	----	10	1.33	2.5	34.11	4.1
Tapura fischeri	----	10	1.33	2.5	21.74	0.85
Antiaris toxicaria	RF, flower	9	1.20	2.25	29.71	2.56
Alangium chinense	----	8	1.07	2	30.78	1.94
Albizia glaberrimes	----	8	1.07	2	73.5	5.86
Trichilia prieuriana	----	8	1.07	2	22.1	1.13

Table 2.5 Total number of trees, density (individuals ha^{-1}), basal area (m^2/ha), mean tree size (cm DBH for trees ≥ 20cm) and the standard error (SE) of tree size for the top 15 food species of the Sonso community, as recorded within the botanical plots

Species	part(s) consumed	Total trees	% of total trees	Density	Basal area	Mean DBH	SE
Ficus mucoso	RF, URF	----	----	----	0	----	----
Cynometra alexandrii	seed	34	3.93	8.5	3.74	64.12	6.73
Broussonetia papyrifera	YL, flower	35	4.04	8.75	0.61	28.83	1.33
Ficus exasperata	RF, URF, YL	15	1.73	3.75	0.50	38.47	3.83
Antiaris toxicaria	RF, flower	26	3.00	6.5	0.57	31.12	2.51
Ficus variifolia	RF, URF, YL	----	----	----	0	----	----
Erythrophleum suaveolens	seed	2	0.23	0.5	0.08	44.50	1.50
Celtis mildbraedii	YL, flower	39	4.50	9.75	1.26	36.23	2.93
Alaphia sp.	RF	----	----	----	0	----	----
Ficus sur	RF, URF	11	1.27	2.75	0.31	35.18	4.51
Ficus natalensis	RF	----	----	----	0	----	----
Antrocarium micrantha	RF	1	0.12	0.25	0.11	75.00	-
Myrianthus holstii	RF	28	3.23	7	0.62	31.64	2.08
Milicia excelsa	RF	5	0.58	1.25	0.30	44.80	16.01
Mango mangifera	RF, URF	1	0.12	0.25	0.13	80.00	-
Total		197	22.75	49.25	8.23	509.89	41.43

Table 2.6 Total number of trees, density (individuals ha^{-1}), basal area (m^2/ha), mean tree size (cm DBH for trees ≥ 20cm) and the standard error (SE) of tree size for the top 15 food species of the Waibira community, as recorded within the botanical plots

Species	part(s) consumed	Total trees	% of total trees	Density	Basal area	Mean DBH	SE
Celtis mildbraedii	YL, flower	167	22.27	41.75	6.11	39.21	1.4
Cynometra alexandrii	seed	93	12.40	23.25	5.26	49.04	2.27
Ficus sur	RF, URF	4	0.53	1	0.22	45.84	15.37
Ficus mucoso	RF, URF	----	----	----	0	----	----
Putranjivace gerrandi	RF	----	----	----	0	----	----
Chrysophyllum albidum	RF	6	0.80	1.5	0.30	47.23	7.44
Ficus saussureana	RF	----	----	----	0	----	----
Ficus exasperata	RF, URF, YL	5	0.67	1.25	0.31	53.9	7.65
Antiaris toxicaria	RF, flower	9	1.20	2.25	0.17	29.71	2.56
Ficus variifolia	RF, URF, YL	1	0.13	0.25	0.10	70	-
Ficus polita	RF	1	0.13	0.25	0.03	40	-
Celtis durandii	RF	36	4.80	9	1.09	36.97	2.2
Maesopsis eminii	RF	5	0.67	1.25	0.34	57.55	6.41
Morus lactea	RF, URF, flower	1	0.13	0.25	0.12	79.58	-
Myrianthus holstii	RF, YL	5	0.67	1.25	0.05	23.36	1.33
Total		333	44.4	83.25	14.1	572.39	46.63

The Sonso community

Fruit availability

For the Sonso community the amount of exploitable resources varied considerably: after an initial phase of relative food scarcity the indices increased in December and January, but then dropped again during the dry months of February and March (Table 2.7). The percentage of trees along phenology trails containing ripe fruit (FAI-1) ranged from 0 – 18%, while FAI-2, which also took into account unripe fruit, young leaves and flowers, varied between 11 and 30%.

Table 2.7 Food availability for the Sonso community
Food availability is expressed as the percentage of trees containing ripe fruit (FAI-1) or ripe fruit and other potential resources (FAI-2). Both indices detected an increase in food availability in December and January, after an initial phase of low food availability. The two indices were not correlated (t = 0.67853, df = 6, p-value =0.523).

Sonso

	FAI-1	FAI-2
Oct 15	0	18.18
Nov 15	4.55	21.36
Dec 15	12.27	29.55
Jan 16	17.73	27.73
Feb 16	10.45	11.36
Mar 16	7.73	10.91
Apr 16	0.85	24.79
May 16	6.41	17.52
mean	7.50	20.18
SD	5.93	6.99

Diet quality

The Sonso community faced a period of largely low-quality food items during October and November 2015 (high quality food items: 32% and 15%, respectively) and another drop in March (Figure 2.4). This analysis, however, did not include time the Sonso community spent feeding on field crops. During times of food scarcity (Oct-Nov 2015; Apr-May 2016) the Sonso community, especially males, supplemented its diet with field crops and may this way have been able to compensate for a lack of high-quality food within the forest boundaries.

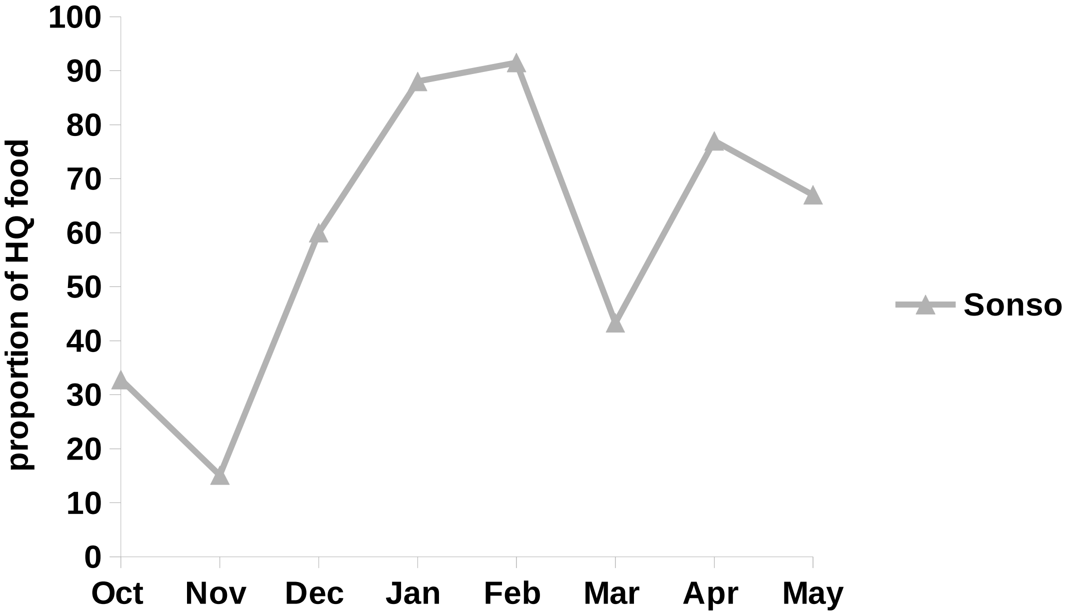

Figure 2.4. Monthly means of observation time (% of total observation time) spend feeding on high quality food items (ripe fruits and seeds) by chimpanzees of the Sonso community

Diet composition

Chimpanzees of the Sonso community spent 35.7% of their time collecting and ingesting food items. During the eight months study period they were observed to feed on more than 36 plant species, as well as three species of monkey (*Colobus guereza, Cercopithecus ascanius, C. mitis*), one species of duiker (*Philantomba monticola*) and different types of soil.

Three species were major food items, each accounting for 18-15% of feeding time. Together these three species accounted for 50% of feeding time and the major twelve species made up more than 80% of feeding time (Table 2.8). Feeding on fruit accounted for 52.4% of feeding time (ripe fruit: 38.7%, unripe fruit: 13.7%), and concentrated mostly on two species

(*Ficus mucusa* and *Ficus exasperata*). This comparatively low value can be ascribed to the heavy reliance on seeds of *Cynometra alexandrii* (16.8%) and flowers and young leaves of *Broussonetia papyrifera* (15.3%) during the study period. Across species, feeding on young leaves and flowers accounted for 21.1% of feeding time.

Table 2.8 Food species of the Sonso community accounting for 0.5% or more of total feeding time
RF = ripe fruit, UF = unripe fruit, YL = young leaves

Species	% of total feeding time	Plant parts consumed
Ficus mucoso	17.60	RF/UF
Cynometra alexandrii	16.82	seeds
Broussonetia papyrifera	15.29	YL/flower
Ficus exasperata	9.31	RF/UF/YL
Antiaris toxicaria	3.76	RF
Ficus variifolia	3.61	RF/UF
Erythrophleum suaveolens	2.94	seeds
Celtis mildbraedii	2.88	YL/flower
Alaphia sp.	2.63	RF
Ficus sur	2.28	RF/UF
Ficus natalensis	2.17	RF
Antrocarium micrantha	2.14	RF
Myrianthus holstii	1.67	RF
Milicia excelsa	1.30	RF
Mango mangifera	1.29	RF/UF
Ficus vallis-choudae	0.94	RF/UF
Pseudospondias microcarpa	0.92	RF
Chrysophyllum gorungosanum	0.71	RF

Some food species were available only in the home range of one community but locally absent in the other community or not fed upon during the study period. For the Sonso community, *B. papyrifera* (rank 3) and *Mango mangifera* (rank 15) were food items that were only available to this community. Three further species (*Erythrophleum suaveolens* (12) *Milicia excelsa* (14) and *Urera camaroonensis* (19)) were present within the forest of both communities, but only the Sonso community fed on these species during the study period.

Diet diversity

Diet diversity of the Sonso community was low. The mean number of species chimpanzees were observed feeding on per month was 12 (median = 12 spp, range: 6-21).

Monthly diversity values, as measured by the Shannon-Wiener diversity index (H′), varied from 1.24 to 1.80 (mean = 1.61, standard error: 0.067; Table 2.9). The standardized Shannon-Wiener index (J′, Hill's (1973) equitability index) ranged from 0.58 to 0.81 (mean = 0.669, standard error: 0.025). Chimpanzees spent each month feeding predominantly on one to two species, while all other food items accounted for only a small proportion of feeding time (see Appendix III).

Table 2.9 Measures of dietary diversity. Presented are the number of species in the diet (n), The Shannon-Wiener index (H') and the standardized Shannon-Wiener index (J'). The standardized index measures diversity on a 0–1 scale, and a score of 1 is indicating that chimpanzees spend completely equal amounts of time feeding on each item in their diet.

Sonso

	n	H'	J'
Oct. 15	9	1.49	0.68
Nov. 15	6	1.24	0.69
Dec. 15	7	1.58	0.81
Jan. 16	11	1.52	0.64
Feb. 16	13	1.72	0.67
Mar. 16	14	1.80	0.68
Apr. 16	21	1.78	0.58
May 16	18	1.74	0.60
mean	12.38	1.61	0.67
median	12		

Fruit availability and diet diversity

Dietary diversity of the Sonso community was not particularly affected by resource availability. FAI-2, which also included unripe fruit, young leaves and flowers, increased slightly when fewer food resources were available, but the effect was not significant (Figure 2.5a and b).

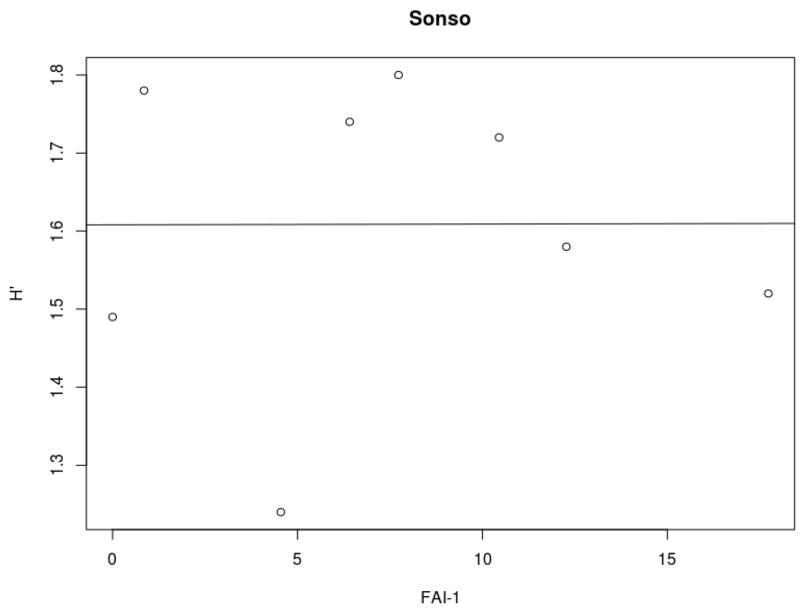

Figure 2.5a Dietary diversity (Shannon-Wiener index H') of the Sonso community in relation to fruit availability as measured by FAI-1 (only availability of ripe fruit)

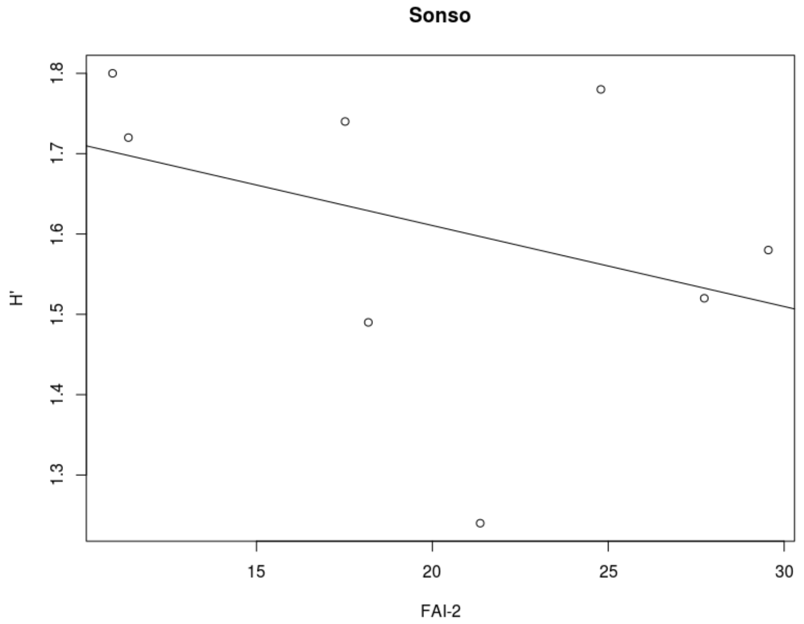

Figure 2.5b Dietary diversity (Shannon-Wiener index H') of the Sonso community in relation to fruit availability as measured by FAI-2 (availability of ripe fruit, unripe fruit, young leaves and flowers). Dietary diversity of the Sonso community increased slightly when fewer food resources were available (r= -0.37, p= 0.367)

Activity budgets

Monthly activity budgets of the Sonso community were quite variable: chimpanzees spent between 17 – 50% of total observation time feeding and time spent resting ranged from 14 – 49% (Figure 2.6a). Time spent traveling alternated less (14 - 27%) and monthly means of time spent grooming varied from 5 – 23%. Observation time only included behaviours recorded within the forest boundaries, but not any crop-foraging forays, which mainly occurred in November, October, April and May. Thus, some of the variation in activity budgets might be related to the fact that some community members, especially males, could not be observed at all times. However, during months of crop-foraging I recorded some of the highest percentages in observation time spent feeding (May: 50%, November: 48%). Since I followed other focal individuals within the forest, when parts of the community engaged in crop-foraging, foraging activities outside of the forest seem to not have disproportionately biased activity budgets reported for the Sonso community. Towards the end of the dry season (March 2016), Sonso chimpanzees spent a lot of time resting near the Sonso river and time spent feeding dropped to only 16% of observation time. During this month, FAI-2 also recorded the lowest level of food availability within the forest (see Table 2.7).

Males and females devoted similar proportions of observation time to feeding and traveling (Figure 2.6b). Females spent more time resting than males (females: 38%, males: 33%), while males devoted more time to grooming (males: 11%, females: 6%). When not feeding or traveling, males thus spent their time more often interacting with each other than females.

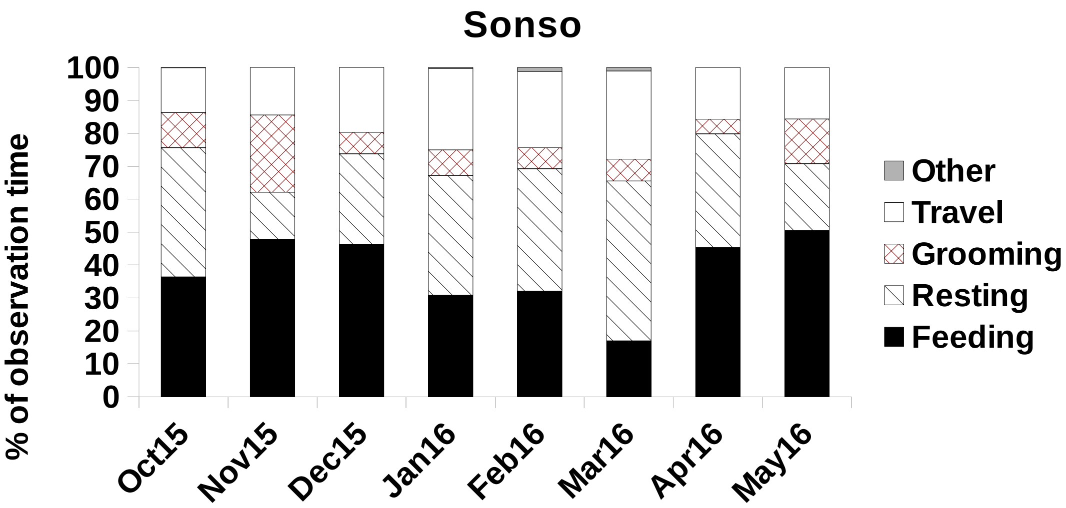

Figure 2.6a Monthly activity budgets of the Sonso community. Percentages of observation time spent feeding, resting, grooming, travel or on other activities. For definitions of behavioural categories see methods. Data pooled across all focal individuals.

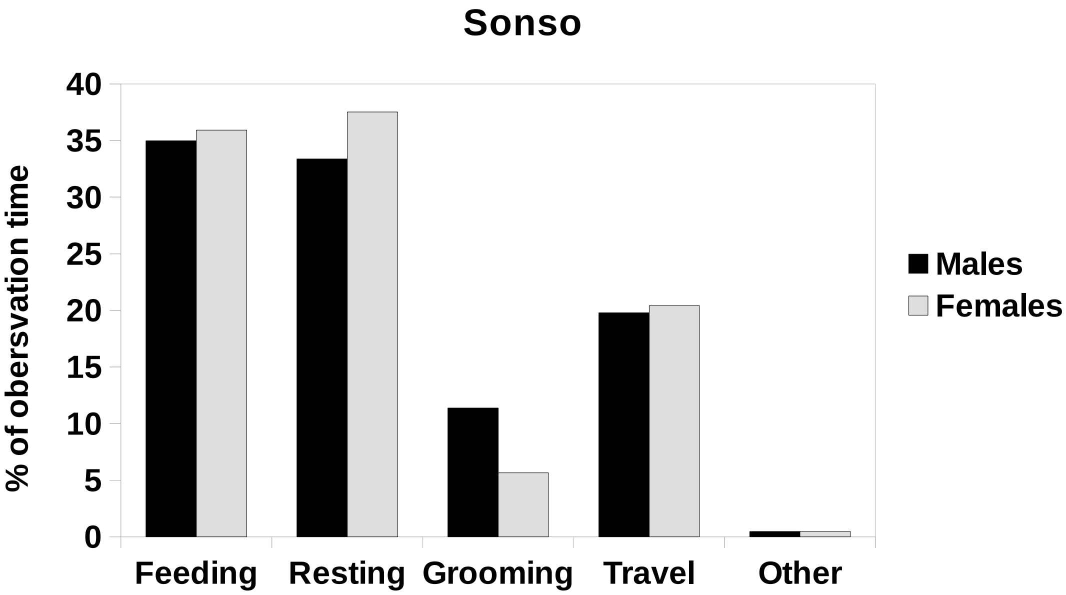

Figure 2.6b Activity budgets of males and females. Percentages of observation time spent feeding, resting, grooming, travel or on other activities. For definitions of behavioural categories see methods.

The Waibira community

Fruit availability

For the Waibira community the amount of exploitable resources remained relatively stable, especially during the first six months of the study (Oct 16 – Mar 17). During these months FAI-2 varied only little, between 11-17% (Table 2.10). Fruit availability peaked in April 2017, when, additionally to other food tree species (such as *Chrysophyllum albidum*, *Ficus sur*, *Myrianthus holstii*, *Maesopsis eminii)* provided ripe fruit.

Waibira

	FAI-1	FAI-2
Oct 16	1.19	10.71
Nov 16	2.98	11.9
Dec 16	1.19	11.31
Jan 17	6.55	16.67
Feb 17	10.12	15.48
Mar 17	7.74	16.07
Apr 17	13.11	32.14
May 17	4.17	10.12
mean	5.88	15.55
SD	4.30	7.18

Table 2.10 Food availability for the Waibira community

Food availability is expressed as the percentage of trees containing ripe fruit (FAI-1) or ripe fruit and other potential resources (FAI-2). The two indices reflect a more stable, yet overall lower food supply. For the Waibira community index 1 and 2 were correlated (t = 3.9568, df = 6, p-value =0.008).

Diet quality

Within the Waibira community, feeding on high quality food items never dropped below 44% of feeding time (Figure 2.6). The availability of high-quality foods was in some months driven by a single, large fruiting tree within the home range. In October 2016, for example, a large part of the community spent almost one week foraging on fruit of an especially large *Ficus mucusa*, which accounted for more than 25% of total feeding time during this month. Similarly, in December 2016, the community returned to one large *Ficus* *saussureana* for an entire week and this single tree amounted to more than 35% of total feeding time.

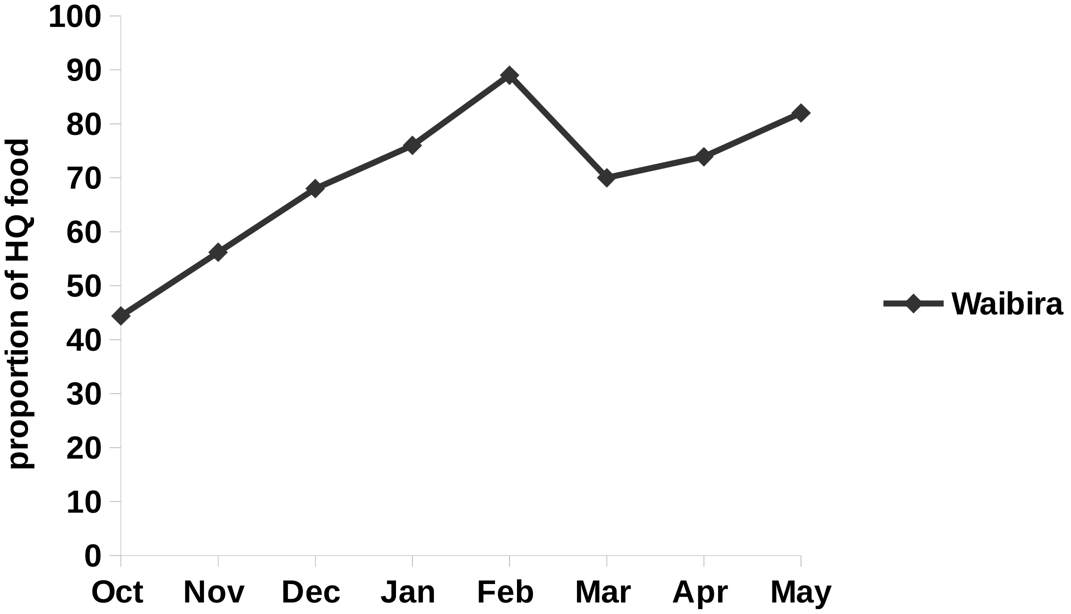

Figure 2.6. Monthly means of observation time (% of total observation time) spend feeding on high quality food items (ripe fruits and seeds) by chimpanzees of the Waibira community

Diet composition

Chimpanzees of the Waibira community foraged during 35.9% of total observation time. They consumed parts of more than 31 different identified plant species and young leaves and fruit from five or more different species of liana. As habituation of this community is still on-going, not all plant food items have yet been identified botanically. During this study, five plant species that chimpanzees consumed regularly and five food items that were consumed once were not yet identified. All of the five plant species consumed regularly were lianas; for two species, chimpanzees fed on unknown fruit and for three young leaves were eaten. Chimpanzees of the Waibira community did not prey on any species of monkey during the study period, only meat consumption of two species of duiker

(*Philantomba monticola, Cephalophus natalensis*) was observed (For a detailed discussion of intergroup variation in chimpanzee hunting behaviour at Budongo, see Hobaiter et al., 2017).

No single species accounted for more than 13% of feeding time. Three major species accounted for 35% of feeding time and the most important ten species accounted for 74% of feeding time (Table 2.11). Feeding on fruit accounted for 58.8% of feeding time (ripe fruit: 54.7%, unripe fruit: 4.1%), with *Ficus sur* being the most important species providing ripe fruit. The food item that chimpanzees relied on most heavily during the study period overall were young leaves of *Celtis mildbraedi*, which accounted for 12.9% of the total feeding time. Similar to the Sonso community, seeds of *Cynometra alexandrii* were a major food source (11.8%).

Table 2.11 Food species of the Waibira community accounting for 0.5% or more of total feeding time
RF = ripe fruit, UF = unripe fruit, YL = young leaves

Species	% of total feeding time	Plant parts consumed
Celtis mildbraedii	12.89	YL
Cynometra alexandrii	11.83	seeds
Ficus sur	10.17	RF/UF
Ficus mucoso	8.00	RF/UF
Putranjivace gerrandi	7.03	RF
Chrysophyllum albidum	5.76	RF
Ficus saussureana	4.90	RF
Ficus exasperata	4.71	RF/UF/YL
Antiaris toxicaria	4.44	RF
Ficus variifolia	4.16	RF/UF/YL
Ficus polita	2.76	RF
Celtis durandii	2.48	RF
Maesopsis eminii	2.23	RF
Morus lactea	1.73	RF/UF/flower
Myrianthus holstii	1.36	RF
Ficus natalensis	0.99	RF
Cordia millenii	0.93	RF/UF
Chrysophyllum muerense	0.85	RF
Lasiodiscus mildbraedii	0.78	YL/flower
Desplatsia dewevrei	0.73	RF/UF
Celtis wightii	0.62	YL
Alaphia sp.	0.51	RF

Putranjivace gerrandi (rank 5) was the only species that was specific to the Waibira home range. A further six species were consumed by Waibira chimpanzees which were not present within the 8-months sample of Sonso (*Chrysophyllum albidum* (6), *Ficus saussureana* (7), *Ficus polita* (11), *Maesopsis eminii* (13), *Cordia millenii* (17) and *Chrysophyllum muerense* (18)). For at least two food species (*C. albidum* and *M. eminii*) these differences can very likely be accounted to inter-annual changes in fruit production; both species produced only little fruit during data collection at Sonso and are therefore only represented within the Waibira sample. Other food species differences might reflect differences in forest composition or foraging preferences across the two communities (see discussion).

Diet diversity

Diet diversity of the Waibira community was moderate. The mean number of species chimpanzees were observed feeding on per month was 13 (median = 13 spp, range: 8-19). Monthly diversity values, as measured by the Shannon-Wiener diversity index (H′), varied from 1.34 to 2.50 (mean = 1.95, standard error: 0.128, Table 2.12). The standardized Shannon-Wiener index (J′, Hill’s (1973) equitability index) ranged from 0.54 to 0.87 (mean = 0.76, standard error: 0.041). During most months of the study period several plant species contributed substantially to the diet (Appendix III).

Table 2.12 Measures of dietary diversity. Presented are the number of species in the diet (n), The Shannon-Wiener index (H') and the standardized Shannon-Wiener index (J'). The standardized index measures diversity on a 0–1 scale, and a score of 1 is indicating that chimpanzees spend completely equal amounts of time feeding on each item in their diet.

Waibira

	n	H'	J'
Oct. 16	13	1.61	0.63
Nov. 16	13	2.11	0.82
Dec. 16	16	2.10	0.76
Jan. 17	12	1.93	0.78
Feb. 17	14	2.19	0.83
Mar. 17	8	1.81	0.87
Apr. 17	19	2.50	0.85
May 17	12	1.34	0.54
mean	13.38	1.95	0.76
median	13		

Fruit availability and diet diversity

Within the Waibira community dietary diversity slightly increased when food availability was high, however, none of these correlations were significant. During April 2017, when a large amount of food resources was available within the forest (Table 2.10), the diet of the Waibira community was most diverse; during this month individual chimpanzees were observed to feed on food items from 19 different species.

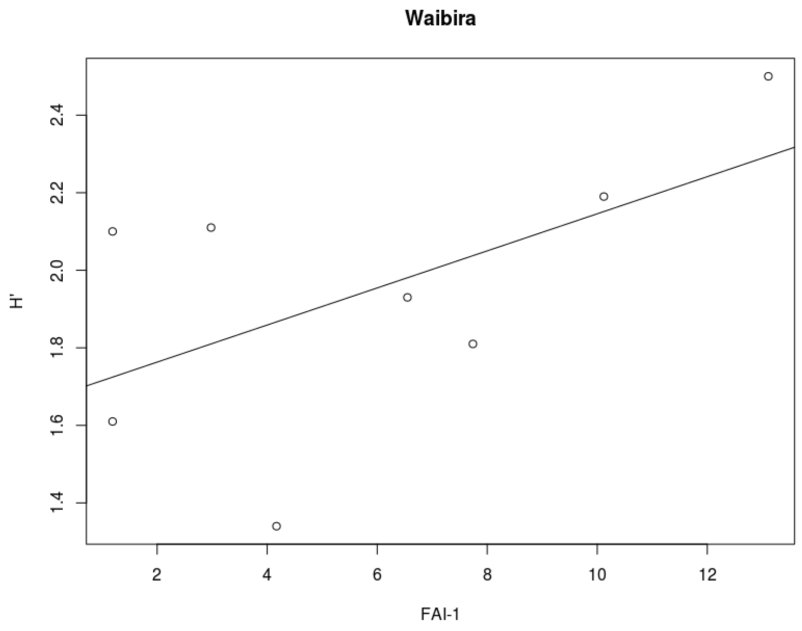

Figure 2.7a Dietary diversity (Shannon-Wiener index H') of the Waibira community in relation to fruit availability as measured by FAI-1 (availability of ripe fruit). Correlation between FAI-1 and diet diversity: r= 0.57, p= 0.142.

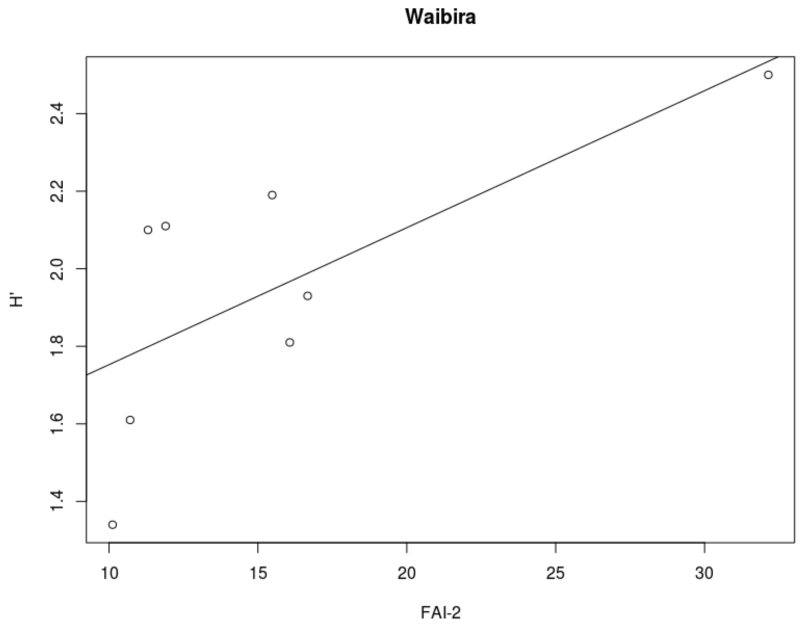

Figure 2.7b Dietary diversity (Shannon-Wiener index H') of the Waibira community in relation to fruit availability as measured by FAI-2 (availability of ripe fruit, unripe fruit, young leaves and flowers). Correlation between FAI-2 and diet diversity: r= 0.70, p= 0.053.

Activity budgets

Monthly activity budgets of the Waibira community were more balanced: the range of deviation within each behavioural category never exceeded 13%. Time spent feeding accounted for 29 – 42%, time spent resting for 25 – 36% and time devoted to resting ranged from 25 – 36% (Figure 2.8a). Monthly means of time spent grooming varied from 7 – 18%. This lower variability in activity budgets was in accordance with the less pronounced seasonal differences in rainfall (Figure 2.3) and fruit production (Table 2.10) during the study period in Waibira.

Activity budgets of males and females within the Waibira community were very similar: for none of the five behavioural categories did the difference between male and female values exceed 3% (Figure 2.8b). The proportion of observation time devoted to feeding was 36% for males and 37% for females. Females spent 31% of observation time on resting and males spent 28% on it. Grooming accounted for 15% of male observation time and 12% of female observation time. Traveling accounted for 21% (males) and 20% (females).

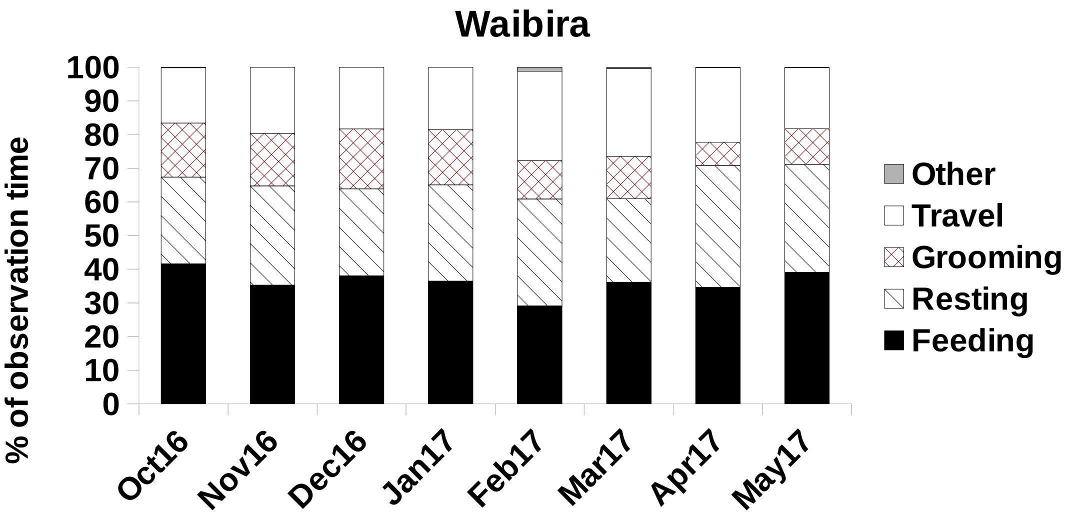

Figure 2.8a Monthly activity budgets of the Waibira community. Percentages of observation time spent feeding, resting, grooming, travel or on other activities. For definitions of behavioural categories see methods. Data pooled across all focal individuals.

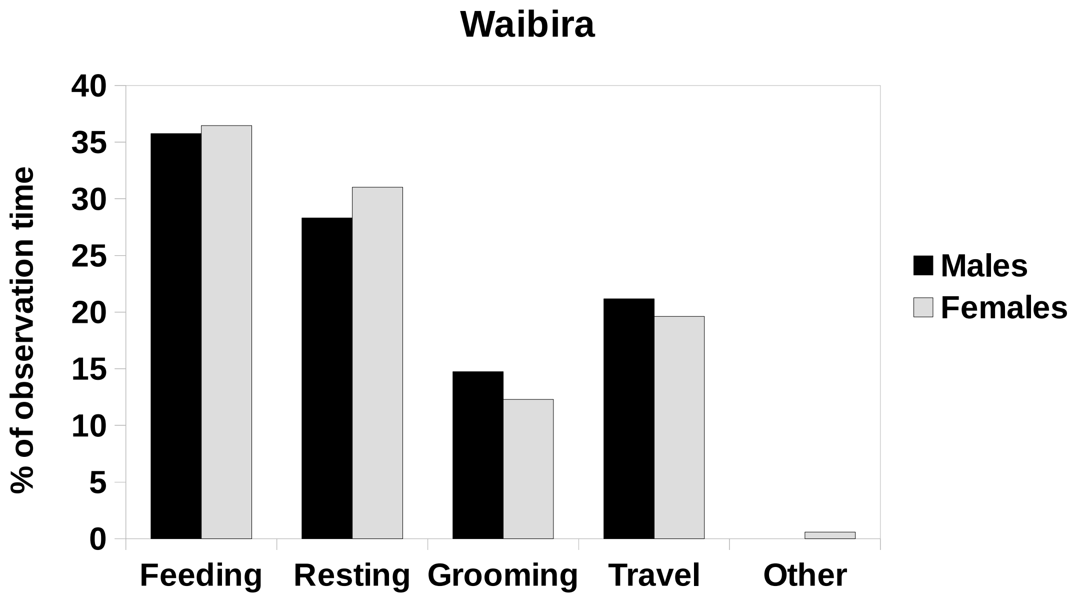

Figure 2.8b Activity budgets of males and females. Percentages of observation time spent feeding, resting, grooming, travel or on other activities. For definitions of behavioural categories see methods.

Discussion

The two study communities at Budongo offer an excellent possibility to gain more insights into sources of within-species variation from interbreeding populations. While a direct comparison of diets and activity budgets was unfortunately not possible during the current study, it identified several promising leads for such an investigation. Below I will first discuss results from each community separately and then present some hypotheses that could be tested based on these results.

The Sonso community

For the Sonso community food availability within the forest varied considerably, as did the proportion of high/low quality food items. In accordance with this variability in food availability and quality, monthly activity budgets were equally unbalanced. For example, during the peak of the dry season, in March 2016, the index of combined food availability (FAI-2) was particularly low; *B. papyrifera* did not offer any fallback foods and there were few field crops available. As a response, chimpanzees spent more time resting (56%) and fed very little (17%). When preferred food is scarce, chimpanzees can adopt two different strategies (Oates, 1987): they can either include a variety of lower quality food items into their diet and /or decrease their level of activity in order to minimise energy expenditure ("energy-saving strategy": Gombe: Wrangham, 1977, Kanyawara: Wrangham et al., 1991; Tai: Doran, 1997) or they can travel further so to maintain a fruit-dominated diet ("increased-searching strategy"; Yamagiwa, 1999). The study by Fawcett (2000) showed that the Sonso community can adopt a mixed strategy: during times of reduced food availability chimpanzees decreased time spent feeding and fed on lower quality food items, whereas during a more severe time of scarcity they travelled further to incorporate seeds of *C. alexandrii* in their diet. During this study Sonso chimpanzees seemed to pursue a mixed strategy as well; during the months of food scarcity in October and November chimpanzees spent some days resting and feeding on low-quality food items, such as flowers and young leaves of *B. papyrifera* (thus “energy-saving”), while on other days they engaged in crop-foraging which meant that they had to travel far (approx 2km) to feed on high-quality resources (“increased-searching strategy”).

Data analysed here did not include crop-foraging behaviour of the Sonso community, which often took place during times when high-quality food was not available within the forest. Thus, some of the variation in activity budgets might be related to the fact that some community members, especially males, could not be observed at all times. When parts of the community engaged in crop-foraging I did, however, follow other focal individuals within the forest, and am thus confident that the activity budgets recorded here represent the activities of chimpanzees within the forest fairly well. Yet, the recent increase in crop-foraging behaviour had clear effects on diet diversity and composition: comparisons to previous studies carried out at Budongo demonstrate that, with the increase of crop-foraging, diet diversity and observations of ripe fruit consumption have decreased. While Newton-Fisher (1999) reported an overall dietary diversity (H′) of 1.80 for the Sonso community, this value had decreased to 1.61 by the time of the current study. The time that Sonso chimpanzees were observed to be feeding within the forest and feeding on ripe fruit decreased as well, by 10% and 5-10%, respectively (total feeding time: Newton-Fisher (1999a): 49%; Fawcett (2000): 53%; this study: 36%; feeding on ripe fruit: Newton-Fisher (1999a): 49%; Fawcett (2000): 44%; this study: 39%). Changes in forest composition are likely to contribute to changes in diet composition as well. Especially fruits of *F. sur* were consumed to a much smaller extent than during previous studies at Budongo: While during the study period of Newton-Fisher (1999a) and Fawcett (2000) fruits of *F. sur* were found to be the most common item in the diet of Sonso chimpanzees, in the present this species was only ranked 10th overall. It seems that trees of this species have become less productive during the past years and have started to die back within the Sonso home range as the forest gradually recovers to its pre-logging composition (F. Babweteera, personal communication).

The Waibira community

Within the Waibira community food availability was more stable, as was the proportion of high-quality food items contributing to the diet of chimpanzees. Activity budgets reflected this stability well: time spent on each behavioural category differed little across month, resulting in an overall more balanced activity budget. As the home range of the Waibira community does not border on any cultivated fields, chimpanzees of this community did not have the possibility to feed on field crops when fruit within the forest was scarce. Possibly as a result of this, diet composition of this community was more variable and diversity was higher. Contrary to previous studies of chimpanzee dietary diversity (Wrangham et al., 1998; Fawcett, 2000), the diet of the Waibira community increased in diversity when food was more abundant, albeit not at a significant level. This might be a way of maintaining a larger overall community size as has been suggested for a group of Indo-Chinese grey langurs (*Trachypithecus crepusculus*) in Wuliangshan, China (Pengfei et al., 2015). The group of langurs studied was 3-10 times larger than other groups of this species, yet it did not travel greater distances per day or devote more time to travel. The authors suggest that the ability to rely on a wide variety of plant foods enabled langurs to live in such a large group. This might be an alternative way of reducing within-community feeding competition and help to maintain a large community size, when habitat productivity alone, as seems to be the case for the Ngogo community (Potts 2009; Potts et al., 2011), is not sufficient.

Although food availability along phenology trails was less variable for the Waibira, monthly FAI scores were comparatively low. These low values might be related to the unusually low amount of rainfall during the second study period. Perhaps as a response to these conditions, chimpanzees of the Waibira community appeared to solely pursue an “energy-saving strategy”: During times of more pronounced fruit scarcity, Waibira chimpanzees fed predominantly on young leaves of *C. mildbraedi* or climbers but did not increase their overall level of time spend resting. Large feeding trees, which attracted a considerable part of the community and provided food for more than a week, nevertheless allowed chimpanzees to maintain a large proportion of high-quality foods within their diets during most months. Two such large feeding trees accounted for 25-35% of total feeding time during October and December 2016, respectively, when little other ripe fruit was available within the home range. Chimpanzees then often stayed within the surroundings of these large feeding trees for entire days and only supplemented their diet with young leaves, spending the day feeding and resting. The Waibira community ranges over a larger area than Sonso (Jakob Villioth, unpublished data); therefore, the home range is more likely to include such large feeding trees with superabundant food amounts. The presence of these large trees, coupled with an "energy-saving strategy" and the approach of diet broadening to avoid feeding competition (see above) might work together in enabling Waibira chimpanzees to maintain a larger community size.

Botanical plots

The preliminary assessment of forest composition and abundance of chimpanzee food tree species across home ranges showed that two important non-fig food species might be more abundant within the Waibira home range. Botanical plots within the Waibira home range contained a higher density of *C. midlbraedii* and *C. alexandrii* than those of the Sonso home range. Although these are regular feeding trees in both chimpanzee communities, chimpanzees only foraged on young leaves of *C. midlbraedii* and *C. alexandrii* produced seeds at a time when other food resources were available to chimpanzees as well. It would thus be premature to link the higher density of only these two species in Waibira to differences in other foraging variables, such as party size or travel distances between food patches (see Chapter 3). While this study focused on behavioural data collection of chimpanzee foraging, this preliminary finding is certainly a promising starting point for more detailed investigations of floristic heterogeneity across the two study communities. As especially fig species were not well represented in the current sample, but contribute significantly to the diet of chimpanzees at Budongo, further studies should aim to better understand the abundance and productivity of important fig species, such as *F. mucoso* and *F. sur*. An efficient way of assessing these, as demonstrated by Potts et al. (2008), is to sample a much larger area of the home range by establishing a large number of plots and then identifying and measuring all large (in Potts et al. (2008): DBH < 80cm) food tree species within these plots. Results from such more in-depth botanical surveys will then allow to soundly test hypotheses about differences in important foraging variables, such as party size, across the two communities. Feeding parties and patch size was larger for the Sonso community (see Chapter 3) and these results could potentially be linked to the size and productivity of fig species. Large trees of *F. mucoso* appeared to be more abundant within the Sonso home range, while medium-sized trees of *F. sur* seemed to be found at a higher density within the Waibira home range (Jakob Villioth, personal observation). It seems likely that the abundance and size of these important food species influences the probability of finding large foraging parties.

The results obtained during the current study could be used to address a range of hypotheses, relating to optimal foraging theory as well as chimpanzee feeding ecology in particular. In order to evaluate the universality of Pott’s findings (Potts 2009; Potts et al., 2011, 2015, 2016), future studies at Budongo could investigate the interaction between community size, forest composition, chimpanzee diets and activity budgets across communities. More specifically a comparative study could test:

1) Does the diet of the larger community (Waibira) contain more ripe fruit than that of the smaller community (Sonso) ?

2) How do activity budgets compare across communities and are they related to potential overall differences in ripe fruit production between home ranges? Do, for example, more abundant and high-quality resources result in less time spend on resting, as for the Ngogo community?

As for investigations that are based on the current study and address the specific conditions at Budongo, the following questions could be answered:

3) Was the “energy-saving” behaviour of the Waibira community documented during the current study related to low rainfall and ripe fruit production – or is it a consistent strategy of this community that might serve as a way of maintaining a large community size in a fragmented habitat?

4) How does diet diversity of the Waibira community relate to food availability within the home range? Was April 2017 an outlier or do Waibira chimpanzees regularly increase diet diversity with increasing food availability?

In order to obtain results that are truly comparable between communities, data collection should be carried out simultaneously in both communities, using identical sampling protocols and inter-observer tests between all researchers involved in data collection (see: Potts et al., 2011). Further, I recommend to collect data from phenology trails at sufficiently short intervals; every two weeks, as done by Fawcett (2000), should be appropriate to also capture more rapid changes in fruit availability, such as from popular food tree species that are quickly depleted (*F.mucoso, F. sur*). In order to answer question 2, behavioural data collection needs to be combined with detailed botanical surveys (as described above).

In both communities, activity budgets of male and female chimpanzees were very similar; both sexes spent almost equal proportions of observation time on feeding, resting, traveling, grooming and other activities. Even though the general assumption is that females need to forage in a different way compared to males (Schoener, 1971; Trivers, 1972; Wrangham and Smuts, 1980; Sterck et al., 1997), most studies have so far failed to find significant differences between activity budgets of male and female chimpanzees: Ghiglieri (1984) and Fawcett (2000) reported differences in the amount of time that males spent traveling, but in both studies males were better habituated than females and could therefore be followed more easily. Wrangham and Smuts (1980) found no sex differences in the time spent feeding and Doran (1997) reported no sex differences for three behavioural categories (feeding, moving and resting). Pott’s study (2011) found differences in time spent resting and feeding between lactating and pregnant females, but none between males and females. Pokempner (2009) found that males and females of the Kanyawara community displayed similar foraging effort, as measured by the time spent feeding and traveling. And at Bossou, Bryson-Morrison (2017) found no differences in time spent foraging between males and females either. If, however, metabolic body mass (MBM) of male and female chimpanzees is taken into account, some differences emerge in terms of macronutrient intake: at Kibale, females showed a higher intake of non-structural carbohydrates and males exhibited a higher absolute intake of calories and protein (Pokempner, 2009). At Bossou in contrast, female chimpanzees displayed higher intakes of protein and NDF from all foods than males (Bryson-Morrison, 2017). Thus, very detailed investigations of male and female feeding efficiency and diet composition are needed, in order to identify any differences between sexes. Taken together, these results suggest that male and female foraging efforts might not be as divergent as current theories of sex differences in foraging postulate.

Dietary profiles revealed that young leaves were an integral part of the diet of both communities. Young leaves were consumed in larger quantities when ripe fruit was scarce, yet even when ripe fruit was abundant chimpanzees still regularly consumed young leaves of several different tree species. Consequently, the food availability index which included unripe fruit, young leaves and flowers of important food species (FAI-2), was able to better capture the amount of food resources available as apparently perceived by the chimpanzees themselves. This index agreed better with monthly activity patterns, especially in the Waibira community; while FAI-1 varied considerably, FAI-2 reported relatively stable amounts of exploitable resources, which corresponded well to the balanced activity budget of the Waibira community. Fawcett (2000), in her study of the Sonso community, arrived at the same conclusion when comparing several different food availability indices: young leaves of *C. mildbraedii* were a highly preferred food item and an index which included the presence of young leaves was more meaningful than one of ripe fruit only. Kuroda (Kuroda et al., 1996) reported *C. mildbraedii* to be a crucial foliage food to chimpanzees when availability of ripe fruit was low and suggested that young leaves of this species are particularly rich in protein. Results from other chimpanzee populations too, show that terrestrial piths and leaves (THV, Wrangham, 1986; or TPL, Wrangham et al., 1991) are regularly consumed by chimpanzees and might play an important role in their overall diet. Marshall and Wrangham (2007) distinguish two types of fallback foods (FBFs): staple FBFs which seasonally can make up the entire diet and which provide foragers with sufficient nutrients to maintain physiological functions – and filler FBFs that never serve as the sole food source and that are insufficient to entirely fulfil nutritional requirements. The authors argue that while in gorillas high-fibre foods such as terrestrial herbs and pith serve as staple FBFs (Remis et al., 2001; Tutin et al., 1991), chimpanzees use such resources only as filler FBFs. Results of this study, in contrast, suggest that young leaves can function as staple FBFs in chimpanzees as well: During periods of low food availability, young leaves and flowers of *B. papyrifera* accounted for a substantial part of the diet in chimpanzees of the Sonso community (October, November 2015). Within the Waibira community chimpanzees foraged exclusively on young leaves of *Celtis mildbraedii* for several consecutive days when fruit was unavailable (November 2016). Although chimpanzees are generally described to be ripe fruit specialists (Ghiglieri, 1984; Watts et al., 2012; Wrangham et al., 1998), the foraging behaviour documented here suggests that chimpanzees are able to sustain themselves solely on a low-quality, folivorous diet for limited periods of time. These findings have important implications for the assessment of food availability and conservation of chimpanzees. Future studies need to consider that nutritional requirements of chimpanzees include fibrous foods, such as young leaves, as well, instead of monitoring the production of fruiting trees only.

The importance of young leaves and THV in chimpanzees diet also stresses the need to reassess chimpanzee foraging strategies. Early studies of primate foraging were commonly based on Optimal Foraging Theory (Emlen, 1966), which focused on the maximization of daily energy intake (Altmann, 1991; Rosenberger and Strier, 1989; Strier, 1992). Since ripe fruit offer a high content of readily digestible sugars, chimpanzees' preferences for such food items conformed to energy maximization models and were viewed as evidence in support of those (Remis, 2002; Reynolds et al., 1998). More recent frameworks of primate nutritional ecology, however, favour a multi-dimensional approach which assumes that foragers attempt to achieve a balanced intake of macronutrients, such as protein, lipids, and carbohydrates (Felton et al., 2009; Raubenheimer et al., 2009). While it was beyond the scope of this study to analyse the nutritional composition of food items, dietary variability documented here suggests that Budongo chimpanzees, at least at times, pursue a strategy of nutrient balancing, rather than one of energy maximization. Support for the importance of protein in chimpanzee diet also comes from a study of a chimpanzee population in a human-disturbed landscape (Bossou: Bryson-Morrison, 2017). Chimpanzees of this populations prioritized a proportional intake of protein, whereas the intake of carbohydrates and lipids varied, and their overall diet showed a consistent balance of protein to non-protein energy. In the light of these more recent frameworks and advances in nutritional analysis techniques (Rothman et al., 2009), investigations of nutrient balancing in chimpanzee foraging are a promising avenue for future research. Questions that could be addressed at Budongo include: Do chimpanzees of the Sonso community use field crops to balance their nutritional requirements in a comparable way to chimpanzees at Bossou? Do nutritional profiles of the two communities at Budongo differ in respect to intake of protein, carbohydrates and lipids? If so, are these differences consistent across multiple years and can they be linked to diet composition or forest composition within the respective home ranges?

Although a direct comparison of data collected at Sonso and Waibira was not possible, this study was able to identify several factors which could potentially contribute to within-species variation in chimpanzees at Budongo. The extent of seasonality, even though not as distinct as between East- and West-African field sites, differed markedly across study periods and had clear effects on fruiting patterns and fruit availability of certain food species, which in turn affected diet composition. At least two food species *(C. albidum and M. eminii*) produced fruit only during the second field season and were therefore only represented within the Waibira sample. Such inter-annual variation in fruit production is common in tropical rainforests and has been documented at other sites of chimpanzee research as well (e.g. Lope, Gabon; Tutin and White, 1998). Generating a truly reliable dietary profile of the two chimpanzee communities at Budongo will thus require comprehensive data collected across several years which can take into account such seasonal changes in fruit production.

Small-scale differences in vegetation composition, as documented for the two home ranges of Budongo chimpanzees, quite likely affected diet composition and responses to food scarcity (see Potts et al., 2009, 2011). The preliminary assessment of forest composition suggested that mature trees of *C. mildbraedii* might be more common within the Waibira home range and were a major food source during this study, especially when ripe fruit was scarce. Sonso chimpanzees, in contrast, benefited from exotic tree species, such as *B. papyrifera*, and the availability of field crops. Habitat changes caused by humans are thus another parameter driving within-species variation (Fischer and Lindenmayer, 2007; Hockings et al., 2015). While chimpanzee communities at the forest edge increasingly incorporate field crops into their diets (Bessa et al., 2015; Bryson-Morrison et al., 2017; Krief et al., 2014; McLennan and Ganzhorn, 2017; Tweheyo et al., 2005),communities at the forest centre might still be characterized by a more “natural” diet and ranging behaviour.

The impact of demography on diet and activity patterns across communities is difficult to quantify. It has not been investigated yet if chimpanzee densities across the two Budongo communities differ as distinctively as in Kibale National Park (Potts, 2008). Given that the Waibira community ranges over an area that corresponds quite well to its larger overall community size (Jakob Villioth, unpublished data), chimpanzee densities of the two communities are probably not substantially different. As outlined above, community size might be linked to diet diversity as well (Pengfei et al., 2015), thus the documentation of natural demographic variation within populations should receive more attention in discussions of within-species variation (Struhsaker, 2008).

This study provides an update of the diet composition and activity patterns of the Sonso community in relation to its increased crop-foraging activities as well as a first description of the foraging behaviour of the Waibira community. It also offers a first, basic assessment of forest composition across the two neighbouring chimpanzee communities and suggests a range of hypotheses that could be tested in order to gain a better understanding of the factors influencing differences in foraging behaviour across communities and within-species variation in primates in general.

Chapter 3

Adjusting the ecological constraints model to fission-fusion dynamics in chimpanzees (*Pan troglodytes*)

Abstract

The ecological constraints (EC) model predicts that an increase in foraging group size leads to higher travel costs, forcing foragers to split into smaller groups once energetic costs of travel exceed energy intake from food patches. Support for this model comes from a number of comparative as well as species-specific studies, but as contradictory results exist, the model's utility has been questioned. This study aimed to rigorously test predictions of the EC model by analysing measurements from distinct food patches and individual inter-patch movements on an appropriately shorter temporal scale from a species characterized by a high degree of fission-fusion dynamics, the chimpanzee (*Pan troglodytes*). I used these results to compare levels of feeding competition across two neighbouring communities, which occupy home ranges of different vegetation composition and differ in overall size. Over a period of 8 months I collected data on food patch characteristics, as well as the occurrence of overt feeding competition and inter-patch distances from individual male and female chimpanzees in each study community. Comparisons of food patch measurements showed that the Waibira community foraged on average in smaller parties and smaller food patches, travelling shorter inter-patch distances when all travel was considered. Three separate generalized linear mixed-effects models (GLMM) demonstrated that larger parties foraged in larger food patches and for longer durations, but only Waibira chimpanzees travelled farther when moving towards a larger food patch, whereas within the Sonso community these two variables were less strongly related. The occurrence of overt contest competition over food increased with party size in both communities. Distinct sex differences in party size and travel distances, as reported from other chimpanzee communities, were not observed during this study and the predictive power of the focal's sex was low compared to that of ecological variables. Findings of this study suggest that, despite certain limitations, the ecological constraints model remains a useful tool to investigate levels of feeding competition in socially foraging animals such as chimpanzees when the level of analysis is appropriately adjusted.

Introduction

Among group-living animals, competition over resources is the main factor that constrains group size and thereby most other aspects of social organization (Janson and van Schaik, 1988; Isbell, 1991; Janson and Goldsmith, 1995; Chapman and Chapman, 2000). The ecological constraints (EC) model posits that, when energy spent on travelling exceeds energy obtained from food resources, foragers will split up into smaller groups in order to fulfil individual energetic and nutritional requirements (Chapman et al., 1995; Chapman, 1990; Chapman and Chapman, 2000). This prediction is, however, not always supported – travel costs alone do not seem to be the only factor constraining group size (Struhsaker and Leland, 1988; Bronikowski and Altmann, 1996; Fashing, 2001; Pengfei et al., 2015). Through decades of research, socio-ecological models have become increasingly complex (Janson, 2000). By now it is widely acknowledged that social organization and group size of primate species is much more flexible than previously thought (Chapman and Rothman, 2009; Harris and Chapman, 2007; Strier, 2009) and that these parameters cannot simply be explained by resource distribution and abundance across primate taxa alone (Sterck et al., 1997; Strier, 2003; Koenig and Borries, 2006; Clutton-Brock and Janson, 2012). A large number of additional factors, such as such as dominance styles (Isbell, 1991), phylogeny and terrestrially (Janson and Goldsmith, 1995), nutritional balancing (Felton et al., 2009; Hohmann et al., 2010), demography (Lehmann and Boesch, 2004; Struhsaker,

2008) and a host of social factors (Isbell and Young, 2002; Sterck et al., 1997) play a crucial role in the interaction between group size and levels of feeding competition as well.

The order Primates has been the focus of the majority of research in this area, as it is characterized by considerable variation in foraging strategies and group size across species. Primates range from solitary, nocturnal species, such as slow loris (*Nycticebus* Geoffroy, 1812), which forage mostly on gum and insects (Starr and Nekaris, 2013), to geladas (*Theropithecus gelada* Rüppell, 1835) which predominantly feed on grass blades and forage in large bands of 50–250 individuals (Dunbar and Bose, 1991; Mac Carron and Dunbar, 2016). This enormous variation of group size and foraging strategies within one Order makes primates particularly suitable for investigating the proposed effects of increased feeding competition (Majolo et al., 2008).

Studying animal species characterized by a high degree of fission-fusion dynamics (Aureli et al., 2008) allows one to include additional considerations into foraging models since the relationship between important foraging variables, such as subgroup size, travel distance and patch size, are expected to be linked more closely in such species. In contrast to animals which forage in cohesive groups, individuals of species with pronounced fission-fusion dynamics travel and forage in small subgroups which frequently change in size and composition throughout the day (parties: Sugiyama, 1968): a foraging behaviour which is interpreted to be a direct response to different levels of feeding competition, due to short-term variation in the distribution and availability of resources (Chapman et al., 1995; Lehmann and Boesch, 2004). Rather than analysing daily averages, in species with highly fluid subgroup composition, it is thus possible to investigate the foraging behaviour of individual animals on a shorter temporal scale, as they move from food patch to food patch, while flexibly adjusting to prevailing ecological, social and their nutritional conditions. Further, the distribution and availability of food resources can be measured directly from the foragers perspective by investigating inter-patch movements on an individual level.

Spider monkeys are characterized by such highly fluid group compositions and illustrate well how using different spatio-temporal scales of data analysis can lead to contrasting results: When habitat-wide measures of food availability and distribution are compared with subgroups size, results are mixed: some studies reported a strong positive relationship between food abundance and monthly or daily subgroup size (Asensio et al., 2009; Chapman et al., 1995; Shimooka, 2003; Symington, 1988), while other studies only found weak correlations (Ospina, 2011) or no relationship at all (Ramos-Fernandez, 2001; Stevenson et al., 1998; Weghorst, 2007). If instead information on the size and food availability of particular patches is used, party size related to these in the predicted manner (Stevenson et al., 1998; Symington, 1988; Wallace, 2008).

Due to their high degree of fission-fusion dynamics the foraging strategies of chimpanzees have been studied extensively as well, yet despite decades of research the picture is far from complete. Research in chimpanzees has so far mostly focused on the relationship between party size and patch size, whereas investigations of the links between patch size and travel distance or patch occupancy are sparse. The majority of studies have found an increase in the size of chimpanzee parties within larger food patches (Ghiglieri, 1984; White and Wrangham, 1988; Isabirye-Basuta, 1993; Newton-Fisher et al., 2000). Patch size alone explained 80% of variance in feeding party size in the Ngogo community but only 23% of variance in party size in the neighbouring Kanyawara community (Potts et al., 2011). Pokempner’s (2009) detailed study of the energetics of feeding competition in male and female chimpanzees of the Kanyawara community found no increase in party size with mean daily fruit patch size at all. The relationship between travel distances and party size (Chapman et al., 1995) and between travel distance and patch productivity (Normand et al., 2009; Pokempner, 2009) corresponds well to predictions of the EC model. In contrast, results on foraging efforts across sexes, as measured by travel distances, are less conclusive. In line with theories of sex differences in foraging effort (Schoener, 1971; Trivers, 1972), females tend to travel shorter distances and move in a more linear way in between feeding trees (Tai forest: Normand and Boesch, 2009; Kibale National Park: Pokempner, 2009; Budongo Forest, Sonso community: Bates and Byrne, 2009). These sex differences, however, disappear when, for example not only fruiting trees but all food patches are considered (Pokempner, 2009) or, instead of daily averages, individual movement phases are analysed (Bates and Byrne, 2009).

This study aimed to test predictions of the EC model rigorously by integrating several important foraging variables into an overall model of chimpanzee feeding ecology. I used an appropriately shorter temporal scale by analysing individual inter-patch movements and parameters of individual food patches. Further, I compared the foraging behaviour of males and females across two neighbouring communities of different demographic structure and in habitats of different vegetation composition. This allowed me to investigate how varying ecological and social parameters might influence the interaction of foraging variables in both sexes. Predictions followed the EC model and theories of sex differences in foraging strategies:

1) I predicted that larger feeding parties can be found in larger food patches and that the formation of larger foraging parties will be linked to longer travel distances in between patches. The predicted relationships between these foraging variables were expected to be stronger in female chimpanzees than in male ones.

Overt contest competition within feeding patches is a reliable indicator of levels of feeding competition. Previous studies have demonstrated that frequencies of food-related agonism are higher in smaller patches when these are further apart (Saito, 1996), when patches offer a smaller numbers of feeding sites and feeding bout length increases (Hanya, 2009; Vogel and Janson, 2007) and when the number of foragers within a patch increases

(Heesen, 2014). Despite this, in chimpanzees’ direct observations of food competition have so far not been related to patch characteristics or male and female foraging behaviour.

2) I predicted that direct contest competition over food will increase with feeding party size and be more frequent in smaller patches. The number of female foragers was expected to better predict the occurrence of food related agonism in patches than numbers of male foragers.

Methods

Study site and communities

Research was conducted within the Budongo Forest Reserve (1°35’ - 1°55’ N, 31°08’ - 31°42’ E), over a period of 16 months. I collected data from two neighbouring chimpanzee communities, Sonso and Waibira, over a period of 16 months. Data on the Sonso community were collected between October 2015 and June 2016, and the second field season, during which data on the Waibira community was collected, lasted from October 2016 to June 2017. The Sonso community has been observed continuously since 1990 (Newton-Fisher, 1997; Reynolds, 2005) and all members of the Sonso community were individually recognized and could be observed at close quarters on the ground. During the study period, the Sonso community contained 71 individuals in total and, following age classifications by Goodall (1986), included 12 adult males (≥16 years old) and 24 adult females (≥14 years old). Habituation of the Waibira community started in 2011 (Samuni et al., 2014) and almost all adult members could be individually recognized as well at the time of this study. Observation distances permitted to study foraging behaviour at a sufficiently close range (see for example also, Hobaiter et al., 2017). The Waibira community consisted of at least 88 known individuals, including 17 adult males and 29 adult females.

Behavioural data collection

I aimed to conduct full-day nest-to-nest follows of individual chimpanzees in both communities to obtain a complete record of the individual’s foraging behaviour, as well as travel between feeding patches. During focal follows, activity of the focal individual was recorded continuously (Altmann, 1974). All behaviours related to food handling – the entire process of picking and ingesting food items – were categorized as feeding. Focal follows started at the morning nest and continued for as long as conditions allowed. Sonso chimpanzees engage in crop-foraging (Tweheyo et al., 2005) and focal follows had to be interrupted when the designated focal left the forest to forage on field crops or during inter-community encounters (mean duration of Sonso follows: 5.6h SD 3.1h, range: 1-12h median: 5h). The ongoing habituation of the Waibira community and their denser habitat made full-day nest-to-nest follows of individual chimpanzees impossible as well (mean duration of Waibira follows: 4.1h SD 2.6h, range: 1-12h median: 4h). At the beginning of each day I selected one focal from a randomised list. When the initial focal individual was lost, I attempted to increase the number of focal samples from individuals that were still underrepresented in the overall sample in order to maintain a balanced sampling regime.

To explore potential sex differences in foraging behaviour, I collected data of male and female chimpanzees in each community: Six adult males and five adult females were selected as focal individuals from the Sonso community, and from the Waibira community ten adult males and nine adult females were chosen. Since the Waibira community is larger in size and it was not always possible to find a predetermined focal individual within the party that was located in the morning, I sampled a larger number of individuals from this community. Males from both communities were of different ages and represented different rank categories (high-, mid- and low-ranking). In Sonso, I followed five females, of which four were lactating and travelled with at least one infant and one juvenile during the study. The fifth female was not lactating and only travelled with her juvenile offspring. In the

Waibira community seven of the focal females were lactating while the other two females were not lactating and only travelled with one juvenile offspring.

Food Patch Characteristics

A feeding patch was defined as an aggregation of food items that allowed uninterrupted foraging movements by the focal animal (White and Wrangham, 1988; Chapman et al., 1994; Pruetz and Isbell, 2000). While in most cases a patch was equivalent to an individual feeding tree, for certain tree species (for example *Broussonetia papyrifera*, *Putranjivace gerrandi*) a patch could consist of multiple trees with overlapping crowns. If the focal animal was able to feed consecutively in such contiguous crowns without extensive travel, all trees were considered to form one patch and patch size measurements (such as DBH, bout length etc.) of all visited trees were summed. If crowns were not overlapping and the focal animal travelled along the ground or through the crown of a non-feeding tree, these were considered different patches.

B. papyrifera only grows in groves, in a certain part of the forest edge within the Sonso community's home range, and individual chimpanzees within a single party often foraged in neighbouring or nearby trees (within 35m). Therefore, the feeding patch was considered to be all trees in which party members were feeding. Foraging by Waibira community chimpanzees on *P. gerrandi* took place in similar groves. However, in these cases the forest consisted more of a mix of tree species and chimpanzees usually spread out over a larger area. Following the same definition of a feeding party, only individuals within 35m were included and therefore feeding events in *P. gerrandi* were recorded as foraging in a number of smaller parties.

Food patches recorded when the chimpanzees' foraging activities and travel was influenced by an inter-community encounter, crop-foraging, hunting or travel to waterholes were excluded from the analysis.

Information on party size, food patch size and travel distance were collected in the following manner:

1) Feeding party size

Feeding party size was defined as the maximum number of individuals that simultaneously occupied a food patch (Strier, 1989). This was achieved by recording changes in feeding party membership as individuals entered or left the patch during each feeding bout. Only adult and adolescent individuals were incorporated into this count, independent individuals below age of adolescence (below 13 years, as defined by Goodall, 1986) were not included. This definition of feeding party size is in line with a previous study of foraging behaviour among the Kanyawara community of chimpanzees (Pokempner, 2009), and assumes that the amount of food removed from a patch by young, weaned chimpanzees is negligible in the analysis of adult chimpanzees' foraging decisions. Observations made during this study confirmed that adult chimpanzees do not seem to view young independent individuals as competitors over food: in none of the cases of high intensity competition (see definition below) which were recorded was the victim a young independent chimpanzee.

2) Patch size

The size of each feeding patch was determined by measuring the DBH (diameter at breast height) of the feeding tree. DBH may not always capture the dynamic nature of fruit availability within trees (Suarez, 2014), yet it is the most widely used method for estimating fruit abundance and thus allows to compare results across study sites and species (Chapman et al., 1992). The measurements were obtained using a tape measure, and were accurate to the nearest cm.

When chimpanzees were foraging on fruits or leaves of lianas, the DBH measurements of all supporting trees were measured and summed. In some cases, it was not possible to measure DBH with a tape measure, for example when a feeding tree was surrounded by dense vegetation or when the tree was so small that it could not be approached without interfering with the foraging animal. In these cases, DBH of the feeding patch was estimated visually. Patches of *B. papyrifera* were quantified by summing DBH measurements across multiple trees considered to be part of the feeding patch, as described above.

3) Patch distance

Patch distance was obtained by following the focal animal's travel path on the ground as closely as possible and recording the distance to the next feeding patch with the help of the track-log function of a handheld GPS (Garmin GPSMAP 64). The track-log function recorded locations at a predetermined interval of two minutes. However, due to certain inaccuracies of these recordings, the function also recorded small movements when chimpanzees remained stationary for longer periods, for example during bouts of resting and/or grooming (Janmaat et al., 2013). As a result, travel distances between food patches were overestimates when resting/grooming bouts occurred. I therefore manually removed all GPS locations that were recorded during resting/grooming bouts using the Garmin BaseCamp software. To investigate the accuracy of locations recorded by the GPS device within the forest, the device was kept in a fixed position for five hours under forest canopy (Bates and Bryne, 2009; Asensio et al., 2009). The average "error" (distance recorded while being in the same place) was 3.97m (N = 499, SD = 2.58 m, range 0-23m). The locations of all food patches visited by the focal animal were also recorded using the GPS. I only included travel within the forest boundaries into the analysis.

The relationship between party size, patch size and travel distance can be influenced by further foraging variables. Foragers usually spent longer periods in larger patches (White and Wrangham, 1988; Janson, 1988; Chapman et al., 1995; Snaith and Chapman, 2005; Wallace,

2008) and the type of food available within patches was expected to affect the interaction of other foraging variables as well (patches of ripe fruit might, for example, allow the formation of larger parties than patches of young leaves). To control for the duration of feeding bouts and the effect of different food types, I therefore included these two variables into foraging models as well.

4) Feeding bout length

Initially, I attempted to base feeding bout length on the occupancy of all chimpanzees in a food patch, an approach that has been used in previous studies of foraging ecology (e.g. Snaith and Chapman, 2005; Vogel and Janson, 2007). However, due to the fission-fusion nature of chimpanzee society, this approach was not possible: often the focal animal would join other chimpanzees in an already occupied food patch or leave a patch when other individuals were still foraging. Focalling potential food patches (Heesen, 2014; Vogel and Janson, 2007) would have been highly inefficient and precludes collection of other foraging data, such as previous/subsequent patches or travel distance between patches. Therefore, feeding bout length in this study refers to the total amount of time which the focal animal spent feeding in a patch, from entering the patch until leaving it (cf. Potts et al., 2011).

5) Food type

For each food patch, the type (fruit, leaves, flowers, seeds, bark, soil, meat), species, and phytophase (ripe, unripe, young, mature), of food items was identified and recorded.

Feeding competition within patches

To investigate contest competition over food, I used a subset of data collected during this study. Within both communities, all agonistic interactions between adult individuals were recorded using a combination of focal follows and all-occurrence sampling (Altmann, 1974). Chimpanzee aggression in usually highly conspicuous to observers (Muller, 2002), thus I am confident that most agonistic interactions could be recorded in this manner. An exception were large feeding trees or occasions when chimpanzees were resting in areas of very dense vegetation: under these circumstances, low intensity aggression, such as displacements or threats, could only be recorded for the focal individuals and other chimpanzees nearby.

Six different types of aggression were distinguished, according to increasing levels of intensity (low intensity competition: displacements, threats and non-directed displays; high intensity competition: charges, chases and attacks; cf. Goodall, 1986; Newton-Fisher, 2017). Further, different contexts of aggression were defined, based on the identity and sex of aggressor and victim, the apparent cause of aggression and the chronological sequence of events. Analyses of this chapter included all aggression that was categorized as feeding competition, which was defined as aggressive interactions occurring within a feeding patch over food items or positions within the feeding tree and that were not of sexual nature.

Statistical analyses

As it is unknown to what extent chimpanzees are able to adjust the size of foraging parties to their individual needs, I designed two models to explore the relationship between party size, patch size and travel distances: Model 1 was constructed with feeding party size as response variable and five predictors: DBH (continuous variable, measured in centimeters), travel distance (continuous variable, measured in meters), feeding bout length (continuous variable, measured in minutes), food type (five categories: ripe fruit, unripe fruit, young leaves, flowers and seeds) and sex of the focal chimpanzee (binary variable, male or female). As feeding party size was count data (max. number of individuals within a feeding patch), this model was a generalized linear mixed-effects model (GLMM) for which I used the function glmer.nb of the R-package MASS (Ripley et al., 2013). As this model showed signs of overdispersion, I used a negative binomial error structure.

In Model 2, travel distance to food patches was set as the dependent variable, whilst feeding party size, DBH, feeding bout length, food type and sex of the focal chimpanzee were fixed factors. For this model I used the function “lmer”, provided by the lme4 package (Bates et al., 2014).

In these two models, identity of the focal was included as a random effect to account for repeated measurements from the same individuals and for between-subject variation (Bolker et al., 2009). A count of daily feeding bouts by each focal was also included as a random factor to take into account that data of consecutive feeding patches could stem from following the same individual over the course of a day.

To test the overall significance of my models, I used a likelihood ratio test (with the R function “ANOVA”; Dobson, 2002) which compares the deviance of the full models with those of the respective null model. The null model included the intercept, random effects and the two variables for which I wanted to control (feeding bout length and food type).

I constructed Model 3 to investigate contest competition over food. The number of aggressive interactions occurring within a feeding patch and involving the focal chimpanzee was insufficient for data analysis; thus, I included every aggression that was observed through a combination of focal follows and all-occurrence sampling (see above). As a result, it was not possible to calculate frequencies of contest competition. Therefore, the occurrence of agonistic interactions within feeding parties entered the model in a binary manner (yes/no): all patches in which at least one instance of overt contest competition occurred were contrasted with food patches in which no feeding competition was recorded.

The presence of feeding competition was set as the dependent variable, whilst DBH, total feeding party size and the proportion of males and females within a party were fixed factors. I used the proportion of male and female chimpanzees within a feeding party to control for the effect of total party size on aggression levels. Since the dependent variable was binary, this model was a GLM with binomial error structure (McCullagh and Nelder, 1989).

The data set used for Model 3 only included food patches with at least two individuals and required a measurement of patch size (DBH). For Sonso chimpanzees, this data set consisted of 311 food patches and 59 aggressive interactions (overt contest competition in 19% of all patches). In Waibira it consisted of 258 food patches and 69 events of food competition (27% of all patches). In contrast to the full data set (see results for: Feeding competition within patches; p. 85), aggression levels in this data set were thus clearly higher within the Waibira community.

All three models were run with the ful data set from both communities and included the interaction term 'community ID' to investigate whether the effects of fixed and random factors on the dependent variable differed across communities.Interaction terms between main predictors and "community ID" were included into initial models and subsequently removed one by one. Only in Model 2 there remained a significant interaction between "community ID" and DBH. To test the significance of this interaction , I compared the full model's deviance with that of a corresponding reduced model not comprising this interaction.

The data used in all models met the assumptions of normality and homoscedasticity of residuals, as determined by visual inspection of diagnostic plots. All continuous variables were centred before running the models to achieve a mean of zero and a standard deviation of one. To check for absence of collinearity between predictors, I examined the variance inflation factors (VIF) (Quinn and Kenough, 2002) using the function "VIF" of the Rpackage "car" (Fox et al., 2012).

For a basic comparison of foraging variables across communities, generalized linear mixed models (GLMM) were used as well, in order to take into account that data from several feeding patches were collected following the same individual over the course of a day. Only for DBH comparisons I used a more simple non-parametric test (Wilcoxon rank sum test), since patch size is independent of the focal chimpanzee.

I used the r.squaredGLMM function to calculate effect size of the GLMM which compared feeding bout lengths across communities and the r.squaredLR function (Nagelkerke, 1991) to calculate effect size of the GLMM which compared feeding party size.

All analyses were conducted in R 3.4.3 (R Development Core Team, 2017).

Results

Food Patch Characteristics

1) Feeding party size

Mean feeding party size (FPS) was significantly higher within the Sonso community than within the Waibira community (Sonso mean: 7.33, SD 5.87; Waibira mean: 4.37, SD 4.01; GLMM : $\beta \pm SE = 0.509 \pm 0.096$, $z = 5.34$, $p < 0.001$, Adjusted R2: 0.126). Small feeding parties (1-3 individuals) made up more than half of all observations in the Waibira community (55%), but only one third (34%) in Sonso. Lone individuals were much more common in Waibira (33% of all feeding bouts) than in Sonso (18% of all bouts). Large parties (more than 10 individuals) accounted for a 32% of feeding parties in Sonso, but only for 12% in Waibira. Lone foragers were more often female than male, in both communities (Sonso: males 37%, females 63%; Waibira: males 40%, females 60%).

2) Patch size (DBH)

Chimpanzees of the Sonso community foraged in significantly larger food patches than those of the Waibira community (Sonso median: 70cm, range: 10-260cm; Waibira median: 63cm, range: 10-200cm; Wilcoxon rank sum test $W = 89282$, $p < 0.001$). To test if this result was due to the large proportion of lone foragers within the Waibira community (see above) the test was repeated excluding data from individuals foraging on their own. The size of food patches still differed significantly across communities, albeit at a lower significance level (Sonso median: 80cm, range:10-260cm; Waibira median: 70cm, range: 10-260cm; Wilcoxon rank sum test $W = 46372$, $p = 0.029$). Small feeding patches (10-30cm DBH) made up 24% of patches in Waibira, but only 12% in the Sonso community. Large patches (DBH above 70cm), in contrast, were more common in the Sonso community (Sonso: 50%, Waibira: 36%).

3) Patch distance

Chimpanzees of the Sonso community travelled longer distances to feeding patches than did those of the Waibira community when the full data set (n = 539) was analysed (Sonso mean = 503m, SD = 422m; Waibira mean = 307m, SD = 368m). Mean travel distance was significantly longer for Sonso chimpanzees than within the Waibira community (LMM: β±SE = 0.805±0.235, X2= 11.74, $p < 0.001$); effect size, however, was small (pseudo-R-squared: marginal 0.092, conditional 0.285).

Males and females of the Sonso community travelled similar distances (male mean: 510m SD 413m, female mean: 471m SD 389m; LMM: β ± SE= -0.006 ± 0.186, $X^2 = 0.001$, p = 0.97), whereas in the Waibira community males travelled further than females (male mean: 354.52m SD 377.19m, female mean: 254.57m SD 352.81m; LMM: β ± SE = 0.615 ± 0.337, $X^2 = 3.324$, p = 0.068; pseudo-R-squared: marginal 0.0508, conditional 0.2804).

Given the differences in habituation level between the two communities, within the Waibira community focal animals often travelled between patches arboreally, especially females (females: 46% of travel bouts, males: 13%); in the Sonso community arboreal travel was rare (females: 5% of travel bouts, males 1%). Therefore, I additionally compared terrestrial travel only. For such terrestrial travel (n = 455), there were no significant differences in travel distance at a community level (Sonso mean: 517m, SD 420m; Waibira mean: 415m, SD 389m; LMM : β ± SE = 0.121 ± 0.143, $X^2 = 0.71$, p = 0.398); similarly, there were no significant sex differences in travel distance when considering terrestrial travel only (Table 3.1).

Chimpanzees of the Sonso community travelled farthest for patches of ripe fruit (602m ± 474) and unripe fruit (574m, ± 467m), whereas Waibira chimpanzees covered the longest distances to reach patches of seeds (397m, ± 408m). When considering only terrestrial travel, this difference across communities remained the same. Distances to patches of young leaves (Sonso: 339m ± 286; Waibira: 331m ±356) and seeds (Sonso: 537m, SD 390m; Waibira: 510m, SD 413m) were comparable across communities (Table 3.2). Flowers were rarely foraged by Waibira chimpanzees (n = 5). To compare distances travelled to patches of BPY, in which Sonso chimpanzees often foraged on flowers and/or young leaves, data of these two food types was pooled (Table 3.2).

Table 3.1. Travel distances (in metres) to food patches by males and females across the two study communities. All travel data includes arboreal as well as terrestrial travel.

Sonso

	n	all travel	*n*	terrestrial travel
Males	146	525 ± 441	144	532 ± 439
Females	134	479 ± 401	128	500 ± 398
total	280	503 ± 422	272	517 ± 420

Waibira

	n	all travel	*n*	terrestrial travel
Males	135	355 ± 377	116	405 ± 381
Females	124	255 ± 353	67	434 ± 405
total	259	307 ± 368	183	415 ± 389

Table 3.2. Travel distances (in metres) to patches of six different food types across the two study communities. All travel data includes arboreal as well as terrestrial travel.

Sonso

	n	all travel	*n*	terrestrial travel
ripe fruit	109	602 ± 474	107	612 ± 472
unripe fruit	38	574 ± 467	37	588 ± 465
young leaves	54	339 ± 286	52	351 ± 285
flowers	25	223 ± 167	25	223 ± 167
seeds	42	537 ± 390	39	576 ± 377
other	12	582 ± 348	12	582 ± 348
total	280	503 ± 422	272	517 ± 420
young leaves & flowers	79	302 ± 259	77	310 ± 259

Waibira

	n	all travel	*n*	terrestrial travel
ripe fruit	145	339 ± 392	106	448 ± 407
unripe fruit	13	274 ± 213	9	365 ± 192
young leaves	71	222 ± 313	44	331 ± 356
flowers	6	389 ± 518	5	465 ± 541
seeds	20	397 ± 408	15	510 ± 413
other	4	174 ± 86	4	174 ± 86
total	259	307 ± 368	183	415 ± 389
young leaves & flowers	77	235 ± 331	49	345 ± 373

4) Feeding bout length

Chimpanzees from the two communities occupied feeding patches for similar durations (Sonso mean = 33.45 min., SD 31.46; Waibira mean = 27.38 min., SD = 25.91). Mean bout length was significantly longer for Sonso than for Waibira (LMM: β ± SE = 0.188 ± 0.077,

$X^2 = 5.99$, $p < 0.014$), effect size, however, was small (pseudo-R-squared: marginal 0.010, conditional 0.071).

5) Food type

Feeding patches of ripe fruit made up a larger proportion of all patches for the Waibira community (Table 3.3). However, while in the Waibira community ripe fruit mostly came from tree species with smaller fruits (*Ficus sur*: 19%, *Putranjivace gerrandi*: 16%), in Sonso the largest share of ripe fruit came from a tree species with large, fleshy fruits (*Ficus mucoso*: 18%). Flowers provided a larger share of the diet of the Sonso community. Especially during October and November 2015, young leaves and flowers of *Broussonetia papyrifera* made up a substantial part of the Sonso community's diet. Overall, young leaves of *Celtis mildbraedii* were the most important food item of the Waibira community.

Table 3.3. Proportion (%) of five different food types to the diets in each community

	Sonso		**Waibira**	
	n	%	*n*	%
Ripe fruit	185	39.96	242	57.48
Unripe fruit	69	14.90	27	6.41
Young leaves	69	14.90	96	22.80
Flowers	49	10.58	10	2.38
Seeds	72	15.55	41	9.74
other	19	4.10	5	1.19
total	463		421	

Feeding competition within patches

For Sonso chimpanzees, 64 events of aggressive behaviour were recorded within 447 food patches (corresponds to: 14% of all patches). Within the Waibira community food competition was recorded in 69 out of 421 food patches (16%). The occurrence of aggressive interactions over food did not differ significantly across communities (LMM: $\beta \pm SE = 0.355 \pm 0.183$, $X^2 = 3.77$, $p = 0.052$).

In both communities, the aggressor was more likely to be male (Sonso: 80%, Waibira: 59%) than female (Sonso: 16%, Waibira: 22%; unknown aggressor: Sonso: 5%, Waibira: 19%). The intensity of aggressive interactions within food patches was similar when two grades of aggression were distinguished: High intensity competition (charges, chases and attacks) made up 58% of events in Sonso and 51% in Waibira. Low intensity competition (non-directed displays within the food patch, threats and displacements) made up 42% of events in Sonso and 33% in Waibira (no data on intensity: Sonso: 0%, Waibira: 16%).

Model 1: Feeding party size

Overall, the full model was highly significant as compared to the null model (likelihood ratio test: $X^2 = 164.17$, $df = 12$, $p < 0.001$). Including patch size, travel distance and sex of the focal thus explained variation in feeding party size better than a model of only feeding bout length and food type.

There was a clear effect of DBH on feeding party size in both communities (Sonso: $\beta \pm SE = 0.817 \pm 0.099$ $z = 8.212$, $p < 0.001$; Waibira: $\beta \pm SE = 0.576 \pm 0.101$ $z = 5.691$, $p < 0.001$; Figure 3.2). The effect of other variables did not vary across communities either. Feeding party size increased with travel distance (Sonso: $\beta \pm SE = 0.128 \pm 0.048$ $z = 2.678$, $p = 0.007$; Waibira: $\beta \pm SE = 0.143 \pm 0.046$ $z = 3.102$, $p = 0.002$) and feeding bout length (Sonso: $\beta \pm SE = 0.153 \pm 0.064$ $z = 2.390$, $p = 0.017$; Waibira: $\beta \pm SE = 0.190 \pm 0.068$ $z = 2.79$, $p = 0.005$). There was no significant effect of sex on feeding party size.

The food type seeds had a significant positive effect on feeding party size for the Sonso community (β±SE = 0.564±0.198 z = 2.853, p = 0.004) but not for the Waibira community (β±SE = -0.481±0.386 z = -1.246, p = 0.213; Table 3.4). I compared patch sizes of seed feeding patches across communities to examine whether the increase in party size for this food type within the Sonso community was simply driven by a larger patch size. Foodpatches of this food type were of similar size (Sonso: 80.49cm ± 11.71, Waibira: 88.61cm ± 5.85) indicating that other factors were responsible for large parties in patches of seed foods in the Sonso community.

Table 3.4 Estimated model coefficients (β), standard errors (SE), z-values and p-values of Model 1, explaining feeding party size within the Sonso and Waibira community. Significant effects (p<0.05) are indicated in bold.

	β	SE	*z*	*p*
Sonso community				
Intercept	1.235	0.177	6.985	*<0.001*
DBH	**0.817**	**0.099**	**8.212**	**<0.001**
Travel distance	**0.128**	**0.048**	**2.678**	**0.007**
Sex (male)	0.239	0.128	1.873	0.061
Feeding bout length	**0.153**	**0.064**	**2.390**	**0.017**
Food type: ripe fruit	0.023	0.177	0.131	0.896
Food type: seeds	**0.564**	**0.198**	**2.853**	**0.004**
Food type: unripe fruit	0.092	0.189	0.487	0.626
Food type: young leaves	-0.003	0.197	-0.016	0.987
Waibira community				
Intercept	1.597	0.330	4.840	*<0.001*
DBH	**0.576**	**0.101**	**5.691**	**<0.001**
Travel distance	**0.143**	**0.046**	**3.102**	**0.002**
Sex (male)	0.098	0.124	0.792	0.429
Feeding bout length	**0.190**	**0.068**	**2.790**	**0.005**
Food type: ripe fruit	-0.415	0.345	-1.204	0.229
Food type: seeds	-0.481	0.386	-1.246	0.213
Food type: unripe fruit	-0.492	0.403	-1.219	0.223
Food type: young leaves	-0.489	0.361	-1.355	0.175

Note: Intercept represents the food type flower and the focal sex female.

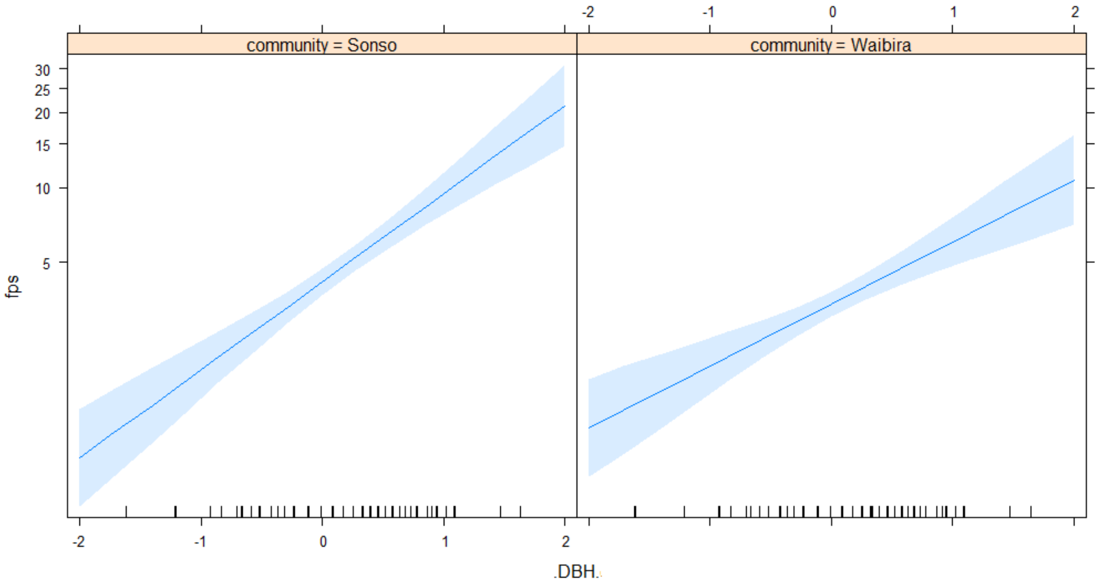

Fig. 3.2 Relationship between patch size (DBH) and feeding party size (fps) across the two communities. The solid line indicates the fitted model. The graph was produced using the "plot effects" command in R and shows the relationship between feeding party size (fps) and patch size (DBH) while controlling for the effect of all other variables.

Model 2: Travel distance to food patches

Overall, the full model was highly significant as compared to the null model (likelihood ratio test: $X^2 = 50.75$, df = 6, $p < 0.001$). Travel distance to food patches was significantly and positively associated with feeding party size in both communities (Sonso: β±SE = 0.024±0.012 z = 2.10, p = 0.036; Waibira: β±SE = 0.034±0.017 z = 2.06, p = 0.040; Table 3.5). The effect of DBH on travel distance varied across communities (interaction between community and DBH: $X^2 = 5.98$, df = 1, p = 0.015) as did the effect of food type ($X^2 = 10.51$, df = 4, p = 0.033). Patch size was predictive of travel distance only for the Waibira community whereas for the Sonso community travel distance was not significantly associated with patch size (Fig. 3.3). Travel distance increased with bout length in both communities (Sonso: β±SE = 0.402±0.198 z = 2.03, p = 0.043; Waibira: β±SE = 0.503±0.215 z = 2.34, p = 0.020). The sex of focal chimpanzees had no significant effect on travel distances and did not vary across communities.

Table 3.5 Estimated model coefficients (β), standard errors (SE), t-values and p-values of Model 2, explaining travel distance to food patches within the Sonso and Waibira community. Significant effects (p<0.05) are indicated in bold.

	β	SE	*t*	*p*
Sonso community				
Intercept	**0.710**	**0.206**	**3.441**	***<0.001***
Feeding party size	**0.024**	**0.012**	**2.104**	**0.036**
Sex (male)	-0.121	0.155	-0.782	0.442
Feeding bout length	**0.402**	**0.198**	**2.033**	**0.043**
Waibira community				
Intercept	**1.209**	**0.376**	**3.215**	**0.001**
Feeding party size	**0.034**	**0.017**	**2.062**	**0.040**
Sex (male)	0.276	0.148	1.871	0.071
Feeding bout length	**0.503**	**0.215**	**2.340**	**0.020**

Note: Results from the variables DBH and food types could not be interpreted in the same manner as those for feeding party size, sex and feeding bout length, due to their interaction with community and are therefore omitted from the table.

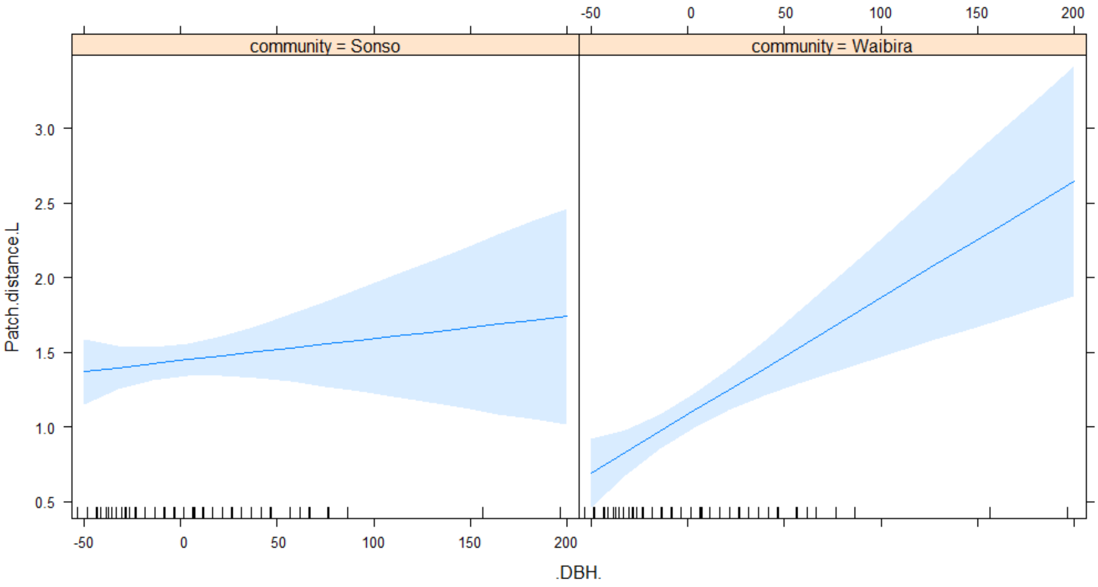

Figure 3.3 Relationship between patch size (DBH) and travel distance to food patches across the two communities The solid line indicates the fitted model. The graph was produced using the "plot effects" command in R and shows the relationship between patch size (DBH) and travel distance while controlling for the effect of all other variables.

Model 3: Contest competition over food

The full model was highly significant as compared to the null model (likelihood ratio test: X^2 = 107.61, df = 9, p < 0.001). In both communities the occurrence of contest competition over food was significantly and positively associated with total party size (Sonso:β±SE = 1.905±0.720 z = 2.65, p = 0.008, Waibira: β±SE = 2.599±0.794 z = 3.28, p = 0.001 Table 3.6). The proportion of males within feeding parties had no significant effect on the occurrence aggression, consequently neither the proportion of females. The proportion of females had a stronger effect on contest competition within the Waibira community (interaction between community and proportion of females: X^2 = 3.96, df = 1, p = 0.047) yet, due to a marginally significant interaction between total party size and the proportion of females (p = 0.083), this results was not conclusive. Patch size (DBH) was not predictive of aggression in either community.

Table 3.6 Estimated model coefficients (β), standard errors (SE), z-values and p-values of Model 3, explaining occurrence of contest competition over food within the Sonso and Waibira community. Significant effects (p<0.05) are indicated in bold.

Aggression model	*β*	SE	*z*	*p*
Sonso community				
Intercept	-7.924	2.408	-3.291	*0.001*
Feeding party size	**1.905**	**0.720**	**2.649**	**0.008**
Proportion males	4.290	3.361	1.276	0.202
DBH	-0.163	0.425	-0.383	0.701
Waibira community				
Intercept	-6.828	2.013	-3.391	*<0.001*
Feeding party size	**2.599**	**0.794**	**3.275**	**0.001**
Proportion males	3.535	2.948	1.199	0.231
DBH	-0.412	0.353	-1.166	0.244

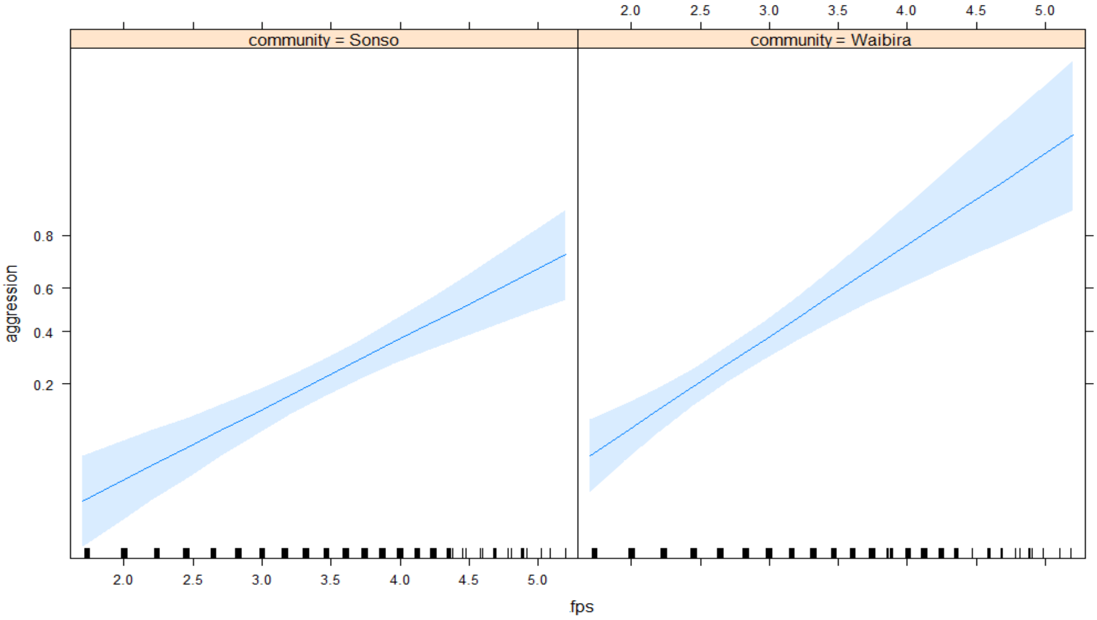

Fig. 3.4 Relationship between feeding party size (fps) and the occurrence of contest competition over food across the two communities. The solid line indicates the fitted model. The graph was produced using the “plot effects” command in R and shows the relationship between feeding party size (fps) and the occurrence of aggression while controlling for the effect of all other variables.

Discussion

Despite differences in vegetation composition across home ranges (see Chapter 2), differences in overall community size and substantial differences in average party and patch size, almost all predictions of the EC model were well confirmed and consistent across the two chimpanzee communities. Larger feeding parties foraged in larger patches and the formation of larger parties required chimpanzees to travel longer distances between patches.

In contrast to previous socio-ecological studies in fission-fusion foragers, in which the relationship between party size and patch characteristics did not follow predictions of the EC model (Busia et al., 2016; Ospina, 2011; Pokempner, 2009; Stevenson et al., 1998), during this study foraging behaviour was analysed on a shorter temporal scale and distribution of resources was quantified based on the behaviour of foragers themselves. Moving beyond daily averages and exploring inter-patch variation in party size, patch size and travel distance is thus clearly a promising approach that deserves broader application. It is now possible to take into account non-systematic (random) variation of individual foragers within their groups (Bolker et al., 2009) and researchers should make use of these novel statistical means to investigate the dynamic responses of foragers to their changing environments.

Travel distances might not always conform to the optimized predictions of the EC model (Chapman and Chapman, 2000). Foragers may not necessarily aim to adjust travel distances to the size of food patches or travelling parties but instead adjust it to the current value a given patch has to them. An individual’s nutritional state and nutritional balancing, for example, strongly affect foraging decisions as well (Nie et al., 2015; Rothman, 2015; Rothman et al., 2011). Nutritional balancing often requires a foraging strategy that is quite different from one that is aimed at maximization of energy intake (Johnson et al., 2017; Rothman et al., 2011), thus foraging animals might not always select the closest or largest feeding patch available. Distances travelled by foragers might therefore be expected to meet cost-benefit calculations only over longer temporal scales, so that analysis of daily averages for this foraging variable can be appropriate to answer certain questions.

For the correlation between subgroup size and patch size, however, daily averages will have very little meaning, especially in fission-fusion species in which foragers are able to readily adjust party size to patch size. This study shows that an analysis at patch-level is a much more appropriate approach in chimpanzees: even though the two communities differed markedly in overall size, home range size (Jakob Villioth, unpublished data) and inhabit areas of different vegetation composition (Chapter 2), the relationship between party size and patch size was strongly linked for individual patches. Previous studies which failed to find predicted correlations between food abundance and daily subgroup size (Ospina, 2011; Pokempner, 2009; Stevenson et al., 1998) might have simply eliminated all meaningful variation of their samples.

Critics of the EC model need to take into account that tests of the model are performed across a variety of primate species with different social organizations, diets and foraging strategies. Unless methods and definitions of central foraging parameters of such studies are effectively standardized, to an extent that standardization is possible and meaningful, conflicting results may simply reflect differences in methodology and/or definitions and should not be used to question the overall applicability of the model. While the incorporation of new research areas, such as nutrient balancing, into the model is certainly required, the complete abolishment of it (Thierry, 2008) seems misguided. Despite certain limitations (Janson, 2000; Koenig and Borries, 2006), the ecological constraints model clearly remains a useful tool to investigate levels of feeding competition in socially foraging animals such as chimpanzees.

At Budongo, two lines of evidence suggested that Waibira chimpanzees faced higher levels of feeding competition. First, the basic comparison of foraging variables revealed that the Waibira community foraged on average in smaller parties and smaller food patches, travelling shorter inter-patch distances when all travel was considered. These differences suggest that the Waibira community inhabits a home range that is less favourable to the formation of large foraging parties; large food patches seem to be spaced too far apart to maintain large parties (Chapman et al., 1995; Chapman and Chapman, 2000). Travel costs thus constrained party size and it was more beneficial to forage in small parties. Within the Sonso home range in contrast, large food patches appeared to be more abundant, allowing for larger foraging parties to be formed and maintained more frequently. To do so, Sonso chimpanzees then travelled longer distances, since such large patches were further apart than potential small patches.

Second, Waibira chimpanzees only travelled farther when moving towards a larger food patch, whereas within the Sonso community these two variables were less strongly related (Fig. 3.3). Thus, Sonso chimpanzees could either sometimes reach larger patches through shorter travel distances; or, at times, they were energetically able to afford to travel longer distances to relatively small patches as well. Both of these explanations can be interpreted as Sonso chimpanzees inhabiting a home range of more abundant food resources than the Waibira community.

A potential third line of evidence is the difference in overt contest competition by female chimpanzees across communities. Within the Waibira community the occurrence of aggressive interactions increased more strongly with the proportion of females within parties than in the Sonso community. This result, however, was not entirely conclusive, as the proportion of females within parties was closely linked to overall party size. A similar tendency was found for the proportion of males within parties as well, albeit at an even lower significance level. This interaction between the proportion of males/females within parties and total party size made it difficult to distinguish between the effect of the number of males/females within a foraging party and the effect of overall party size. Yet, in the light of the other two lines of more conclusive evidence, more detailed research on potential differences in the level of overt contest competition across communities hold a lot of promise. Capturing all aggressive interactions within feeding trees proved to be difficult, thus a specific study on contest competition should ideally include several observers that can monitor different parts of the tree. With more focal data on overt competition it will also be possible to calculate frequencies of aggression and to move beyond this first, rather simplistic, binary model of the current study.

The number of food-related competition events increased as predicted with party size, in both communities. In several other non-human primates such a direct measure of food competition has been useful for testing theories of socio-ecological models (Hanya, 2009; Heesen, 2014; Saito, 1996; Vogel and Janson, 2007; Wheeler et al., 2013), suggesting that results obtained during this study can indeed be interpreted as evidence for overall more intense feeding competition in larger parties. Contrary to expectations, aggressors in food patches were much more likely to be male chimpanzees than female ones. These results contrast with findings of feeding competition in capuchin monkeys (*Cebus capucinus*: Vogel and Janson, 2007) in which female, but not male, party size was predictive of aggression in food patches. In chimpanzees males are generally the more aggressive sex (Muller, 2002; Muller et al., 2007; Wrangham and Peterson, 1996) and it is possible that results of this study reflect the overall aggressiveness of chimpanzee males. However, the analysis was restricted to aggressive interactions that were clearly linked to competition over food. Male aggression usually takes place in the context of male dominance interactions or sexual competition, whereas aggression in female chimpanzees is more frequently related to competition over food (Muller, 2002), thus high levels of male competition within food patches were not expected. Another possibility is that males, which were more often initiators of aggression, used aggression within feeding patches as well to ensure their dominance over other, lower-ranking, individuals. None of the foraging models revealed greater foraging efforts in females (see below). Thus, it should not be ruled out that males of the two study communities may in fact be more concerned with food acquisition than current theories of male foraging strategies acknowledge. Male ranging and association patterns are not always explained by the search for fertile females but might to an equal extent reflect the need for male-male interactions (Newton-Fisher, 2014) or efficient foraging in familiar areas (Murray et al., 2008).

Contrary to predictions, patch size (DBH) was not predictive of aggression levels in food patches in either community. Since there was a strong positive relationship between patch size and party size in both communities, chimpanzees might have been able to adjust the size of foraging parties quite readily to available food amounts and this way avoided higher levels of contest competition in smaller food patches. It might be possible to test this hypothesis using a more detailed measure of fruit availability within food patches (Vogel, 2005; Vogel and Janson, 2007). During this study a uniform measure of food availability across food types and different tree species could not be achieved, since the types of available foods and their visibility in trees varied substantially across species.

Two confounding factors need to be considered for the comparisons that I have drawn between communities: first, differences in habituation level might have influenced the size of parties which were recorded. For example, average party size in Waibira might have been lower, because less habituated individuals were reluctant to join parties followed by human observers or remain at the periphery of a party. Larger parties, on the other hand, were more tolerant of human observers (personal observation) which could have biased data collection in Waibira towards larger parties. Overall, my impression was that habituation levels had little impact on party sizes recorded during this study. Lone individuals could be followed easily in each community and were, in fact, more common in the Waibira community.

Second, fruiting patterns of chimpanzee food species differed markedly across the two field seasons of data collection (see Chapter 2). Whether resource abundance is thus indeed consistently lower within the Waibira home range will therefore require more detailed data on food availability and foraging efforts by chimpanzees in each community. Since the home range of the Waibira community has been logged more intensely and more recently (Plumptre, 1996), and, as a result, is still more fragmented today, it seems nevertheless likely that possibilities to maintain larger parties are generally lower for this community.

Distinct sex differences in party size and travel distances, as reported from other chimpanzee communities (Kibale National Park: Wrangham 2000; Pokempner 2009; Gombe: Williams et al., 2002; Tai forest: Normand and Boesch, 2009) and in a previous study at Budongo (Bates and Byrne, 2009) were not observed during this study. Females foraged slightly more often on their own and in smaller food patches than did male chimpanzees. However, when females joined parties, they fed in patches of comparable size than males. In the Waibira community travel distances to food patches differed between males and females, but this difference was driven by certain female focals that travelled only arboreally during some days of observations. In the two foraging models, which investigated party size and travel distance, the predictive power of the focal's sex was low compared to that of ecological variables, and the investigation of overt feeding competition revealed surprisingly high levels of male-initiated conflict over food (see above). Taken together, results of these analyses suggest that overall males and females foraged in similar ways.

In her detailed study of the energetics of feeding competition in male and female chimpanzees of the Kanyawara community, Pokempner (2009) found little difference in overall intake and foraging effort across sexes and suggested that short-term energetic costs for males and females may in fact be similar (Key and Ross, 1999). This possibility is supported by contrasting results of travel distance and linearity at different levels of analysis: while females travelled more directly to fruiting trees, there was no differences in directness between males and females when all food patches are considered (Pokempner, 2009). And while lactating females travelled shorter daily distances, both sexes travelled similar distances per movement phase (Bates and Bryne, 2009). Such results and these of the current study indicate that foraging efforts by male and female chimpanzees may not be as fundamentally different as commonly assumed (Wrangham 2000; Williams et al., 2002), even if females seem to be more susceptible to increased levels of feeding competition (Pokempner, 2009).

Compared to previous investigations of chimpanzee foraging strategies, this study focused on food patches only, rather than including information on parties and travel of the entire day. A lack of sex differences in foraging behaviour could thus potentially be ascribed to differences in methodology. However, it seems unlikely that sex differences should be absent within food patches and only quantifiable when entire days are investigated. In fact, sex differences in foraging should be more pronounced during behaviour that is clearly linked to food acquisition, as was studied here. The low predictive power of sex during this study might instead reflect differences in food abundance and distribution across chimpanzee communities. Peripheral females of the Sonso community are more gregarious than in other East African populations (Reynolds, 2005; Thompson and Wrangham, 2006), which suggests that costs of grouping at Budongo may be lower. Females in Budongo forest might thus be less constrained by resource availability and not required to maximize feeding efficiency significantly more than males.

This study is the first to test predictions of the EC model across two neighbouring chimpanzee communities. Despite differences in vegetation composition across home ranges and substantial differences in overall community size, interactions between party size and patch characteristics followed predictions of the EC model in both communities. My results underline the applicability of the EC model in the study of feeding competition and demonstrate that analysing individual inter-patch movements and parameters of individual food patches is a much more appropriate approach in foragers of high levels of fission-fusion dynamics than the use of daily average values. Findings of this study also revealed that at Budongo sex differences in foraging strategies were less pronounced than predicted, suggesting that foraging efforts in male and female chimpanzees might be less divergent than in other chimpanzee populations.

Chapter 4

Introducing discrete-choice models to chimpanzee feeding ecology

Abstract

Optimal foraging theory (OFT) has guided much of the research on foraging behaviour in the past five decades and the notion of optimal foraging is deeply embedded in most models of foraging today. However, by assuming that all foragers strive to maximize a certain predefined "currency", such as the amount of food per unit time, or have in fact already achieved an optimal strategy, little can be learned about which factors influence foraging decisions and if or how individual foragers attempt to meet energy or other nutritional goals. Here I apply a novel approach to study foraging decisions in two communities of wild chimpanzees: the discrete-choice model. Such models do not assume an optimal strategy as starting point but instead examine the foraging decisions themselves by allowing animals to choose from a set of "option trees". Over a period of 16 months I collected data on patch characteristics and inter-patch distances from male and female focals in two chimpanzee study communities, Sonso and Waibira, in the Budongo Forest Reserve. From these, I created a set of 422 foraging decisions (Sonso: 205, Waibira: 217) which were used to investigate the influence of several foraging variables on patch choice. Despite considerable differences in community size and forest composition, foraging strategies of Sonso and Waibira chimpanzees were remarkably similar: Across sexes and communities, chimpanzees exhibited a clear preference for closer as well as novel food patches. The size of food patches did not predict foraging decisions as expected; only for males of the Waibira

community was DBH a significant predictor of patch selection. Chimpanzees of both communities frequently chose to forage on food patches providing young leaves, which highlights the importance of this food type in their diet. This study demonstrates that new insights can be gained from integrating several important foraging variables of chimpanzee feeding ecology into a coherent model of foraging choices. My findings provide the first direct evidence that chimpanzees consider travel distance, patch novelty and patch size when choosing foraging sites.

Introduction

Studies of foraging behaviour have traditionally followed optimality models (Charnov, 1976; Parker and Smith, 1990; Schoener, 1971). In this approach, foraging organisms are assumed to have complete spatial and temporal knowledge of available resources and are therefore able to choose foraging options which allow them to optimize net intake rates (Giraldeau and Caraco, 2000; Krebs and Davies, 2009). This central assumption has, however, been questioned since it seems more plausible that individual foragers are, to some extent, uncertain about foraging conditions (Houston et al., 2007; Mangel, 1990; Pyke, 1984). Further, the environments in which social animals forage are often highly complex, making it unlikely that even experienced foragers constantly make optimal decisions (Fawcett et al., 2014).

Discrete-choice models, which have been developed in the field of economics (Ben-Akiva and Lerman, 1985; Train, 2009), allow for an approach that does not assume an optimal strategy as the starting point (Cooper and Millspaugh, 1999; Manly et al., 2002). These models have recently been used to study foraging decisions in wild populations of chacma baboons (*Papio ursinus*, Marshall et al., 2012), black bears (*Ursus americanus*, Lewis et al., 2015) and mantled howler monkeys (*Alouatta palliata*, Hopkins, 2016), amongst others. Discrete-choice models are based on the concept of utility, where utility can be thought of as the most profitable of available options to the animal, be it in terms of energy intake (Emlen, 1966), nutrient balancing (Felton et al., 2009; Raubenheimer et al., 2009) or some other, unknown utility. In data analysis, the foraging animals are allowed to choose from a set of resources (the “choice set”) and are assumed to choose the option from which, at this moment, it can gain the maximum utility. Instead of judging the foraging success of animals based on the capability to optimize a predefined currency, discrete-choice models thus study the foraging decisions themselves, thereby allowing us to understand which factors truly influence decisions and how individual foragers attempt to meet energy or other nutritional goals across different habitats (Marshall et al., 2012). Such models also more easily allow for the optimised currency to shift or to accommodate multiple currencies at the same time, for example if an animal is both trying to maximise its energy intake and meet particular nutritional requirements (Felton et al., 2009).

Here I apply a discrete-choice model to investigate the foraging behaviour of chimpanzees (*Pan troglodytes*) within the Budongo Forest Reserve. Chimpanzees are a popular model for the validation of foraging models due to their high degree of fission-fusion dynamics (Chapman and Chapman, 2000). In this type of grouping and foraging behaviour, individuals within a community travel and forage in small subgroups which frequently change in size and composition throughout the day (parties: Sugiyama, 1968). Fission-fusion sociality is thought to be an efficient foraging strategy in large-bodied animals which can afford temporary small subgroups due to low predations risks (Chapman, 1990; Symington, 1988; Wrangham, 1977). The foraging behaviour of individuals or subgroups is interpreted as a direct response to different levels of feeding competition, which change due to short-term variation in the distribution and availability of resources (Aureli et al., 2008; Chapman et al., 1995; Lehmann and Boesch, 2004). Thus, the relationship between important foraging variables, such as subgroup size, travel distance and patch size, are expected to be linked more closely in species with pronounced fission-fusion dynamics, in contrast to group-foraging animals in which the need for cohesive grouping prevents animals from pursuing more individualistic foraging strategies. Chimpanzees’ fission-fusion dynamics therefore represents an excellent opportunity in which individual foraging decisions can be examined relatively free of grouping constraints and links to foraging variables can rigorously be established.

Previous research suggests that chimpanzees are able to navigate through their territory using a combination of long-term spatial memory (Janmaat et al., 2013) and a Euclidean map (Normand & Boesch, 2009). While such cognitive mechanisms are a prerequisite for effectively locating food resources and travel in between them, this study does not further test any of the mechanisms proposed for primate spatial cognition (Byrne 2000; Garber 2000; Garber & Dolins, 2014). Instead it aims at establishing the importance of certain ecological criteria that chimpanzees use to select feeding trees. Previous studies of chimpanzees have identified a range of such ecological parameters which are influential in foraging decisions, such as patch size and the size of foraging parties (Ghiglieri, 1984; White and Wrangham, 1988; Isabirye-Basuta, 1993; Newton-Fisher et al., 2000), distance between food patches (Normand et al., 2009; Pokempner, 2009) and the duration of feeding bouts within patches (Normand and Boesch, 2009). While in other non-human primates, the relationship between several of these variables has been investigated (*Cercopithecus aethiops*: Isbell et al., 1998; *Trachypithecus crepusculus*: Pengfei et al., 2015; *Ateles geoffroyi*: Busia et al., 2016), research on chimpanzees has so far mostly focused on the relationship between party size and patch size, whereas links between patch size and travel distance or bout length have remained largely unexplored. I hypothesized that in chimpanzees, as in other primates which exploit discrete depletable patches, selection of a food patch will be a trade-off between the value of a particular patch and the travel costs to reach it.

Foraging theory predicts that energetic costs of travel should have a strong impact on foraging strategies (Chapman and Chapman, 2000; Majolo et al., 2008). Multiple studies have shown that travel distance to food patches is a crucial parameter during foraging behaviour, constraining group size (Chapman et al., 1995; Isbell, 1991; Janson and Goldsmith, 1995; Steenbeek and Van Schaik, 2001) and predicting size and productivity of the patches in which animal choose to forage (Normand et al., 2009; Pokempner, 2009; Suarez, 2014). In chimpanzees, detailed studies of travel distance to food patches have thus far focused on sex differences. In several communities females tend to travel shorter distances and move in a more linear way in between feeding trees (Tai forest: Normand and Boesch, 2009; Kibale National Park: Pokempner, 2009; Budongo Forest, Sonso community: Bates and Byrne, 2009). These sex differences, however, disappear when, for example not only fruiting trees but all food patches are considered (Pokempner, 2009) or, instead of daily averages, individual movement phases are analysed (Bates and Byrne, 2009). As a conservative hypothesis, I expected chimpanzees of both sexes to minimize travel distances between patches:

Hypothesis 1:

All things being equal, chimpanzees will choose feeding patches closer by over those further away.

The value of a give patch will depend upon the quantity and quality of available resources in that patch; in case of multiple visits to the same patch, foragers might also use information from previous feeding bouts to decide whether to revisit it (Vogel and Janson, 2007). The link between the size of a food patch and the amount of food it provides has been well established through different fruit-quantification methods (Chapman et al., 1992; Peres, 1994) as well as through the behaviour of foragers; larger food patches can accommodate a larger number of foragers (Asensio et al., 2009; Symington, 1988) or provide food for longer periods than smaller patches (Janson and van Schaik, 1988; Chapman, 1990; Chapman et al., 1995; Snaith and Chapman, 2005), correlations which apply to chimpanzee foraging parties as well (Ghiglieri, 1984; White and Wrangham, 1988; Isabirye-Basuta, 1993; Newton-Fisher et al., 2000; Lehmann and Boesch, 2004). I therefore predicted that chimpanzees would use patch size as a way of estimating the potential amount of a food within a patch and, across all food types, select larger patches over smaller ones:

Hypothesis 2:

Chimpanzees select larger food patches over smaller ones; the probability of choosing a patch increases with patch size.

The amount of available resources within a patch will not only depend upon its size but also on how depleted it is (Charnov, 1976). The influence of patch depletion has so far mostly been investigated in terms of patch departure times; that is: when foraging animals should decide to leave a patch (Altmann, 1998; Grether et al., 1992; Johnson et al., 2017; Plante et al., 2014) whereas in non-human primates patch depletion has rarely been used to assess patch value or to predict probabilities of foragers to return to a given patch. Suarez (2014) demonstrated that time since the last visit to a feeding patch can be an influential factor in predicting revisits to patches in spider monkeys (*Ateles belzebuth*): the probability of revisiting a patch was initially low, peaked after an interval of 2.5 - 3.5 days and then sharply declined for intervals of four or more days. This was interpreted as monkeys selecting patches after an interval when sufficient unripe fruit had ripened to make a return visit worthwhile. As ripe fruit specialists, chimpanzees can be expected to prefer patches which still contain a large amount of ripe fruit. Novel food patches should provide a larger amount of resources but might also contain more unripe fruits that are not yet edible. Previously visited trees, on the other hand, could be preferred since animals already had a possibility to assess patch value which further allows to time a productive revisit. However, as chimpanzees forage in several loose groups simultaneously, some parties may deplete patches independently which makes scheduling productive revisits to the same patch nearly impossible.

I therefore predicted to find a preference for novel food patches in chimpanzees:

Hypothesis 3:

Novel patches are preferred over patches that have been visited before.

The quality of a patch, from a forager's perspective, will strongly depend on the kind of resource that patches offers. Chimpanzees are considered to be ripe fruit specialists and try to maintain a frugivorous diet even when fruit availability is low (Ghiglieri, 1984; Watts et al., 2012; Wrangham et al., 1998) - when available, chimpanzees select foods which offer a high content of easily digestible macronutrients, such as non-structural carbohydrates and lipids (Hohmann et al., 2010; Remis, 2002). Several studies in other non-human primates demonstrated that foraging decisions are strongly affected by an individual's nutritional state (Nie et al., 2015; Rothman, 2015; Rothman et al., 2011). Nutrient balancing between protein and non-protein energy (fats, non-structural carbohydrates, and digestible fibre) was found to best predict food patch occupancy time in black-and-white colobus monkeys (*Colobus guereza*: Johnson et al., 2017). Gorillas similarly prefer a stable non-protein energy (NPE) intake, which remained at similar levels during high-fruit periods and when leaves dominated gorilla diets (Rothman et al., 2011). In spider monkeys, in contrast, subgrouping patterns were best explained by the amount of protein in food patches that were visited during each day, which suggests that digestible protein content is a key nutritional factor in this species (Busia et al., 2016). Theories of nutrient balancing have not yet been investigated in wild chimpanzees, but previous research at Budongo has shown that Sonso chimpanzees incorporate a comparatively high proportion of young leaves into their diet (Newton-Fisher, 1999a; Chapter 2 of this study).

I therefore set out to test whether Budongo chimpanzees conform to other chimpanzee populations in showing a marked preference for ripe fruit over other food types:

Hypothesis 4:

Patches of ripe fruit are preferred over all other types of food patches.

Feeding bout length is another important measure of patch value; it is considered a more subjective, primate-based measure of patch value and has been found to be a reliable indicator of patch size (Chapman et al., 1995; Chapman, 1990; Janson, 1988; Symington, 1988), predictive of food-related agonism (Vogel and Janson, 2007) and might also reflect the quality of a patch (Normand et al., 2009; Suarez, 2014). However, how long individual foragers feed in patches of different food types might depend on energy and nutrients acquired from previous patches and patch departure can also be influenced by social factors, such as the number of co-feeders (Kazahari and Agetsuma, 2008; Snaith and Chapman, 2005). A short stay within a feeding tree might thus not necessarily indicate a patch of low quality or quantity. However, since bout length could theoretically reflect quantity as well as quality of a patch, I expected to overall find a positive relationship between feeding bout lengths and the likelihood of choosing food patches:

Hypothesis 5:

The probability of selecting a patch increases with feeding bout length.

This study thus simultaneously integrates several important foraging variables of chimpanzee feeding ecology into a discrete-choice model. Using data from two neighbouring communities, I investigated how varying ecological and social parameters might influence the interaction of a range of foraging variables, thereby furthering our general understanding of the significance of these variables as well as their importance to chimpanzee feeding ecology.

Methods

Study site and communities

Data collection took place within the Budongo Forest Reserve (1°35’ - 1°55’ N, 31°08’ - 31°42’ E), over a period of 16 months. Foraging decisions were investigated in two neighbouring chimpanzee communities, Sonso and Waibira. Between October 2015 and June 2016, I observed chimpanzees of the Sonso community and, during a second field season (October 2016 to June 2017), chimpanzees of the Waibira community. During the study period, the Sonso community contained 71 individuals in total and, following age classifications by Goodall (1986), included 12 adult males (≥16 years old) and 24 adult females (≥14 years old). All members of the Sonso community could be observed at close quarters and were individually recognized, as this community has been studied continuously since 1990 (Newton-Fisher, 1997; Reynolds, 2005). Habituation of the Waibira chimpanzees started in 2011 and is still ongoing (Samuni et al., 2014). At the time of this study almost all adult members could be individually recognized as well and observation distances permitted to study foraging behaviour at a sufficiently close range (see for example also, Hobaiter et al., 2017). This Waibira community consisted of at least 88 known individuals, including 17 adult males and 29 adult females.

Behavioural data collection

In order to obtain a complete record of the individual’s foraging decisions during a follow, I aimed to conduct full-day nest-to-nest follows of individual chimpanzees in both communities. Focal follows started at first feeding tree of the day and continued for as long as conditions allowed. As Sonso chimpanzees engage in crop-foraging (Tweheyo et al., 2005), focal follows in this community had to be interrupted when the designated focal left the forest to forage on field crops or during inter-community encounters (mean duration of Sonso follows: 5.6h SD 3.1h, range: 1-12h median: 5h). This kind of foraging was excluded from the analysis. Waibira chimpanzees have no possibilities to forage on field crops, but the ongoing habituation of the Waibira community and their denser habitat made full-day nest-to-nest follows of individual chimpanzees impossible as well (mean duration of Waibira follows: 4.1h SD 2.6h, range: 1-12h median: 4h). I selected one focal from a randomised list at the beginning of each day. In order to maintain a balanced sampling regime, I attempted to increase the number of focal samples from individuals that were still underrepresented in the overall sample, when the initial focal individual was lost.

In order to investigate foraging decisions of males and females, I followed male and female focals in each community: In the Sonso community, six adult males and five adult females were selected as focal individuals, and in the Waibira community I collected data on ten adult males and nine adult females. I sampled a larger number of individuals from the Waibira community since this community is also larger in size. Males from both communities varied in age and occupied different ranks (high-, mid- and low-ranking). Female focals from Sonso were lactating and travelled with at least one infant during the study, except for one female that was not lactating and only travelled with her juvenile offspring. From the Waibira community seven females were lactating while the other two females were not lactating and only travelled with one juvenile offspring.

During focal follows, activity of the focal individual was recorded continuously (Altmann, 1974). All behaviours related to food handling – the entire process of picking and ingesting food items – were categorized as feeding. A feeding patch was defined as an aggregation of food items that allowed uninterrupted foraging movements by the focal animal (White and Wrangham, 1988; Chapman et al., 1994; Pruetz and Isbell, 2000). While in most cases a patch was equivalent to an individual feeding tree, for certain tree species (for example *Broussonetia papyrifera*, *Putranjivace gerrandi*) a patch could consist of multiple trees with overlapping crowns. Food patches recorded when the chimpanzees' foraging activities and travel was influenced by an inter-community encounter, crop-foraging, hunting or travel to waterholes were excluded from the analysis.

The discrete choice model

For data analysis, I used a mixed logit model (Hole, 2007). The advantage of a mixed logit model, compared to multinomial logit models (e.g. Marshall et al., 2012) or conditional logit models (e.g. Hopkins, 2016), is that it allows for different preferences (random coefficients) across individuals instead of applying fixed coefficients to all decision-makers (Train, 2009). This way it was possible to sample a larger number of individuals, and chimpanzees of both sexes, and consolidate possibly diverging foraging decisions of individuals into a general foraging strategy for each community. The mixed logit model also enabled me to investigate foraging decisions of individual chimpanzees within their fission-fusion social organization, which goes beyond the analysis of foraging behaviour in coherent groups that is typical of many other non-human primates (Strier, 2016).

I analysed foraging decisions in the following manner. Each time a focal chimpanzee left a food patch, it could choose between a discrete choice set of “option trees”. These option trees included all food patches that chimpanzees had visited during the past three days and all trees that were visited during the day of the focal follow. The limit of three days was based on the average interval between visits to the same food patch, which was comparable in both communities (Sonso: 3.57 days, Waibira: 3.09 days). This time frame was also in line with results from previous studies of frugivorous primates (Cunningham and Janson, 2007; Hopkins, 2016, 2008; Suarez, 2014), especially those of re-visitation patterns to food trees by chimpanzees (Normand et al., 2009). Although chimpanzees are able to remember the location of fruit trees over much longer time-spans (Janmaat et al., 2013), this average interval between visits should be a conservative estimate of patch depletion. Based on focal follows (for details see Chapters 2 and 3), I created a set of 422 foraging decisions across both communities (Sonso: 205, Waibira: 217). The mean number of option trees per decision was 6 (SD: 4; range 2-19). For each of the option trees the following variables, which represented either costs of choosing this particular food patch (*travel distance*) or estimates for the value of a patch (*DBH, visits, food type, feeding bout length*), entered the model:

a) Travel distance

During focal follows the locations of all food patches visited by the focal animal were recorded using a handheld GPS (Garmin GPSMAP 64). For each foraging decision, I later digitally measured the straight-line distance (in metres) that the focal would have to travel to reach each of the available option patches using the Garmin BaseCamp software.

b) DBH (diameter at breast height)

DBH is a widely used measure to estimate the size of a feeding patch, and thus the amount of food resources that are potentially available (Chapman et al., 1994). This measure may not always capture the dynamic nature of fruit availability within trees, yet due to its frequent application and as it allows to compare results across study sites and species (Chapman et al., 1992), DBH was used during this study as well. The measurements were obtained using a tape measure, and were accurate to the nearest cm. When chimpanzees were foraging on fruits or leaves of lianas, the DBH measurements of all supporting trees were measured and summed. In some cases, it was not possible to measure DBH with a tape measure, for example when a feeding tree was surrounded by dense vegetation or the tree was so small that it could not be approached without interfering with the foraging animal. In such cases, DBH of the feeding patch was estimated visually.

The Sonso community foraged extensively on flowers and young leaves of a specific tree species (*Broussonetia papyrifera)* during October and November 2015. This species only grows in groves, in a certain part of the forest edge within the Sonso community's home range, and individual chimpanzees within a single party often distributed themselves across a large area within such groves. I assumed that chimpanzees chose to forage in these patches because they offered a large quantity of quickly replenishing resources. To adequately capture foraging events in these groves, in contrast to foraging in individual feeding trees, I distinguished 7 spatially separated "BPY plots" of different sizes. I then calculated the total number of trees within each plot based on the overall plot size, which was measured using a handheld GPS unit. Based on DBH measurements obtained during foraging events within

BPY plots, I used an average DBH of 30cm for each tree and then calculated the DBH sum of all trees in each plot. The total DBH values of these BPY plots varied between 210cm (plot 2) and 4200cm (plot 3).

c) Visits

To test whether chimpanzees prefer novel food patches over previously visited trees, I incorporated the number of visits to each patch into the model. In species with a fission-fusion social organization it is not possible to follow all individuals or parties at all times. Therefore, all food patches that had been visited during follows were registered with a unique patch number, so that any revisits to previous patches, also with other focal individuals, were not considered as foraging events in a "novel" patch. Since chimpanzees could only choose from a limited number of large food patches on any given day (revisits to small food patches never occurred), I am therefore confident that novel patches are indeed so, in the sense that the focal individual decided to forage in a patch that had not previously been visited before.

d) Food type

I distinguished five different food types: (i) ripe fruit, (ii) unripe fruit, (iii) young leaves, (iv) flowers and (v) seeds. These five food types were the most common food times on which chimpanzees in both communities foraged. Other food types, which were eaten only occasionally, such as bark, raisins or soil, were excluded from this analysis due to small sample sizes. Since I tested whether chimpanzees prefer patches of ripe fruit over those of other food types, I selected ripe fruit as the base category against which each of the other food types were compared to.

e) Feeding bout length

For patches which were visited only once, feeding bout length, refers to the total amount of time which the focal animal spent feeding in a patch, from entering the patch until leaving it (cf. Potts et al., 2011). In cases where patches were visited several times, the sum of bout lengths across all visits was included in the model, on the assumption that an increase in bout length due to re-visits would represent stronger desirability for this patch. After several visits, however, a longer bout length might equally describe a more depleted patch, thus past a certain value the relationship between bout length and desirability should reverse, i.e. higher values of bout length will indicate low desirability. I therefore included a quadratic term of bout length into the model as well (Marshall et al., 2012; Suarez, 2014).

In addition to variables which represent costs and benefits of a patch, I incorporated a further variable which described the number of food patches that the focal has already visited during each focal follow (food patch 2, food patch 3 etc.). This variable (*daycount*) was included to test whether foraging strategies of chimpanzees changed throughout the day. Rather than representing a characteristic of the feeding patch, this variable represents the state of the foraging animal: e.g. levels of hunger or energy.

Data analysis

The mixed logit model required the data set to be in the long-form, that is: each row represented one option tree and contained information as to whether the tree had been chosen (0/1), and values for each of the variables outlined above. Every decision had an ID (1-422) to chronologically group foraging events into distinct choice sets. Within each set, each option tree had a unique patch number (tree ID) to control for individual patch effects and investigate potential re-visits to the same patch. It was, however, not possible to include tree species into the model due to the large sample size of total tree species or the small sample size within each tree species. Further, focal ID was included into each choice set to take into account that each individual contributed unequal numbers of foraging decisions to the data set. *Travel distance*, *DBH*, *feeding bout length* and *daycount* entered the model as continuous variables, while the variables *food type* and *visits* were dummy-coded.

Initially, the variable *visits* was dummy-coded to distinguish between patches that had never been visited (0) and those that had been visited once (1), twice (2), three times (3) or more than three times (4). However, since results from both communities were similar and showed that the largest difference occurred between no visits and one visit, I ultimately only differentiated between novel food patches and patches that had been visited before (binary: 0/1).

During travel to food patches or while resting, chimpanzees occasionally fed on young leaves of saplings or smaller trees (personal observations). For this type of foraging, chimpanzees fed on young leaves from a large number of species, thus did not appear to be very selective. To take such opportunistic foraging on nearby sources of young leaves into account, I created a hypothetical option tree providing young leaves within each choice set. Values for DBH, travel distance and feeding bout length for this option were stable across choice sets and based on average values from foraging events in small (DBH of up to 20cm) young leaf patches in each community. The average values for DBH (Sonso: 11cm; Waibira: 13cm) and feeding bout length (Sonso: 12 min; Waibira: 10 min) were similar across communities, while travel distance (Sonso: 342m; Waibira: 99m) was significantly higher for the Sonso community (Wilcoxon rank sum test: $W= 540.5$, $p< 0.001$; $n=24$). Final models were then run without (Model 1) and with (Model 2) young leaf option trees to investigate how providing such a hypothetical option would influence foraging decisions. I further ran Model 1 and 2 for each community separately (Model 1 *Sonso*; Model 2 *Sonso*; Model 1 *Waibira*; Model 2 *Waibira*) in order to compare the predictive power of foraging variables between communities; as well as for males and females only (Model 1 *male*; Model 2 *male*, Model 1 *female*; Model 2 *female*), so as to compare male and female foraging choices. All discrete-choice models were run in Stata 15.

Prior to running discrete-choice models, I carried out a quantitative comparison of all foraging variables across the two study communities, using non-parametric tests (Wilcoxon rank sum test) for all continuous data (*Travel distance*, *DBH*, *feeding bout length*). These analyses were conducted in R 3.4.3 (R Development Core Team, 2017).

Results

Foraging variables

a) Travel distance

Travel distance to all option trees in this study varied from 10-3800m, with a mean of 654.12m ± 556.70m (Sonso: 840.51m ± 597.43m; Waibira: 494.14m ± 462.91m). The distance to food patches which were chosen by chimpanzees varied between 10-1800m, with a mean of 304.17m ± 304.46m. Sonso chimpanzees on average travelled further distances to food patches than chimpanzees of the Waibira community (Sonso: 369.05m ± 323.41m; Waibira: 241.92m ± 271.64m; Wilcoxon rank sum test: W = 28522, $p < 0.001$).

b) DBH

Patch size of all option trees varied from 10-4200cm, with a mean of 106.08cm ± 325.40cm (Sonso: 161.63cm ± 471.26cm; Waibira: 58.40cm ± 35.88cm). The DBH of food patches which were chosen by chimpanzees varied between 10-4200cm as well, with a mean of 304.17cm ± 304.46cm (Sonso: 327.53cm ± 793.74cm; Waibira: 59.69cm ± 36.66cm). Excluding the large BPY patches of the Sonso community lead to an overall average DBH of 64.25cm ± 37.70cm for selected feeding patches, and a mean of 69.68cm ± 38.29cm for selected feeding patches within the Sonso sample. The average DBH of chosen trees was larger within the Sonso community, also when BPY patches were excluded (Wilcoxon rank sum test: W = 22552, $p = 0.003$).

c) Food type

Across all option trees, patches of ripe fruit accounted for the largest share (51.3%), followed by young leaves (19.9%) and seeds (15.1%). Within the Sonso community patches of ripe fruit (40%) and young leaves (19%) were chosen most frequently. Chimpanzees of the Waibira community showed a clear preference for ripe fruit (54.7%) and often selected patches of young leaves as well (29%, Table 3.0).

Table 3.0 Proportion (%) of different food types across all option trees (n= 4095) and chosen feeding trees (n= 419)

	all option trees	Sonso	Waibira
ripe fruit	51.3	41.3	59.9
unripe fruit	9.0	14.3	4.3
flower	4.4	7.8	1.6
seeds	15.1	20.9	10.1
young leaves	19.9	15.1	24.1
other	0.3	0.6	0.0

	chosen trees	Sonso	Waibira
ripe fruit	47.5	40.0	54.7
unripe fruit	9.1	12.2	6.1
flower	6.0	10.2	1.9
seeds	12.9	17.6	8.4
young leaves	24.1	19.0	29.0
other	0.5	1.0	0.0

d) Visits

Most feeding patches were visited only once (Sonso: 76% Waibira: 89%). Two visits to the same patch accounted for 11% of the chosen patches within the Sonso community and for 7% within the Waibira community. Patches that were visited more than twice accounted for 13% (Sonso, range: 3-14) and 4% (Waibira, range: 3-6), respectively.

e) Feeding bout length

Feeding bout length within all food patches ranged from 1-875min, with a mean of 36.59min ± 54.17min (Sonso: 44.7min ± 59.65min; Waibira: 29.63min ± 47.91min). Chimpanzees foraged on average for 46.18min ± 92.12min in food patches which were selected. Sonso chimpanzees fed in food patches for longer durations than chimpanzees of the Waibira community (Sonso: 54.69min ± 79.10min; Waibira: 38.02min ± 102.60min; Wilcoxon rank sum test: W = 26020, $p < 0.001$).

Discrete-choice foraging models

In Model 1 (without a hypothetical young leaf option), several foraging variables were highly significant in predicting foraging choices across both communities: distance to food patches, feeding bout length and the number of visits were strongly related to the probability of selecting certain food patches.

Hypothesis 1 was clearly supported: as distance to food patches increased, patches were less likely to be chosen by foragers ($z = 9.12$, $p < 0.001$, Table 3.1). This effect was even stronger within the Waibira community and, as separate models for males and females showed, Waibira males selected closer trees than did Sonso males (com:distance: $z = -2.43$, $p = 0.015$, Table 3.2), whereas across communities females did not differ in this respect (Table 3.3).

Hypothesis 2 was not supported: the probability of choosing a patch did not increase with patch size ($z = 0.54$, $p = 0.586$) in the overall model which included data from males and females of both communities. Waibira males, however, chose patches in a different manner from Sonso males, with respect to DBH (com:DBH: $z = 1.99$, $p = 0.047$, Table 3.2). Model 1 Waibira revealed that DBH was a significant predictor of patch selection for males in this community ($z = 2.04$, $p = 0.042$, Table 3.5).

Hypothesis 3 was supported: chimpanzees of both communities showed a distinct preference for novel food patches over patches that had been visited before. The size of this effect differed between communities (com:visits: $z = -2.38$, $p = 0.017$, Table 3.1) since females of the Waibira community selected novel food patches more often over alternative choices than did Sonso females.

Preferences across food types (Hypothesis 4) did not follow predictions: while patches of ripe fruit were preferred over those of seeds ($z = -2.76$, $p < 0.006$) and unripe fruit ($z = -2.40$, $p = 0.016$) they were not preferred over patches of flowers ($z = -0.64$, $p =0.525$) or of young leaves ($z = -0.70$, $p = 0.487$). While the sample size for flowers was rather small

(Sonso: n = 21, Waibira: n = 4), sample size for young leaves was sufficiently large to conclude that results for young leaves are statistically meaningful. While the overall model suggested that the effect of unripe fruit on patch choice might differ between communities, single-community models revealed that this difference was driven by a preference for unripe over ripe fruit by Waibira females (z = 2.26, p = 0.024, Table 3.5), which is probably an artefact of the small sample size for patches of unripe fruit chosen by females in that community (n = 6).

Hypothesis 5 received support: as feeding bout length increased, the probability of selecting a patch increased as well (z = 3.74, p< 0.001). Feeding bout length affected patch selection in the same manner across both communities and in both sexes. The quadratic term of bout length was not significant, although there was a negative trend (z = -1.82, p = 0.069, Table 3.1), i.e. an increase in the quadratic term of feeding bout length lead to a lower probability of patch selection. This suggests that very long bout lengths might reflect food patches that have almost been depleted and which are therefore less preferred by foragers. Finally, the variable *daycount* showed no predictive power for patch selection at all, suggesting that foraging strategies of chimpanzees were stable across the course of the day.

Table 3.1 Results of discrete-choice Model 1 (without a hypothetical young leave option), comparing the influence of foraging variables across communities. Results for each community include male and female data.

Model 1: Sonso vs Waibira

	β	z score	p value
Distance	**-0.0036**	**-9.12**	**<0.001**
Com:distance	**-0.0026**	**-3.30**	**0.001**
DBH	0.0001	0.54	0.586
Com:DBH	0.0075	1.79	0.073
Food type – flowers	-0.2996	-0.64	0.525
com:flowers	-0.1410	-0.16	0.877
Food type –seeds	**-0.9268**	**-2.76**	**0.006**
com:seeds	-0.2023	-0.35	0.728
Food type – unripe fruit	**-0.7870**	**-2.40**	**0.016**
com:unripe fruit	**1.4962**	**2.52**	**0.012**
Food type – young leaves	-0.2231	-0.70	0.487
com:young leaves	0.1395	0.32	0.749
Visits	**-3.5761**	**-11.73**	**<0.001**
com:visits	**-1.2946**	**-2.38**	**0.017**
Fbl	**0.0174**	**3.74**	**<0.001**
Com:Fbl	-0.0025	-0.39	0.698
Fbl squared	0.0000	-1.82	0.069
com:Fbl squared	0.0000	0.99	0.323
daycount	13.8192	0.01	0.993

Fbl - feeding bout length, *Fbl squared* - quadratic term of feeding bout length, *daycount* - number of food patches that the focal had already visited during each follow

Note: The Sonso community was selected as a baseline to which data from the Waibira community was compared. Solitary entries (e.g. distance) refer to results from the Sonso community, followed by entries for the Waibira community, labelled by com (e.g. com:distance), which represent differences from the Sonso community. For example: the coefficient for the variable distance within the Sonso community is -0.0036; the coefficient for com:distance is -0.0026, which represents the difference from the Sonso community coefficient, in this case a lower value (-0.0036 – 0.0026 = -0.0011).

Table 3.2 Results of discrete-choice Model 1 *male*, comparing the influence of foraging variables across males of both communities

Model 1: data from males only

	β	z score	p value
Distance	**-0.0038**	**-6.56**	**<0.001**
Com:distance	**-0.0026**	**-2.43**	**0.015**
DBH	0.0003	0.99	0.324
Com:DBH	**0.0118**	**1.99**	**0.047**
Food type – flowers	-1.3519	-1.58	0.114
com:flowers	-0.5360	-0.33	0.740
Food type –seeds	-0.6495	-1.52	0.127
com:seeds	-0.5214	-0.66	0.507
Food type – unripe fruit	-0.7273	-1.49	0.137
com:unripe fruit	0.6881	0.85	0.395
Food type – young leaves	-0.0523	-0.10	0.922
com:young leaves	0.1601	0.24	0.808
Visits	**-3.9803**	**-7.50**	**<0.001**
com:visits	-0.4596	-0.60	0.546
Fbl	**0.0198**	**2.95**	**0.003**
Com:Fbl	-0.0059	-0.40	0.688
Fbl squared	0.0000	-1.29	0.198
com:Fbl squared	0.0000	0.06	0.953

Fbl - feeding bout length, *Fbl squared* - quadratic term of feeding bout length

Table 3.3 Results of discrete-choice Model 1 *female*, comparing the influence of foraging variables across females of both communities

Model 1: data from females only

	β	z score	p value
Distance	**-0.0037**	**-6.15**	**<0.001**
Com:distance	-0.0024	-1.92	0.055
DBH	0.0001	0.34	0.732
Com:DBH	0.0007	0.10	0.918
Food type – flowers	0.1499	0.25	0.800
com:flowers	0.2622	0.22	0.830
Food type –seeds	**-1.3853**	**-2.39**	**0.017**
com:seeds	0.1534	0.17	0.866
Food type – unripe fruit	-0.7902	-1.74	0.082
com:unripe fruit	**2.7747**	**2.80**	**0.005**
Food type – young leaves	-0.3132	-0.72	0.474
com:young leaves	0.1459	0.22	0.827
Visits	**-3.5391**	**-8.75**	**<0.001**
com:visits	**-2.1548**	**-2.34**	**0.019**
Fbl	**0.0206**	**2.65**	**0.008**
Com:Fbl	-0.0015	-0.14	0.887
Fbl squared	0.0000	-1.73	0.083
com:Fbl squared	0.0000	1.13	0.258

Fbl - feeding bout length, *Fbl squared* - quadratic term of feeding bout length

Table 3.4 Results of discrete-choice Model 1 *Sonso*, for males and females of the Sonso community

Model 1: Sonso community	β	z score	p value
Males			
Travel distance	**-0.0038**	**-6.55**	**<0.001**
DBH	0.0003	0.98	0.326
Food type – flowers	-1.3506	-1.57	0.115
Food type – seeds	-0.6494	-1.52	0.127
Food type – unripe fruit	-0.7274	-1.49	0.137
Food type – young leaves	-0.0524	-0.10	0.922
Visits	**-3.9804**	**-7.49**	**<0.001**
Fbl	**0.0198**	**2.95**	**0.003**
Fbl squared	0.0000	-1.29	0.198
Females			
Travel distance	**-0.0037**	**-6.15**	**<0.001**
DBH	0.0001	0.34	0.732
Food type – flowers	0.1498	0.25	0.800
Food type – seeds	**-1.3854**	**-2.39**	**0.017**
Food type – unripe fruit	-0.7902	-1.74	0.082
Food type – young leaves	-0.3131	-0.72	0.474
Visits	**-3.5391**	**-8.75**	**<0.001**
Fbl	**0.0206**	**2.65**	**0.008**
Fbl squared	0.0000	-1.73	0.083

Fbl - feeding bout length, *Fbl squared* - quadratic term of feeding bout length

Table 3.5 Results of discrete-choice Model 1 *Waibira*, for males and females of the Waibira community

Model 1: Waibira community

	β	z score	p value
Males			
Travel distance	**-0.00634**	**-7.19**	**<0.001**
DBH	**0.01207**	**2.04**	**0.042**
Food type – flowers	-1.88863	-1.38	0.168
Food type – seeds	-1.17174	-1.77	0.077
Food type – unripe fruit	-0.04117	-0.06	0.949
Food type – young leaves	0.10628	0.27	0.784
Visits	**-4.44140**	**-8.11**	**<0.001**
Fbl	0.01405	0.99	0.321
Fbl squared	-0.00002	-0.20	0.840
Females			
Travel distance	**-0.00608**	**-5.52**	**<0.001**
DBH	0.00081	0.12	0.907
Food type – flowers	0.41206	0.39	0.699
Food type – seeds	-1.23198	-1.75	0.080
Food type – unripe fruit	**1.98457**	**2.26**	**0.024**
Food type – young leaves	-0.16732	-0.33	0.741
Visits	-5.69383	-6.87	**<0.001**
Fbl	**0.01903**	**2.50**	**0.012**
Fbl squared	-0.00001	-1.52	0.129

Fbl - feeding bout length, *Fbl squared* - quadratic term of feeding bout length

In Model 2, which included a young leaf option tree within each choice set, *Distance*, *feeding bout length* and *visits* predicted the choice of food patches in a similar way as Model 1 (Table 3.6). Yet, Model 2 differed to some degree in the explanatory value assigned to the variables *distance*, *DBH* and the food type ‘young leaves’.

While distance was a significant predictor of selecting food patches, the magnitude of its effect did not differ across communities (com:distance: z = -1.53, p = 0.126, Table 3.6) in contrast to Model 1, nor were there any sex differences. Model 2 suggested a trend for an overall preference of larger patches across both communities and sexes (z = 1.86, p = 0.064): as with Model 1, *DBH* was a significant predictor of patch selection for males from the Waibira community, but Sonso males in Model 2 showed a trend for a preference of larger patches as well (z= 1.73, p = 0.083, Table 3.7). The inclusion of a young leaf option tree also had a strong effect on the likelihood of chimpanzees choosing the food type ‘young leaves’: while in Model 1 the selection of young leaves did not differ significantly from those of ripe fruit, Model 2 reported a significant preference for ripe fruit over young leaves in chimpanzees from both communities and sexes (z = -7.25, p< 0.001, Table 3.6).

Table 3.6 Results of discrete-choice Model 2 (with a hypothetical young leave option), comparing the influence of foraging variables across communities. Results for each community include male and female data.

Model 2: Sonso vs Waibira

	β	z score	p value
Distance	**-0.0030**	**-8.59**	**<0.001**
Com:distance	-0.0009	-1.53	0.126
DBH	0.0003	1.86	0.064
Com:DBH	**0.0161**	**4.40**	**<0.001**
Food type – flowers	-0.5849	-1.28	0.201
com:flowers	0.2744	0.31	0.753
Food type –seeds	**-0.8705**	**-2.75**	**0.006**
com:seeds	0.0356	0.07	0.945
Food type – unripe fruit	**-0.6600**	**-2.11**	**0.035**
com:unripe fruit	0.7104	1.26	0.207
Food type – young leaves	**-2.1118**	**-7.25**	**<0.001**
com:young leaves	0.5653	1.46	0.144
Visits	**-3.1351**	**-11.43**	**<0.001**
com:visits	**-0.9681**	**-2.27**	**0.023**
Fbl	**0.0146**	**3.15**	**0.002**
Com:Fbl	-0.0028	-0.41	0.682
Fbl squared	0.0000	-1.65	0.099
com:Fbl squared	0.0000	0.72	0.473
daycount	0.2613	0.33	0.743

Fbl - feeding bout length, *Fbl squared* - quadratic term of feeding bout length, *daycount* - number of food patches that the focal had already visited during each follow

Table 3.7 Results of discrete-choice Model 2 *male*, comparing the influence of foraging variables across males of both communities

Model 2: data from males only

	β	z score	p value
Distance	**-0.0034**	**-6.43**	**<0.001**
Com:distance	-0.0009	-1.10	0.270
DBH	0.0005	1.73	0.083
Com:DBH	**0.0247**	**4.70**	**<0.001**
Food type – flowers	-1.5096	-1.72	0.085
com:flowers	-0.0608	-0.04	0.969
Food type –seeds	-0.6155	-1.54	0.123
com:seeds	-0.5828	-0.82	0.413
Food type – unripe fruit	-0.7884	-1.66	0.096
com:unripe fruit	0.7335	0.97	0.332
Food type – young leaves	**-2.4167**	**-5.47**	**<0.001**
com:young leaves	**1.2626**	**2.29**	**0.022**
Visits	**-3.3491**	**-7.37**	**<0.001**
com:visits	-0.7430	-1.19	0.233
Fbl	**0.0168**	**2.61**	**0.009**
Com:Fbl	0.0127	0.89	0.376
Fbl squared	0.0000	-1.22	0.224
com:Fbl squared	-0.0001	-1.35	0.179

Fbl - feeding bout length, *Fbl squared* - quadratic term of feeding bout length

Table 3.8 Results of discrete-choice Model 2 *female*, comparing the influence of foraging variables across females of both communities

Model 2: data from females only

	β	z score	p value
Distance	**-0.0027**	**-5.69**	**<0.001**
Com:distance	-0.0011	-1.17	0.243
DBH	0.0004	1.32	0.185
Com:DBH	0.0051	0.81	0.417
Food type – flowers	-0.3158	-0.56	0.573
com:flowers	0.6226	0.50	0.617
Food type –seeds	**-1.3862**	**-2.56**	**0.011**
com:seeds	0.7328	0.93	0.353
Food type – unripe fruit	-0.5087	-1.21	0.227
com:unripe fruit	0.9435	1.13	0.259
Food type – young leaves	**-1.8850**	**-4.60**	**<0.001**
com:young leaves	-0.0882	-0.15	0.883
Visits	**-3.1261**	**-8.59**	**<0.001**
com:visits	-1.2905	-1.91	0.056
Fbl	**0.0177**	**2.46**	**0.014**
Com:Fbl	-0.0095	-0.98	0.326
Fbl squared	0.0000	-1.79	0.073
com:Fbl squared	0.0000	1.50	0.134

Fbl - feeding bout length, *Fbl squared* - quadratic term of feeding bout length

Discussion

Within the complete sets of option trees and also across chosen options, distances to food patches were larger for the Sonso community, as was the average size of feeding patches and average feeding bout length. Chimpanzees of the Sonso community thus travelled longer distances, but foraged in larger patches and for longer durations than did Waibira community chimpanzees. Despite these differences in foraging behaviour, and considerable differences in community size and forest composition, foraging strategies of Sonso and Waibira chimpanzees were remarkably similar. For all foraging variables of sufficient sample size, the discrete choice models reported comparable effects on food patch choice in both communities: Across sexes and communities, chimpanzees exhibited a clear preference for closer as well as novel food patches.

This is the first study to demonstrate directly that chimpanzees consider travel distance to food patches when choosing foraging sites. Travel distance has been identified as a strong predictive variable in patch choice across several small-bodied primates (*Cebus apella*: Janson, 1998; *Ateles belzebuth*: Suarez, 2014, *Alouatta palliata:* Hopkins, 2016). Chimpanzees are large-bodied primates in which travel is expected to be energetically more costly than in smaller foragers (Garland, 1983), thus it is of little surprise that they aim to minimize distance between feeding patches. Females, as well as males, of both communities incorporated estimates of inter-patch distance into foraging decisions, which suggests that energetic constraints of travel are indeed an important cost in chimpanzees.

The preference for novel food patches, which contrasts with results of a similar study in Howler monkeys (Hopkins, 2016), is likely to be linked to chimpanzees' fission-fusion social organization. Howler monkeys (*Alouatta palliata*) were more likely to revisit previous fruit patches after a certain interval that allowed sufficient unripe fruit to ripen instead of exploring novel food patches. In chimpanzees, returning to former foraging sites was avoided, presumably because such patches could have been depleted by other foraging chimpanzees in the meantime. Results of this study therefore highlight that scheduling revisits to food patches is not a particularly profitable option in animals that are characterized by fission-fusion dynamics. I could not confirm results presented by Bates and Bryne (2009) who found that females of the Sonso community were more likely to revisit previous feeding patches than males. This discrepancy can probably be ascribed to differences in methodology: while in Bates and Bryne's (2009) study, focal animals were followed for up to three days, focals were chosen on a daily basis during this study. Thus, revisits on an individual level will have been more apparent during the former study. Such considerations illustrate the trade-offs of different study designs and the need for focal follows over consecutive days in order to investigate certain aspects, such as revisit rates, in foraging strategies. While Bates and Bryne's (2009) study focused on sex differences in movement patterns, this study investigated foraging decisions across two different communities. For such a purpose it was essential to sample a larger number of male and female chimpanzees from each community, in order to go beyond individual foraging preferences of only few chimpanzees.

The chimpanzee-based measure of patch value, *feeding bout length*, consistently predicted patch selection, despite a variety of factors that might affect patch residence/departure time (Marshall et al., 2013). Indicators of patch desirability that are based on the behaviour of foragers themselves were highly diagnostic in monkey foraging models (*Cebus capucinus*: Vogel and Janson, 2007; *Ateles belzebuth*: Suarez, 2014) and, as results of this study indicate as well, offer a promising alternative to researcher-based measures, such as DBH. The quadratic term of bout length further appeared to be a reliable measure of patch depletion in chimpanzees, as patches of very long bout lengths were less likely to be selected. Similar to foraging monkeys, chimpanzees thus not only remember the location of previous feeding trees (Garber, 1988, 1989; Janmaat et al., 2006; Janson, 1998; Normand et al., 2009), but seem to also integrate information about the value of previous food patches when deciding where to forage.

The size of food patches did not predict foraging decisions as expected, despite the body of research that highlights the importance of patch size (White and Wrangham, 1988; Janson, 1988; Chapman, 1990; Chapman et al., 1995; Chapman and Chapman, 2000; Newton-Fisher et al., 2000; Snaith and Chapman, 2005; but see: Fashing, 2001; Pengfei et al., 2015). This discrepancy may in part result from the fact that the size of foraging parties could not be included into the discrete choice models applied here. Due to chimpanzees' fission-fusion nature most option trees were at great distances from chosen food patches and therefore a simultaneous assessment of party size at all option trees was not feasible. Marshall et al. (2012), studying foraging behaviour in cohesive baboon groups, were able to include the number of potential co-feeders across option patches into a discrete-choice model and showed that the number of patch occupants considerably affected patch choice. The size of foraging groups is linked to patch size in a range of foraging animals (Janson, 1988; Chapman, 1990; Chapman et al., 1995; Chapman and Chapman, 2000; Snaith and Chapman, 2005), also in chimpanzees (Ghiglieri, 1984; White and Wrangham, 1988; Isabirye-Basuta, 1993; Newton-Fisher et al., 2000). And, as results from Chapter 3 show, feeding party size is significantly and positively associated with DBH in both chimpanzee communities at Budongo as well. It is therefore to be expected that decisions of individual chimpanzees regarding patch size will be influenced by current party size and the number of co-feeders that chimpanzees expect within alternative food patches. Correcting for party size during foraging decisions might thus result in an effect of DBH which is more in line with previous studies. Yet, other variables, such as travel distance and feeding bout length, were predictive of foraging decisions despite the lack of a party size variable. This suggests that DBH was indeed not as influential in chimpanzee foraging strategies as expected.

In one group, however, DBH was a significant predictor of patch selection: Waibira males. According to theory, females are expected to be more concerned with the maximization of energetic and nutritional intake than males (Schoener, 1971; Trivers, 1972; Wrangham and Smuts, 1980; Sterck et al., 1997). This distinction supposedly applies to chimpanzees as well, as with all mammals females invest more parental efforts through gestation, lactation and infant care than males (Pokempner, 2009; Wrangham, 2000). That Waibira males based foraging decisions more strongly on patch size than females of both communities and Sonso males suggests that large food trees provided important opportunities to males in the Waibira community. One possible explanation is that males in this larger community had to search actively for opportunities to associate with large numbers of other adult males. Chimpanzee males benefit from associations with other males in a number of ways: by establishing social bonds with specific individuals through coalitions, meat sharing, grooming and joint border patrols, males can increase social status and mating opportunities (Duffy et al., 2007; Kaburu and Newton-Fisher, 2015; Newton-Fisher, 1999b, 1997; Nishihara and Hosaka, 1996; Watts and Mitani, 2002). Rather than simply searching for potential mates, male ranging might thus reflect this need for male-male interactions (Newton-Fisher, 2014). Results of this study hint at the possibility that chimpanzee males are in fact more invested in searching for food and one another than current theories of male association patterns acknowledge. The majority of studies investigating foraging behaviour focus solely on female strategies, following the rationale that female foraging is more likely to reflect optimality and thus more informative (Hopkins, 2016, 2008; Normand et al., 2009; Normand and Boesch, 2009; Suarez, 2014). Here I decided to instead pursue a comparative approach of male and female foraging behaviour. Results of this study confirm the importance of comparing male and female foraging behaviour in order to rigorously test theories of foraging strategy, as has been stressed previously (Pokempner, 2009).

Despite a distinct preference for ripe fruit, chimpanzees of both communities frequently chose to forage on food patches providing young leaves. As ripe fruit were not available at all times, such choices might not necessarily demonstrate a preference for young leaves but instead simply necessity. Yet, these results support the notion that fibrous food are an important component of the chimpanzee diet (Wrangham et al., 1991; Chapter 2). The importance of non-fruit food items, such as young leaves and THV, in the chimpanzee diet has significant implications for studies that use chimpanzees as a model species to test socio-ecological theories of foraging behaviour. It has so far generally been assumed that chimpanzees, as highly frugivorous foragers, feed on discrete and depletable patches (Chapman et al., 1995; Pokempner, 2009). If, however, chimpanzees regularly forage in patches of young leaves and THV which are more abundant and depleted more slowly or not at all, this assumption cannot be maintained. Chimpanzees certainly are selective when foraging on young leaves (Kuroda et al., 1996; Takemoto, 2003; Carlson et al., 2013), just like some other folivorous primates that exhibit preferences for particular plant parts and plant species (Snaith and Chapman, 2007). Thus, patches of young leaves and THV are depletable to a certain extent as well. Yet, at Budongo, young leaves were highly abundant and virtually undepletable during several months of the study period: chimpanzees of the Sonso community foraged in large groves of *B. papyrifera* in October and November 2015 and foragers in Waibira fed on highly abundant young leaves of *C. mildbraedii* in October and November 2016. Under such circumstances chimpanzee might behave more similar to folivorous foragers and some basic assumptions of, for example the ecological constraints model (Chapman and Chapman, 2000), are not given. Feeding competition might not limit group size as expected for frugivorous foragers: large groups can form at lower costs if food patches are not depleted and travel distances to other patches are short. However, less energy, in the form of soluble sugars, can be obtained from young leaves compared to ripe fruits (McLennan and Ganzhorn, 2017). If chimpanzees respond to fruit scarcity by spending more time resting and feeding more on such low quality food items (“energy-saving strategy”), instead of travelling further to search for high quality food resources (“increased-searching strategy”), then a clear relationship between group size, patch size and travel distances might not be discernable anymore. A prediction that follows from these considerations is that in chimpanzees relationships between foraging variables, as predicted by the EC model, should be more clear during times of high fruit abundance than at times of food scarcity. Future studies that test socio-ecological theories of foraging behaviour in chimpanzees should take into account that this species not only feeds on discrete and depletable patches and that for data analysis a distinction between different food or patch types is needed.

In line with results from the previous chapter, Waibira females exhibited signs of a foraging strategy adapted to higher levels of feeding competition. In addition to travelling shorter distances between food patches and more arboreally than males, they further showed a stronger preference for novel, undepleted patches than Sonso chimpanzees. Sample sizes for individual females were too small for a more detailed analysis, yet during focal follows it was evident that in Waibira several lactating females employed a strategy of solitary foraging within smaller areas, possibly their core areas. None of the female focals of Sonso showed such restricted range use during foraging, even when foraging alone. Some females of the Waibira community thus showed foraging and ranging patterns of high site fidelity which have been described for other East African chimpanzee communities (Gombe: Wrangham and Smuts, 1980; Williams et al., 2002; Kanyawara, Kibale National Park: Wrangham et al., 1992; Mahale Mountains National Park: Hasegawa, 1990) and are interpreted as indicators of high costs of grouping. Sonso females, in contrast, were less concerned with feeding competition, employing foraging strategies more similar to West African female chimpanzees, where habitats are more productive and less seasonal (Boesch, 1996; Lehmann and Boesch, 2005).

Demographic effects might account for some of the observed differences in foraging strategies as well. Associations between males and females tend to increase, creating a more cohesive community structure, when communities decrease in size (Lehmann and Boesch, 2004). Peripheral females of the smaller Sonso community are indeed more gregarious than in other East African populations (Emery-Thompson and Wrangham, 2006). Differences in overall community size, as well as home range size, across the two study communities could thus affect male and female association and foraging strategies in a similar manner, resulting in more cohesive foraging groups in Sonso. Ultimately, however, levels of food availability and distribution need to be sufficiently favourable in order to allow formation of cohesive groups, no matter what the demographic structure of a community may be like.

Chimpanzees of the Waibira community showed a stronger preference for food patches close by than those of the Sonso community. I can not exclude the possibility that this result reflects the fact that focal follows within the Sonso community were longer and more continuous than in Waibira. Yet, it seemed to me that foraging within the Waibira community took place more often in a certain area of the home range, whereas the Sonso community, which occupies a smaller overall home range (Jakob Villioth, unpublished data), ranged more widely for foraging, travelling more frequently across the entire home range. Therefore, option trees of the Waibira community appeared more clumped, also across several days, than those of the Sonso community. Levels of forest fragmentation might contribute to these differences in spatial foraging strategies. The forest compartment which corresponds to the home range of the Waibira community has been logged more intensely and more recently (Plumptre, 1996) and, as a result, forest cover seems to have recovered further within the home range of the Sonso community; botanical plots in Sonso contained more trees above a DBH of 20cm, thus tree size appears to be more homogeneous in this area (see Chapter 2). Within the Waibira home range, some areas of unlogged primary forest still exist in more hilly parts, while other plots contained only few mature trees. The forest of the Waibira home range hence is still more fragmented today.

The foraging strategy of the Waibira community resembled the one described by Hopkins (2008) in her study of mantled howler monkeys (*Alouatta palliata*). This study demonstrated that the selection of foraging sites was strongly influenced by the presence of further resources in the surrounding area. Foraging animals seemed to not select specific feeding trees but rather chose productive foraging areas within their home range which allowed efficient food acquisition throughout the day. Within the large home range of the Waibira community chimpanzees appear to follow a similar foraging strategy: a large part of the community (often most adult males) were usually found within a certain area of the home range for several consecutive days, especially when food availability was low. After some days in that area chimpanzees then moved to a different part of the home range and exploited resources there. The possibility of exploiting food calls from nearby foraging parties (Chapman and Lefebvre, 1990; Clark and Wrangham, 1994), coupled with the flexibility of the fission-fusion social organization seems to make this an effective foraging strategy which minimizes travel costs and thus optimizes foraging pay-offs across a large area of rather fragmented forest. Whether there is indeed a consistent difference in spatial foraging strategies across communities will require a more detailed comparative study of home range utilization.

The discrete choice model

Discrete choice models utilized here proved to be a valuable tool to gain a better understanding of foraging decisions in chimpanzee communities of different demographic structure and habitat. One key advantage of discrete choice models, when compared to other statistical approaches, is that they specifically investigate individual foraging decisions and that available options change from one decision to the next one. This adds an important element of realism to the model (Marshall et al., 2012). Chimpanzees, like other foragers, do not have complete knowledge of their current environment and available foraging options – but the DC model allows us to gain some insights into how they make decisions in such an environment, for example how chimpanzees use certain ecological criteria to select feeding trees. In accordance with predictions of foraging theory and results from previous studies of foraging behaviour in non-human primates, the models were successful in identifying the effects of several ecological variables on patch choice decisions. Further, this study demonstrates that choices from a large number of animals which forage independently of each other can be analysed in a meaningful manner through the application of mixed-logit models. Mixed-logit models allow a highly flexible data analysis, which is of immense use for any study that samples many individuals possessing possibly different preferences.

There are, however, some limitations to discrete-choice models that need to be acknowledged. Such an approach requires a biologically reasonable definition of “option trees”, thus what resources are available to the forager at a given moment in time. As there is no standardized method for measuring such resource availability, this definition might vary in between different studies. Consequently, the use of a discrete-choice model requires careful and detailed considerations prior to data collection. Selection of focal individuals, duration of follows and data collection on ecological (and possibly social) parameters for all available foraging options have to be well aligned to the foraging animals that are being studied in order for the discrete-choice model to make any sense.

While a discrete-choice model allows to gain insights into the selection feeding trees based on certain criteria, such a model is not able to distinguish between a deliberate choice of a food patch nearby and opportunistic foraging events on small and close food patches on the way to larger patches. Other approaches, such as the change point test (Byrne et al., 2009; Janmaat et al., 2013) or tests of linearity (Noser & Byrne, 2007) are better suited to investigate the ultimate destination of travelling foragers, but even these have difficulties to clearly identify opportunistic foraging. Apparently opportunistic foraging might seem so to an observer, because the animal is trying to fulfil a current nutritional need, because little other valuable options are available or simply because the animal is waiting for other group members to move on.

In order to explore the possible influence of abundant, small and often herbaceous food resources on foraging decisions, I ran Model 2 that included hypothetical young leaf option trees close by. A comparison to Model 1, without such young leaf option trees, provides a useful example of the workings of a discrete-choice model: since the young leaf option included within each choice set was only a hypothetical one, and thus never actually selected by chimpanzees, the properties of this option affected the predictive power of other variables. For example, a young leaf option that is present in the choice set but never chosen, naturally reduces any preferences that the model assigns to this food type in comparison to the baseline of ripe fruit. Also, since the average DBH value utilized for young leaf option trees was very low in both communities (Sonso: 11cm; Waibira: 13cm), the fact that this option was never chose was interpreted as a stronger preference for large food patches by the model. The same reasoning applies to the variable distance: as the average value of distance for young leave option trees was very low (Sonso: 340m, Waibira: 99m), inclusion of this option resulted in an apparently stronger preference for closer patches within the Sonso community as well, negating the difference across communities attested by Model 1. When the average value of distance for young leave option trees within the Sonso community was adjusted to that of the Waibira community (both 99m), the model reported again a significant difference across communities. Changing estimates for certain variables, such as patch distance to the option tree, thus had a strong influence on model results; apparent differences across communities could be attributed solely to these changes made to hypothetical option trees. The disparities between Model 1 and 2 demonstrate that a model without further hypothetical options is more useful in detecting true differences in foraging strategies across communities.

This study is the first to explicitly study foraging decisions in wild chimpanzees with the help of discrete choice models. It integrated several important ecological variables into a coherent model of foraging choices and showed that distance to patches, feeding bout length and patch novelty were crucial factors to chimpanzees of both sexes across communities in deciding where to forage.

Chapter 5

Conclusion

Chimpanzee feeding ecology

A major objective of this thesis was to further our understanding of chimpanzee feeding ecology with regard to ecological as well as social parameters. The results reported here include two significant findings that have broader implications for our general notion of chimpanzee feeding ecology: the first is concerned with chimpanzee diet and the associated specialisation; the second relates to predicted sex differences in foraging effort.

With regard to diet, chimpanzees are typically described as ripe fruit specialists (Ghiglieri, 1984; Watts et al., 2012; Wrangham et al., 1998) and this study confirmed that chimpanzees prefer to forage on ripe fruit, if these are available. Compared to many cercopithecine species, which show a generalist foraging strategy and maintain a higher percentage of non-fruit plants in their diet regardless of fruit abundance (*Cercopithecus ascanius:* Cords, 1986; Blue monkeys, *Cercopithecus mitis*: Kaplin et al., 1998; *Lophocebus albigena:* Wrangham et al., 1998; *Papio anubis*: Okecha and Newton-Fisher, 2006), chimpanzees seem, therefore, to be more specialized in their dietary profile.

Insights into the feeding flexibility and dietary options of primates can be gained from examining digestive retention times (Milton, 1993), as many plant parts containing fibre require substantial fermentation before they can be used as an energy source: long retention times usually indicate higher levels of fermentation (Lambert, 1998). Consequently, many primate species with long retention times are characterized by a generalist diet which can include a large proportion of high-fibre foods. Retention times of cercopithecine species, compared to those of chimpanzees, are slower, supporting the view that chimpanzees are specialized on a more frugivorous diet (Lambert, 2002).

However, in terms of habitat occupation and distribution, chimpanzees can clearly be considered ecological generalists (Russak and McGrew, 2008). They have the broadest geographical distribution of the great apes (Caldecott and Miles, 2005), inhabiting a large range of different habitats, from evergreen lowland rainforest (Taï National Park, Boesch and Boesch-Achermann, 2000) to mosaic savanna habitats (Bogart and Pruetz, 2008). Compared to, for example, gorillas (*G. gorilla*), which are closed-canopy specialists (Hvilsom et al., 2014; Fünfstück and Vigilant, 2015), chimpanzees can be found over a geographical range that is typical of a generalist species. While many studies have stressed chimpanzees' reliance on readily digestible sugars (Wrangham et al., 1998; Lambert, 2002; Remis, 2002; McLennan and Ganzhorn, 2017), their remarkable ability to adapt to a wide variety of habitats has been rather under-appreciated (Russak and McGrew, 2008). Generalist species are not only defined by dietary breadth, but also by their ability to adapt to a large variety of environmental conditions (MacArthur, 1972; Pianka, 1988). As chimpanzees demonstrably possess this ability, it seems appropriate to consider them as a generalist species.

Despite a more narrow, specialized diet than that of some other primates, this study demonstrates that some features of a generalist diet can be found in chimpanzees as well. While ripe fruit made up a large proportion of Budongo forest chimpanzees' diet when available, other food types were crucial components of their diet as well. The most common food item in the diet of the Waibira community were young leaves of *C. mildbraedii,* while the Sonso community relied heavily upon young leaves and flowers of *B. papyrifera* during periods of fruit scarcity. Chimpanzees of both communities were able to sustain themselves solely on such a folivorous, high-fibre diet for limited periods of time. This suggests that, despite a preference for ripe fruit and certain physiological adaptations to a frugivorous diet (Lambert, 2002), the chimpanzees of Budongo were able to shift their diets considerably, similar to species that are characterized by a generalist feeding strategy. Chimpanzees of the

Waibira community responded to lower levels of food availability by adopting an “energy-saving strategy”, similar to the Kanyawara community in Kibale National Park (Potts et al., 2011), while Sonso community chimpanzees reacted to temporal periods of fruit scarcity by either foraging increasingly on field crops or by resting more and foraging on low-energy foods. At Bossou, chimpanzees adjust activity budgets to fruit availability and microclimate in the forest, such as rainfall, temperature and humidity, showing an increase in resting behaviour and arboreality during cool periods to reduce thermoregulation costs (Takemoto, 2004). Such an “energy-saving strategy” is also adopted by more generalist species during periodic shortages of high energy foods, for example by western black-and-white colobus (*Colobus polykomos:* Dasilva, 1992).

Monthly dietary diversity values of the two study communities were lower than for forest cercopithecines (e.g. Grey-cheeked mangabeys: *Lophocebus albigena*, Ham, 1994; Poulsen et al., 2001) or other large-bodied frugivorous (e.g. Sakis: *Chiropotes sagulatus*, Shaffer, 2013). Yet, young leaves were consumed year-round by chimpanzees of both communities, not only as fallback foods but also at times when fruit was abundant and other food types, such as unripe fruit, flowers, bark, soil and animal prey were eaten regularly. In many chimpanzee populations, fibrous foods offer an additional source of carbohydrate energy (Wrangham et al., 1991; Fawcett, 2000) and, since fruits contain little protein (Matsumoto-Oda and Hayashi, 1999; McLennan and Ganzhorn, 2017), chimpanzees require high-quality leaves to cover protein demands (Carlson et al., 2013; Takemoto, 2003). Nutritional requirements of chimpanzees thus include fibrous foods as well, and the importance of this food type, as demonstrated here, shows that dietary breadth goes beyond that of a true specialist.

A high degree of fission-fusion dynamics allows chimpanzees to efficiently exploit habitats with a patchy distribution of high-quality food resources (Lehmann and Boesch, 2004). As demonstrated here, a general foraging strategy that minimizes travel and grouping costs, as predicted by the ecological constraints model, enables chimpanzees to cope with habitat variability across different forest environments. Chimpanzees of both study communities adjusted foraging party size and travel distances in a manner to patch characteristics that effectively minimized feeding competition, even though forest composition and the size and distribution of food patches varied substantially between communities. Chimpanzees thus flexibly employed a general strategy to maximize foraging success across these different habitats.

Across distinctly different habitat types, chimpanzees can exploit a variety of different food resources. Some communities in evergreen lowland rainforest of West Africa, such as the ones in Taï National Park, supplement their diet by nut-cracking during the dry season (Boesch and Boesch-Achermann, 2000). In the mosaic savanna habitat in south-eastern Senegal, the Fongoli community feeds on termites continuously throughout the year (Bogart and Pruetz, 2008). And at Bossou, in West-Africa, chimpanzees feed on oil-palm kernel and oil-palm pith (Yamakoshi, 1998) or succulent fruits, such as oranges, in farmlands when there is little ripe fruit available in the forest (Hockings et al., 2009; Bryson-Morrison, 2017). More recent studies, such as Potts et al. (2011, 2015, 2016) and the current study, have demonstrated that even on a small spatial scale, chimpanzees can adjust their foraging strategies to more subtle differences in habitat productivity and resource distribution. Taken together, a high degree of fission-fusion dynamics, coupled with the ability to adjust activity patters and dietary composition and diversity, make chimpanzees foragers that, even if not as versatile as baboons, nevertheless deserve to be called true ecological generalists.

Female chimpanzees are expected to be more concerned with food acquisition and to employ more efficient foraging strategies than males (Schoener, 1971; Trivers, 1972). Contrary to these predictions, male and female chimpanzees of both communities had nearly identical activity budgets and foraged in a very similar manner. Except for four females of the Waibira community, who foraged solitarily on some days of observations, no substantial sex differences in foraging strategies and decisions could be detected. These findings are in line with results of activity budgets from males and females in other chimpanzee communities (Wrangham and Smuts, 1980; Doran, 1997; Potts et al., 2011; Bryson-Morrison, 2017) and also those by Pokempner (2009), the only available study that has investigated the energetics of feeding competition in male and female chimpanzees in a detailed comparative approach. Male and female chimpanzees of the Kanyawara community had similar overall caloric and daily macronutrient intake and foraging effort, as measured by the time spent feeding, was virtually the same. Males in Pokempner's (2009) study even exhibited a higher overall net foraging efficiency than females, as calculated from energy intake and expenditure. Consequently, Pokempner (2009) concluded that, apart from certain phases such as conception when females tend to peak in energy requirements (Thompson, 2005), short-term energetic costs for males and females seem in fact to be similar (Key and Ross, 1999). Results of this study and Pokempner (2009) thus question the general assumption that female chimpanzees need to forage in a fundamentally different way compared to male chimpanzees.

Previous studies of foraging efforts in female chimpanzees have mostly focused on female association patterns (Wrangham, 2000; Williams et al., 2002; Wakefield, 2008; Riedel et al., 2011). Females of most East African populations spend more time on their own and female gregariousness generally decreases during periods of food scarcity (Nishida, 1968; Goodall, 1986; Hasegawa, 1990; Wrangham et al., 1992; Pepper et al., 1999; Mitani et al., 2002; Lehmann and Boesch, 2008). This has been viewed as evidence that females are more likely to suffer from resource competition than males (Wrangham and Smuts, 1980; Wrangham, 2000): According to this explanation, the female foraging "strategy" is to avoid costs of increased scramble competition by foraging more often alone. Foraging strategies, however, go beyond mere association patterns; such strategies are also concerned with how animals adjust activity patterns (Dasliva, 1992; Potts et al., 2011), which food resources are chose as fallback foods (Wrangham et al., 1991; Marshall and Wrangham 2007; Pokempner, 2009), and, as investigated during this study, how foragers can maximize foraging success based on patch characteristics and inter-patch travel (Bates and Byrne, 2009; Normand et al., 2009). Further, female association patterns are not only influenced by ecological factors, but also by social ones: mothers with young infants of the Kanyawara community spent less time in groups with many adult males to protect their offspring from aggressive interactions (Otali and Gilchrist, 2006). And males, just like females, focus their foraging efforts onto familiar areas to increase their foraging efficiency when travelling alone (Murray et al., 2008).

While female association patterns are certainly different from those of males in some chimpanzee populations, this study shows that the general way in which male and female chimpanzees make foraging decisions seems to be very similar. If a high degree of fission-fusion dynamics allows chimpanzees to adjust their foraging efforts efficiently to different levels of feeding competition, then males and females will benefit from this possibility in the same way. I therefore suggest that a way forward in understanding male and female foraging behaviour is to select an equal starting point: instead of assuming that females commonly need to employ more efficient foraging strategies, our working hypothesis should be that nutritional requirements of male and female chimpanzees, and the general manner in which food resources are acquired, are similar at most times. Potential research questions that could be investigated with such a starting point include: How do female foraging strategies (association patterns, diet composition, activity patterns) change during periods of increased energy and nutritional demands? At what point does it become beneficial for females to associate more with other community members again, and which factors influence this transition?

Socio-ecological models of foraging

A further goal of this thesis was to test socio-ecological models of chimpanzee feeding behaviour by pursuing novel methodological approaches. Results presented in Chapter 3 demonstrate that using a species characterized by a high degree of fission-fusion dynamics as a model to test theories relating to group size, patch size and travel distance is a very fruitful approach – although only when the level of analysis is adjusted accordingly. Daily averages of travel distance may be appropriate when larger temporal scales are investigated, but in interactions between subgroup size and patch size daily averages will have very little meaning. Studies that have used habitat-wide measures of fruit abundance (Chapman et al., 1995; Stevenson et al., 1998; Ramos-Fernandez, 2001; Shimooka, 2003; Weghorst, 2007) or daily averages of patch and group size (Pokempner, 2009; Busia et al., 2016) in fission-fusion foragers often failed to find predicted correlations between food availability and party size. Presumably, the dynamic response by fission-fusion foragers to short-term changes in food availability, nutritional requirements and social factors is lost when averaging values of important foraging variables over an entire day. The current study shows that an analysis of individual food patches and travel distances by specific foragers is a successful approach for testing the ecological constraints model in chimpanzees: Across both communities, the relationships between party size, patch size, travel distance and feeding bout length corresponded very well to predictions, despite differences in forest composition and overall community size. The EC model, despite certain limitations, thus remains a useful tool to investigate links between the abundance and distribution of food resources, and grouping patterns and levels of feeding competition, in socially foraging animals.

Simple models of a limited number of foraging variables will never be able to explain the full range of variation in primate social organization and foraging behaviour (Janson, 2000). Yet, these simple models provide a starting point from which initial hypotheses can be tested and to which more detailed predictions can be added. For example, more recent frameworks of primate nutritional ecology take a multi-dimensional approach to macronutrient intake (Felton et al., 2009; Raubenheimer et al., 2009) and thanks to recent advances in nutritional analysis techniques (Rothman et al., 2009), elements of nutritional ecology are a new facet that could be added to existing foraging models. Deriving testable predictions from such extended models will be a promising avenue for future research. Exploring within-species variation in feeding ecology is another way of improving existing socio-ecological models (Strier, 2009, 2003, Struhsaker, 2008, 2000) and was also pursued as part of this study. Over the last three decades there has been a large accumulation of data on the diets and foraging behaviour of wild primates, so that it now possible to go beyond a comparative approach that places species or genera in categories based on average behavioural characters. A better understanding of mechanisms that lead to variation within interbreeding populations can help to inform current models and might result in novel predictions for variation between species. To distinguish behaviour patterns that are phylogenetically conservative from those that are simply a response to local conditions, more studies of interbreeding populations that inhabit different ecological conditions are required (Chapman and Rothman, 2009) and the current study is the first to provide a detailed description of the feeding ecology in two neighbouring chimpanzee communities. While differences in habitat types, seasonality in food supply and demography are known to affect within-species variation (Struhsaker, 2008), results presented in Chapter 2 demonstrate that small-scale differences in forest composition and habitat changes caused by humans can be further parameters that drive within-species variation.

Finally, Chapter 4 provides an example of the application of a novel model that goes beyond the traditional assumptions of optimal foraging (Emlen, 1966; MacArthur and Pianka, 1966). The discrete-choice model, which I for the first time applied to chimpanzee feeding ecology, successfully identified the effects of several ecological variables on patch choice decisions. Results of this study also showed that mixed-logit models allow for a highly flexible data analysis, including choices from a large number of animals that may possess different foraging preferences. Discrete-choice models offer a tool to investigate how foragers come to make decisions under varying ecological and social conditions, for example how foraging decisions can differ across habitat types or according to the number and identity of co-foragers (Marshall et al., 2012). While this is a different approach from traditional socio-ecological models, discrete-choice models provide the ability to consider a large number of foraging variables simultaneously. Such models therefore correspond better to the complex environments in which most social animals forage and offer a large array of possible applications. For example, discrete-choice models avoid the common problem of having to quantify (or at least classify) the patchiness of food distribution (Isbell et al., 1998). Rather than assuming that food resources of folivorous animals are uniformly distributed and those of frugivorous ones are located in discrete patches, a discrete-choice model model can instead compare what food type a given species values most, and what other factors influence patch selection in foragers of different species or food type specialisation. Discrete-choice models enable researchers to investigate what particular species (or populations of a species) actually need when foraging and how they fulfil their energetic and nutritional requirements under varying conditions. Understanding these processes better has an enormous potential for developing a more informed view of what shapes their sociality. Discrete-choice models can also be combined with other methodological approaches, such as nutritional ecology to explore in more detail how foragers' nutritional status affects foraging decisions. It is now possible to investigate macronutrient intake of individual chimpanzees in much more detail (Pokempner, 2000; Bryson-Morrison, 2017) and non-invasive markers of individual's metabolic status, such as C-peptide, have successfully been tested in several wild apes (orangutans: Emery Thompson and Knott, 2008; chimpanzees: Emery Thompson et al., 2009; bonobos: Surbeck et al., 2015). Applying discrete-choice models to foraging data, while simultaneously monitoring foragers' energetic status and food intake would, for example, allow a test of whether wild free-ranging animals make different foraging decisions when energy-reserves are low (Houston and McNamara, 1988; McNamara, 1990).

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Appendix

Appendix I. Total number of trees, density (individuals ha^{-1}), mean tree size (cm DBH for trees ≥ 20cm) and the standard error of tree size for the all species within Sonso plots

	Species	Species code	Total trees	% of total trees	Density	Mean DBH	SE
1	*Alangium chinense*	ALC	5	0.58	1.25	34.60	14.00
2	*Albizia glaberrimes*	AGL	10	1.15	2.5	64.50	8.47
3	*Alstonia boonei*	AB	12	1.39	3	75.00	11.49
4	*Aningeria altissima*	AAL	7	0.81	1.75	23.42	1.84
5	*Antiaris toxicaria*	ANT	26	3.00	6.5	31.12	2.51
6	*Antiocarion sp.*	ANC	2	0.23	0.5	37.00	19.80
7	*Antrocarium micrantha*	ANM	1	0.12	0.25	75.00	-
8	*Balsamocitrus dawei*	BD	1	0.12	0.25	38.00	-
9	*Bosquea phoberos*	BP	17	1.96	4.25	33.16	5.91
10	*Bridelia brideliifolia*	BRB	1	0.12	0.25	33.00	-
11	*Broussonetia papyrifera*	BPY	35	4.04	8.75	28.83	1.33
12	*Caloncoba schweinfurthii*	CLS	30	3.46	7.5	30.87	1.84
13	*Celtis durandii*	CDU	38	4.39	9.5	40.26	2.13
14	*Celtis mildbraedii*	CMI	39	4.50	9.75	36.23	2.93
15	*Celtis zenkeri*	CZE	62	7.16	15.5	30.17	1.58
16	*Chrysophyllum albidum*	CAL	7	0.81	1.75	43.71	8.07
17	*Chrysophyllum muerense*	CMU	2	0.23	0.5	25.00	-
18	*Chrysophyllum perpulchrum*	CPR	9	1.04	2.25	38.11	5.64
19	*Cleistopholis patens*	CP	7	0.81	1.75	39.71	7.37
20	*Cordia millenii*	COM	9	1.04	2.25	55.22	5.26
21	*Croton sylvaticus*	CSY	25	2.89	6.25	40.48	2.53
22	*Cynometra alexandrii*	CYA	34	3.93	8.5	64.12	6.73
23	*Desplatsia chrysochlamys*	DC	1	0.12	0.25	30.00	-
24	*Desplatsia dewevrei*	DD	8	0.92	2	30.75	3.52
25	*Dichrostachys cinerea*	DCC	1	0.12	0.25	21.00	-
26	*Dombeya mukole*	DOM	1	0.12	0.25	45.00	-
27	*Drypetes spp.*	DSP	2	0.23	0.5	25.00	-
28	*Drypetes ugandensis*	DU	1	0.12	0.25	19.00	-
29	*Ehretia cymosa*	EC	7	0.81	1.75	34.29	5.41
30	*Entandrophragama angolense*	ENA	13	1.50	3.25	31.77	2.56
31	*Erythrophleum suaveolens*	ES	2	0.23	0.5	44.50	1.50
32	*Fagara angolensis*	FAN	2	0.23	0.5	33.00	3.00
33	*Fagaropsis angolensis*	FAA	1	0.12	0.25	25.00	-
34	*Ficus barteri*	FB	1	0.12	0.25	45.00	-
35	*Ficus exasperata*	FE	15	1.73	3.75	38.47	3.83
36	*Ficus polita*	FPO	1	0.12	0.25	75.00	-
37	*Ficus saussureana*	FSS	2	0.23	0.5	26.50	2.50
38	*Ficus sur*	FSU	11	1.27	2.75	35.18	4.51
39	*Ficus vallis-choudae*	FVL	9	1.04	2.25	26.22	1.93
40	*Funtumia elastica*	FUE	139	16.05	34.75	26.43	0.56
41	*Guarea cedrata*	GC	8	0.92	2	35.50	5.77
42	*Holoptelea grandis*	HG	1	0.12	0.25	67.00	-
43	*Khaya anthoteca*	KA	53	6.12	13.25	50.04	3.35
44	*Kigelia africana*	KIA	1	0.12	0.25	21.00	-
45	*Klainedoxa gabonensis*	KLG	2	0.23	0.5	33.00	12.00
46	*Lasiodiscus mildbraedii*	LM	13	1.50	3.25	22.62	0.74
47	*Lychnodiscus cerospermus*	LYC	4	0.46	1	19.25	0.25
48	*Macaranga lancifolia*	ML	1	0.12	0.25	28.00	-
49	*Macaranga monandra*	MM	2	0.23	0.5	52.50	7.50
50	*Macaranga schweinfurthii*	MS	2	0.23	0.5	33.00	14.00
51	*Maesopsis eminii*	ME	13	1.50	3.25	72.18	8.96
52	*Majidea fosteri*	MF	1	0.12	0.25	80.00	-
53	*Mango mangifera*	MMA	1	0.12	0.25	80.00	-
54	*Margaritaria discoideus*	MDI	20	2.31	5	53.50	3.18
55	*Markhamia platycalyx*	MP	1	0.12	0.25	33.00	-
56	*Melanodiscus sp.*	MEL	1	0.12	0.25	20.00	-
57	*Mildbraediodendron excelsum*	MIE	2	0.23	0.5	45.00	22.00
58	*Milicia excelsa*	MEX	5	0.58	1.25	44.80	16.01
59	*Mitragyna stipulosa*	MST	2	0.23	0.5	92.00	38.00
60	*Morus lactea*	MOL	2	0.23	0.5	46.50	17.50

	Species	Species code	Total trees	% of total trees	Density	Mean DBH	SE
61	*Myrianthus holstii*	MYH	28	3.23	7	31.64	2.08
62	*Paropsia guineensis*	PG	1	0.12	0.25	38.00	-
63	*Pseudospondias microcarpa*	PSM	2	0.23	0.5	100.00	20.00
64	*Ricinodendron heudelotii*	RH	2	0.23	0.5	110.00	-
65	*Rinorea ardisiaeflora*	RI	1	0.12	0.25	20.00	-
66	*Sapium ellipticum*	SE	1	0.12	0.25	20.00	-
67	*Schrebera arborea*	SA	1	0.12	0.25	80.00	-
68	*Strombosia sp.*	SS	2	0.23	0.5	35.50	12.50
69	*Tabernaemontana holstii*	TH	9	1.04	2.25	22.22	1.12
70	*Tapura fischeri*	TAF	16	1.85	4	24.00	0.89
71	*Teclea nobilis*	TN	1	0.12	0.25	23.00	-
72	*Tetrapleura tetraptera*	TT	7	0.81	1.75	24.43	0.87
73	*Tetrorchidium didymostemon*	TD	2	0.23	0.5	23.00	3.00
74	*Trichilia prieuriana*	TRP	29	3.35	7.25	26.03	1.02
75	*Trichilia rubescens*	TRR	18	2.08	4.5	25.00	1.35
	unkown	unknown	14	1.62	3.5	28.23	
	Total		865				

Appendix II. Total number of trees, density (individuals ha^{-1}), mean tree size (cm DBH for trees ≥ 20cm) and the standard error of tree size for the all species within Waibira plots

Species	Species code	Total trees	% of total trees	Density	Mean DBH	SE
1 *Alangium chinense*	ALC	8	1.07	2	30.78	1.94
2 *Albizia glaberrimes*	AGL	8	1.07	2	73.5	5.86
3 *Albizia zygia*	AZ	1	0.13	0.25	42.34	-
4 *Alstonia boonei*	AB	7	0.93	1.75	63.93	12.94
5 *Aningeria altissima*	AAL	5	0.67	1.25	45.4	14.41
6 *Antiaris toxicaria*	ANT	9	1.20	2.25	29.71	2.56
7 *Belonophora hypoglauca*	BEH	1	0.13	0.25	23.87	-
8 *Bosquea phoberos*	BP	4	0.53	1	48.41	8.07
9 *Caloncoba schweinfurthii*	CLS	7	0.93	1.75	26.01	1.97
10 *Celtis africana*	CAF	2	0.27	0.5	30.24	4.78
11 *Celtis durandii*	CDU	36	4.80	9	36.97	2.2
12 *Celtis mildbraedii*	CMI	167	22.27	41.75	39.21	1.4
13 *Celtis wightii*	CWI	2	0.27	0.5	21.65	1.59
14 *Celtis zenkeri*	CZE	25	3.33	6.25	31.45	2.15
15 *Chrysophyllum albidum*	CAL	6	0.80	1.5	47.23	7.44
16 *Chrysophyllum muerense*	CMU	6	0.80	1.5	57.41	2.99
17 *Chrysophyllum perpulchrum*	CPR	5	0.67	1.25	45.9	11.48
18 *Cordia millenii*	COM	5	0.67	1.25	44.37	11.97
19 *Croton sylvaticus*	CSY	33	4.40	8.25	34.91	2.02
20 *Cynometra alexandrii*	CYA	93	12.40	23.25	49.04	2.27
21 *Desplatsia dewevrei*	DD	1	0.13	0.25	19.74	-
22 *Diospyros abyssinica*	DIA	2	0.27	0.5	29.76	2.39
23 *Dombeya mukole*	DOM	1	0.13	0.25	40.11	-
24 *Drypetes spp.*	DSP	1	0.13	0.25	24.83	-
25 *Ehretia cymosa*	EC	3	0.40	0.75	27.27	6.22
26 *Entandrophragama angolense*	ENA	1	0.13	0.25	20.37	-
27 *Erythrina excelsa*	EE	1	0.13	0.25	21.65	-
28 *Erythrophleum suaveolens*	ES	2	0.27	0.5	77.9	10.49
29 *Fagara angolensis*	FAN	4	0.53	1	29.6	3.98
30 *Fagaropsis angolensis*	FAA	2	0.27	0.5	40	15
31 *Ficus exasperata*	FE	5	0.67	1.25	53.9	7.65
32 *Ficus polita*	FPO	1	0.13	0.25	40	-
33 *Ficus sur*	FSU	4	0.53	1	45.84	15.37
34 *Ficus variifolia*	FVR	1	0.13	0.25	70	-
35 *Funtumia africana*	FUA	2	0.27	0.5	23.55	3.82
36 *Funtumia elastica*	FUE	53	7.07	13.25	24.91	0.58
37 *Greenwayodendron suaveolens*	GS	1	0.13	0.25	28.58	1.81
38 *Guarea cedrata*	GC	1	0.13	0.25	32.79	-
39 *Harungana madagascariensis*	HM	1	0.13	0.25	28.97	-
40 *Holoptelea grandis*	HG	2	0.27	0.5	54.78	10.22
41 *Khaya anthoteca*	KA	5	0.67	1.25	47.3	10.22
42 *Klainedoxa gabonensis*	KLG	1	0.13	0.25	33.42	-
43 *Lasiodiscus mildbraedii*	LM	63	8.40	15.75	22.36	0.45
44 *Leptaulus daphnoides*	LPD	5	0.67	1.25	28.2	3.81
45 *Lychnodiscus cerospermus*	LYC	2	0.27	0.5	27.86	4.62
46 *Macaranga monandra*	MM	10	1.33	2.5	34.11	4.1
47 *Macaranga schweinfurthii*	MS	1	0.13	0.25	95	-
48 *Maerua duchesnei*	MD	7	0.93	1.75	22.78	1.52
49 *Maesopsis eminii*	ME	5	0.67	1.25	57.55	6.41
50 *Margaritaria discoideus*	MDI	19	2.53	4.75	45.32	3.5
51 *Markhamia platycalyx*	MP	3	0.40	0.75	36.29	4.2
52 *Mildbraediodendron excelsum*	MIE	1	0.13	0.25	20.69	-
53 *Milettia spp.*	MIL	3	0.40	0.75	45.31	13.61
54 *Monodora angolensis*	MOA	2	0.27	0.5	31.04	7.17
55 *Morus lactea*	MOL	1	0.13	0.25	79.58	-
56 *Myrianthus holstii*	MYH	5	0.67	1.25	23.36	1.33
57 *Paropsia guineensis*	PG	5	0.67	1.25	45.71	4.76
58 *Ricinodendron heudelotii*	RH	3	0.40	0.75	51.46	18.97
59 *Rinorea ardisiaeflora*	RI	3	0.40	0.75	22.18	1.54
60 *Sterculia dawei*	STD	1	0.13	0.25	65	-

	Species	Species code	Total trees	% of total trees	Density	Mean DBH	SE
61	*Strombosia sp.*	SS	1	0.13	0.25	23.87	-
62	*Strychnos mitis*	SM	33	4.40	8.25	45.93	3.77
63	*Tapura fischeri*	TAF	10	1.33	2.5	21.74	0.85
64	*Teclea nobilis*	TN	4	0.53	1	22.6	1.59
65	*Tetrapleura tetraptera*	TT	4	0.53	1	32.31	5.18
66	*Tetrorchidium didymostemon*	TD	5	0.67	1.25	39.28	6.4
67	*Trema orientalis*	TO	2	0.27	0.5	35.02	3.19
68	*Trichilia dregeana*	TRD	2	0.27	0.5	27.53	5.57
69	*Trichilia prieuriana*	TPR	8	1.07	2	22.1	1.13
70	*Uvariopsis congensis*	UC	6	0.80	1.5	22.07	0.91
		unknown	11	1.47	2.75	30.06	5.48
	Total		750				

Appendix III. Species names and number of individual trees that were monitored each month along phenology trails in Sonso and Waibira. The Sonso trail comprised 17 food species, the Waibira trail 15 food species.

Sonso

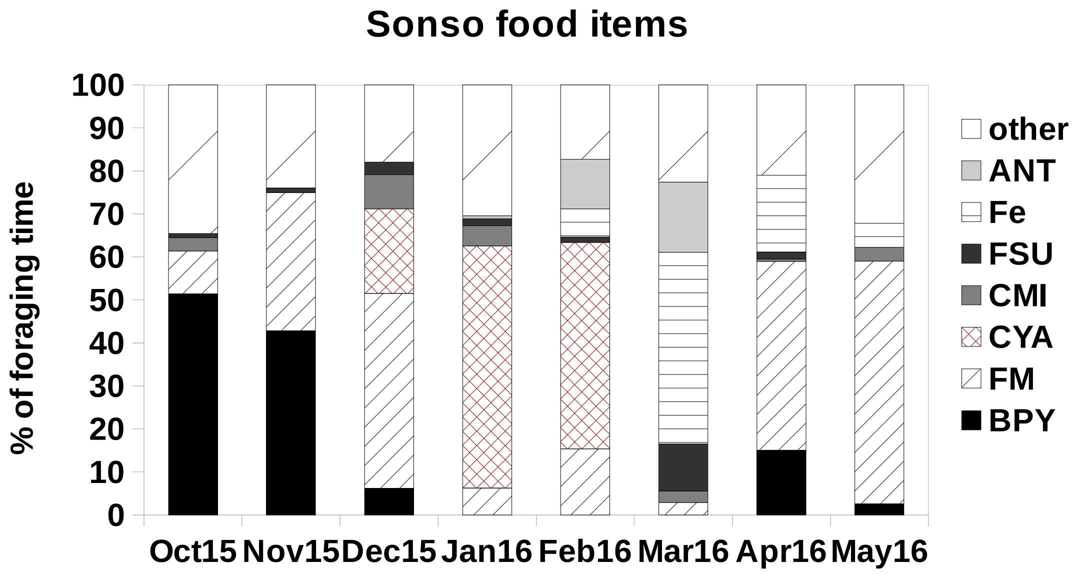
Species	Trees monitored
Ficus mucoso	15
Ficus sur	15
Mildbraediodendron excelsum	15
Ficus exasperata	15
Cordia millenii	15
Chrysophyllum albidum	15
Morus lactea	15
Maesopsis eminii	15
Celtis mildbraedii	15
Celtis durandii	15
Ficus variifolia	15
Cynometra alexandrii	15
Milicia excelsa	15
Broussonetia papyrifera	15
Antrocarium micrantha	15
Ficus barteri	4
Ficus natalensis	8
Total	237

Waibira

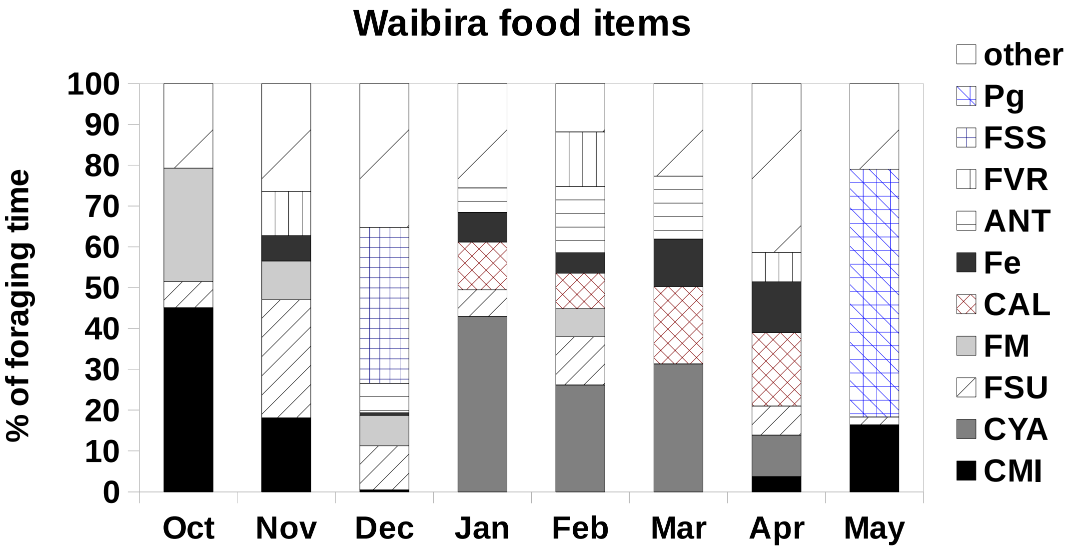
Species	Trees monitored
Ficus mucoso	15
Ficus sur	12
Mildbraediodendron excelsum	10
Ficus exasperata	15
Cordia millenii	15
Chrysophyllum albidum	15
Morus lactea	5
Maesopsis eminii	15
Celtis mildbraedii	15
Celtis durandii	15
Ficus variifolia	6
Cynometra alexandrii	15
Croton sylvaticus	15
Strychnos mitis	15
Chrysophyllum gorungosanum	2
Total	185

Appendix IV. Monthly proportion of feeding time devoted to the most important food species, within the Sonso community (top) and the Waibira community (bottom)

Chimpanzees of the Sonso community spent each month feeding predominantly on one to two species, while all other food items accounted for only a small proportion of feeding time. Within the Waibira community, in contrast, several plant species contributed substantially to the diet during most months.



Legend codes: ANT (*Antiaris toxicaria*); Fe (*Ficus exasperata*); FSU (*Ficus sur*); CMI (*Celtis mildbraedii*); CYA (*Cynometra alexandrii*); FM (*Ficus mucoso*); BPY (*Broussonetia papyrifera*)



Legend codes: Pg (*Putranjivace gerrandi*); FSS (*Ficus saussureana*); FVR (*Ficus variifolia*); ANT (*Antiaris toxicaria*); Fe (*Ficus exasperata*); CAL (*Chrysophyllum albidum*); FM (*Ficus mucoso*); FSU (*Ficus sur*); CYA (*Cynometra alexandrii*); CMI (*Celtis mildbraedii*)