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Dissertação apresentada à Universidade de Coimbra para cumprimento dos requisitos necessários à obtenção do grau de Mestre em Evolução e Biologia Humana, realizada sob a orientação científica da Professora Doutora Eugénia Cunha (Universidade de Coimbra) e da Professora Doutora Kimberley Hockings (Universidade Nova de Lisboa e Oxford Brookes University)

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Abstract

Chimpanzees are our closest living relatives, sharing some behaviours once thought unique to humans. Much is known about chimpanzee behaviour and socio-ecology, but we have a very limited understanding of how they adapt their behaviour to the costs and benefits of inhabiting human-influenced habitats. This dissertation presents the first data on the feeding ecology of the most westerly community of chimpanzees (*Pan troglodytes verus*) studied to date, in the forest-savannah-mangrove-farm mosaic of Caiquene-Cadique, Cantanhez National Park, Guinea-Bissau. The main aim of this research was to better understand temporal variations in chimpanzee feeding behaviour, including identification of food species consumed, and relate it to the seasonal availability of plant foods. A combination of data collection methods were employed during the 9-month field study: indirect recording (faecal samples and feeding traces), direct opportunistic observations of chimpanzees, and phenology quadrats. The Caiquene-Cadique chimpanzees experienced marked seasonal variations in the availability of plant foods, but maintained a high proportion of ripe fruit in the diet across months. In addition to fruits, they also ingest a variety of other plant parts, including leaves, piths, flowers, bark and sap. Chimpanzees at Caiquene-Cadique regularly consumed cultivars, including cashew, mango and orange, which represent 13,4% of all consumed species. Honey is frequently consumed, and was obtained from both natural and man-made beehives. There was no evidence of hunting or meat consumption, even though preferred prey species were available, and evidence for the consumption of social insects, such as termites or ants, was not found. However, there was indirect evidence of possible smashing and consumption of giant African snails (*Achatina sp.*). An episode of plant food-sharing *(Treculia africana)* was also recorded, supporting the theory that large, easily divisible plants are more commonly shared among apes than smaller, less easily divisible foods. The clearing of forestland for slash-and-burn cultivation is constant, and constitutes a significant threat to survival of this and other chimpanzee communities within the Park. Although ‘conflicts’ over access to space and resources appear uncommon, it is likely they will become more frequent with increasing human populations and encroachment.

Key-words: *Pan troglodytes*; diet; plant food sharing; habitat destruction

Resumo

Os chimpanzés são os nossos parentes mais próximos, partilhando alguns comportamentos que se pensava serem exclusivos dos humanos. Sabemos hoje bastante acerca do comportamento e ecologia social dos chimpanzés, mas temos uma compreensão muito limitada de como adaptam esse comportamento aos custos e benefícios de viverem num habitat antropogénico. Esta dissertação apresenta os primeiros dados sobre a ecologia alimentar da mais ocidental comunidade de chimpanzés (*Pan troglodytes verus*) estudada até ao momento, no mosaico de floresta-savana-mangual-campo-agrícola de Caiquene-Cadique, Parque Nacional de Cantanhez, Guiné-Bissau. O principal objectivo da investigação consistiu em compreender melhor as variações temporais no comportamento alimentar dos chimpanzés, incluindo a identificação de espécies consumidas, e relacioná-las com a disponibilidade sazonal de alimentos vegetais. Durante os 9 meses de trabalho de campo foi utilizada uma combinação de métodos de recolha de dados: métodos indirectos (amostras fecais e vestígios de alimentação), observações oportunistas de chimpanzés, e quadrados-amostra de fenologia. Os chimpanzés de Caiquene-Cadique experimentam variações sazonais acentuadas na disponibilidade de alimentos vegetais, mas mantém uma elevada percentagem de frutos maduros na dieta ao longo dos vários meses. Para além de frutos, ingerem também uma multiplicidade de outras partes de planta, incluindo folhas, caules, flores, casca e seiva. Em Caiquene-Cadique consumiram regularmente espécies agrícolas, incluindo caju, manga e laranja, as quais representam 13,4% de todas as espécies consumidas. O mel é frequentemente consumido, sendo obtido quer a partir de colmeias naturais, quer artificiais. Não foram encontrados indícios de caça ou consumo de carne, apesar da presença de espécies-presas preferenciais, nem indícios de consumo de insectos sociais, como térmitas ou formigas. Contudo, houve indício indirecto de possível esmagamento e consumo de caracóis gigantes africanos (*Achatina sp.*). Um episódio de partilha de alimento vegetal (*Treculia africana*) foi também registado, apoiando a teoria de que plantas grandes, facilmente divisíveis, são mais comummente partilhadas entre estes primatas do que alimentos de menor dimensão, menos fáceis de dividir. O desmatamento de floresta para cultivo de corte-e-queimada é constante e constitui uma ameaça significativa para a sobrevivência desta e de outras comunidades de chimpanzés do Parque. Apesar de os 'conflitos' em torno do acesso a espaço e recursos aparentem ser incomuns, é provável que se venham a tornar mais frequentes com o aumento da população humana e correspondente ocupação de terrenos.

Palavras-chave: *Pan troglodytes*; dieta; partilha de alimentos; destruição de habitat

Acknowledgments

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Table of Contents

List of Chapter Covers

List of Figures

List of Tables

Chapter 1

Introduction

1. Introduction

1.1 Theme and main goals of research

This dissertation falls within the scope of a Master's degree programme in Human Evolution and Biology, at the Department of Life Sciences, the University of Coimbra, and is part of a Fundação para a Ciência e a Technologic (FCT) funded project entitled "Where humans and chimpanzees meet: assessing sympatry throughout Africa using a multi-tiered approach" (PTDC/CS-ANT/121124/2010; Principle Investigator, Kimberley. J. Hockings). All data and results presented in this dissertation are based on nine months of intensive fieldwork, conducted by Joana Bessa in Cantanhez National Park, Guinea-Bissau, on an un-habituated community of western chimpanzees (*Pan troglodytes verus*). The main goal of the research was to better our understanding of the behavioural ecology of a largely unstudied community of wild chimpanzees living in a forest-savannah-mangrove-agricultural mosaic habitat around the villages of Caiquene and Cadique, Central Cantanhez National Park (hereafter the Caiquene-Cadique chimpanzee community). More specifically, it sought to identify food species consumed by this community and relate chimpanzee feeding strategies to seasonal patterns of wild food availability. This was the first in-depth research conducted on the Caiquene-Cadique chimpanzee community, the most westerly community studied to date. This thesis will contribute important data to better our understanding of chimpanzee behavioural adaptations in anthropogenic habitats, and where appropriate, findings are placed in an evolutionary framework. During the development of the research, a poster entitled " Size matters: the importance of plant food size in wild chimpanzee sharing behaviour" (see Appendix A) was produced, to be presented in August 2014 at the International Primatological Society XXV Congress in Vietnam (authors Bessa, J.; Sousa, C.; Hocking, K.). Two academic papers are also in preparation: Bessa, J.; Sousa, C.; Hocking, K. In prep. Size Matters – the role of plant food size in wild chimpanzee sharing behaviour; Bessa, J.; Sousa, C.; Hocking, K. In prep. Chimpanzee feeding ecology in a human-influenced habitat.

1.2 The importance of wild chimpanzees in studies of human evolution

Chimpanzees are humans' evolutionary cousins, and share at least 98% of our DNA (Sequencing, 2005). As chimpanzees are our closest living relatives (along with the bonobos, *Pan paniscus*) and we share a common ancestor, chimpanzees are frequently used as models for human evolution (McGrew, 2010a). Furthermore, humans and chimpanzees share numerous behavioural characteristics which were once considered unique to humans (e.g. flexible tool use, facultative bipedality, food sharing between unrelated individuals etc.).

In the 1960s, Louis Leakey sent Jane Goodall, Dian Fossey and Birute Galdikas to study great apes in their natural habitats, knowing that such data would significantly develop our understanding of human evolution (Morell, 1993). Over the last few decades many authors have used chimpanzees as anatomical and behavioural models for early hominins (e.g. McGrew, 1992; Stanford, *et al.,* 1994; Richmond *et al.,* 2001; Pruetz and Bertolani, 2009; Carvalho *et al.,* 2012). Wrangham and Pilbeam, (2002) even refer to the African Apes as "time machines" in the study of the Last Common Ancestor (LCA).

Despite strong arguments for the use of chimpanzees as models of our Last Common Ancestor, certain authors have strongly criticized it. Sayers and Lovejoy (2008) accused some primatologists of "chimpocentrism", which has caused other evolutionary relevant species, such as bonobos or capuchin monkeys, to be overlooked when reconstructing human evolution. Moreover, they consider that chimpanzees are not unique in their so-called 'human-like' behaviours, and that there are many examples of nonhuman vertebrates, such as sea otters, dolphins or woodpecker finches who are also known tool users, or big cats that hunt cooperatively in groups. They argue that studying these other species as behavioural models for human evolution is as justified as the use of chimpanzees. Sayers and Lovejoy (2008:99) are clear in their opinion that chimpanzees "are not humans and, most important, are not australopithecines".

In addition to existing knowledge on *Ardipithecus kadabba* (Haile-Selassie and WoldeGabriel, 2009), *Orrorin tugenensis* (Senut *et al.,* 2001) and *Sahelanthropus tchadensis* (Brunet *et al.,* 2002; Zollikofer *et al.,* 2005), new findings on *Ardipithecus ramidus* (White *et al.,* 2009) highlighted further reasons for the inadequacy of chimpanzees as models in human evolution (Lovejoy, 2009; Sayers *et al.,* 2012). For example, *Ar. ramidus* was capable of full bipedality with associated pelvis and foot modifications, and had lost the chimpanzees' characteristic projecting canine teeth (two anatomical characteristics considered exclusive to hominins) (Lovejoy, 2009). However, it still had the capacity to manoeuvre arboreally because of a grasping big toe. The authors argued that these unique characteristics meant that it was no longer possible to "simply [compare] humans to extant apes, because no ape exhibits an even remotely similar evolutionary trajectory to that reviled by *Ardipithecus*" (Lovejoy, 2009: 74).

Despite such criticisms, these authors do not regard chimpanzees as unimportant in the reconstruction of human evolution, and are ready to admit that they "provide crucial anatomical and behavioural information" (Sayers *et al.,* 2012: 120). But due to their highly specialized anatomy and behaviour, chimpanzees cannot be seen as exemplars of our LCA (Sayers and Lovejoy, 2008; Lovejoy, 2009; Sayers *et al.,* 2012). This suggests that these authors (Sayers and Lovejoy, 2008; Lovejoy, 2009; Sayers *et al.,* 2012) think that using chimpanzees as models for our LCA means treating them as the same species. However, most researchers that defend the use of chimpanzees as behavioural models emphasise that early hominins and chimpanzees are different and that their behavioural repertoires are not expected to be exactly the same (e.g. Whiten *et al.,* 2010; Carvalho and McGrew, 2012). Such supporters argue that, as chimpanzees are our closest extant relatives, and under certain conditions they face many of the same environmental pressures as early hominins, then it is likely that they have generated similar adaptive behavioural responses (Haslam *et al.,* 2009; Toth and Schick, 2009; Whiten *et al.,* 2010; Carvalho and McGrew, 2012; Pickering and Domínguez-Rodrigo, 2012).

Although early hominins appear to have some distinct anatomical and behavioural characteristics to chimpanzees, there are still features shared by both. In evolutionary research, shared features of related *taxa* are parsimoniously attributed to their LCA (Whiten *et al.,* 2010; Pickering and Domínguez-Rodrigo, 2012). Behaviour does not fossilize (Stanford, 2012); hence research on chimpanzees is our best hope to develop an understanding of the potential effects of ecological pressures on the behaviour of our LCA. This is especially relevant if chimpanzees inhabit similar habitat types to those of early hominins, such as the savannah-forest mosaics and woodland habitats (Pruetz and Bertolani, 2009; Pruetz and LaDuke, 2010; Carvalho *et al.,* 2012). Despite Sayers and Lovejoy (2008) attesting to the banality of human-like behaviour across the animal kingdom, the reality is that only nonhuman great apes, in particular the chimpanzee, possess the diversity of human-like characteristics. For example, unlike other species, they habitually make and use a wide variety of tools (e.g. McGrew, 2010b; Carvalho and McGrew, 2012), they hunt in groups with some communities exhibiting signs of cooperation (e.g Boesch *et al.,* 2006), alliance formation (e.g. de Wall, 2007) and reconciliation (e.g. Wittig and Boesch, 2005), they frequently share meat (Gilby, 2006) and some communities share plant foods albeit rarely (e.g. Hockings *et al.,* 2007). Interestingly, differences between communities in social and feeding behaviours, including tool-use, are not always explained by environmental factors and might instead reflect local traditions or cultures (e.g. Biro *et al.,* 2003; Whiten *et al.,* 2001).

McGrew (2010a:3267) defends the approach of modelling “the last common ancestor (…) based on current ethological and ecological knowledge of our closest living relations”. He argues that even if a very small part of what has been learned so far about wild chimpanzees “is applicable to the LCA (...), then the case has been made for preserving them”. It is impossible for us to determine exactly how our LCA lived, but cautiously using chimpanzees, and in some cases other apes, as behavioural models is currently our best chance to indirectly shed some light on this fascinating question. Authors may disagree on the validity of chimpanzee models, but one thing is for sure: all of them defend, in some way, the importance of our closest living relatives in the study of human evolution.

1.3 Integrating chimpanzee and early hominin behavioural ecology

Early hominins appear to have originated and lived in woodland habitats with forest patches, with no evidence of closed canopy tropical rainforest or subdesertic vegetation (WoldeGabriel *et al.,* 2009; White *et al.,* 2009). White *et al.,* (2009) state that chimpanzees inhabit the opposites of the earliest hominin paleohabitats (i.e. rainforests and savannahs). However, this is incorrect. Chimpanzees inhabit a wide variety of habitats from evergreen forests to grassland savannahs, and mosaic of woodland and deciduous forest (Butynski, 2003).

Moreover, their behavioural flexibility allows them to successfully exploit (if offered a degree of protection from hunting) highly fragmented and mosaic habitats with high human and agricultural presence (Hockings *et al.,* 2012; Hockings and Sousa, 2013; McLennan, 2013).

The habitat of early hominins appears to have been highly seasonal with temporal variations in food availability (Lovejoy, 2009). Seasonality also has a strong effect on the distribution and availability of foods to chimpanzees across tropical Africa (McGrew *et al.,* 1981; Pruetz, 2006; McLennan, 2013). Variations in the availability of resources to chimpanzees directly impacts their feeding behaviour; understanding such responses to food scarcity are important when considering how early hominins might have responded under similar conditions. For example, at Bossou, chimpanzees use tools to exploit 'keystone resources', such as the oil-palm *(Elaeis guineensis)*, especially during periods of fruit scarcity (Yamakoshi, 1998). Furthermore, Carvalho *et al.* (2012) demonstrate how bipedal transport increases when chimpanzees are presented with unpredictable resources (Carvalho *et al.,* 2012), and argue that the availability of certain food items and preferred tools might have been a strong selective force for bipedal locomotion in the earliest ape-like hominins (also see Lovejoy, 2009).

Chimpanzees are considered ripe fruit specialists (Wrangham *et al.,* 1998). Nevertheless, they are omnivorous, eating a wide range of foods such as: fruits, flowers, young leaves, tubers, bark, sap, honey, soil, invertebrates and small mammals (Morgan and Sanz, 2006). They also consume vertebrates, especially preying upon monkeys (McGrew, 2010a), with red colobus monkeys (*Procolobus badius*) a preferred prey species (Watts and Mitani, 2002). In human-influenced habitats, where many typical prey species are absent, chimpanzees still engage in hunting behaviours, albeit infrequently (Hockings *et al.,* 2012).

Despite such a diverse diet, some authors consider *Ar. ramidus* "more omnivorous" than chimpanzees, based on size, shape and enamel thickness of their teeth (Gibbons, 2009; Suwa *et al.,* 2009). They describe *Ar. ramidus'* diet as being mainly comprised of woodland plants such as ripe fruit (e.g. figs), supplemented by nuts and tubers, and with occasional insects, small mammals and bird eggs (Gibbons, 2009). Although these authors state that this is a completely different type of diet from that of wild chimpanzees, chimpanzees in fact consume all the food types outlined above. Moreover, certain foods exploited by chimpanzees require specific and complex processing techniques. Chimpanzees are habitual tool users (McGrew, 2010b), and depending on the community, employ rich and varied *tool kits*, which are used in complex sequences (*tool sets*) and combinations (*tool composites*) (McGrew, 2010b). Each community has its unique repertoire of tool use behaviour (McGrew, 2004), which allows the exploitation of resources that would otherwise be difficult to access, such as the rich interior of palm oil nuts (nut-cracking – Boesch *et al.,* 1994; Carvalho *et al.,* 2008), underground storage organs (Hernandez-Aguilar *et al.,* 2007; Hockings *et al.,* 2010a), termites (termite fishing – Goodall, 1986; Sanz *et al.,* 2009), ants (ant dipping – Humle and Matsuzawa, 2002), honey (Boecsh *et al.,* 2009), water (leaf sponges – Sousa *et al.,* 2009) and even bushbabies (*Galago senegalensis*) (tool assisted hunting - Pruetz and Bertolani, 2007). In addition to subsistence, chimpanzees use tools in their daily life for numerous social reasons and for personal hygiene (McGrew, 2010b). This impressive technological repertoire is considered one of the most important reasons for using chimpanzees as models in human evolution, and has led to the development of promising fields such as ‘Primate Archaeology’ (Haslam *et al.,* 2009; McGrew, 2010b; Carvalho and McGrew, 2012).

1.4 Dissertation structure

As outlined, the main goal of this research is to gain a better understanding of the behavioural ecology an un-habituated community of western chimpanzees inhabiting a human-influenced mosaic habitat in Caiquene and Cadique. For that purpose, this dissertation has been divided into seven main chapters. Following this Introduction, Chapter 2 describes the study species and study site. Chapter 3 provides an overview of all the methodology used during the fieldwork, including faecal and feeding trace analyses, opportunistic observations of chimpanzee behaviour, and the phenological study of forest plant species. In Chapter 4 the phenology and availability of wild plant food species to the chimpanzees is presented, and in Chapter 5 a detailed list of plant foods consumed by this chimpanzee community, as well detailed analysis of their feeding behaviour is given. Chapter 6 describes a rare yet important observation of plant food sharing between adult individuals. To conclude, Chapter 7 draws together the main findings of the study and suggests future directions for research.

Chapter 2

Study species and site

2. Study species and site

2.1 A closer look at chimpanzees (*Pan troglodytes*)

2.1.1 Social behaviour

Chimpanzees are highly social and intelligent, with a high degree of behavioural and social flexibility (McGrew, 2010a). The average size of a community is around 35 individuals, but can range from 12 (at Bossou Guinea: Hockings *et al.,* 2012) to 150 (Kanyawara in Uganda: Potts *et al.,* 2011). Chimpanzees exhibit fission-fusion dynamics whereby temporary and unstable parties are formed as a subset of the whole community (Kummer, 1971). This allows flexible responses to social and ecological change over short timescales (Aureli *et al.,* 2008).

Chimpanzees have a slow life history. In the wild, individuals can live for more than 40 years (Matsuzawa *et al.,* 2011). Typically, females migrate to other communities around the age of puberty (i.e. at around 10 years of age), and males remain in their natal community (Goodall, 1983). When a female reaches puberty her menstrual cycle starts and is accompanied by a very noticeable swelling of the perineal skin (Mori *et al.,* 2007). Chimpanzee reproductive rate is very slow due to the complete dependency of infants during the first 5 years of age. Females typically give birth every 6 years, and have an average of three to four offspring during their lifetime (Inskipp, 2005).

Chimpanzees build nests every night, and sometimes during the day. Nests are usually constructed in trees, but there have been reports of ground nests in several communities (for example at Nimba in Guinea: Koops *et al.,* 2007). In West Africa, chimpanzees often build nests in oil-palm trees *(Elaeis guineensis)* (Humle and

Matsuzawa, 2004; Sousa *et al.,* 2011) that are abundant, especially on the forest edges.

2.1.2 Chimpanzee numbers, distribution and conservation

The African chimpanzee (*Pan troglodytes,* Blumenbach, 1799) is the most abundant and widespread of all Great Apes. There are four subspecies of chimpanzees: the East African chimpanzee (*Pan troglodytes schweinfurthii*, Giglioli, 1872), the Central African Chimpanzee *(Pan troglodytes troglodytes,* Blumenbach, 1799), the West African chimpanzee (*Pan troglodytes verus,* Schwarz, 1934) and the Nigeria-Cameroon chimpanzee (*Pan troglodytes ellioti*, Gray, 1862).

It is estimated that there are between 173.000-300.000 individuals in the wild (Butynski, 2003), the East African chimpanzee being the best-represented subspecies with 76.400-119.600 individuals, followed by the Central African chimpanzee with 70.000-116.500 individuals. The West African chimpanzee has a much lower representation with 21.300-55.600 individuals in the wild, and at the bottom is the Nigeria-Cameroon chimpanzee with a mere 5000-8000 individuals.

Chimpanzees are the most widely distributed of the great apes, and are present in 22 countries, from 13ºN to 7ºS latitude with a geographic range of 2.342.000km^2 and inhabit altitudes from sea level to 2600m (Inskipp, 2005; Butynski, 2003) (see Figure 1). The East African chimpanzee is present from Ubangi River/Congo River in Central African Republic and Democratic Republic of Congo (DRC) to Western Uganda, Rwanda and Western Tanzania; relict populations are present in Burundi and South-eastern Sudan (Butynski, 2003; IUCN, 2013; WWF, 2014). The Central African chimpanzee occurs in Gabon, Cameroon and Republic of Congo, with a few populations in the Central African Republic, Equatorial Guinea and Angola (Butynski, 2003; IUCN, 2013; WWF, 2014). The West African chimpanzee is distributed from southern Senegal eastwards as far as the Niger River in Nigeria, and is present in Guinea Bissau, Côte D'Ivoire, Guinea, Sierra Leon, Nigeria, and Liberia, with relict populations in Mali, Ghana and Senegal. It is regionally extinct in Benin and Togo and, is also likely extinct in Burkina Faso (Brownell, 2003; Butynski, 2003; IUCN, 2013; WWF, 2014). The Nigeria-Cameroon chimpanzee is only found in Nigeria and Cameroon (Butynski, 2003; IUCN, 2013; WWF, 2014).

Chimpanzees have been classified as endangered by the IUCN since 1996, and this species is also listed under Appendix I of the Convention of International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2013). The main threats that this species faces are the loss and modification of habitat to other land-uses such as agriculture, increased human-chimpanzee 'conflict' which might result in retaliatory killings, poaching for bush meat, the pet trade, and the transmission of infectious disease with potential outbreaks due to the increasing number of encounters with humans (e.g. Ebola) (Butynski, 2003; IUCN, 2014).

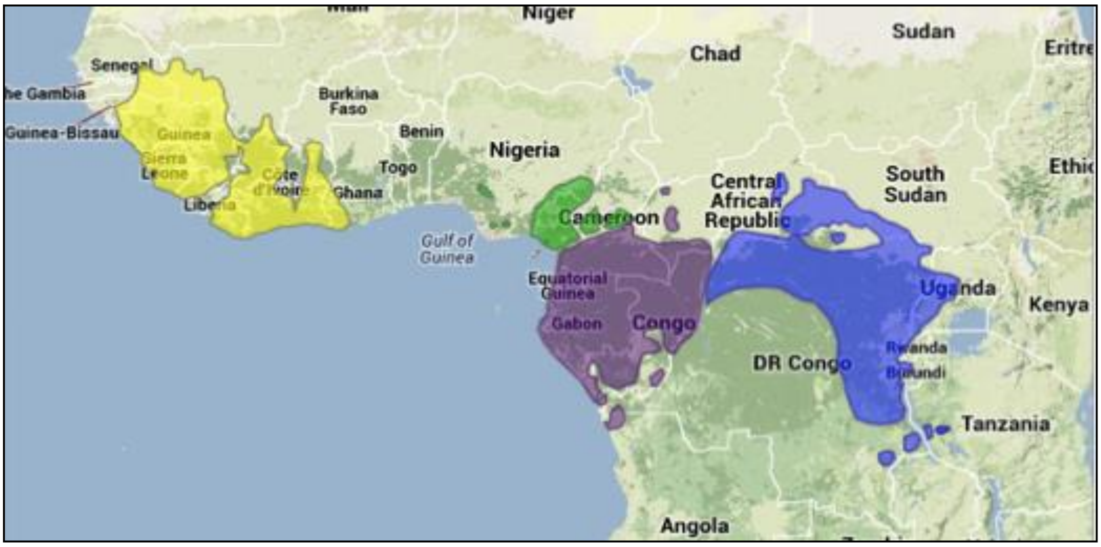


Figure 1 A map of distribution of the different sub-species of *Pan troglodytes*. Yellow: Western chimpanzee distribution; Green: Nigeria-Cameroon chimpanzee distribution; Purple: Central chimpanzee distribution; Blue: Eastern chimpanzee distribution. Map adapted from: http://wwf.panda.org/what_we_do/endangered_species/great_apes/chimpanzees/

2.1.3 The under-studied chimpanzees of Guinea-Bissau

Guinea-Bissau is one of the smallest countries in Africa's Atlantic West Coast. With an area of 36.125 km^2, it shares boarders with Senegal (to the North) and Guinea (to the South and East). It has a small number of offshore islands (the Bijagos archipelago) and the continental part is divided into coastal lowlands, interior plain and North-eastern highlands (Hocking and Sousa, 2011). In terms of topography, the highest altitude is 300m (CIA, 2014). The climate is classified as tropical humid with two distinct seasons: from May to November is the rainy season, and from December to April is the dry season. Annual mean temperature is 25.5ºC, with a low fluctuation rate across months, and average humidity levels is 69% (INEC, 2005).

The human population is estimated at 1.693.398 people (survey conducted in July 2014), and people belong to more than 20 different ethnic groups, the largest of which include Balanta (30%), Fula (20%), Manjaca (14%), Mandinga (13%) and Papel (7%). Other ethnic groups, such as the Nalu, are present in specific regions of Guinea-Bissau. Fifty% of the population is Muslim, 40% holds Animistic beliefs, and the remaining 10% are Christian (CIA, 2014).

Guinea-Bissau is one of the poorest countries in the world (16th place, Global Finance, 2014) and its population depends greatly on fishery and traditional agriculture, especially rice farming in mangrove areas and slash and burn agriculture (Sousa and Moreira, 2010; Sousa *et al.,* 2014). It is the sixth biggest exporter of unprocessed cashew nuts and forests and arable lands in Guinea-Bissau are being converted into cashew plantations at an approximate rate of 4% per year (Barry *et al.,* 2007). In the year 2000, 60% of the land was covered by forest, including primary and secondary forest and mangroves (FAO, 2000), and ten years later this area had been reduced to 55.9% (FAO, 2010).

Closed broad-leaved forest can be found in the lowland plains, with areas of primary forest being found in the Southwest (Tombali and Quinara regions) and Northwest (Cacheu regions) (see Figure 2; Gippoliti and Dell Omo, 2003). Forests are dominated by *Afzelia Africana*, *Alstonia congensis*, *Antiaris africana*, *Ceiba pentandra*, *Dialium guineense*, *Ficus spp.* and *Parinari excelsa* (Scott, 1992).

Guinea-Bissau has high biodiversity, with 12 orders of mammals represented, with 11 species from the Primate order (Casanova and Sousa, 2007). The western chimpanzee (*Pan troglodytes verus*) is the only great ape to be found in the country. However, the chimpanzee was considered extinct in Guinea-Bissau until 1988 (Lee *et al.,* 1988; Scott, 1992), but now it is estimated that there are between 600-1000 individuals. Their range is believed to extend through the Boé region in the South (borders with Guinea), and the South-eastern regions of Quinara and Tombali (Gippoliti *et al.,* 2003). Like across Africa, in Guinea-Bissau, a primary threat to chimpanzee persistence is high levels of deforestation for slash and burn agriculture, which is leaving chimpanzee habitat severely fragmented. Due to species-specific taboos, chimpanzees are not hunted for meat (Gippoliti *et al.,* 2003; Sousa *et al.,* 2005; Casanova and Sousa, 2007; Costa *et al.,* 2013). However, occasionally, body parts might be used in traditional medicine (Minhós *et al.,* 2013a) and accidental deaths might occur due to illegal snares or by farmers protecting their crops (Gippoliti *et al.,* 2003). The pet trade might also represent a threat to the species (Casanova and Sousa, 2007).

2.1.3.1 Cantanhez National Park

Cantanhez National Park (CNP) is situated in the South-western part of the Tombali administrative region (Northeast limit 11º22'58''N, 14º46'12''W and

Southwest limit 11º02'18''N, 15º15'58''W) (INEC, 2013) (see Figure 2). It was considered a hunting reserve from the mid 1980's, but in 2008 was formally declared National Park (Hockings and Sousa, 2011). However, the CNP holds 110 villages with an estimated population size of 22.505 people (Hockings and Sousa, 2011). This means that throughout the National Park people and wildlife live in close proximity. At least since the 15th century, when the first Portuguese arrived in Guinea-Bissau, the Nalu people have been considered the traditional owners of the land in Cantanhez (Temudo, 2009).

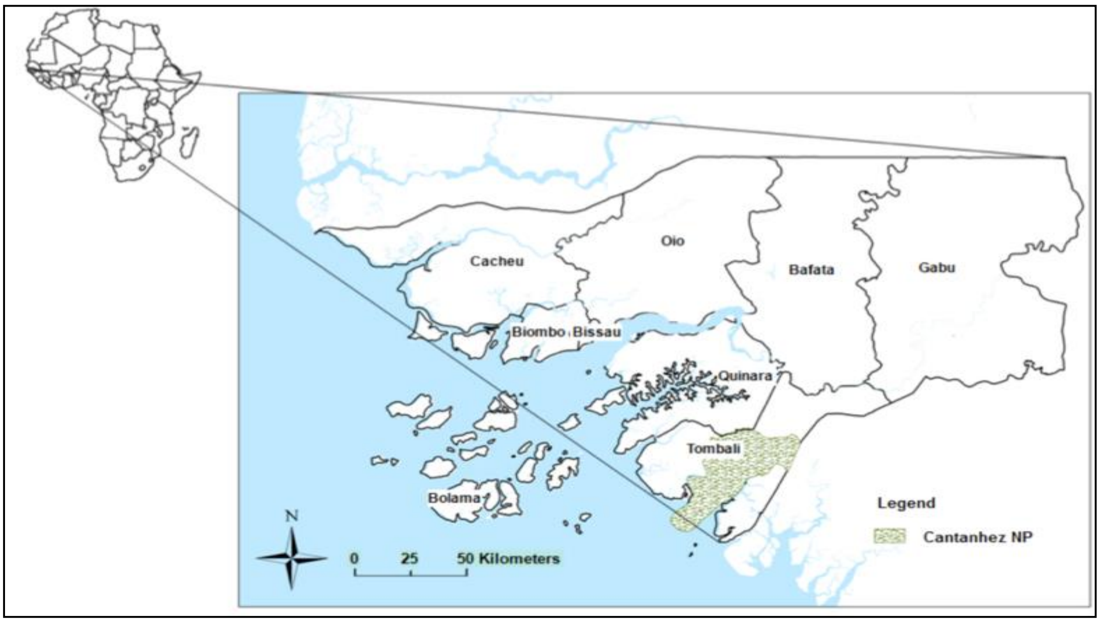


Figure 2 Location of Guinea-Bissau in west Africa and Cantanhez National Park (Tombali Region) (Adapted from Hockings and Sousa, 2011)

The environment is a mosaic of evergreen and semi-deciduous forest, savannah, mangroves and cultivated fields (Gippoliti and Dell'Omo, 2003; Catarino, 2004) supporting a large portion of Guinea-Bissau's primary subhumid forest (Oom *et al.,* 2009). The CNP is very rich in wildlife having six species of diurnal primates – western chimpanzee (*Pan troglodytes verus*) red colobus (*Procolobus badius temminckii*), black and white colobus (*Colobus polykomos*), Guinea baboon (*Papio papio*), green monkey (*Chlorocebus aethiops sabaeus*), Campbell's monkey

(*Cercopithecus campbelli*) - and one species of nocturnal primates, which is presumed to be the Senegalese bushbaby (*Galago senegalensis*) (Gippoliti and Dell'Omo, 1996; Minhós *et al.,* 2013b; Silva *et al.,* 2014).Due to the importance of its subhumid forests, CNP was considered by the WWF as one of the 200 most important ecoregions in the world, and has also been regarded as one of the seven priority areas in West Africa for chimpanzee conservation (Hocking and Sousa, 2011). The current chimpanzee population in CNP is estimated at 400 individuals (Casanova and Sousa, 2007; Hocking and Sousa, 2011). Even though it was declared a National Park, CNP does not benefit from much formal protection. 'Slash and burn' agriculture for subsistence crops and the increasing number cashew plantations, that transform closed forest into open forest and savannah woodlands, are the main drivers of deforestation in the region (Hockings and Sousa, 2011).

2.2 Location of the study site

2.2.1 Caiquene and Cadique Nalu

Caiquene (6,602m^2) and Cadique Nalu (28,485m^2) are two small villages situated in CNP (latitude 11º 12'-11º 15' N and longitude 15º 04'-15º 06' W), hereafter Caiquene-Cadique (see Figure 3). The ethnicities of local people vary however most people are Nalu, with some other ethnic groups present including Balanta. Islam is the main practiced religion.

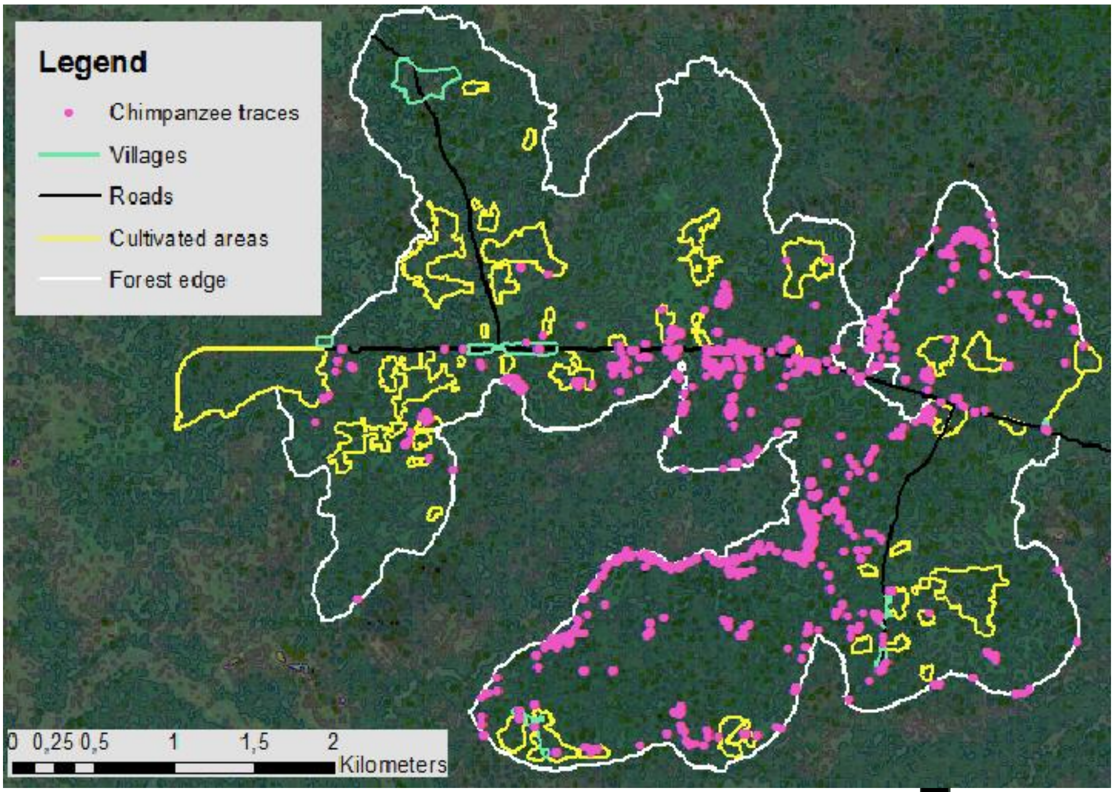


Figure 3 A map of the Cadique-Caiquene area in CNP. The roads are shown in black ■ the villages of Cadique Ialá (top left), Cadique Nalu (middle left) and Caiquene (bottom right) are shown in light green 🟩 and forest edge is shown in white □ cultivated areas are in yellow 🟨 and chimpanzee traces (including observations, feeding traces, faecal samples, tool use, nests, other) collected during the study period are highlighted in pink 🟪

2.2.2 Climate and vegetation

In terms of climate, there are two distinctive seasons: dry (from November to mid-May) and rainy (from mid-May to October). From February 2013 to January 2014, the mean temperature was of 27,47ºC with a minimum temperature of 21ºC in

May, with a maximum temperate of 36,3ºC in April. The total rainfall was of 1964mm with peaks in July and August (see Figure 4).

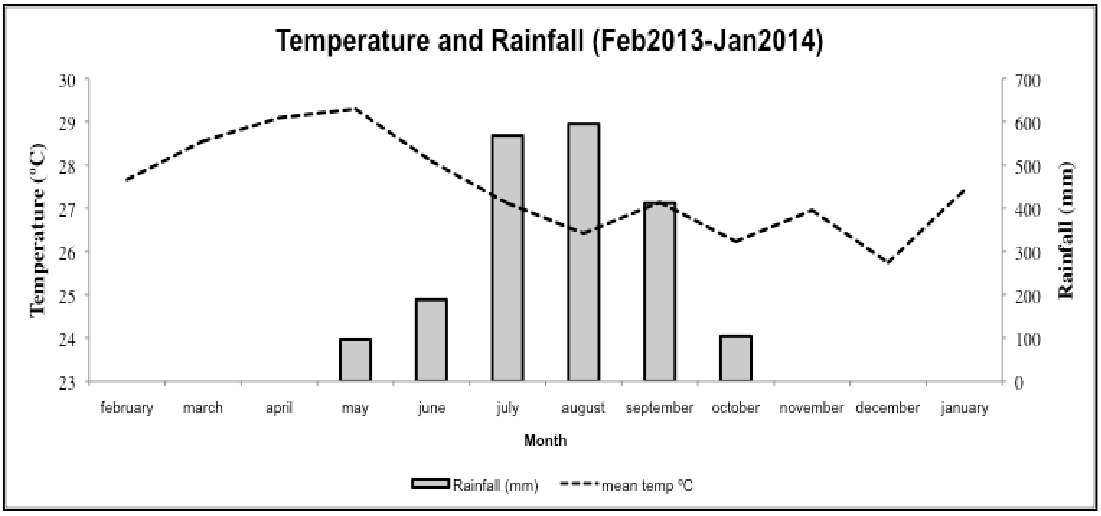


Figure 4 Rainfall and temperature data from Cadique Nalu (CNP), Guinea Bissau, between February 2013-January 2014.

The habitat is comprises a mosaic of primary subhumid forest, secondary forest, mangroves, savannah, and agricultural fields and orchards, especially cashew fields (see Figure 5). Common tree species include *Pavetta corymbosa, Monodora tenuifolia, Terminalia macroptera, Dialium guineense, Aedesia glabra, Elaeis guineensis.*

2.2.3 The Caiquene-Cadique chimpanzee community

Based on behavioural observations (sightings, vocalizations, road-crossing points) of chimpanzees, the location of chimpanzee sign (nests, faeces, knuckle prints, feeding remains), local reports and natural and man-made barriers, Hockings and Sousa (2013) proposed that several different chimpanzee communities are present in the forested areas of central-southern CNP; this is supported by genetic analyses (Sá, 2013). The home range of the Caiquene-Cadique chimpanzees is of ~7.93km^2 (see Figure 3).

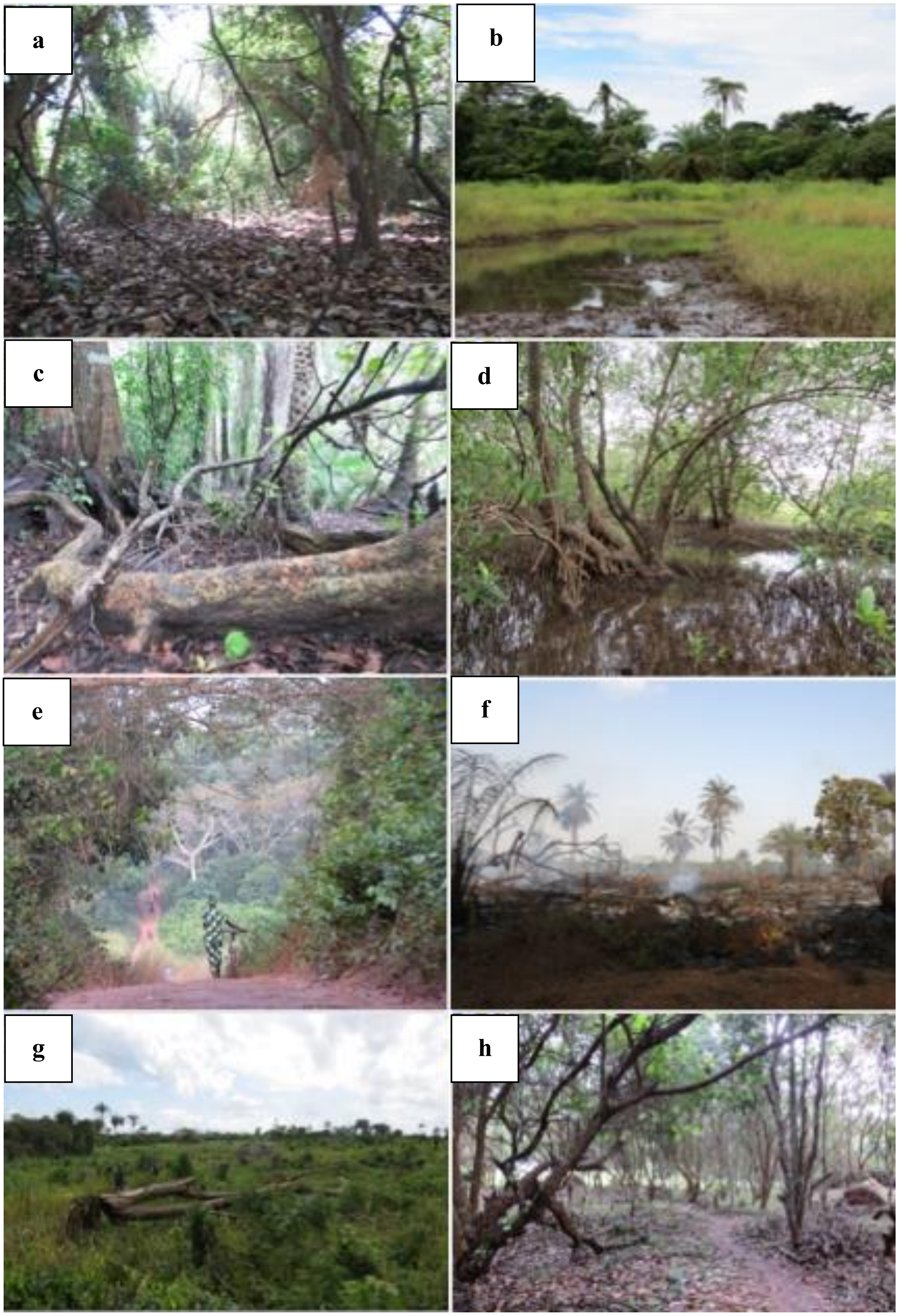


Figure 5 – Photographs showing the different habitat types found in Caiquene-Cadique**. a)** Secondary forest **b)** Palm-savannah-mangrove mosaic **c)** Subhumid forest **d)** Mangrove forest **e)** Secondary forest divided by a road **f)** Forest cleared through 'slash and burn' **g)** Cultivated field, and **h)** Cashew orchard

This un-habituated chimpanzee community has a minimum of 39 individuals (minimum 15 adult females and 11 adult males) (confirmed through filmed observations of road-crossings; Bessa unpublished data). One partially tarmacked road that leads from Jemberem to Cadique-Nalu divides the chimpanzees' home range (see Figure 3). This road is frequented by human and vehicle traffic including bicycles and motorbikes. The chimpanzees cross this road daily at specific crossing points, which change depending on the season (Bessa, unpublished data). Chimpanzees at Caiquene-Cadique often display curiosity towards local people and researchers (see Figure 6), and compared to other sites across Africa (e.g. Bossou – Hockings *et al.,* 2009, Bulindi – McLennan, 2013), currently show very little aggression towards local people and researchers (Hockings and Sousa 2013; Bessa pers. obs.).

Figure 6– a) An adult male chimpanzee and a local man walking down the road **b)** An adult female chimpanzee crossing the road while two locals walk towards her, Cadique Nalu (CNP).

Chapter 3

Study Methods

3. Study Methods

3.1 Overview of methods

This research comprises a set of direct and indirect data: phenology plots, chimpanzee observations and trace collection. All data related with the chimpanzees' feeding ecology were collected by the researcher (Joana Bessa) with the help of three local guides (Mamadu Cassamá, Djibi Indjai and Iaia Camará). For consistency, Mamadu Cassamá accompanied the researcher daily except on rare occasions (e.g. illness). When a part of the territory wasn't explored or wasn't fully known by the main guide, another with more knowledge of that specific area would join the research group.

3.2 Study period

The phenology data were collected continuously from February to November 2013. Chimpanzee feeding data were collected for a period of 9 months, from February 2013 to October 2013.Data was collected for equal periods in the dry season (1st February- 14th May) and the rainy season (15th May – 14th October). During the study period, data were collected for 6 days a week, with some exceptions (e.g. illnesses, religious holidays for the guides).

3.3 Chimpanzee habituation levels and visibility

The Caiquene-Cadique chimpanzee community is un-habituated. To-date, very limited behavioural data have been collected at this site (but see Hockings and Sousa, 2011; Hockings *et al.,* 2012 and Sousa *et al.,* 2013 for information on crop feeding; Sá *et al.,* 2013 for information on parasite loads; and Sousa *et al.,* 2013 for chimpanzee nesting). The chimpanzees encounter local people on a daily basis when crossing roads and exploiting anthropogenic parts of their habitat.

Opportunistic encounters with the chimpanzees often took part during road crossing events, where visibility was good. Observations in the forest were difficult due to poor visibility.

The goal of this research was not to habituate this chimpanzee community. Although certain in-depth questions can only be answered by researching habituated individuals, habituating chimpanzee communities, especially those that live in proximity to people, throws up many ethical issues that must very carefully be considered before habituation takes place (McLennan and Hill, 2013).

3.4 Rainfall and temperature

At the beginning of the study period, a weather station was built at the base camp. The thermometer was placed in an outside shelter in the shade, and the rain gauge was positioned in an open area nearby. Minimum and maximum temperatures (ºC) as well as the precipitation levels (mm) were collected daily at 18h, from February 2013 to January 2014.

3.5 Phenology

Eight randomised 50x50m plots were set up in February 2013, totalling 20,000m^2, this constitutes approximately 0.25% of the known chimpanzees' home range. Plots cover different habitat types, and cultivated and open savannah areas were avoided.

A random GPS point was generated. A 50 m line was traced from that point Northwards using a compass. From there, a 50m perpendicular line in a Westerly direction was traced and so forth until a 50x50m^2 square was marked. Habitat disturbance was kept as low as possible, and machetes were only used when absolutely essential to avoid opening up any habitat to hunters.

All trees and lianas with a diameter of greater than 10 cm at breast height (DBH) were marked with metal numbered tags. For each tagged tree, the species common names (in as many local languages as possible), DBH and tree height were recorded. The local guides had excellent botanical knowledge, but for accuracy, plant names were also checked in *Plantas vasculares e Briófitos da Guiné-Bissau* (Catarino *et al.,* 2006). When a species was unknown, a sample was collected for later identification at the herbarium of the Tropical Sciences Research Institute in Lisbon.

Every first and third week of the month a researcher accompanied by one or more guides monitored the plots. Availability of fruit (unripe and ripe), flowers and young leafs was recorded with a scale of abundance from 0 to 4 (0 being absent, 1 between 1 and 25% coverage, 2 between 26 and 50%, 3 between 51 and 75% and 4 between 76 and 100%) (Hockings *et al.,* 2009).

Information was recorded when a tree died by natural causes or was cut down.

3.6 Data collection

Data were collected by the researcher, Joana Bessa, and at least one guide. The guide(s) was familiar with the area as well as with the location of chimpanzee paths, nesting sites and large fruiting trees. He would help to find and identify new traces and was importantly able to distinguish chimpanzee traces from those of other sympatric primates *(*see Chapter 2 of this dissertation). GPS points were taken when new faecal samples, traces, nests, were located, along with all encounters with chimpanzees (see Appendix A).

3.6.1 Faecal sampling

Faecal sampling, processing and analysis during the research period followed trialled-and-tested methods proposed by McGrew *et al*. (2009) and McLennan (2010). All faecal samples that were fresh (≤ 1 day) or recent (≤ 2 days), and without evidence of insect activity, were collected. They were normally found in known chimpanzee trails, underneath fresh nests or in places where the chimpanzees had recently been (McGrew *et al*., 1988). The samples were easily distinguishable by size, smell, colour and form from other sympatric species' dung. When in doubt, samples were not collected. Only one sample was collected if faecal matter looked like it was from the same individual (McLennan, 2010). The faecal samples were picked up using a zip lock plastic bag. All external matter that didn't make part of the dung (e.g. dry leafs and twigs) was carefully discarded (McGrew *et al*., 2009).

The collected samples were stored at camp in a shelter and within the plastic bag. Every two days the samples were washed in a 1 mm mesh sieve. Faecal washing took place in a covered yet open space by the researcher with the help a guide. As there was no running water or nearby streams, buckets of water were used instead. After the entire soft matrix of the faeces was washed away, and any accidental external matter and dung insects were removed, the remaining part was positioned carefully on newspaper sheets where it was immediately analyzed while wet. Seeds were separated from foliage and other matter. Faecal matter was rated using percentages of fruit (pulp and seeds), foliage (leaves, pith and bark), flower (all flower parts) and other (honey, insects, etc). When possible, the seeds and any other parts such as leaves were identified. The numbers of species in each faecal sample were counted and percentages of fruit, foliage, flower and other were attributed. Every new seed, leaf, flower or other matter was photographed and preserved in 70% alcohol or dried. Unidentified species were taken to be identified at the herbarium of the Tropical Sciences Research Institute in Lisbon or the Kew Gardens in London.

3.6.2 Feeding traces

Only chimpanzee feeding traces that were identified with certainty were recorded. Confirmation that a trace was made by chimpanzees was made when other chimpanzee signs (e.g. knuckle prints) were associated, if it was a species-specific sign (e.g. fruit wadges), if an individual was seen doing it, or if it was known that a feeding party had been in that place very recently (Pruetz, 2006; McLennan, 2010; Morgan and Sanz, 2006). Only traces that were fresh or recent (≤ 3days old) were recorded, with the exception of traces that were found in new parts of the habitat that were not previously known to be visited by the chimpanzees.

To ensure the independence of data points, only one record was taken if various traces, of the same estimated age and species, were found together (i.e. in the case of a large feeding party; McLennan 2010).

Every time a trace of a new species or species part was encountered, a photograph was taken, and the sample was collected for later identification.

3.6.3 The snail trail

Early on in the study period, the research team suspected that chimpanzees at Caiquene-Cadique might be smashing open and consuming Giant African land snails (*Achatina sp*.). The local guides were certain the chimpanzees engaged in this behaviour. However, it must be noted that mongooses (*Atilax paludinosus*) also reportedly smash snails and are present at this site (see Hicks, 2010 for similar reports at Bili-Uele in DRC; and Eisner and Davis, 1967 for other mongoose smashing).

A 'snail trail' of potential snail-smashing sites was created. Once a potential smashing site was found, the surrounding area was carefully checked for evidences of further smashed snails and any signs of smashing, especially on tree buttresses and roots. Shell fragments of more than 1 cm width were counted and the number of fragments per site was recorded. An estimation of the minimum number of individual snails smashed was based on the number of *columella* found (internal pillar of the shell), as this appeared to be the part of the shell that was able to resist the smashing. Fragments greater than 2 cm in length were marked with a cross using waterproof black marker to ensure that they would not be confused with new signs when returning to the smashing site. When possible, the distance between the shell apex and *columellar truncation* was recorded to get an approximation of the size of the snail.

Where possible, a conservative estimation of the age (in days, weeks, months) was attributed to those large snail fragments that included the *apex* or *collumella*. Age was estimated based on the following shell characteristics whilst considering season: soil sedimentation, discoloration, mucus residue and any fleshy parts left in the shell. Smashing sites were determined by marks (e.g. removed bark; embedded shell) that were frequently generated through the force of the smashing behaviour on wooden surfaces (e.g buttress roots; lianas, bifurcated trunk). The species of tree(s) used for smashing was recorded, as well as its DBH, the existence of adequate smashing surfaces, and all signs of smashing.

The maximum distance (i.e. the farthest distance snail fragments were found from the smashing point), and the spread (i.e. the distance between the fragments that were furthest apart and surrounding the smashing site), were recorded. Any indirect evidence of chimpanzee presence that was possibly associated with the smashing signs was recorded. During the dry season, confirmed smashing sites with more than 3 smashed snails were revisited once a month. As snails come out of hibernation and breed during the rainy season, snail smashing sites were revisited every two weeks.

3.6.4 Opportunistic encounters

Encounters with chimpanzees were opportunistic. If a chimpanzee group was heard nearby and the research team felt they could observe the chimpanzees without causing them too much stress, the researcher and guide would try to get closer to observe. Chimpanzees were sometimes encountered when walking in the forest, or close to the villages, or on the road when cycling between the forest patches.

As reported at other sites (e.g. Bossou: Hockings, 2007), it proved more difficult to encounter the chimpanzees during the rainy season, making fresh indirect data sometimes difficult to collect. On such occasions, more effort was placed on finding the chimpanzees. When chimpanzees were encountered, a safe distance was always maintained by the researcher and research team kept as quiet as possible, keeping any communication (e.g. calling) or reaction (e.g. laughing) towards the chimpanzees to an absolute minimum. If individuals started to become restless or agitated (i.e. fear grin or high levels of rough self-scratching, Hockings *et al.,* 2007) the researcher and guide would move further away until this behaviour stopped or leave altogether.

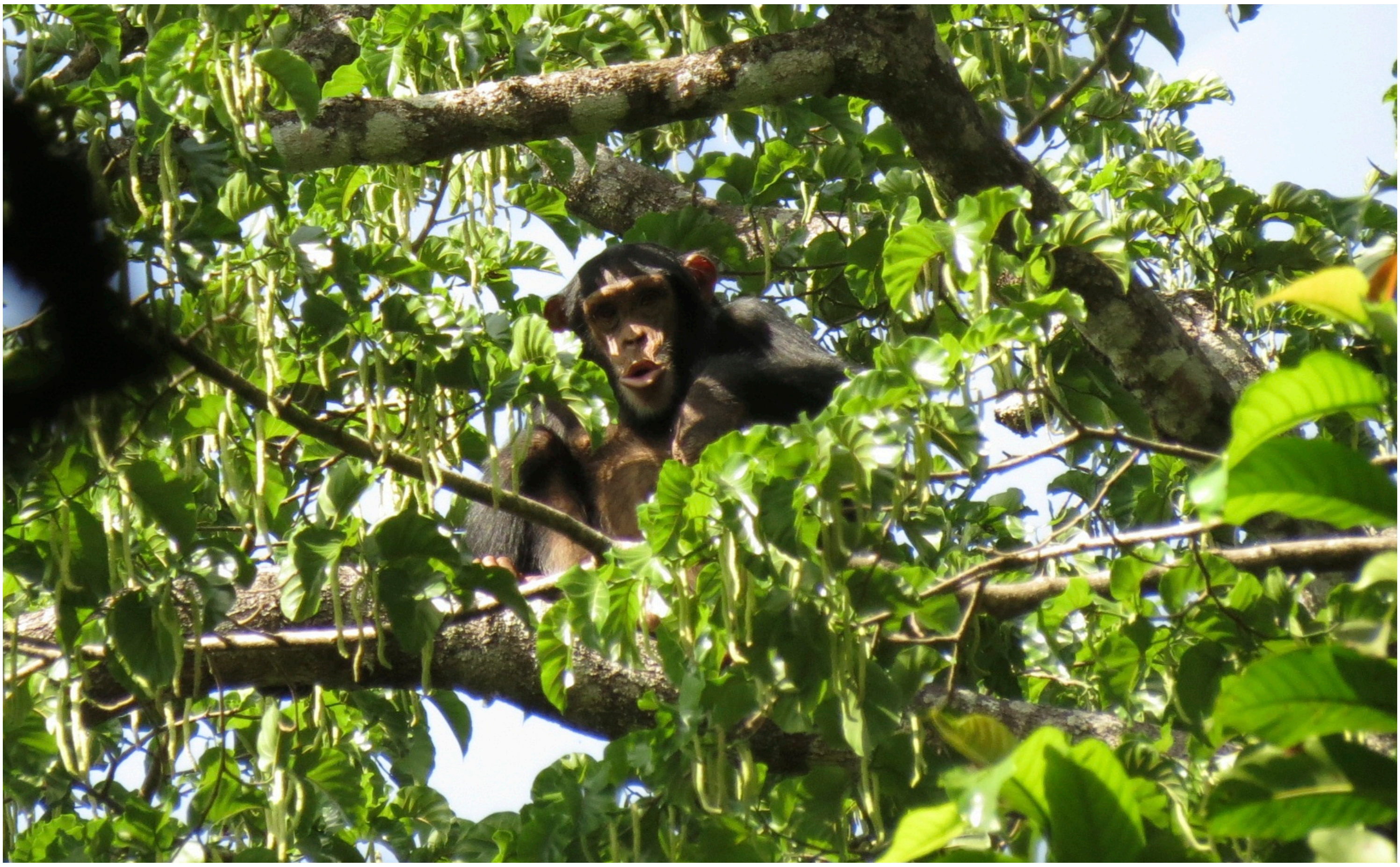
Although full descriptions of all encounters were taken by the researcher (including start and end times, number of confirmed individuals in the party, estimated ages and sexes of the individuals, visible behaviours, reactions towards the researcher), these data are not presented in this thesis due to space limitations. Photographs and videos were taken when possible.

3.7. Data Analyses

Data were analysed using SPSS 20, Microsoft Excel 2008, Garmin Basecamp 4.2.4. and ArcGIS 10.2.1. All data were checked for normality and where possible transformed (Field, 2009). All the hypotheses considered were two tailed and tested at 0.05. Details of all statistical tests are presented in each data chapter.

Chapter 4

Phenology and Food Availability



4. Phenology and Food Availability

4.1. Introduction

Food availability in tropical forests is highly seasonal (Sun *et al.,* 1996; Chapman *et al.,* 1999; Fawcett, 2000; Chapman *et al.,* 2005; Ting *et al.,* 2008; Hockings *et al.,* 2009; McLennan, 2013). Rainfall, temperature and sun radiation are some of the most common factors that determine food availability (Chapman *et al.,* 1999; Anderson *et al.,* 2005; Chapman *et al.,* 2005).

The seasonal or temporal availability of foods can impact population densities and determine a species geographical distribution (Chapman and Chapman, 1999). Understanding the temporal availability of food to a particular species is crucial when examining the drivers of behavioural patterns, including animal feeding strategies (Hockings *et al.,* 2012; McLennan, 2013). It is also an important ecological force that shapes primates social systems (Marshall *et al.,* 2009). Moreover, it is essential to study community-level patterns of food availability since differences in food availability can occur even when comparing study sites that are only a few kilometres from each other (Anderson *et al.,* 2005; Chapman *et al.,* 2005).

Even though chimpanzees are considered ripe fruit specialist (Wrangham, 1977), they are in fact omnivorous and during periods of fruit scarcity they are known to increase their consumption of other plant parts (e.g. leaves and pith – Morgan and Sanz, 2006; tubers - Hockings *et al.,* 2010a). When examining chimpanzee feeding ecology, phenological data should be collected on the availability of young leaves as well as ripe fruits.

Correlating the availability of food parts with their consumption by chimpanzees will allow identification of potential fallback and preferred foods. Fallback foods are present year-round (or at least during the majority of the year), with poor nutritional value (considered low in calories and minerals) and whose consumption is inversely proportional to the availability of preferred foods (Marshall and Wrangham, 2007)[1]. However, fallback foods have high seasonal importance. Even though they represent low preference items, they might be fed upon during the whole year and provide a reliable source of food (Marshall *et al.,* 2009; Marshall and Wrangham, 2007). In many chimpanzee communities across Africa, figs (*Ficus spp.)* are particularly important fallback foods (Fawcett, 2000; Marshall *et al.,* 2009; McLennan, 2013).

4.1.1 Monitoring food availability

The most commonly used methods to measure fruit availability are fruit traps, fruit trails, and phenology transects/quadrats (outlined in Chapman *et al.,* 1994).

- Fruit traps consist of a structure that collects fallen fruits, flowers or leaves that are systematically collected, counted and weighed.
- Fruit trails monitor key species (i.e. those known to be eaten by the chimpanzees) along establish trails.
- Phenology transects or quadrats involve the establishment of areas where a subset of all tree species within the sampling areas are systematically monitored for food availability. Trees are selected based on diameter at breast height (DBH), usually >10cm.

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[1] Preferred foods are items that are overselected, sometimes even disproportionally to their relative abundance in the animals' home range (Marshall and Wrangham, 2007).

Choosing a method depends on its accuracy, the knowledge of the chimpanzee community's feeding ecology and the amount of time available for sampling (Chapman *et al.,* 1994). Chapman *et al*. (1994) compared all three methods simultaneously, and concluded that only estimates derived from fruit trails and phenology transects/quadrats were correlated. Moreover, the possibility of randomly establishing a large number of transects or quadrats within a species home range allows for better descriptions of the habitat itself, and accuracy of food availability estimates will be positively related to the proportion of sampled area.

In addition to selecting the appropriate sampling method, it is necessary to choose how food availability is recorded. The most straightforward methods include recording the presence/absence of food (e.g. Anderson *et al*., 2005) or giving a score (usually on a scale of 0-4) to the crop size (Chapman *et al.,* 1994) . Some authors argue that both methods are equally accurate (e.g. Fawcett, 2000; McLennan, 2010) whereas others stress the importance of scoring due to visible longterm variations in the proportion of the fruiting population and the abundance produced during each fruiting episode (Chapman *et al*., 2005).A food availability index (FAI) is calculated from the crop score and DBH. The DBH provides an accurate indicator of a tree's size and hence its ability to produce fruit, with high inter-observer reliability (Chapman *et al*., 1994).

The objective of this chapter is to describe monthly variations in the availability of wild foods to the Caiquene-Cadique chimpanzees, for analyses and discussion in the following chapter.

4.2 Hypotheses

1. The food available to chimpanzees will vary seasonally.
2. Certain species will fruit year round, i.e. present in times of food scarcity.

4.3 Methods and analyses

For complete methods see chapter 3.

4.3.1 Food availability

To calculate FAI the following formula was used (replicated from Hockings *et al.,* 2009):

$$\mathbf{FAI = [\ \Sigma\ (Pi \times Fi)] \,/\, [\ \Sigma\ (\ Pi \times 4)\ ] \times 100}$$

Pi is the basal area of the tree (cm^2) and Fi is the food (flower, fruit or leaf) score of the tree (0-4).Food score: 0 is absent, 1 is between 1 and 25% of canopy coverage, 2 is 26 to 50% coverage, 3 is 51 to 75% coverage, 4 is 76 to 100% coverage.Twice-monthly FAI (first and third weeks of the month) was calculated for all species present in the quadrats. From this, a mean monthly FAI was calculated.

Following Hockings (2007), two species groups were established from all the plant species monitored in the quadrats:

- "Community-wide species" – representing all monitored species.
- "Chimpanzee food species" – representing only the confirmed food species that chimpanzees consumed during this study period.

4.3.2 Statistics

In total, 19 surveys were conducted. Data were checked for normality using *Shapiro-Wilk* test and normality *Q-Q plot*. When data were non-normally distributed, the data were transformed using a *log-10* function (Field, 2009). Parametric *Linear regression* tests were used to test relationships between dependent and independent variables. When the assumptions for parametric test were not met, non-parametric *Spearman's rank correlation coefficient* was used. All statistical analysis was done using SPSS version 20.

The relationship between twice-monthly variations in community-wide and chimpanzee food species (including all parts) were examined using Parametric *Linear regression* tests, and a descriptive analysis of temporal variation in different food parts was conducted.

To assess if the phenology of the three most common chimpanzee food species found in the quadrats - *Monodora tenuifolia, Dialium guineense, Elaeis guineensis* - influenced the total phenology, parametric *Linear regression* tests were conducted.

To examine the effects of seasonality on phenology, parametric *Linear regression* tests were used for temperature and non-parametric *Spearmen correlation coefficient* for rainfall.

4.4 Results

A total of 1994 trees and lianas from 129 (82 known and 47 unknown) species were tagged and monitored in eight quadrats (see methods section). Of these, 37 were chimpanzee food species representing a total of 834 trees and lianas. During the study period, 64 trees were cut down or died naturally, 31 of them being chimpanzee food species. The ten most common species found in the quadrats are shown in Table 1. Four are chimpanzee food species.

Table 1 List of the 10 most common plant species in the quadrats survey in the forest of Caiquene-Cadique, including counts, density (plants per hectare), and whether or not the plant is a chimpanzee food species (0: no; 1:yes)

Scientific name (Family)	Count	Density	Chimpanzee food species
Pavetta corymbosa (Rubiaceae)	140	70	0
Monodora tenuifolia (Annonaceae)	127	63,5	1
Terminalia macroptera (Combretaceae)	121	60,5	0
Dialium guineense (Leguminosae / Fabaceae)	97	48,5	1
Aedesia glabra (Compositae)	91	45,5	0
Elaeis guineensis (Palmae / Arecaceae)	86	43	1
Anthostema senegalense (Euphorbiaceae)	84	42	0
Synsepalum pobeguinanum (Sapotaceae)	75	37,5	0
Malacantha alnifolia (Sapotaceae)	49	24,5	1
Erythrina senegalensis (Leguminosae / Fabaceae)	40	20	0

Species density (i.e. number of individual trees of a species per ha) and relative density (i.e. percentage of total tree density) were calculated for all tree species found in the quadrats (data are presented in Appendix C). To calculate the food availability index of community-wide and chimpanzee food species only trees and lianas, which were not cut down/died naturally were used. This includes a total of 1930 plants, 803 of which are chimpanzee food species.

4.4.1 Food Availability

As chimpanzees rarely consume unripe fruits (Hockings 2007), and data on the availability of unripe fruits will not be included in the analyses presented in subsequent chapters, these data were omitted for clarity.

Flowers

Flower availability of community-wide and chimpanzee species were positively correlated ($R^2=0.953$, $p<0.001$).

For both community-wide and chimpanzee food species (see Figures 7 and 8), flowering peaked in March, and fell from July to November, and was at its lowest in August.

Ripe Fruit

Twice-monthly availability of ripe fruit for community-wide and chimpanzee food species was strongly positively associated (see Figure 9; $R^2=0.964$, $p<0.001$). Ripe fruit availability peaked from March to May, with March the most productive month (see Figures 7 and 8). From June to November, the availability of ripe fruit is lower, with the month of August showing the lowest levels of ripe fruit productivity. During the study period, I identified two potential fallback foods. *Elaeis guineensis* fruited across all months and *Ficus spp*. fruited in 8 of the 10 studied months.

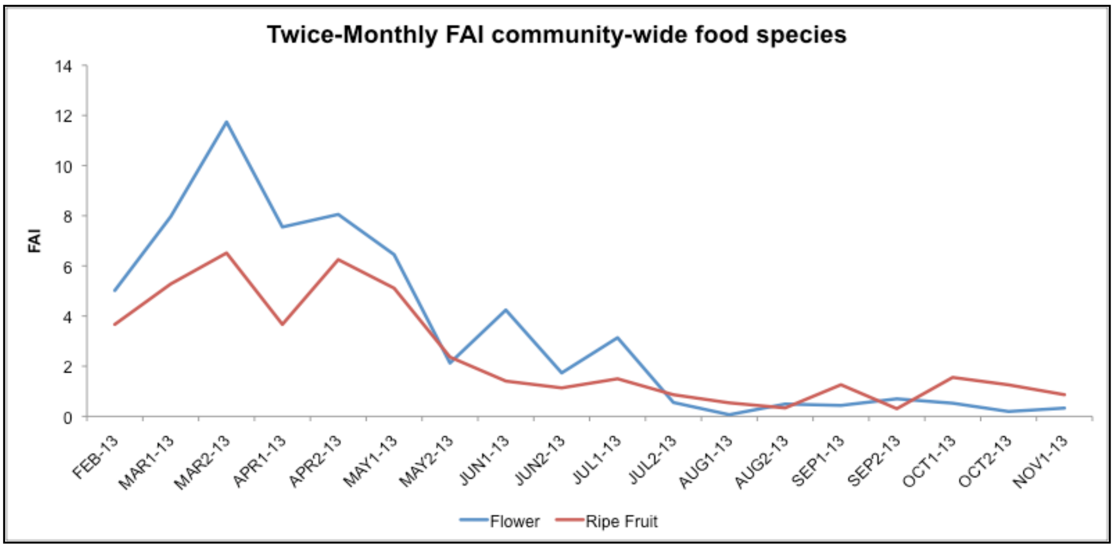

Figure 7. Twice-monthly availability of ripe fruit and flowers in community-wide species.

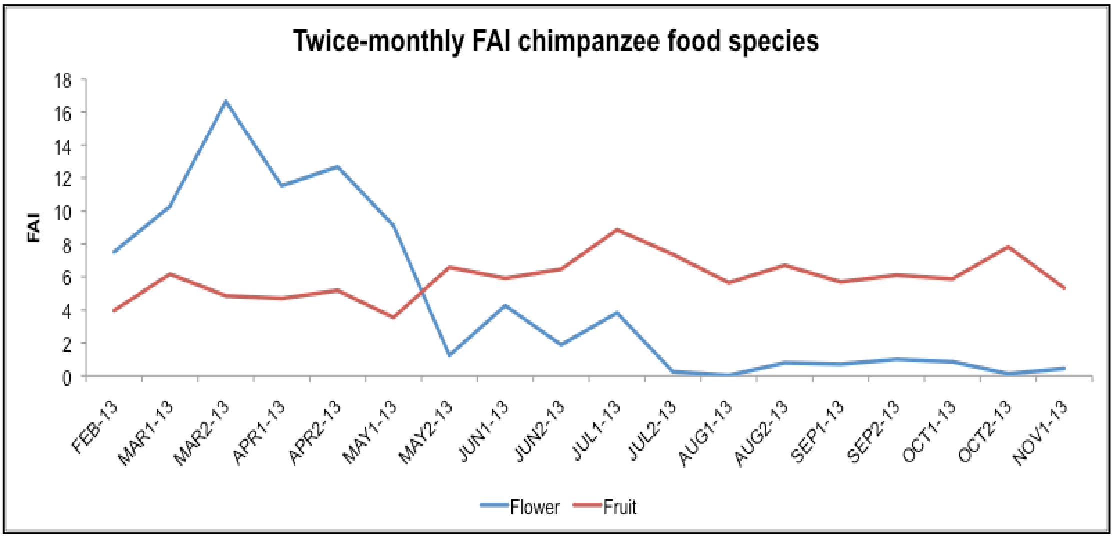

Figure 8 Twice-monthly availability of ripe fruit and flowers in chimpanzee food species.

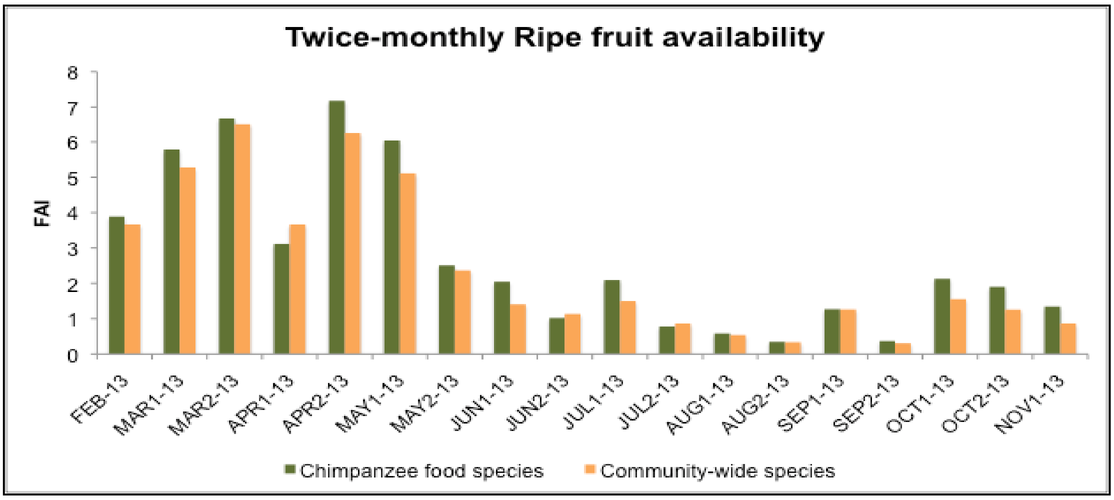

Figure 9. Twice-monthly availability of ripe fruit in chimpanzee food species and community-wide food species

New Leaves

New leaf availability for community-wide and chimpanzee food species were significantly correlated (see Figure 10; R^2=0.664, p<0.001). New leaves were available throughout the study period, with peaks in August. February had the lowest availability for both community-wise and chimpanzee food species. As availability of community-wide and chimpanzee food species are highly correlated, the following analyses focus on chimpanzee food species only.

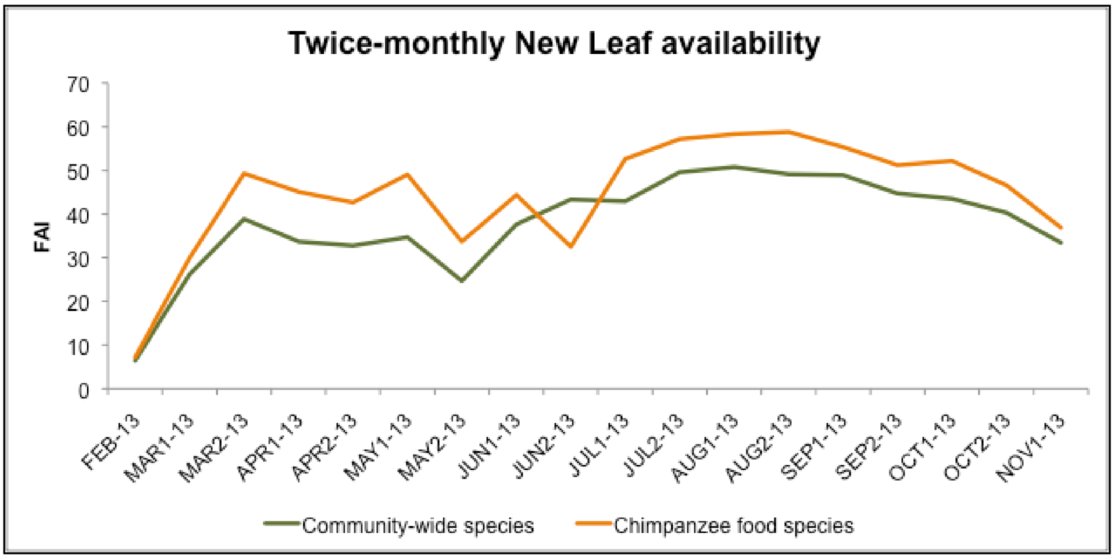

Figure 10. Twice-monthly availability of new leaves in chimpanzee food species and community-wide food species.

4.4.2 Common plant species

Neither *Monodora tenuifolia* nor *Elaeis guineensis* ripe fruiting patterns were associated with variations in availability of ripe fruit in chimpanzee food species (R^2=0.088, ns; R^2=0.066, ns respectively). In contrast, availability of *Dialium guineense* ripe fruit was significantly correlated to ripe fruiting patterns in chimpanzee food species (R^2=0,383, p=0.006) (see Figure 11).

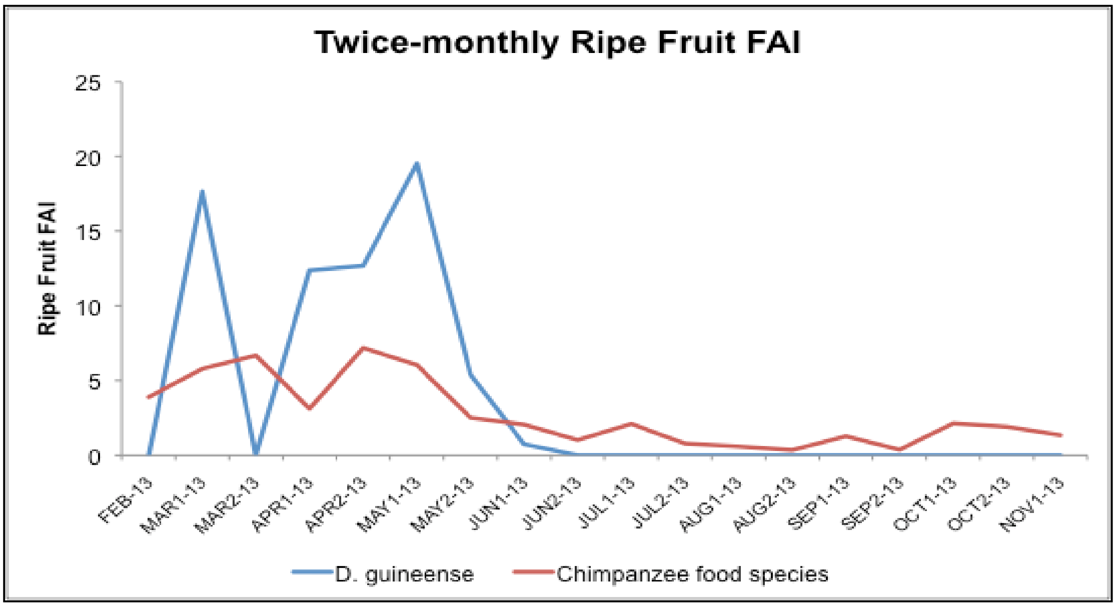

Figure 11 Twice-monthly ripe fruit availability in *Dialium guineense* versus overall chimpanzee food species

Leaf flushing of Chimpanzee food species was significantly associated with availabilities in the new leaves of *Monodora tenuifolia (*R^2=0.568, p<0.001)*, Dialium guineense* (R^2=0.480; p=0.02) and *Elaeis guineensis* (R^2=0.448; p=0.003).

4.4.3 Effects of seasonality

The availability of flowers was significantly positively influenced by temperature, accounting for 65,8% of variation (p<0.001). Likewise, ripe fruit productivity increased with temperature (Fig 12a; R^2=0.362; p=0.01), whilst leaf flushing decreased (Fig. 12b; R^2= 0.331; p=0.02). Ripe fruit availability was inversely associated with rainfall (R_s=-0.805, p≤0.001), as was flower availability (R_s =-0.641; p=0.004). During the study period, ripe fruit was mostly available during the dry season from February to May (mean ripe fruit FAI: dry season 5.54±0.66 versus rainy season 1.53±0.34). In contrast, leaf flushing was positively associated with rainfall (R_s =0.733; p=0.001).

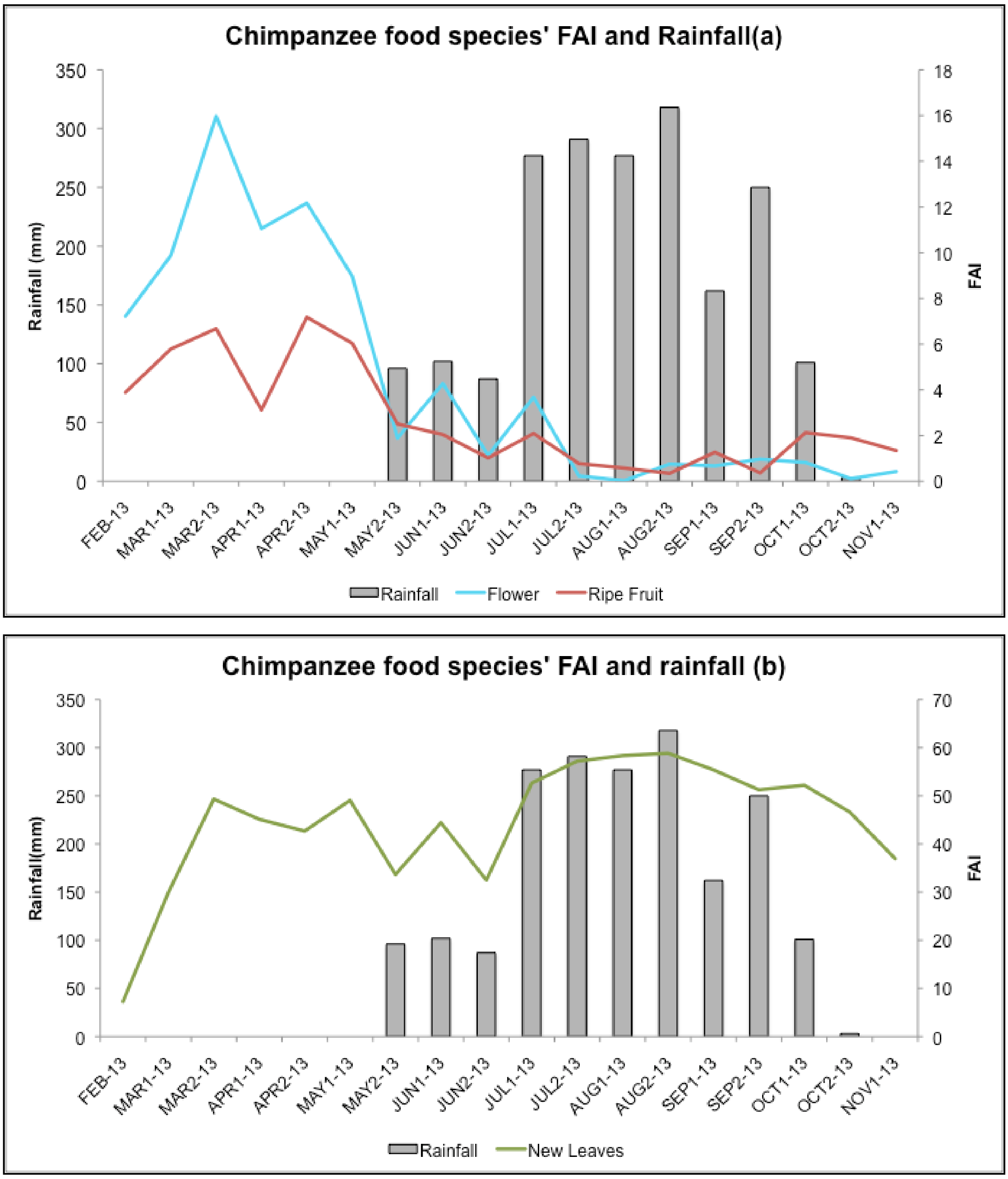

Figure 12. (a) Rainfall in 2013-2014 plotted against ripe fruit and flower availability of chimpanzee food species; (b) Rainfall in 2013-2014 plotted against new leaf availability of chimpanzee food species

4.5 Discussion

4.5.1 Methods and Phenology variations

In this study, phenology quadrats were chosen since there was no previous information on the feeding ecology of this chimpanzee community, which excluded the possibility of establishing fruit trails. Additionally, the scoring method was chosen to capture as much variation in food availability as possible (Chapman *et al.,* 2005). Differences in FAI may occur when comparing twice-monthly and monthly data (Chapman, *et al.,* 1994), potentially due to the presence of frugivorous species that might quickly consume ripe fruits (Fawcett, 2000; McLennan, 2013). Hence, twice-monthly surveys were used in this study to avoid underrepresentation of ripe fruit availability. These results are intended to establish background information to allow detailed examination of this chimpanzee community's feeding behaviour. As such, they are not intended to provide a detailed botanical analysis of Caiquene-Cadique forest.

As predicted, there are strong seasonal variations in the availability of wild fruit, flowers and new leaves at Caiquene-Cadique. Months of high ripe fruit availability were from March to May and low fruit availability from June to November. Ripe fruit availability is higher during the dry season than the rainy season. Conversely, leaf flushing is higher from July to August and lower from May to June, which represents an increase in new leaves during the rainy season.

Variation in phenological patterns is likely related to numerous factors; however, both temperature and rainfall appear to strongly influence food availability at this site. Like many other chimpanzee sites (e.g. Anderson *et al.,* 2005; Hockings, 2007; McLennan, 2010), fruiting is positively correlated with temperature and negatively correlated with rainfall. When analysing phonology data, it is important to examine whether common species drive (or strongly impact) overall fruiting, flowering or flushing patterns and hence drive the FAI. For example, at Bulindi, *Phoenix reclinata* fruit accounts for 90% of the total variation in fruit availability (McLennan, 2010). At Caiquene-Cadique, *Dialium guineense* influenced overall levels of ripe fruit abundance for chimpanzee food species. During the dry season both *D. guineense* and ripe fruit availability for all chimpanzee food species were at their highest. Nevertheless, fruit of *D. guineense* was only available during the dry season. This means that the fruiting patterns for all chimpanzee food species during the dry season might have been driven by *D. guineense*, but the overall fruit availability across both seasons was not. *Monodora tenuifolia* and *Elaeis guineensis* did not impact overall levels of ripe fruit availability, but *Monodora tenuifolia*, *Dialium guineense* and *Elaeis guineensis* did drive patterns of leaf flushing and may have resulted in seasonal variations of new leaf availability.

4.5.2 Fallback foods

Elaeis guineensis and *Ficus spp*. were the best candidates for potential fallback foods. *E. guineensis* is a common species in the forest of Caiquene-Cadique and represents one third of the most common chimpanzee food species in the quadrats. This, and the fact that chimpanzees are known to feed not only on the fruits but also on other parts of the plant (e.g. flower and pith) in many communities (Yamakoshi, 1998; Humle and Matsuzawa, 2004), makes this palm a good potential fallback food. Although, figs are less common than oil-palm, as for other chimpanzee communities (Fawcett, 2000; Marshall *et al.,* 2009; McLennan, 2013), their fruiting patterns across months also makes them good fallback candidates.

Understanding which species function as important fallback foods can assist chimpanzee conservation efforts through the targeted conservation of specific species. At sites where human presence and activities are increasing, every effort should be made to spare important fallback species during slash and burn agriculture. Furthermore, the maintenance of ecological corridors allowing chimpanzees to move between areas containing vital fallback foods might be essential for chimpanzee health and survival during periods of food scarcity (Marshall *et al.,* 2009), in addition to potentially reducing crop feeding activities (Hockings *et al.,* 2009).

4.5.3 Final remarks

During the study period, there is marked seasonal variation in the availability of flowers, ripe fruit and new leaves in Caiquene-Cadique which must be taken into account when investigating the chimpanzees feeding ecology. As this study did not cover a full year, some chimpanzee food species likely remain unidentified (i.e. those that flower, fruit or produce new leaves in December or January) and a food availability index for certain months was not generated. It should also be noted that in addition to inter-monthly variations, variations in food availability are expected to occur inter-annually.

Chapter 5

Feeding ecology of the Caiquene-Cadique chimpanzees

5. Feeding ecology of the Caiquene-Cadique chimpanzees

5.1 Introduction

Habitat loss is one of the main drivers of chimpanzees' decline across Africa (for a more in-depth discussion, see Chapter 2). A growing number of chimpanzee communities now occupy anthropogenic habitats, with growing proximity to human populations (Hockings *et al.,* 2012; Hockings and Sousa, 2012; McLennan, 2013). Until quite recently, very little was known about chimpanzee behavioural adaptations to, and survival in, anthropogenic habitats, including forest-farm mosaics. We are just starting to grasp the complexities of how these great apes exploit such habitats, although there are still many unanswered questions (Hockings *et al.,* 2012; McLennan, 2013). Studying a species feeding ecology in human-influenced environments is one of the most effective ways to assess their ability to cope with changing conditions (Tutin *et al.,* 1997; Chapman *et al.,* 2002; Chapman *et al.,* 2004). Hence, site-specific information on the feeding ecology of a specific chimpanzee community is fundamental in developing appropriate conservation management strategies (Hockings and Humle, 2009; McLennan, 2010; Hockings *et al.,* 2012).

Diet

As ripe fruit specialists (see Chapter 1), ripe fruit represents between 31% and 88% of chimpanzee feeding time (data from 12 study sites; Morgan and Sanz, 2006), with high variation in dietary repertoire across sites (Wrangham, 1977; Nishida and Uehara, 1983; McGrew *et al.,* 1988; Yamagiwa *et al.,* 1996; Fawcett, 2000; Tweheyo and Lye, 2005; Morgan and Sanz, 2006; Pruetz, 2006; Watts *et al.,* 2012; McLennan, 2013). Fruits are rich in sugars, but might be lacking in other nutrients (Milton, 1999). To ensure adequate intake of proteins, fats, fiber and minerals, chimpanzees also consume other food parts including leaves, pith, seeds, flowers, underground storage organs, and insects, among other things (Wrangham, 1977; McGrew *et al.,* 1988; Fawcett, 2000; Tweheyo and Lye, 2005; Morgan and Sanz, 2006; Pruetz, 2006; Hicks, 2010; Hockings *et al.,* 2010a; Potts *et al.,* 2011; Watts *et al.,* 2012; McLennan, 2013). The ingestion of these non-fruit foods varies across communities, and types of foods that might be important in one community might be less important in another. For instance, in the Goualougo Triangle feeding on leaves comprises up to 37% of feeding time (Morgan and Sanz, 2006), whereas in Budongo leaves constitute only 20% of feeding time (Fawcett, 2000, Tweheyo *et al.,* 2004), and at other sites, including Kibale, less than 10% (Thompson and Wrangham, 2008). Flower consumption also varies across sites. For example, it constitutes 4% of feeding time in the Goualougo Triangle (Morgan and Sanz, 2006) and almost 13% at Fongoli and Budongo (Fawcett, 2000; Pruetz, 2006). The use of non-plant foods also varies between communities, with chimpanzees most commonly feeding on ants, termites, larvae, honey (McGrew, 2014), as well as vertebrates such as monkeys. Interestingly, Hicks (2010) reports the potential smashing of giant African land snails by chimpanzees at Bili, Democratic Republic of Congo. However, as mentioned in Chapter 3, mongooses also show this smashing behaviour (Müller, 2010; McAuliffe and Thornton, 2012) limiting the conclusion that can be drawn.

Across chimpanzee sites, fruit availability is highly seasonal (see Chapter 4) and in times of fruit scarcity chimpanzees adjust their diets. This can be achieved in many ways: increasing dietary diversity (e.g. Fawcett, 2000), reducing frugivory or ingesting fallback and staple foods (e.g. McLennan, 2010), feeding on cultivars (e.g. Hockings *et al.,* 2009; McLennan, 2013) and/or expanding foraging range (e.g. Fawcett, 2000; Morgan and Sanz, 2006; Tutin *et al.,* 1997). Although untested, it is likely that chimpanzees inhabiting fragmented and shrinking natural habitats will be under more pressure to adapt their feeding behaviour with reduced potential to expand foraging ranges.

Crop raiding

Cultivated resources are palatable, energy-rich, with low toxicity levels and easily digestible (Forthman-Quick and Demment, 1988; Strum, 1994; Hockings *et al.,* 2009). Additionally, these desirable crops are normally found in clumped distribution (e.g. in orchards and fields), which makes them easily accessible and potentially increasing foraging efficiency (Hockings *et al.,* 2009). These characteristics make them highly desirable, especially in times of wild fruit scarcity (Hockings *et al.,* 2009; Hockings and McLennan, 2012).

On a survey of crop feeding, Hockings and McLennan (2012) showed that there were at least nineteen chimpanzee study sites where cultivar consumption was confirmed. Chimpanzees consume at least thirty-four plant parts from twenty-four cultivated species. As expected crop fruit species are preferred, but chimpanzees also raid a variety of other crop food parts (e.g. sugar cane, banana and rice piths, avocado and papaya leaves) (Hockings and McLennan, 2012).

The degree of exposure to agriculture was found to be related to crop feeding and number of crops consumed (Hockings and McLennan, 2012) (see Figure 13). Even though cultivar consumption is shown to be an increasing and potentially problematic behaviour (Hockings and Humle, 2009), systematic data are lacking on the utilisation of cultivars by different chimpanzee communities. Aside from the present study, crop feeding by chimpanzees has only been studied in depth at two sites: Bossou and Bulindi (see Figure 13).

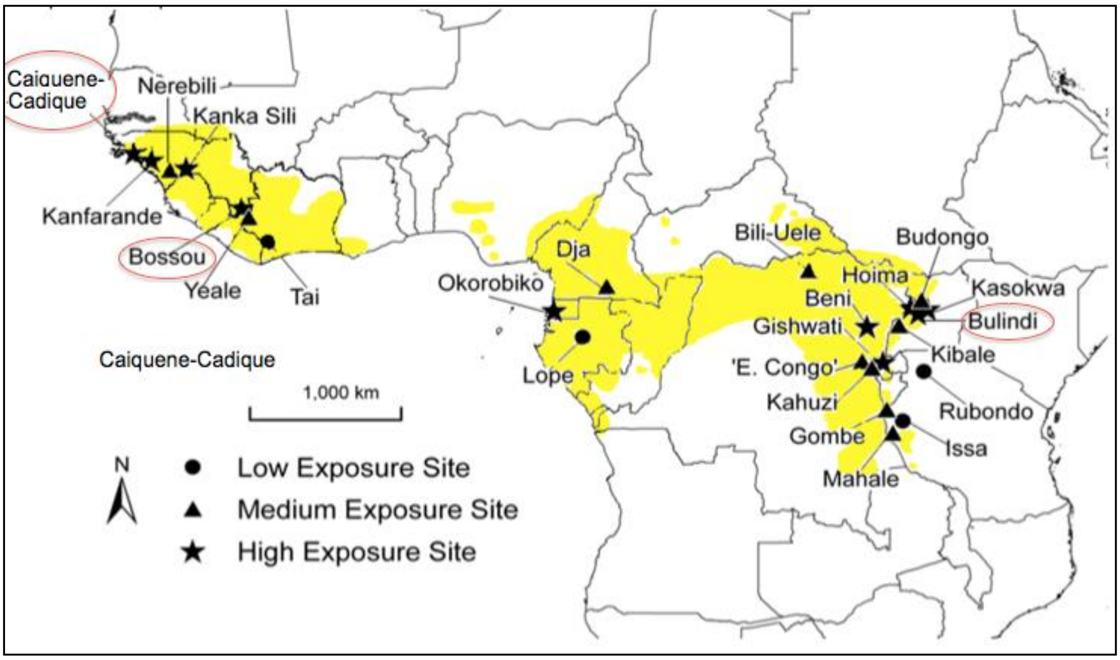

Figure 13 Exposure level to agriculture. In yellow chimpanzee distribution in sub-Saharan Africa; in red are the three sites (Bossou, Bulindi and Caiquene-Cadique) were systematic data on crop feeding has been collected. Adapted from Hockings and McLennan (2012)

Fallback and important foods

When examining chimpanzee feeding ecology, many authors refer to the importance of fallback foods for the survival of this species (Hockings *et al*., 2010; Marshall and Wrangham, 2007; McLennan, 2013; Pruetz, 2006). To standardise the definition of the term ‘fallback food’, Marshall and colleagues (2009) suggest it be used when referring to a food that is consumed by a particular animal species at an inverse proportion to the availability of the said species’ preferred foods. Another particularly vital food group is referred to as ‘important food’; these are the foods that are most frequently consumed when available (Marshall *et al.,* 2009; McLennan, 2013). As these two classes of foods likely have significant roles in chimpanzee survival, special effort should be taken to identify them, and where possible, incorporate them into site-specific habitat and biodiversity management strategies (Pruetz, 2006; Marshall *et al.,* 2009; McLennan, 2013).

Methodological considerations

When working with populations that are fully habituated, researchers normally only rely on observational data (e.g Nishida and Uehara, 1983; Reynolds, 2005; Tweheyo and Lye, 2005), but when populations are not fully habituated the collected data will be biased towards certain foods due to the visibility of the individuals (Wrangham *et al.,* 1991). In un-habituated communities, observations of the chimpanzees are rare and opportunistic. Under these circumstances, authors rely on the analyses of faecal data (McGrew *et al.,* 1988; Hernandez-Aguilar, 2006; Moscovide *et al.,* 2007; McLennan, 2010; Hicks, 2010; Phillips and McGrew, 2014). However, faecal data are not free from bias either. Chimpanzees tend to ingest fruits whole and, because of the dispersal adaptations of many plants, their seeds normally pass through the chimpanzee’s gut intact (Tutin and Fernandez, 1993). This translates to an overestimation of fruits in diet vs. non-fruit food parts (e.g Lambert, 1998; Doran *et al.,* 2002; Pruetz, 2006; McLennan, 2013; Phillips and McGrew, 2013; 2014). Phillips and McGrew (2014:9), after comparing faecal analyses and feeding observations from the same chimpanzee community, concluded “that quantified proportions of frugivory, folivory, and faunivory in faecal samples are valid proxy measures of time spent feeding on various food items”. Therefore, as long as the sampling and analyses are done in a continuous and standardized way, indirect methods are the best option (Phillips and McGrew, 2013; 2014).

This chapter will present detailed information on the feeding ecology of the chimpanzees at Caiquene-Cadique in order to better understand their strategies in coping with variations in wild food availability and the costs and benefits of inhabiting an anthropogenic habitat. This community is the most westerly chimpanzee community studied to date, and inhabit a unique mosaic of forest, savannah, mangrove, and agricultural areas, which makes understanding their feeding adaptations all the more interesting.

5.2 Hypothesis

1. Certain foods that are available year-round or during periods of food scarcity will be consumed at greater levels during periods of food scarcity – fallback foods.
2. Certain fruit species will be eaten at higher proportions than others when available – important foods.
3. In times of fruit scarcity, the chimpanzees will increase their ingestion of non-fruit foods.

5.3 Methods and analyses

For complete methods, see chapter 3.

5.3.1 Data analyses

5.3.1.1 Food classification

The data collected during the study period was compiled and is presented in the form of a species list. This list contains all information concerning all plant foods consumed, including species and family names, life forms (tree, shrub, herb, climber or grass) and part ingested (fruit, leaf, pith, flower, seed, bark and sap). Scientific nomenclature and life forms followed *Plantas vasculares e Briófitos da Guiné-Bissau* (Catarino *et al.*, 2006). Subsequent analyses only include faecal data unless otherwise stated. Following McLennan (2010:104) definitions for the classification of chimpanzee fruits (see Table 2), important fruits (i.e. present in ≥50% samples in ≥1 month or >10% of total faecal samples) were identified. An attempt to identify preferred, fallback and staple foods was also made.

Table 2 Definition of food classifications (taken from McLennan, 2010)

Classification	**Definition**
Important fruit species	Present in ≥50% of faecal samples in one or more months or in >10% of all samples
Preferred fruit species	Presence in faecal samples increases with the increase of its availability
Staple food	Present throughout the year, not necessarily in accordance with availability
Fallback food	Available year-round or extended periods (>6 months), present in samples inversely to fruit availability and/or fruit consumption

5.3.1.2 Analyses of faecal sample data

During the study period, 377 faecal samples were collected in total with high monthly variation (monthly mean= 41.9±7.480 N=9, range 7-70). The samples were collected on an average of 9.2 days per month (±1.5 SD, range 2-16). The mean number of samples collected per day (excluding days where no samples were collected) was 4.2 (±0.5 SD). High monthly variation in the number of samples collected and the number of days that samples were collected is a direct consequence of only two weeks spent collecting data in June and October. For this reason, monthly faecal data were divided into two groups, month 1 (first and second weeks of the month) and month 2 (third and fourth weeks of the month). The months of June and October only represent a group each. Hereafter, this data will be referred to as *twice-monthly* faecal data.

For each half month a food score of average percentage of a food type was calculated. To evaluate if twice-monthly sample size affected measures of fruit consumption, the same approach as Doran *et al*. (2002) was used. Using *parametric Linear regression tests*, the effect of number of samples collected was tested for: i) twice-monthly mean number of fruit species per sample (R^2=0.068, ns); ii) total number of fruit species in samples per month (R^2=0.138, ns); iii) fruit score, i.e. percentage of fruit in diet (R^2=0.007, ns). The number of samples collected did not affect any of the assessments of fruit diversity or fruit quantity.

5.3.2 Statistics

Only twice-monthly FAI values of chimpanzee food species were used in this chapter. In order to compare them with the data from faecal samples, 16 twice-monthly groups of faecal data were created. Data were checked for normality using

Shapiro-Wilk test and normality *Q-Q plot*. When data were not normally distributed, a *square root* transformation was done. Parametric *Linear regression* tests were used to test relationships between dependent and independent variables. When the assumptions for parametric test were not met, non-parametric *Spearmen correlation coefficient* was used (Field, 2009). All statistical analysis was done using SPSS version 20.

5.4 Results

5.4.1 Dietary composition – Plant foods

5.4.1.1 Species list

A list of the plant food species consumed by chimpanzees at Caiquene-Cadique, between the months of February to October 2013 is shown in Table 4. This list compiles data from direct observations, feeding traces and faecal samples.

A minimum of 83 plant food items from 66 species (57 identified and 9 unidentified), from at least 28 families were consumed during the study period. Nine of these species were cultivars. There was no evidence that mangrove species were consumed. It was not possible to distinguish some species of the genus *Ficus* due to the size and similarity of seeds found in faecal samples. This means that the known list of food species may be underestimated. Five seeds found in the chimpanzees' faeces and four species found in feeding traces could not be identified and are referred in Table 4 as *unknowns*. Evidence of consumption for the majority of food items was indirect. 41 food items were found in faecal samples, 58 found in feeding traces and 8 were observed being eaten. Only 6 species were confirmed by all three methods.

5.4.1.2 Parts eaten

Table 3 shows the percentage of each food part eaten by this chimpanzee community. Fruits dominated the diet, representing 64.3% of total food items consumed. The fruits of at least 52 species were consumed, with fruits of the Moraceae family consumed the most (a total of six species). Fruits were normally eaten ripe, but in the rainy season, when fruit was scarce a small percentage of certain fruits were consumed unripe (e.g. *Mangifera indica* and *Landolphia heudelotti)*.

In addition to fruits, other plant parts consumed included leaves, pith, bark, flowers and sap. The only non-plant food that was confirmed to be eaten by this community of chimpanzees was honey, which was confirmed in 30 faecal samples (7.97% of samples).Leaves from at least 17 species were eaten (20.2% of plant foods). Of these, at least four species were swallowed whole (*Antiaris toxicaria, Chasmopodium caudatum, Ficus exasperata* and *Tetracera potatoria*) and were easily identifiable in the faeces; however, these appeared in a very low percentage (1.6%) of faecal samples. Pith of at least 7 species and bark of at least 3 species were confirmed in faeces. The ingestion of only two species of flowers and the sap of one tree were also confirmed.

Table 3 Breakdown of plant food species consumed by chimpanzees at Caiquene-Cadique by part eaten.

Plant Part Eaten	n	%
Fruit	53	64.3
Leaf	17	20.2
Pith	7	8.3
Bark	3	3.6
Flower	2	2.4
Sap	1	1.2
Total	83	100

Table 4 List of plant food items consumed by chimpanzees at Caiquene-Cadique (in alphabetical order), from February to October 2013. For each species or species group the following information is listed: family, life form, part eaten, criteria used to determine consumption, and months in which the species was recorded eaten (Table layout adapted from McLennan 2010).

No.	Scientific name	Family	Life form	Part eaten	Criteria	Feb 13	Mar 13	Apr 13	May 13	Jun 13	Jul 13	Aug 13	Sep 13	Oct 13
1	*Adansonia digitata* *	Bombacaceae	Tree	Fr / L	T / F	●	●			◇	●	◇●		
2	*Aframomum alboviolaceum*	Zingiberaceae	Herb	Fr	F									◇
3	*Aframomum sp.*	Zingiberaceae	Herb	P	T					●	●			
4	*Albizia ferruginea*	Leguminosae / Fabaceae - Mimosoideae	Tree	L	F	◇								
5	*Ampelocissus bombycina*	Vitaceae	Vine	Fr	T / F						●		●◇	●◇
6	*Anacardium occidentale* *	Anacardiaceae	Tree	Fr	T / F / O		●	●◇	●◇★					
7	*Anisophyllea laurina*	Rhizophoraceae	Tree	Fr	F			◇	◇					
8	*Antiaris toxicaria*	Moraceae	Tree	Fr / L	F	◇	◇							
9	*Borassus aethiopum*	Palmae / Arecaceae	Tree	Fr	T				●					
10	*Cajanus cajan* *	Leguminosae / Fabaceae - Papilionoideae	Shrub	Fr	T	●								
11	*Carica papaya* *	Caricaceae	Tree	Fr / L / P	T							●	●	
12	*Ceiba pentandra*	Bombacaceae	Tree	Fr / Fl / B	T / F	●◇	●◇	●◇						
13	*Chasmopodium caudatum*	Gramineae / Poaceae	Grass	L	F				◇				◇	
14	*Citrus aurantifolia* *	Rutaceae	Tree	Fr	F						◇	◇	◇	
15	*Citrus sinensis* *	Rutaceae	Tree	Fr	T / F	◇					●		●	
16	*Combretum micranthum*	Combretaceae	Shrub	Fr	T	●								
17	*Detarium senegalense*	Leguminosae / Fabaceae - Caesalpinioideae	Tree	Fr	T	●								
18	*Dialium guineense*	Leguminosae / Fabaceae - Caesalpinioideae	Tree	Fr / L	T / F	●◇	●◇	●◇	●◇	●◇	●◇	●◇	◇	
19	*Diospyros heudelotii*	Ebenaceae	Tree	Fr	T						●			
20	*Drypetes floribunda*	Euphorbiaceae	Tree	Fr	T / F							●◇		

No.	Scientific name	Family	Life form	Part eaten	Criteria	Feb 13	Mar 13	Apr 13	May 13	Jun 13	Jul 13	Aug 13	Sep 13	Oct 13
21	*Elaeis guineensis*	Palmae / Arecaceae	Tree	Fr / FL / L / P	T / F / O	●◇★	●◇	●◇★	●◇	●◇★	●◇	●◇	●◇★	●◇
22	*Ficus exasperata*	Moraceae	Tree	L	F	◇						◇	◇	
23	*Ficus sansibarica*	Moraceae	Tree	Fr / B	T	●								
24	*Ficus sp.*	Moraceae	Tree	Fr / B	T / F/O	●◇	●◇	●◇★	●◇	◇	◇	◇	◇	
25	*Ficus sur*	Moraceae	Tree	Fr	T			●	●	●		●		
26	*Hibiscus sabdariffa* *	Malvaceae	Herb	L / P	T				●					
27	*Landolphia heudelotti*	Apocynaceae	Climber	Fr	T / F / O			●◇	●◇★	●◇	●◇	◇	◇	◇
28	*Landolphia hirsuta*	Apocynaceae	Climber	Fr (?) / P	T								●	
29	*Lecaniodiscus cupanioides*	Sapindaceae	Shrub	Fr	T						●			
30	*Macrosphyra longistyla*	Rubiaceae	Tree	Fr	F	◇	◇							
31	*Mafer phyllanthus*	Euphorbiaceae	Shrub	Fr	T / F		●	●	◇					
32	*Malacantha alnifolia*	Sapotaceae	Tree	Fr	F					●◇	●◇			
33	*Mangifera indica* *	Anacardiaceae	Tree	Fr	T / F		●	●	●◇	●				
34	*Memecylon afzelii*	Melastomataceae	Tree	Fr	T							●		
35	*Milicia regia*	Moraceae	Tree	Fr / L	T / F	●◇	◇	◇	◇			●		
36	*Monodora tenuifolia*	Annonaceae	Tree	Fr	T / F						●	◇	◇	
37	*Neocarya macrophylla*	Chrysobalanaceae	Tree	Fr	T / F	●◇	◇							
38	*Newbouldia laevis*	Bignoniaceae	Tree	L	T	●		●			●			
39	*Parinari excelsa*	Chrysobalanaceae	Tree	Fr / L	T / F / O	●◇	●◇	●◇						
40	*Parkia biglobosa*	Leguminosae / Fabaceae - Mimosoideae	Tree	Fr	T / O				●★	●	●			
41	*Pentaclethra macrophylla*	Leguminosae / Fabaceae - Mimosoideae	Tree	Fr	T	●								
42	*Phoenix reclinata*	Palmae / Arecaceae	Tree	Fr	F					◇	◇			
43	*Pseudospondias microcarpa*	Anacardiaceae	Tree	Fr	T / F	◇		●◇	◇					
44	*Ricinodendron heudelotii*	Euphorbiaceae	Tree	Fr / S	T / F							◇	●◇	◇
45	*Rothmannia whitfieldii*	Rubiaceae	Shrub	L	T								●	

No.	Scientific name	Family	Life form	Part eaten	Criteria	Feb 13	Mar 13	Apr 13	May 13	Jun 13	Jul 13	Aug 13	Sep 13	Oct 13
46	*Saba senegalensis*	Apocynaceae	Climber	Fr	T / F		●	●	●	●◇	●◇			
47	*Saccharum officinarum* *	Gramineae / Poaceae	Herb	P	T								●	
48	*Sarcocephalus latifolius*	Rubiaceae	Climber	Fr	T						●	●	●	
49	*Spondias mombin*	Anacardiaceae	Tree	Fr	T / F						◇	◇	●◇	◇
50	*Strombosia pustulata*	Olacaceae	Tree	Fr	F	◇								
51	*Tabernaemontana africana*	Apocynaceae	Shrub	Fr	T		●	●	●					
52	*Tetracera potatoria*	Dilleniaceae	Tree	L	F								◇	
53	*Treculia africana*	Moraceae	Tree	Fr	T / F / O	●◇	●◇★	●◇	●◇		●	●◇	◇	
54	*Trichilia monadelpha*	Meliaceae	Tree	L	T							●		
55	*Triclisia patens*	Menispermaceae	Climber	Fr	T / F						●◇			
56	*Uvaria chamae*	Annonaceae	Climber	Fr	T / F							◇	●◇	●◇
57	*Vitex doniana*	Verbenaceae	Tree	Fr	F									◇
58	*unknown #1*	unknown	-	L	T								●	
59	*unknown #2*	unknown	-	Fr	F						◇			
60	*unknown #3*	unknown	-	Fr	F					◇	◇			
61	*unknown #4*	unknown	-	Fr	T / F						●◇			
62	*unknown #5*	unknown	-	Fr	F						◇			
63	*unknown #6*	unknown	-	Fr	F									◇
64	*unknown #7*	unknown	-	P	T				●					
65	*unknown #8*	unknown	-	Fr	T						●			
66	*unknown #9*	unknown	Tree	L	O		★							

Part eaten: FR= Fruit; L=Leaf; P=pith; Fl=Flower; B=Bark; Sp= Sap
Criteria: F=Faecal sample; T= feeding trace; O=Observation
Symbols: ◇= Faecal sample; ● = Feeding traces; ★= Observation; *= Cultivar

5.4.1.3 Frugivory

Fruit was consumed in all sampled months, and was consistently the most represented food part (see Figure 14).

Fruit was present in 97.9% of faecal samples. The average monthly fruit score was 79.51 (±2.8 SD, range 71.3-94.4). May, June and July were the months with the highest fruit scores (≥87%), whereas March had the lowest fruit score (71.3%). The availability of ripe fruit was not a predictor of chimpanzees twice-monthly fruit score (R^2=0.023, ns).

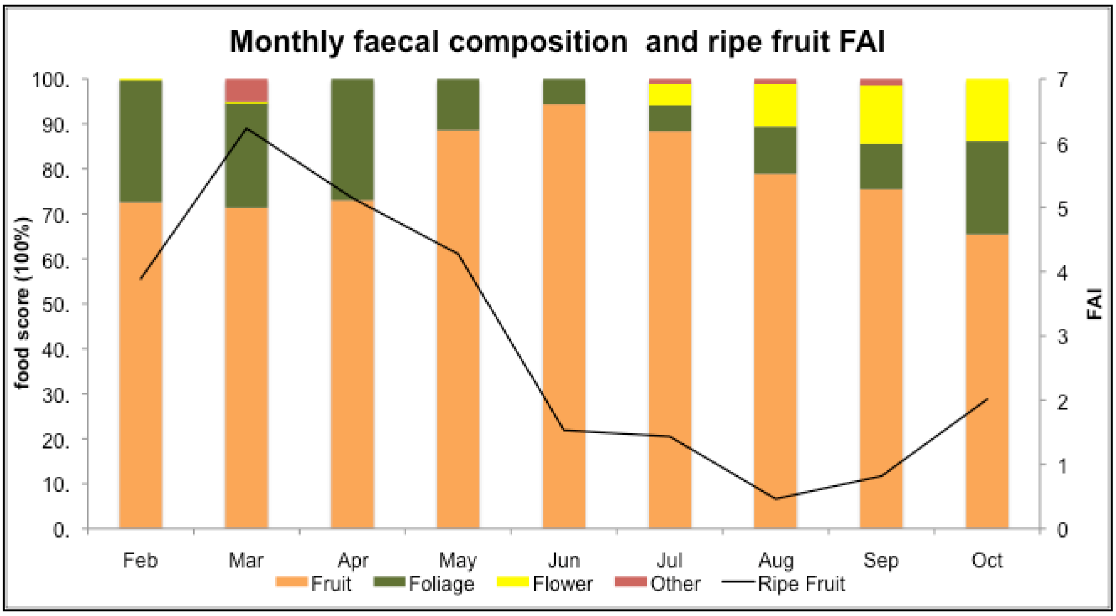

Figure 14 Monthly faecal composition (fruit score; foliage score; flower score; other score) vs. Ripe fruit availability (FAI)

Diversity of fruit in the diet

The mean number of fruit species per dung was 2.4 ± 0.05 SD (range 0-6). It is important to note that in many samples it is possible that the number of fruit species present exceeded the ones that were recorded. This is because the number of species was mainly obtained from seeds present in samples and not from soft parts, which are difficult or even impossible to identify to a taxonomic level. Like fruit scores, the mean number of species per sample was not significantly related to FAI of ripe fruit (R^2=0.151, ns). The average number of total food species found each month was 11,9 ±0.68 SD (range 9-14), and showed no significant relation ripe fruit FAI values (R^2=0.176, ns).

Important fruit species

The chimpanzees' diet was dominated by certain fruit species that were present every month and in the majority of samples. Ten species (including one species group) were identified as being *important food* species for this chimpanzee community (see Table 5). These include seven tree species and three lianas. The mean number of important species that were present in ≥50% of monthly samples ranged from one to two. This number was not related to fruit score (R_S=0.188, p>0.05) nor fruit availability (R_S=-0.598, p=0.089), although an inverse tendency was apparent in the latter.

Preferred food species

Fruit availability for all ten important species was monitored in the quadrats. Eight of these species (*Ceiba pentandra, Dialium guineense, Landolphia heudelotti, Parinari excelsa, Saba senegalensis, Spondias mombin, Treculia africana, Uvaria chamae)* fruited seasonally, with fruiting periods of between 2 to 5 months. Chimpanzees fed heavily on these species when they were fruiting, which fits the definition of preferred food species. However, some of these fruits would appear in the faecal samples after their recorded fruiting season which is explained by the number of trees that were monitored, and that the same tree species in different parts of the habitat might have slightly unsynchronized fruiting.

Fallback foods

The other two ‘important food’ species had different fruiting patterns, and were available during all or most of the monitored months (see Chapter 4). As such, these species, *Ficus spp*. and *Elaeis guineensis,* were considered potential fallback foods.

Different fig *species* could not be distinguished taxonomically in the faecal samples, and for that reason *Ficus* was analysed as group. Figs were present in 45,6% of all faecal samples, with an average monthly score of 13%. *Ficus spp*. scores in the faecal samples were not related to its availability (R^2=0.001, ns). Fig intake did not depend on overall fruit consumption (R^2=0 p>0.05).

The fruits of *Elaeis guineensis* were present in 20.2% of all faecal samples, with an average monthly score of 4.18% ± 1.50 SD (range 0-20.41). Oil-palm fruit score was inversely related to its availability (R^2=0.310, p=0.025), but its use was not correlated with total fruit score (R^2=0.004, p>0.05).

Furthermore, other parts of the oil-palm were frequently eaten (also see following sub-section on foliage consumption). The flower of *Elaeis guineensis* appeared in 17.5% of all faecal samples, with an average monthly score of 4.70% ±1.65 SD (range 0-16.50). The flower score of oil-palm was not related to its availability (R_s=-0.003, p>0.05), ripe fruit availability (R_s=-0,448, p=0.062), or fruit score (R_s=0.89, p>0.278).

Table 5 Important fruit species in the diet of chimpanzees at Caiquene-Cadique, from February to October 2013. Data from total faecal sample (N=377)

Species	**Life form**	**% Total samples**	**% Monthly samples containing each important species**									**Mean monthly % in sample**	**# Months in sample**	**# Months in ≥50% samples**
			Feb	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**			
Ficus spp.	Tree	45,1	**88,1**	**63,6**	45,3	**53,5**	12,5	32,7	43,6	1,9	-	38,6	8	3
Dialium guineense	Tree	33,4	7,1	31,2	**64,2**	**55,8**	**62,5**	**58,2**	7,7	1,9	-	32,2	8	4
Elaeis guineensis	Tree	30,8	9,5	2,6	7,5	14,0	25,0	47,3	**51,3**	**90,4**	**71,4**	35,0	9	3
Spondias mombin	Tree	17,2	-	-	-	-	-	1,8	**64,1**	**73,1**	14,3	17,0	4	2
Landolphia heudelotti	Shrub/Climber	14,1	-	-	-	-	-	40,0	38,5	15,4	14,3	12,2	4	0
Parinari excelsa	Tree	14,1	**64,3**	29,9	5,7	-	-	-	-	-	-	11,1	3	1
Treculia africana	Tree	11,4	11,9	19,5	22,6	9,3	-	-	5,1	3,8	-	8,0	6	0
Saba senegalensis	Climber	10,9	-	-	-	-	**50,0**	32,7	-	-	-	9,2	2	1
Ceiba pentandra	Tree	10,3	9,5	39,0	9,4	-	-	-	-	-	-	6,4	3	0
Uvaria chamae	Shrub/Climber	7,7	-	-	-	-	-	-	2,5	44,2	**71,4**	13,1	3	1
# fruit species in ≥50% of monthly samples			**2**	**1**	**1**	**2**	**2**	**1**	**2**	**2**	**2**			

5.4.1.4 Foliage consumption

Foliage comprised leaves and piths, and was present in 48.27% of all samples, representing an average monthly score of 16.03% (±3.03 SD, range 5.63-27.19) (see Figure 14). February to April and October were the months with the highest foliage scores. The months with the lowest scores were June and July (5,6% in each month).

Foliage scores were positively related with fruit availability ($R^2=0.260$, $p=0.030$), i.e. when there was high availability of fruit the percentage of foliage consumed was higher. However, foliage scores were negatively correlated with fruit score ($R^2=0.645$, $p<0.001$): fruit consumption explained a high proportion of variance in foliage consumption

Leaf consumption

Leaves were present in faecal samples across all months, in a total of 36.9% of all faecal samples, with an average monthly score of 12.27% (±2.55 SD, range 2.22-23.57). Leaf scores were significantly positively related to fruit availability ($R^2=0.26$, $p=0.031$), but not significantly related to leaf availability ($R^2=0.066$, $p>0.05$). Leaf scores were negatively related to fruit scores ($R^2=0.493$, $p=0.002$). The consumption of leaves did not depend on its availability but it increased when less fruit was consumed.

Pith consumption

Pith was present in 18.57% of all faecal samples, with an average monthly score of 3.67% (±1.78 SD, range 0-10.76). Pith intake was not related to fruit availability ($R^2=0.082$, $p>0.05$), but was negatively related with fruit score ($R^2=0.256$, $p=0.046$). The consumption of pith increased when fruit consumption fell.

5.4.1.5 Flower consumption

Flowers were present in 18.57% of all faecal samples, with an average monthly score of 4.8% (±2.11 SD, range 0-15.71). In Figure 14 there is a noticeable increase in flower consumption from July to September. Flower consumption was greatly correlated with oil-palm flower consumption ($R_s=0.97$, $p\leq0.001$), and inversely correlated with flower availability ($R_s=-0.531$, $p=0.023$). However, it was not significantly related to either fruit availability ($R_s=-0.308$, $p=0.078$) or fruit score ($R_s=-0.393$, $p>0.05$). Flower consumption was driven by oil-palm flower consumption.

5.4.2. Cultivar consumption

Cultivar species represented 13.4% (n=9 of 66) of all consumed species. From the nine species of cultivars, ten food parts were eaten. Seven were fruits, two were leaves and one was pith. Only five cultivar species were present in faecal samples: *Adansonia digitata* (baobab); *Anacardium occidentale* (cashew), *Citrus aurantifolia*[1] (lime), *Citrus sinensis* (orange) and *Mangifera indica* (mango). Cultivars were present in 3.98% of all faecal samples, with a low monthly average score of 0.7% (±0.39 SD, range 0-2.67). Lime was found in 5 faecal samples (1.33%), baobab and cashew in 3 faecal samples (0.79%), orange and mango in 2 faecal samples (0.53%). Variations in the consumption of cultivars were not related to fruit scores ($R_s=0.301$, $p>0.05$) nor fruit availability ($R_s=-0.404$, $p>0.05$): cultivars were not consumed when wild fruit consumption was low or when wild fruits had low availability (See Table 6).

The characteristics of cultivars consumed by chimpanzees at Caiquene-Cadique (e.g. lack of seed for cashew; or very large size of seed for mango) likely resulted in an underestimation of cultivars consumed through analyses of faecal traces

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[2] This is a species of lime, and even though it is likely to be *Citrus aurantifolia* there is no confirmation to date.

only. Therefore feeding trace data were also analysed to gain a more comprehensive understanding of the importance of cultivars to this community. Of 463 feeding traces, 61 were crops (13.17%). Of these, chimpanzees mostly consumed cashew fruit[3] (3.89%; n=18) and mango fruit (3.89%; n=18), followed by orange fruit (1.30%; n=6), baobab fruit (1.30%; n=6) and sugar cane pith (*Saccharum offinarum*; 1.30%; n=6), papaya fruit, leaf and pith (*Carica papaya,* 0.65%; n=3), and pigeon pea seed (*Cajanus cajan,* 0.43%; n=2). Only one trace (0.22%) of hibiscus leaf consumption (*Hybiscus sabdariffa*) was found.

The chimpanzees were rarely observed feeding on cultivars: only twice on cashew (1.96% of total observation; N=102) and once attempting to feed on oranges at the back of a house.

Table 6 Crop species consumed by chimpanzees at Caiquene-Cadique, including part eaten and percentages found in faeces and feeding traces.

Crop species	**Part(s) eaten**	**% faecal samples**	**% feeding traces**
Adansonia digitata	Fruit	0.79	1.30
Anacardium occidentale	Fruit	0.79	3.89
Cajanus cajan	Fruit	-	0.43
Carica papaya	Fruit / Leaf / Pith	-	0.65
Citrus aurantifolia	Fruit	1.33	-
Citrus sinensis	Fruit	0,53	1.30
Hybiscus sabdariffa	Leaf	-	0.22
Mangifera indica	Fruit	0.53	3.89
Saccharum offinarum	Pith	-	1.30
Total		**3.98**	**13.17**

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[3] The cashew fruit is in fact a pseudofruit (Hockings and Sousa, 2012)

5.4.3 Dietary composition – Non-plant foods

5.4.3.1 Honey consumption

Only one non-plant item – honey - was confirmed to be eaten by the Caiquene-Cadique chimpanzees. Honey was present in 7.96% of all samples with a low monthly average score of 0.97% (±0.55 SD, range 0-5.10) (see Figure 14). Honey consumption was not related to fruit score (R_s=0.054, p>0.05) nor fruit availability (R_s=0.423, p>0.05).

5.4.3.2 Snail-smashing – chimpanzees or mongooses?

Potential indirect evidence of giant African land snail (*Achatina sp.*) smashing and consumption was found in humid parts of the Caiquene-Cadique forest. Although snail-smashing remins unconfirmed, data are presented in this thesis due to the rarity of the behaviour across chimpanzee communities and the potential subsistence importance to the chimpanzees. However, caution is urged when interpreting these results.

During the study period thirty-nine "snail-smashing sites" were identified. These smashing sites were associated with trees with big buttress roots and lianas, or trees with adequate smashing surfaces (e.g. bifurcation of trunk). Smashing sites contained the fragmented shells of giant African land snails and smashing surfaces, often with smashing marks in their surface. On two occasions (include dates), the discarded half-eaten meaty parts of the snails were found.

At the beginning of the study period in the dry season, 30 smashing sites were found with an average estimated age of 6.7 months (0.55 SD, range 1-12). During the rainy season (when the snails come out of hibernation to breed: Plummer, 1975), 9 new smashing sites were identified, and 5 of the previously identified sites had new signs of smashing. The average estimated age for these new sites was 8.3 days (1.78 SD, range

1-21). The total number of snails confirmed was 127, with a total of 704 shell fragments (of greater than 1cm in size) identified. The mean number of snails found per site was 3.1 (0.6 SD), but ranged between one and 17 snails. The average number of fragments at each site was 17.2 (4.83 SD, range 1-146). The mean shell spread from the smashing surface was 107.4 cm (18.63 SD, range 0-400). The mean maximum distance of fragments from the smashing site was 61.3 cm (12.3 SD, range 10-200). Overall, 8 smashing sites had evidence of being re-used, i.e. shells of dissimilar age were found with different degrees of discoloration and soil sedimentation.

There was no evidence in chimpanzee faeces that confirmed the consumption of snails by this community nor were there any direct observations of the behaviour. The best evidence that chimpanzees do in fact engage in this smashing behaviour is circumstantial. On one occasion the chimpanzees vocalised in proximity to an identified snail-smashing site. When JB visited the site 2.5 hours later, large teeth marks (canine teeth marks that were approximately 10cm apart) consistent with a chimpanzee bite were found in the meaty part of a snail that was discarded. The large size of the bite marks are not consistent with mongoose jaw size, and as chimpanzees are neophobic (e.g. Ueno and Matsuzawa, 2005), it is unlikely that an individual would bite into the discarded food remains of another species.

5.5 Discussion

5.5.1 Dietary composition

Chimpanzees' dietary diversity has been found to be positively correlated with study duration and time devoted to data collection (Nishida and Uehara, 1983; Tutin and Fernandez, 1993; McLennan, 2010). It is also influenced by the type of data collection, whether indirect methods are used to determine feeding behaviour, such as faecal samples (see Figure 15) and traces (see Figure 16), or direct observations (see Figure 17) of the feeding itself. In this study, 83 plant food items from 66 species were identified as being part of the Caiquene-Cadique chimpanzee community's diet. This is consistent with other short term studies investigating the feeding ecology of un-habituated chimpanzees (see Table 7). For example, McLennan (2010) confirmed 96 food parts from 82 species in a 16 month study at Bulindi in Uganda. However, as expected, it is significantly less that figures reported from long-term studies; for example 16 year studies at Mahale in Tanzania (Nishida and Uehara, 1983) and Bossou in Guinea (Humle, 2011) identified a rich dietary diversity of plant food consumed, including 328 food parts from 198 species and 246 food parts from 226 species respectively. Our data support the idea that study duration is positively related to diet diversity. For detailed information of chimpanzee's diet composition across Africa, see Table 7. Although the Caiquene-Cadique chimpanzee community inhabits a fragmented and disturbed habitat their diet is not as impoverished as might have been expected, and they manage to maintain a varied diet comparable to other chimpanzee communities with comparable short-term research histories and data collection techniques, including Bulindi in Uganda (McLennan, 2010). There was no evidence that mangrove species were consumed at this site, although chimpanzees did rave through the mangrove area at low tide.

Of the 84 plant food items recorded consumed at Caiquene-Cadique, 64% were fruits followed by 20% leaves. All other food items represented less than 10% of the chimpanzee diet. Morgan and Sanz (2006) calculated, that the mean proportion of fruits in chimpanzee diets across Africa is 55% (range 31%-88%), and 18.7% for leaves. The results from Caiquene-Cadique fall within this range. However, due to indirect data collection techniques, these preliminary data are most likely biased towards an overestimation of fruit compared to non-fruit.

More specifically, in agreement with the hypothesis, the intake of fruit (i.e. % of fruit in faecal samples) was higher than any other food part during all months, with a monthly average of 79.5%. The average number of fruit species found per sample was 2.4, which is again comparable to other chimpanzee communities (see McLennan, 2010). This value might be underestimated since fruit pulp and skin are difficult to identify in dung and only seed species were used to estimate the number of fruit species per dung. Contrary to expected, fruit intake did not vary with the availability of wild ripe fruit, nor did the total number of species consumed per month. These results may be due to several non-mutually exclusive reasons. Firstly, phenology quadrats might have not been an exact sample of the habitat's trees, even though more than 50% of food species were present in the quadrats. Secondly, fruiting patterns across the habitat might be unsynchronised. Or lastly, during certain periods, the chimpanzees might explore different parts of the habitat and exploit different food species, although due to human settlements and cultivated areas the potential for this is limited. Nevertheless, it was evident that during the rainy season chimpanzees were more dispersed within their home range and foraged in smaller parties. In the same period, chimpanzees increased consumption of liana fruits, such as *Landolphia heudelotii*, *Saba senegalensis* and *Uvaria chamae*, which were generally non-fleshy and located in closed secondary forest and forest-savannah and mangrove edge.

As hypothesised, during the study period ten species including *Ficus spp*. were identified as important fruits to chimpanzees at Caiquene-Cadique, forming the majority of their diet in one or more months. For eight of these species, consumption increased with availability. Fig had an almost constant availability and as its intake did not depend on this, and consumption showed variations across time, it is classified as a non-preferred food.

Fallback foods

Fallback foods have already been described as fundamental for chimpanzee's survival, especially in anthropogenic habitats (Pruetz, 2006; Marshall, *et al.,* 2009; Hockings *et al.,* 2010a; McLennan, 2013). Although this was a short-term study and data collection did not cover a complete year, the potential for certain species and parts to act as fallback foods for this community are outlined. In total, three plant species and their parts that showed year-round presence were tested for their potential 'fallback' role: Ficus fruit, oil-palm fruit, and oil-palm flower. *Ficus spp*. were present in 45.6% of all samples, a value which is quite high, but lower than other sites (e.g. at Bulindi in Uganda, *Ficus spp* were present in 65-99% of samples; McLennan, 2010). This species group has been identified as a fallback food at many chimpanzee sites across Africa (Tutin *et al.,* 1997; McLennan *et al.,* 2013), whereas at others it has been considered preferred or staple food (e.g. Pruetz, 2006; Yamagiwa and Basabose, 2009). For chimpanzees at Caiquene-Cadique, fig fruit consumption was not inversely correlated with wild fruit availability nor overall fruit intake, and it did not vary with fig availability. For this community, figs do not function as preferred or fallback foods, but fit the description of a staple food.

Lipid rich *Elaeis guineensis* fruits were present in 20.2% of all faecal samples. At many sites, palm fruits have been identified as fallback foods (e.g. Tutin *et al.,* 1991; Yamakoshi, 1998). At Caiquene-Cadique, like figs, oil-palm fruit consumption was not related to ripe fruit availability, palm fruit availability or overall fruit intake, indicating that palm fruits are a staple food for chimpanzees, but do not fit the descriptions of preferred or a fallback foods.

Oil-palm flower was tested as a potential fallback, as it was available year-round and its consumption started to increase during the time of fruit scarcity. It was present in 17.5% of all faecal samples but statistical analyses did not find a significant relationship between its consumption and wild fruit availability, palm flower availability or overall fruit intake. Even though feeding traces were not analysed, 13.6% (n=63) of all feeding traces were of this flower. Oil-palm flower is a staple food, but not a preferred food to this community. Further data are required to more thoroughly examine the role of oil-palm flower as a potential fallback food.

Leaves and pith were present in around half of all faecal samples. Leaves were consumed more by this community than was pith. However, it was virtually impossible to attribute leaves and pith found in faeces to a particular species. On the rare occasion when leaves were swallowed whole they were identifiable; leaf swallowing without chewing is consistent with plant medicinal use by chimpanzees (e.g. Huffman *et al.,* 1996; 2013; Fowler *et al.,* 2007; McLennan and Huffman 2012;). Interestingly, the levels of both leaf and pith consumption by the chimpanzees increased when fruit in the diet decreased, indicating that chimpanzees were substituting a lack of fruit in the diet with lower quality leaves and pith. This is consistent with the definition of fallback foods. However, leaf consumption was also positively related to wild fruit availability, which makes interpretation of these results difficult. These results are contrary to what has been reported at other sites (Tutin *et al.,* 1991; Fawcett, 2000; McLennan *et al.,* 2010). Additional data are required to further test the relationship between the consumption of different food parts and wild food availability. Only two species of flower were confirmed to be eaten by chimpanzees at this site. As a result of this, oil-palm flower consumption is a major predictor of total flower consumption. Like foliage consumption, its use did not vary with wild fruit availability or fruit consumption, but its intake increased during the rainy season. Flowers are rich in sugar and their consumption might have been related to the consumption of lower quality foods during the same period.

Table 7 Comparison of chimpanzee diet composition in chimpanzee study sites across Africa, adapted from Morgan and Sanz (2006). T = feeding trace; F = faecal sample; O=obsercations.

Study site	Start year	Methods	%Fruit	%Seeds	%Leaves	%Pith	%Flowers	%Bark	%Other	Plant food items	Plant species	Reference
Assirik, Senegal	1976	F / T / O	57	10	10	3	10	7	3	60	-	McGrew *et al.,* 1988
Bafing, Mali	2004	F / T / O	-	-	-	-	-	-	8	45	-	Duvall, 2008
Belinga, Gabon	1980	F / T	85	-	4	7	-	-	4	46	43	Tutin and Fernandez, 1985
Bossou, Guinea	1976	O	52	7	18	13	5	3	2	246	226	Sugiyama and Koman, 1992; Humle, 2011
Budongo, Uganda	1990	O	-	-	-	-	-	-	-	118	58	Newton-Fisher, 1999
Budongo, Uganda	1997	O	-	-	-	-	-	-	-	91	49	Fawcett, 2000
Bulindi, Uganda	2006	F / T / O	66	3	18	9	2	1	-	96	82	McLennan, 2010
Bwindi, Uganda	2000	F	50	-	-	-	-	-	-	60	34	Stanford and Nkurunungi, 2003
Caiquene-Cadique, Guinea-Bissau	**2013**	**F / T / O**	**64**	**-**	**20**	**8**	**2**	**4**	**1**	**83**	**66**	**Present study**
Fongoli, Senegal	2001	F / O	53							60	47	Pruetz, 2006
Gishwati, Rwanda	2009	F / O	N=23	-	-	-	-	-	-	-	>23	Chancellor *et al.,* 2012
Gombe, Tanzania	-	O	43	7	27	8	10	-	7	201	-	Wrangham, 1977
Gualago, Rep. Congo	1999	F / T / O	56	7	16	8	8	3	2	158	116	Morgan and Sanz, 2006
Kahuzi, D.R.C.	1991	F / T/ O	38	-	31	19	-	6	5	99	75	Yamagiwa *et al.,* 1996
Kahuzi, D.R.C.	1994	F / T / O	40	3	30	17	5	2	4	156	110	Basabose, 2002
Lope, Gabon	1983	F / T	66	11	12	5	4	2	1	161	132	Tutin and Fernandez, 1993
Mahale, Tanzania	1965	O	31	5	36	11	9	4	5	328	198	Nishida and Uehara, 1983
Ndoki, Rep. Congo	1989	F / T / O	88	-	3	5	2	-	3	114	108	Kuroda *et al.,* 1996
Semiliki, Uganda	1996	O	39	15	30	9	3	3	-	33	-	Hunt and McGrew, 2002

5.5.2 Cultivar consumption

In a three-month study conducted in 2008, Hockings and Sousa (2012) identified ten species of cultivars eaten by this chimpanzee community at Caiquene-Cadique, including papaya, cashew, cow bean (later identified as pigeon pea, *Cajanus cajan*) mango and orange. All of the above cultivars were also confirmed eaten during the present study period. Overall cultivars represented 13,4% of all eaten species. Only four of the nine confirmed species were identified in faecal samples, and their presence in faecal samples was very low. Due to difficulties in identifying most cultivars in faeces (e.g. seedless cashew fruit), the consumption of cultivars by chimpanzees at this site was unquestionably underestimated. When feeding traces were analysed, cultivar consumption increased 4-fold from 2.9% to 13% of all samples, providing a better representation of the importance of cultivars to this community. The observation of chimpanzees in fields and orchards was not a priority of this research, hence cultivar feeding was rarely observed directly. In addition to the characteristics of cultivars in Caiquene and Cadique, the way chimpanzees consumed them contributed to their underestimation in faeces. For example, when chimpanzees feed on oranges they spit the seeds out instead of ingesting them, or when feeding on cashew, that pulp wadges are discarded and only the juice ingested (as previously described by Hockings and Sousa, 2012) (see Figure 17). In agreement with McLennan (2013), relying on faecal samples to quantify crop feeding by un-habituated chimpanzees is problematic. It is important to collate data obtained through different sampling methods and triangulate results.

Chimpanzees did not consume cultivars in response to periods of wild fruit scarcity as shown at other sites (e.g. Bossou: Hockings *et al.,* 2009; Bulindi: McLennan, 2013), hence they were not used as fallback foods. Unlike chimpanzees at

Bossou in Guinea who balance their intake of crops and wild foods on a daily basis, chimpanzees at Caiquene-Cadique cultivar use was not related to fruit consumption. Even though data on crop availability were not collected during the study period, most crops in this area were only seasonally available, and chimpanzees likely fed on each particular species accordingly. This was especially noticeable with cashew, orange, and mango, which means that these cultivars might qualify as preferred foods. Although the percentage of crops consumed by the Caiquene-Cadique community appears to be high, it is important to notice that the sampling methodology is different between sites, resulting in an underestimation of total plant food species consumed in Caiquene-Cadique and Bulindi. During this study, the majority of feeding traces found in cultivated areas were located on the edges of the villages, in some cases, even in single trees planted at the back of houses. In other highly disturbed areas (see Table 8), crops are frequently consumed in abandoned cultivated areas (McLennan, 2010; Hockings *et al*., 2012). Differences in levels of crop raiding might be explained by the fact that there are few abandoned cultivated areas in Caiquene-Cadique, and the ones that exist are mainly individual trees or small clusters of trees that were left from abandoned villages.

Crop raiding has been shown to increase the likelihood of negative human-chimpanzee interactions, increasing the potential for retaliatory killing of chimpanzees (e.g. Hockings and Humle, 2009). There is currently no strong evidence of agonistic behaviour from local people in Caiquene and Cadique towards chimpanzees, apart from the occasional throwing of sticks or small stones to scare away individuals. A possible explanation for this lack of aggression between humans and chimpanzees may be related to the type of crops raided. The most heavily consumed crop by chimpanzees was cashew. From data collected on the same chimpanzee community, Hockings and Sousa (2012) showed that this constituted a 'low conflict' crop since humans and chimpanzees importantly exploited different parts of the plant. Nevertheless, Hockings and McLennan (2012) categorised two of the crops raided at this site, sugar cane and mango, as 'high-risk' of generating conflict, and another, papaya, as a potentially high-risk crop. Of these, mango was the most heavily raided crop. However, the variety that was eaten by the chimpanzees was never sold for money by local people, and currently has no commercial value. Similarly to cashew fruit, it is socially acceptable for anyone to pick and eat these mangos. This variety was mostly found on the edge of the village and there was no evidence that mango trees were protected from wildlife.

Further data are required to fully examine the role of cultivars in the foraging strategies of chimpanzees at Caiquene-Cadique. Longer term data sets will allow us to determine whether this behaviour will increase over time in response to further habitat fragmentation and conversion to other land-uses including agriculture. Moreover, comparisons with other 'human-influenced' sites will illuminate the degree to which these communities vary in their reliance on crops depending on other environmental, anthropogenic and social factors.

Table 8 Chimpanzee crop consumption at chimpanzee research sites with high exposure to agriculture and where systematic data have been collected to specifically examine the role of cultivars in the diet

Chimpanzee site	**Exposure***	**Study duration (months)**	**Data collection methods**	**No. wild species in diet**	**No. crop species in diet**	**% crops in diet**	**Average monthly score crop in diet**
Bossou[a]	High	12	O	140	17	12	14%
Bulindi[b]	High	21	T / F	74	10	14	-
Caiquene-Cadique[c]	High	9	T / F / O	67	9	14	0.28% (F) 14.36 (T)

*As classified by Hockings and McLennan (2012)

[a] Hockings *et al.,* 2009; [b] McLennan, 2010; [c] Present study

Direct methods: O=observation

Indirect methods: F= Faecal, T=Feeding trace

5.5.3 Non-plant foods consumption

Bee-honey was frequently ingested by this community, but it is not classified as an important food species (see Figure 18). Its consumption was independent of plant food consumption and availability, and appeared opportunistic. Although data are lacking on honey availability, it is possibly a preferred food in this community. In addition to chimpanzees feeding from natural hives in the forest, some local people occasionally reported honey raiding from human-made beehives within the villages.

Honey feeding is not an uncommon behaviour in chimpanzees (Morgan and Sanz, 2006; McLennan, 2010; Chancellor *et al.,* 2012). Tools are often associated with honey collection at these other sites (e.g. Loango National Park – Boesch *et al.,* 2009; Goualougo Triangle - Sanz and Morgan, 2007; 2009), but no evidence of tool-use to access honey was found during this study period. Raided natural beehives were not found and man-made beehives appear to be easily opened and the honey inside consumed manually (see Figure 18). However, further in-depth research is required on the techniques employed to exploit honey by chimpanzees at this site.

Apart from honey consumption there was one other non-plant food that is potentially eaten by this chimpanzee community: Giant African land snails. Snails are a good source of protein, minerals and calcium (Adeyeye and Afolabi, 2004; Özogul *et al.,* 2005; Hicks, 2010). Even though there is no faecal evidence or direct observations of chimpanzees smashing and consuming snails, it is highly likely that identified snail-smashing sites and snail remains were left by chimpanzees and not by other sympatric wildlife (e.g. mongooses). This behaviour has only been described in two other chimpanzee communities: Nimba (Republic of Guinea – Matsuzawa and Yamakoshi, 1996) and Bili-Uele (D.R.C. – Hicks, 2010). The behaviour has not yet been confirmed in Nimba (Matsuzawa and Yamakoshi, 1996; Humle, 2011). In Bili, Hicks (2010) found 142 snail-smashing sites on the main land, and for most of which, there was nearby evidence of chimpanzee presence (e.g. faeces, nests). Nevertheless, he also found evidence of snail smashing in an island where chimpanzees were absent. A species of mongoose (*Atilax paludinosus*) was likely responsible. Hicks (2010) compared these 'island' smashing sites with others on the main land, and states to have "found that the strike marks on the trees were shallow and superficial, and that the bark was discoloured but not broken where the snails had been struck" (Hicks, 2010:227) The number of smashing sites found on the island was low compared to the ones identified on the mainland and**,** for some, only small fragments of shell were found.

The species of mongoose described can be found in the forest of Caiquene-Cadique and it might be responsible for some of the smashed snails. However, when comparing the smashing site characteristics described by Hicks' (2010) and the ones identified during this study, there are several similarities:

1. Smashing sites at both sites are associated with wooden surfaces suitable for cracking.
2. There is evidence of great force being used to smash the snails (with damage and shell bits embedded in the smashing surfaces).
3. A large number of snails and fragments were found at both sites.
4. There is evidence of smashing site re-use.
5. The majority of smashing sites occur in proximity to locations where chimpanzee presence was confirmed (faeces, paths, etc) during the study period.
6. As described in the results, canine teeth marks left in a discarded piece of snail meat at Caiquene-Cadique were too distant apart (approximately 10cm) to be attributed to a mongoose (see Figure 19).

Although these data suggest that chimpanzees do smash and consume Giant African land snails, further data are required, including direct observations of the behaviour, to confirm its presence in this community's behavioural repertoire.

Contrary to what was expected, and aside from the snail-smashing, there was no evidence of consumption of other invertebrates (e.g. army ants or termites) or vertebrate preys (e.g. monkeys). The consumption of other animals by chimpanzees has been described at most other study sites (e.g. McGrew and Rogers, 1983; Boesch and Boesch, 1989; Pruetz, 2006; Hicks, 2010; Hockings *et al.,* 2012) but no evidence was found for this particular community. Similar results were reported for the Gishwati community in Rwanda that inhabits a very small and fragmented forest (Chancellor *et al.,* 2012). However, it is likely that chimpanzees at Caiquene-Cadique do consume meat opportunistically, but only further research can confirm this. Although chimpanzees share the forests with primates, including red colobus, a preferred prey species to chimpanzees (Watts and Mitani, 2002), it appears that their numbers are quite low, likely due to human hunting pressure. However, the fact that no invertebrate consumption was recorded is puzzling. Faunivory is underestimated when analysing faecal samples, although exoskeletons of invertebrates are found in faecal samples (e.g. Phillips and McGrew, 2014). They might have been overlooked during faecal analyses, but this is unlikely since particular importance was given to the smaller food fragments found in the samples.

Additionally, tools normally associated with the exploitation of invertebrates such as termites and ants (McGrew, 2014) were never recovered. This is quite puzzling given the location in Caiquen-Cadique in West Africa, and the fact that this chimpanzee subspecies (*Pan troglodytes verus*) is known for their extensive 'tool kits' (e.g. Boesch and Boesch, 1990).

One might expect that, in places where preferred foods are less available, that other food resources, such as termites, would be exploited to ensure a balanced diet (Duvall, 2008). But this appears not to be the case for this chimpanzee community. More data are needed from this community and those in surrounding areas in the Cantanhez National Park.

Due to the apparent uniqueness of this chimpanzee community, further research on its faunivoury and honey collection is imperative.

5.5.4 Ethical considerations

The use of indirect methods may not be ideal when examining chimpanzee feeding ecology. Direct observation of well habituated individuals is of course the best way to record what chimpanzees consume. However, as touched upon earlier, it is important to consider the consequences of intensive habituation, especially in areas where chimpanzees and local people encounter each other on a daily basis (McLennan and Hill, 2013). By its very nature, habituating chimpanzees reduces their fear of people, potentially resulting in increased aggression towards local people (Hockings *et al.,* 2010b), increased levels of potentially problematic behaviours such as crop-raiding (Deblauwe and Janssens, 2008; Hockings *et al.,* 2009) and increased risk of disease transmission (Köndgen *et al.,* 2008; Woodford *et al.,* 2002).

5.5.5 Final remarks

Overall, the plant diet composition of this community conforms to what was expected. A diet rich in carbohydrates that are found in fruits and flowers, proteins that are found in leaves, and fats found in oil palm fruits. The fact that other foods, such as seeds and other species of invertebrates, did not appear to be eaten, suggests that the metabolic demands of this chimpanzee community are being fulfilled. These results give some hope for populations living in anthropogenic habitats, and highlights chimpanzees' capacity for behavioural plasticity. However, if patterns of deforestation for slash and burn agriculture are maintained the long-term persistence of this chimpanzee community might be at risk.

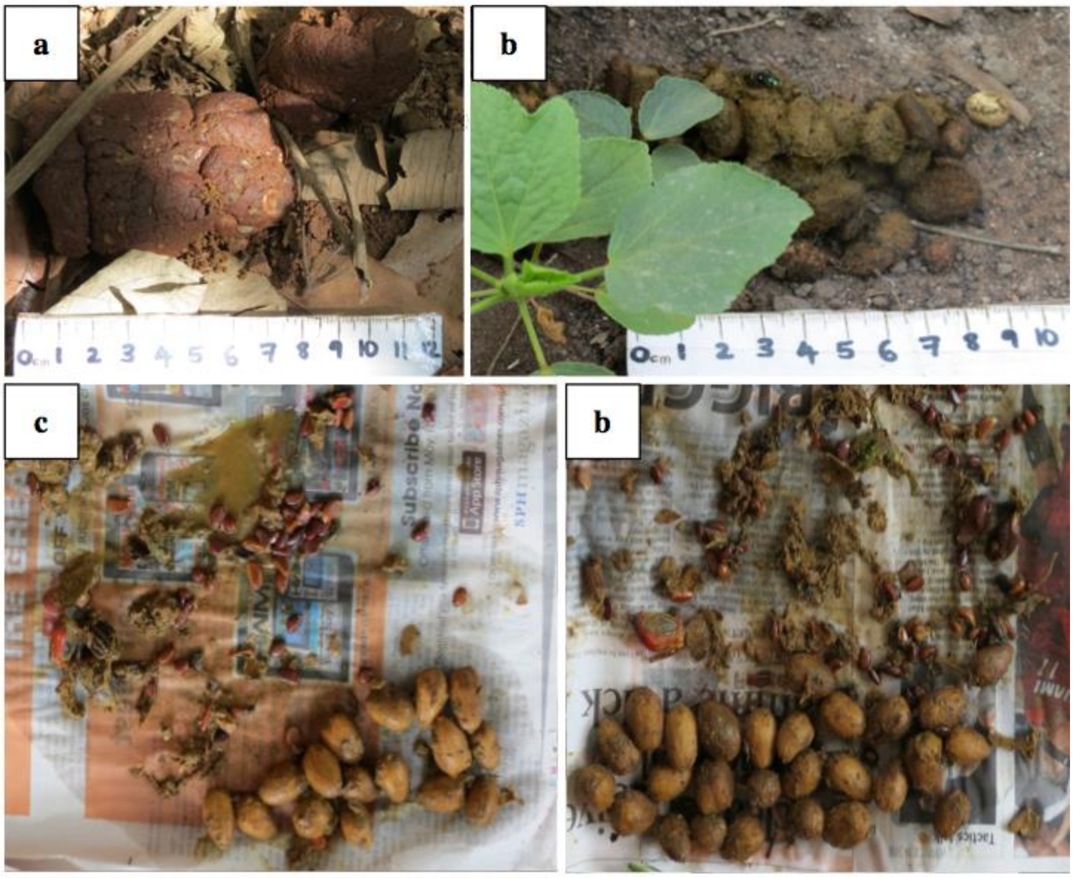

Figure 15 Faecal samples: a) fresh dung with *Dialium guineense* seeds; b) fresh dung with *Saba senegalensis* seeds (found in a cultivated area); c, d) washed faecal samples.


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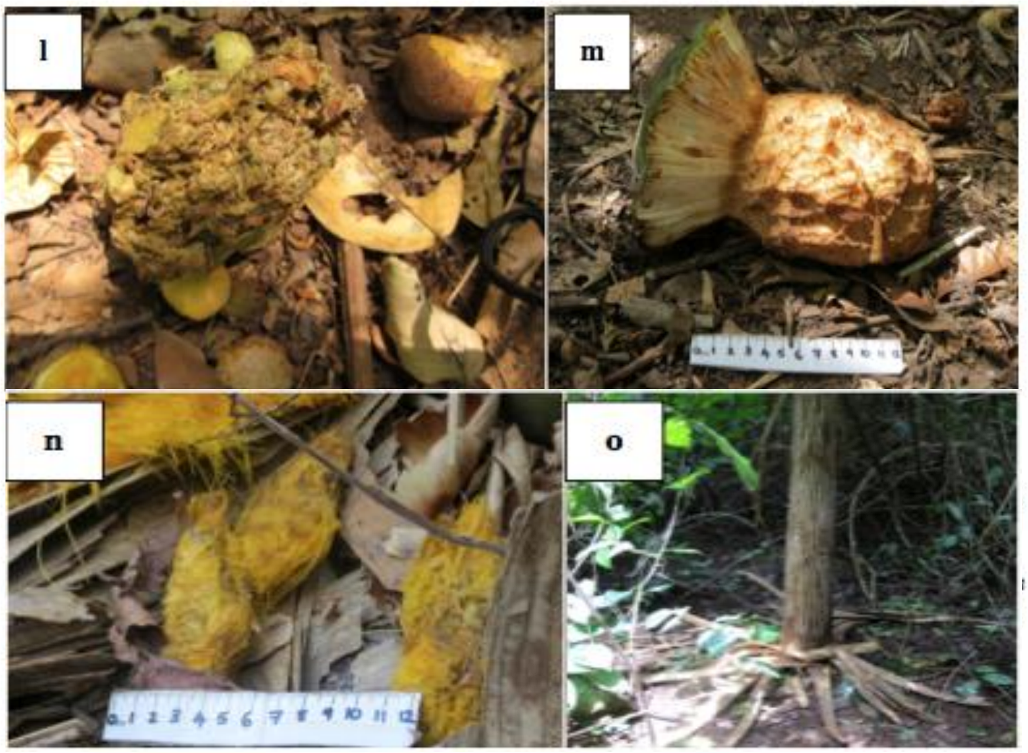


Figure 16 Chimpanzees feeding traces of **a)** Orange (*Citrus sinensis*) ripe fruit, pulp and seeds discarded; **b)** mango (*Mangifera indica*) ripe fruit, with teeth marks; **c)** papaya (*Carica papaya*) unripe fruit, with teeth marks; **d)** cashew (*Anacardium occidentale*) ripe fruit wadge**; e)** baobab (*Adansonia digitata*) ripe fruit, with teeth marks; **f)** *Saba senegalensis* ripe fruit; **g)** *Dialium guineense,* ripe fruit**; h)** *Ceiba pentandra* ripe fruit, with teeth marks; **i)** palm (*Elaeis guineensis*) flower with teeth; **l)** *Parinari excelsa* ripe fruit wadge; **m)** *Treculia africana* ripe fruit and wadge; **n**) *Borassus aethiopum* ripe fruit wadge; **o**) *Ricinodendron heudelotii* sap consumption

Figure 17 Chimpanzees feeding: **a, b** and **c)** juvenile chimpanzee feeds on cashew fruit, making a wadge of several fruits. **d)** two adult female chimpanzees feed on fig fruits (*Ficus sur*). **e)** Adult male chimpanzee feeds on *Treculia africana* fruit.

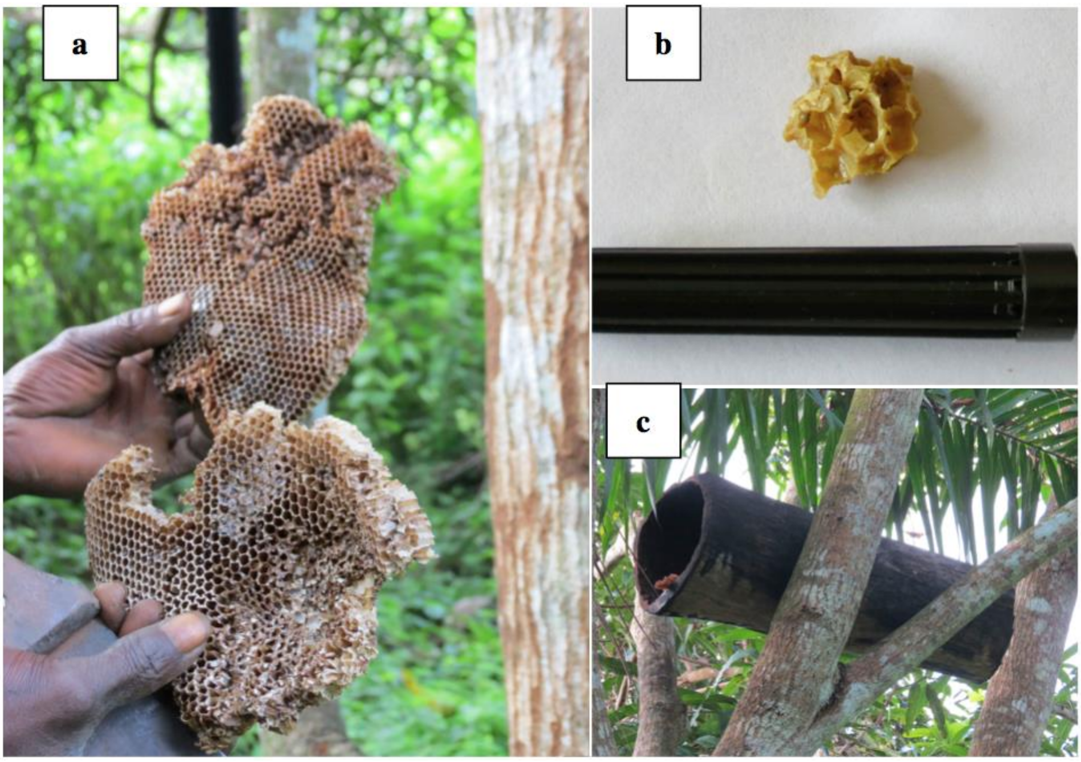


Figura 18. Honey feeding by chimpanzees: **a)** local holding honey comb left behind by raiding chimpanzees; **b)** honey comb found in faecal sample**; c)** raided artificial bee hive on the village of Caiquene.

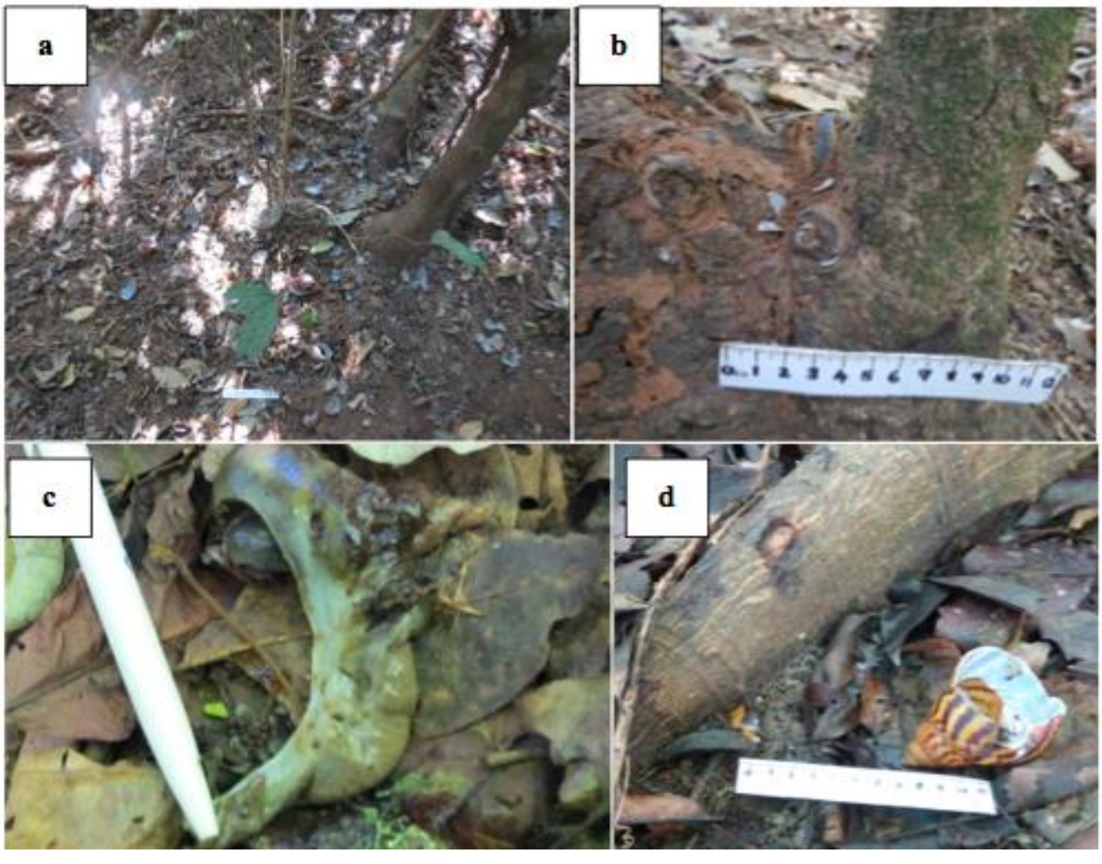


Figure. 19 Snail-smashing: **a)** smashing site with fragmented snails; **b)** snail shell embedded on tree trunk; **c)** teeth marks on the meaty part of the snail; **d)** damaged trunk from snail smashing

Chapter 6

Size Matters –the role of plant food size in wild chimpanzee sharing behaviour

6. Size Matters – the role of plant food size in wild chimpanzee sharing behaviour

6.1 Introduction

Food sharing consists of the unopposed transfer of a monopolized food from a possessor to a recipient (see 6.2.2 for definitions of different types of food transfer; Feistner and McGrew, 1989; Stevens and Gilby, 2004). In human foraging communities, food sharing is universal (Jaeggi *et al.,* 2010; Jaeggi and Gurven, 2013a). In these communities it has been studied in an effort to model the evolution of altruism and cooperation in the human lineage (Gurven, 2004; Stevens and Gilby, 2004; Kaplan *et al.,* 2009; Silk *et al.,* 2013). Sharing is most commonly witnessed when it is 'riskier' to obtain a certain food and collaboration between individuals is needed (Jaeggi and Gurven, 2013a), suggesting that food sharing functions as a reciprocity tool.

Food sharing is also universal among the genus *Pan (*Pruetz and Lindshield, 2011), occurring most frequently between mother and offspring (Goodall, 1986; Nishida and Turner, 1996). In *P. paniscus* (hereafter bonobo), plant food sharing between adults occurs often (Kano, 1980; Kuroda, 1980; 1984; White, 1996), but among *P. troglodytes* (hereafter chimpanzee) the behaviour is reported as more frequent when meat is involved (Teleki, 1973; Goodall, 1986; Boesch and Boesch, 1989; Gomes and Boesch, 2009).

Plant food sharing has been observed at numerous chimpanzee sites but at very low frequencies (see Table 9). Fruits provisioned by humans (bananas -

McGrew, 1975 and sugar cane – Nishida, 1970), as well as crops (Hockings *et al.,* 2007), are the most commonly shared items, while wild fruits appear to be shared rather infrequently (Nakamura and Itoh, 2001; Wrangham, 1975; Bethell *et al.,* 2000; Slocombe and Newton-Fisher, 2005). Interestingly, a recent study at Fongoli in Senegal showed that plant food sharing in this community of savannah-living chimpanzees is more frequent than reported at other sites, with 26 sharing events in 34 months (Pruetz and Lindshield, 2011). Crick *et al.* (2013), suggest that sharing behaviour is influenced by the accessibility of food, with sharing more likely when food is more difficult to obtain.

One factor that appears important in determining plant food sharing in chimpanzees is the size of the food, regardless of whether the food item is from a cultivated or wild source (Bethell *et al.,* 2000; Boesch and Boesch-Achermann, 2000; Slocombe and Newton-Fisher, 2005; Hockings *et al.,* 2007; Ohashi, 2007; Nakamura and Itoh, 2001; Pruetz and Lindshield, 2011). Large plant foods, usually fruits, are easily divisible due to their size, and have been considered predictors of sharing, since the cost of sharing decreases as food size increases (Hockings *et al.,* 2007). Bethell *et al.* (2000) compared the ease at which large plant foods can be potentially shared to the sharing of animal carcasses. However, the low availability of large fruits at chimpanzee sites has been provided as a possible explanation for observed differences in sharing frequency between chimpanzees and bonobos (White, 1996). Overall, sharing appears to be more frequent when the seasonal availability of the shareable food item is high (Hockings *et al.,* 2007; Pruetz and Lindshield, 2011), especially for species that have a low density in the chimpanzee's territory (Nakamura and Itoh, 2001; Pruetz and Lindshield, 2011).

Three main hypotheses have been suggested to explain meat sharing among chimpanzee communities, however they might equally apply to the sharing of plant foods: Firstly, sharing under pressure whereby owners may relinquish part of the food if the cost of defending it is too high, i.e. sharing increases with harassment (Wrangham, 1975; Gilby, 2006); secondly, to enhance ones status through sharing with higher rank individuals (Moore, 1984); and lastly, reciprocal sharing which suggests social benefits to the sharer. This includes, 'food-for-sex', where males share with maximally swollen females to gain immediate access to mating opportunities (e.g. Goodall, 1986) or to increase the likelihood of future mating opportunities (Tutin, 1979); 'grooming-for-food', where individuals share more frequently with others that previously groomed them (de Waal, 1997); and 'food-for-support', where males share food with others to insure support in future conflicts (Mitani and Watts, 2001). However, these hypotheses are not mutually exclusive and differences of social behaviour or habitat between communities might explain differences in sharing strategies.

Pruetz and Lindshield (2011) suggest that the high frequency of plant food sharing at Fongoli might be explained by the dry savannah environment they inhabit. Although the authors don't specify what habitat characteristics they are referring to, it is likely that the more distant and scattered distribution of ripe fruit might increase the value of these foods, increasing the likelihood of sharing. Hockings *et al.* (2007) show that crops that were obtained under 'riskier' scenarios (including a village location, further from the forest edge, and in the presence of local people), were frequently transported back to the forest to be shared (see Carvalho *et al.,* 2012 for details of crop transport). These authors compare the sharing of difficult-to-obtain crops at Bossou to meat sharing (which occurs infrequently at this site), and suggest sharing by adult males to unrelated females of reproductive age is a strategy used to obtain "food-for-sex and -grooming", but also might be a 'showing-off' strategy by males.

In the majority of plant food sharing cases, males are the 'possessors' and share frequently with unrelated females (Bethell *et al.,* 2000; Slocombe and Newton-Fisher, 2005; Hockings *et al.,* 2007; Pruetz and Lindshield, 2011), which superficially appears to support the "reciprocity" hypothesis. However, at sites where plant food sharing occurs more frequently it appears that maximally swollen females are not specifically shared with, but that cycling females are often preferred (Hockings *et al.,* 2007; Pruetz and Lindshield, 2011). This suggests that the sharing of plant foods might be a longer-term social strategy for chimpanzees in anticipation of future mating opportunities (Crick *et al.,* 2013).

Plant food sharing appears to be neglected in the literature compared to meat sharing (e.g. Jaegii *et al.,* 2010). Although plant food sharing among chimpanzees is not as rare as once thought, plant foods are shared infrequently. Hence any observation provides valuable insight into this behaviour. In this chapter, I provide an overview of plant food sharing in chimpanzees across Africa, and provide a detailed description of a plant food sharing event in the Caiquene-Cadique chimpanzee community.

6.2 Methods

The food sharing episode was observed from the road using binoculars from a distance of 100m. The sharing event was video-recorded and a detailed analysis was made afterwards. Because visibility was not always optimal (due to the positioning of the individuals and ~~leaves~~ vegetation), the video image was sometimes unclear. To ensure as much of the sharing event was recorded as possible, detailed notes were taken during the observation by JB with the help from MC and IC who were positioned at different sides of the road. Chimpanzees at this site are very used to people being present on this road (see Chapter 2), and it is unlikely that human observer presence impacted sharing behaviour in any way.

Additionally, data on plant food sharing across Africa were compiled. Information on the number of sharing events, type of plant food species shared, and their estimated sizes were incorporated into analyses.

The size of plant foods can vary, even within species. For that reason, when specific information was absent from the published description of the sharing event, each plant food part was categorised as either small, medium or large. These were based on diameter when the food part was round, on length when it was oblong, and on weight if the food was higher than 1 kg.

- Small - <5cm length or diameter
- Medium - ≥5cm to <15 cm length or diameter
- Large - ≥15 cm length or diameter or ≥1kg

For more information on the methods, see Chapter 3.

6.2.1 Important definitions

Sharing event: when a possessor shares an item of food with one or more recipients during a single feeding bout.

Sharing types: The following definitions are adapted from Pruetz and Lindshield (2011).

- Recovery: The receiver takes the item that has been dropped or placed on the ground by the owner, and the owner tolerates the action.
- Passive-sharing: The receiver takes part of the item which is held by the owner, and the owner passively tolerates the behaviour.
- Active-sharing: The owner actively divides the item so that the receiver is able to take a portion, or the owner presents the receiver with a portion while keeping the majority.
- Giving: The owner presents the majority of the item to the recipient.

- Begging occurs when an individual approaches a possessor, but does not restrict the possessor's movement. Begging includes sitting and staring at the possessor, holding out the hand and gesturing towards, but not touching, the possessor or food (Hockings, 2007).

6.3 Results

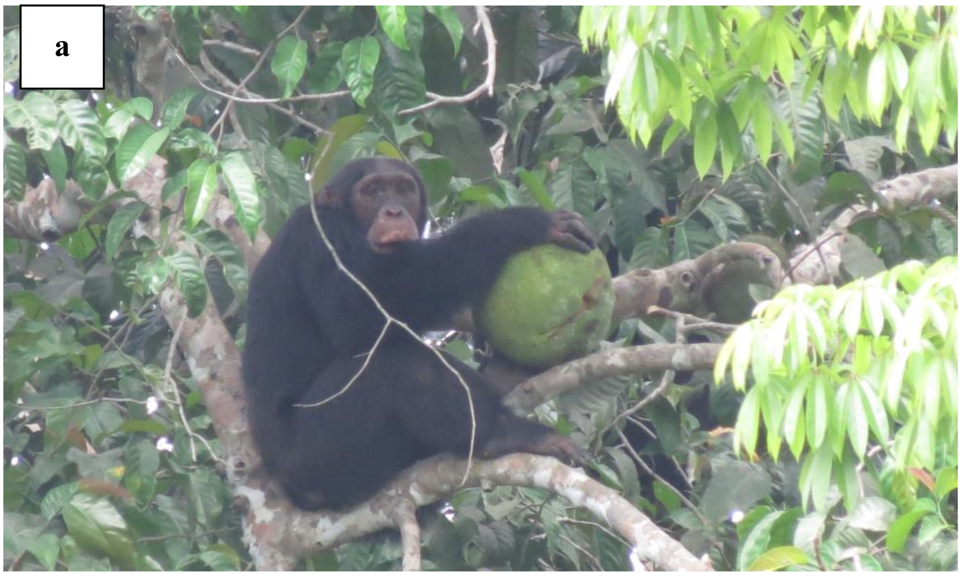
6.3.1 A case study of *Treculia africana* sharing

At 1514h on the 23rd of March 2013, a mixed-party of chimpanzees were observed approximately 17m high in a large *Treculia africana* tree (approx. 22 m high) that is located on the edge of a forest patch. Initially there were at least 8 individuals in the tree, including three adult males, two adult females, one unidentified adult and two juveniles, one of whom was female. Other individuals were heard on the ground, although remained out of site. The observers (JB, MC and IC) sat in silence on the road, approximately 100m from the chimpanzee group, with good visibility of the *T. africana* tree.

At 1514h, an adult male (AM1) was seen carrying a large green *T. africana* fruit (~40cm diameter) tripedally for ~5 meters and subsequently sat on an exposed *T. africana* branch and held the fruit on the branch [Figure 20.a]. *T. africana* fruits have a thick and fibrous mesocarp with a woody core, and their skin is tough but not hard (Watts, 2008). At 1515h AM1 started to feed on the fruit, whilst occasionally glancing at the human observers. At 1516h AM1 moved ~5m onto a different branch carrying the *T. africana* tripedally*,* then continued to feed on the fruit with his back to the observers.

At 1526h (11 minutes after AM1 had started feeding) a maximally swollen female (AF1) sat directly next to AM1. The female did not display any begging gestures, and at 1527h AF1 started to feed on the *T. africana* fruit that was being held between AM1's feet [Figure 20.b]. Both AM1 and AF1 continued to feed face-to-face with their feet touching and the fruit positioned between them. Periodically whilst feeding, both individuals stood bipedally holding the branch with one hand and tearing off part of the fruit with the other. At 1534h, AM1 turned his back on AF1, and he continued to tear off pieces of fruit with his hand and consumed them. At 1538h AF1 moved and stood holding on to a branch whilst facing AM1 who continued to hold and feed on the fruit. Once again AF1 was not observed begging, but at 1539h AF1 resumed feeding on the *T. africana*. AM1 did not move away and they both calmly fed. At 1552h, AF1 moved out of sight, and AM1 continued to feed. No mating was observed between AM1 and AF1.

At 1556h, a second adult female (AF2), with a partial swelling, sat next to AM1, and started to feed on the *T. africana* fruit that was being held by AM1. At the same time a juvenile female (JF1) moved to inspect (i.e. touch and smell) a small unripe *T. africana* fruit (~15cm diameter), that was still attached to the tree, approximately 4m from AM1 [Figure 20c]. At 1558h, JF1 continued to inspect the fruit, but did not 'pick' the fruit. She then climbed down and sat 0.5m from AM1. AM1 was positioned with his back to JF1, and continued to feed with AF2. At 1559h JF1 tried to look at the *T. africana* fruit, then at1600h AF2 left with a piece of *T. africana* fruit and JF1 followed her. AF2 subsequently climbed down the tree to the ground and went out of sight, while JF1 remained ~5m away from AM1 and continued to look at the fruit. At 1610h AF1 returned and sat next to AM1, and they resumed feeding together. At1621h AM1 turned his back on AF1 and continued to feed [Figure 20.d]. At that point, approximately one half of the fruit was still left. AF1 remained seated approximately 1m from AM1 for 5 minutes then left. At 1702h, individuals on the ground vocalised (pant-hoots) and the individuals in the tree responded and left the tree. The half-eaten *T. africana* fruit was left in the tree.


a


b


c

Figure 20 Food sharing: a) AM1 with a large *T. africana* fruit; b) AM1 and AF1 feeding on the fruit; c) JF1 investigates a smaller unripe *T. africana* fruit; d) AM1 turns his back on AF1 and continues feeding

6.3.2 *Treculia africana* availability and consumption

At Caiquene and Cadique, *Treculia africana* trees occurred at a low density (6.5 trees/ha). The trees had a mean DBH of 71.77cm (range=13-250; SD=21.23) and a mean height of 10.15m (range=3.5-23; SD=2.11) *T. africana* produced fruits from February to May and then again in September, peaking in April (5 of 13 monitored trees produced fruit during the study period; see Figure 21). However, the availability of ripe fruit may have been underestimated, as when fully mature, these fruits fall to the ground.

The *T. africana* fruit was an important (i.e. consumed frequently during one or more months) and preferred food (i.e. consumption increases with availability) species for this chimpanzee community (see Chapter 5). *T. africana* fruit was present in 11,41% of all faecal samples and 7,34% of all feeding traces were attributed to this species. Consumption peaked in March.

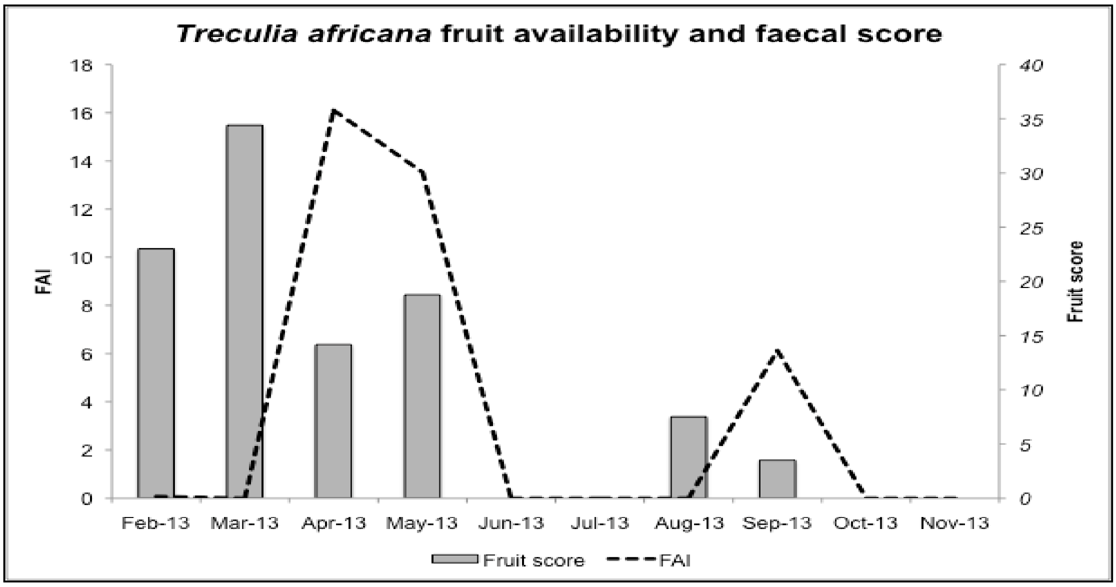


Figure 21 *Treculia africana* fruit availability and fruit faecal score from February to November 2013

6.3.3 Plant food sharing across Africa

Plant food sharing has been recorded at nine chimpanzee study sites (including the present). Four are situated in West Africa *(Pan troglodytes verus)* and 5 are in East Africa *(Pan troglodytes schweinfurthii)*. A total of 646 plant food sharing episodes have been recorded from the wild; of these, 533 concern the sharing of human provisioned plant foods, excluding crops. Fruits are most frequently shared of all plant parts, representing 71,9% of all non-provisioned plant food parts shared. Larger sized fruits are the most shared, representing 66,7% of all shared fruits, and *T. africana* appears to be the species that is most commonly shared across chimpanzee study sites (n=3). For detailed information see Table 9. Of the non-provisioned plant foods, crops are most frequently shared: 63 episodes in Bossou (Guinea) and 4 in Bulindi (Uganda), with one observation of chimpanzees at Mahale (Tanzania) sharing lemon obtained from an abandoned trees. The site with the highest record of wild plant food sharing is Fongoli (Senegal) (n=26).

Table 9 Reports of plant food sharing between adult chimpanzees across East and West Africa.

Study site	**Sharing events**	**Plant food species**	**Plant part**	**Type**	**Estimated size**			**References**
					Dimensions (cm)	**Measurements (kg)**	**Score**	
Bossou, Guinea§	9	*Carica papaya*	Fr	*C*	-	-	L	Ohashi, 2007
	36	*Carica papaya*	Fr	*C*	~30cm length x 20cm width	-	L	Hockings *et al.*, 2007; pers.comm. 2014
	3		Le		~40cm length x 30cm width	-	L	
	4		Wt		= tree trunk size	-	L	
	5	*Citrus aurantifolia*	Fr	*C*	~10cm diam x 10	-	M	
	3	*Ananasa comosus*	Fr	C	~25cm length x20cm w	-	L	
	3	*Manihot esculenta*	Tb	C	~25cm length x 10cm w	-	L	
	2	*Theobroma cacao*	Fr	C	~15cm length x 10cm w	-	L	
	1	*Zea mays*	Fr	C	~20cm length x 8cm w	-	L	
	1	*Ficus exasperata*	Le	*C*	~10cm length	-	M	
Budongo, Uganda§	1	*Monodora myristica*	Fr	*W*	~ 15 cm diameter^{a}	1kg	L	Slocombe and Newton-Fisher, 2005
	5	*Ficus mucoso*	Fr	*W*	-	-	S	Reynolds, 2005
		Desplatsia dewevrei	?	*W*		-		
		Raphis farinifera	?	*W*		-		
	1	*Treculia africana*	Fr	*W*	~ 20 cm diameter^{a}		L	Bethell *et al.*, 2000
Bulindi, Uganda$^{\#}$	4	*Artocarpus heterophyllus*°	Fr	*C*	-	18Kg (can reach 34kg)	L	McLennan, personal communication 2014

Study site	Sharing events	Plant food species	Plant part	Type	Estimated size			References
					Dimensions (cm)	Measurements (kg)	Score	
Caiquene-Cadique, Guinea-Bissau *	1	*Treculia africana*	Fr	*W*	~ 40 cm diameter	-	L	Present study
Fongoli, Senegal#	1	*Oncaba spinosa*	Fr	*W*	5-7 cm	-	M	Pruetz and Lindshield, 2011
	3	*Ficus sp*	FR	*W*	<5cm^a	-	S	
	1		Le	*W*	-		L	
	7	*Piliostigma thonningii*	Fr	*W*	10-20 cm^a	-	M/L	
	2	*Hymenocardia acida*	Fl	*W*	<1 m (branch)^a	-	L	
	10	*Adansonia digitata*	Fr	*W*	7.5 – 55 cm^a	-	M/L	
	2	*Oxytenanthera abyssinica*	Pi	*W*	-	-	L	
Gombe, Tanzania§	4	*Strychnos sp.*	Fr	*W*	-	-	M	Wrangham, 1975
	1	*Sterculia quinqueloba*	Fr	*W*	-	-	M	
	457	*Musa sp.*	Fr	*P*	-	-	L	McGrew, 1975
Mahale, Tanzania§	1	*Citrus limon*	Fr		-	-	M	Nakamura and Itoh, 2001
	1	*Voacanga Africana*	Fr	*W*	~ 15 cm	1 kg	L	
	76	*Saccharum officinarium*	Pi	*P*	-	-	L	Nishida, 1970
Taï Forest, Ivory Coast §	-	*Treculia africana*	Fr	*W*	-	-	L	Boesch and Boesch-Achermann (2000)
	-	*Coula edulis*	Fr	*W*	-	-	S	Boesch, 2009
	-	*Panda oleosa*	Fr	*W*	-	-	S	
Tongo, DRC§	1	*Clematis sp.*	Tb	*W*	~25cm diameter	5kg	L	Lanjouw, 2002

Fr= fruit; Le=leaf; Tb=tuber; Wt=woody tissue; Fl= flower; Pi= pith

Semi-habituated community; § Habituated community; *Un-habituated community

S= small size; M= medium size; L= large size

6.4 Discussion

As in many other communities (see Table 9) the fruit shared at Caiquene-Cadique was large, easily divisible and presumed to be energy rich. *Treculia africana* is one of the largest fruits available to wild African apes, and fruits can be more than 40cm in diameter. They are dense and fibrous, and require a considerable force (from the teeth and jaw, neck and shoulder muscles) to open (Watts, 2008). In the Tai National Park, chimpanzees smash these fruits against branches and roots to facilitate consumption (Whiten *et al.,* 2001) and at Nimba Mountains in Guinea there is indirect evidence that chimpanzees use stone and wooden 'clevers' as well as stone 'anvils' to open and exploit this large fruit (Koops *et al.,* 2010).

The sharing incident recorded took place in the dry season, when the availability of ripe fruit, including *T. africana*, is high. This is consistent with findings from other west African sites (Bossou: Hockings *et al.,* 2007; Fongoli: Pruetz and Lindshield, 2011) The overall density of *T. africana* trees is low in Caiquene and Cadique, which is again consistent with reports from other sites where low density species were shared more often (Mahale: Nakamura and Itoh, 2001; Fongoli: Pruetz and Lindshield, 2011). Interestingly, and similar to observation from Budongo (Slocombe and Newton-Fisher, 2005), when this sharing episode occurred, other large *T. africana* fruits were available on the same tree and on the ground beneath.

The observed passive sharing event at Caiquene-Cadique occured over 188mins between adult chimpanzees: one male possessor and two females recipients, one maximally swollen. As these chimpanzees are unhabituated and relatively little research has been conducted at this site, we do not have information on relatedness between individuals. However, based on chimpanzee dispersal patterns (females leave their natal community before reaching sexual maturity), it is very unlikely that the adult male was related to the two adult females that were both mature but too young to be his mother. No intense begging was observed, although the recipients sat in proximity to the possessor and stared at him and the food. The possessor did not show signs of anxiety nor aggression towards the females. However, on two occasions he did move away from the maximally swollen female, but once she tried to reinitiate feeding, he did not refuse. Like observations from other sites where adult males share with unrelated adult females, no observable distinction was made between maximally swollen and other cycling females during the sharing episode, and no harassment occurred. These results, although anecdotal, do not support the 'sharing under pressure' hypothesis which is commonly used to explain meat-sharing in chimpanzees (Gilby, 2006), and is more likely to be related to the potential for future benefits, such as sex or affiliative relationships.

During the 9 month study period only one episode of food sharing was recorded. Although at first glance this seems low compared to other sites where plant food sharing has been reported (see Table 9), the Caiquene-Cadique community is one of only two un-habituated communities represented and encounters with the chimpanzees occur opportunistically. During this study period, chimpanzees were not confirmed to consume animal prey, even though the preferred chimpanzee prey species is available (red colobus, Watts and Mitani, 2002). It is possible that chimpanzees at Caiquene-Cadique do hunt, but due to presumed low colobus numbers, this might occur more sporadically. Like instances of meat-sharing reported at other sites (Gilby, 2006), multiple individuals were involved in the reported plant food sharing episode. As suggested by Hockings *et al.* (2007) the sharing of plant foods may provide some of the same social benefits as meat-sharing at this site.

Obtaining the *T. africana* fruit did not involve any obvious risk (such as those described in crop raiding and hunting forays). Even though the *T. africana* tree is in proximity to a road, surprisingly little attention was given by the chimpanzees to to passers-by or researchers.

T. africana is an important food resource for chimpanzee communities across Africa (Whiten *et al.,* 2001), including chimpanzees at Caiquene-Cadique. It is interesting that this large fruit appears to be the species most commonly shared by bonobos (e.g. White, 1994; Hohmann and Fruth, 1996) and it is shared in 3 of the 9 chimpanzee sites, albeit infrequently (see Table 9). The size of the *T. africana* fruit, and the fact that it is an important and preferred food item for the Caiquene-Cadique community might provide one explanation for the sharing of this fruit at different sites. Another explanation is that *T. africana* fruits might be difficult to 'pick' from the tree. If the potential weight of a fruit is considered, the part that attaches the fruit to a branch must be very strong and potentially difficult to break. The result of this might be that adult males are more easily able to remove these fruits. Like findings from other sites that adult males crop-raid and –share under 'risky' conditions which might make these crops 'monopolisable' by males, the potential difficulties to remove *T.africana* might also result in sex differences in acquisition.

This research supports the idea that plant food sharing in wild populations occurs in situations where food possessors can provide large benefits to receivers at a low cost to themselves (Jaeggi and Gurven, 2013b). This might be in part due to the large size of the plants shared. Captive experiments of chimpanzee plant food sharing behaviours might be able to further examine the role of food size. In human forager communities, this sharing "cost" has resulted in long-term correlations between the giving of food and the receiving of food or other benefits (Kaplan *et al.,* 2009; Jaeggi and Gurven, 2013a). Studies the focus on chimpanzee plant food sharing behaviours might be important to better understand this universal trait in human foraging communities (Kaplan *et al.,* 2009; Jaeggi and Gurven, 2013a). Chimpanzees are ripe fruit specialists, and some authors have argued that the sharing of plant foods is phylogenetically older than meat sharing (McGrew, 1975; Kuroda, 1984).

In conclusion, further research is required to tease apart the factors that promote plant food sharing in wild chimpanzees, with the hope to shed some light on the origins of food sharing and reciprocity in humans. Particular attention should be paid to chimpanzee communities inhabiting anthropogenic habitats, with increasing exposure to large-sized and highly sought after crops and shrinking wild food supplies.

Chapter 7

Conclusion

7. Conclusion

The present dissertation explores the feeding ecology and behaviour of an un-habituated chimpanzee community (*Pan troglodytes verus*), inhabiting presence human-influenced habitat. The results are based on nine months of fieldwork (from February to October 2013), which took place at Caiquene-Cadique in Cantanhez National Park, Guinea-Bissau. Here, the main findings and conclusions of this research are briefly summarised and their importance to understanding this chimpanzee community, as well as what these data contribute to the general field, are discussed.

7.1 Summary of findings

There was marked seasonal variation in the availability of flowers, ripe fruit and new leaves in Caiquene-Cadique (Chapter 4). During the dry season (February to May) fruit availability peaked and with the start of the rainy season (May to October) fruit productivity decreased. Some species fruited for long periods and, for that reason, were selected as good candidates as potential fallback food for chimpanzees.

A preliminary list of plant species consumed by the Caiquene-Cadique chimpanzee community was produced using direct and indirect data collection techniques (Chapter 5). The effects of seasonal variation on the feeding behaviour of this community were analysed. As expected, the chimpanzees mostly consumed ripe fruits, but surprisingly their fruit intake did not vary according to fruit availability. None of the proposed fallback fruit species identified in the previous chapter were used by chimpanzees when wild fruit availability or fruit consumption was low. Moreover, leaf consumption did not increase when fruit availability was lower but a particular flower species, *Elaeis guineensis*, was identified as a fallback food during times of fruit scarcity. Nine species of cultivars (cashew, mango, orange, lime, papaya, baobab, sugar cane, hibiscus and pigeon pea) were found to be consumed by this chimpanzee community. However, further data are needed to determine the dietary importance of these resources to the chimpanzees since crop feeding levels are likely underestimated. A high rate of honey consumption was identified. The honey was sometimes raided from the villages' artificial beehives, but this raiding appeared to be opportunistic and not related to wild food availability.

There was no evidence of hunting and meat consumption, nor was there evidence of the consumption of social insects (e.g. ants or termites). No extractive tools that are typically used by other West African chimpanzees were found, with the exception of leaf sponges for drinking water. Interestingly, there was indirect evidence of the possible smashing and consumption of giant African snails. This type of behaviour has yet to be confirmed at any chimpanzee site, making this behaviour even more intriguing. Plant food sharing is not frequent in chimpanzee communities, which normally share meat, and has been neglected in wild chimpanzee studies (Chapter 6). This research supports the idea that large and easily divisible plant foods are more commonly shared than smaller foods. Sharing a large item reduces the cost to the possessor whilst providing potential benefits. . Such data are invaluable when examining the evolutionary significance of food sharing and reciprocity in humans.

The data presented in this dissertation are preliminary and it is expected that future research will identify additional wild and cultivated foods, as well as occasional meat and invertebrates that are consumed by the Caiquene-Cadique chimpanzees. New chimpanzee behaviours will certainly emerge, as the apes adapt to their continuously shrinking mosaic habitat.

7.2 The future of the Caiquene-Cadique chimpanzee community

Chimpanzees have been classified as endangered since 1996 (CITES, 2013). The main threats to their survival are deforestation and the modification of habitat, poaching, live animal trade, retaliatory killing in response to crop damage or protection, and disease transmission (Butynski, 2003; IUCN, 2014). Even though the Caiquene-Cadique community inhabit a protected Cantanhez National Park, the land is under pressure from an expanding local human population, as well as immigration from neighbouring countries. As with many other chimpanzee communities across sub-Saharan Africa chimpanzees at Caiquene-Cadique inhabit a fragmented forest-farm mosaic in which wild fruit availability is low during certain periods of the year. As observed at these other sites, it is likely that crops and other human resources (e.g. honey) will occupy growing importance in the apes' subsistence strategies in the coming years, especially as forests are cut and crops become increasingly available. As witnessed during the study period, the clearing of forestland for slash-and-burn agriculture is constant, constituting the main threat for this community's survival. With increasing anthropogenic pressure, human-chimpanzee proximity is also likely to increase in this small corner of Guinea-Bissau. Even though it seems that human-chimpanzee 'conflicts' are uncommon, this trend might change in future years. Crop and honey raiding are not uncommon in this community, but due to local Nalu people's tolerance, these behaviours (at least at their current levels) appear not to cause to many problems.

Despite all of the pressure and difficulties that chimpanzees at Caiquene-Cadique face, there are reasons for hope. The community comprises a minimum of thirty-nine individuals, with a high number of infants and juveniles. This is one indication that the community is healthy and apparently reproducing. Chimpanzees are highly adaptable, resourceful and intelligent, and their plasticity to changing environments is considerable (Hockings *et al.,* 2012; Pruetz and Bertolani, 2009). To cope during periods of fruit scarcity, this chimpanzee community maintains a high intake of fruit through targeting the fruits of liana species. They also exhibit high levels of feeding on sugar rich oil-palm flowers. It is likely that the chimpanzees use this species as a fallback food, which makes it valuable for chimpanzee persistence and conservation. The identification of key plant species (such as fallback foods) to chimpanzees can contribute to the development of targeted conservation strategies (for example, when clearing forest patches for cultivation, local people can be encouraged to keep certain wild species that might buffer against crop raiding, although care would have be taken that their presence doesn't attract chimpanzees to crops). Like other communities, chimpanzees at Caiquene-Cadique appear to fission across their home range, emphasising the importance that forest corridors are maintained between fragments to allow chimpanzees to travel to find food. Certain crops were targeted by chimpanzees, including cashew and mango. However, these do not appear to constitute 'high-conflict' crops in this area. For cashew, humans and chimpanzees exploit different plant parts (Hockings and Sousa 2012), and mango does not have any monetary value. However, the value of crops can change along with changing economic and political climates. For example, at Bossou oranges went from having very low monetary value to being highly sought after and expensive to purchase, changing local people's tolerance to chimpanzee orange-raiding. This emphasises the dynamic nature of anthropogenic habitats.

To conclude, further cross-disciplinary data are needed from human and chimpanzee perspectives to understand the complexities and sustainability of interactions at Caiquene-Cadique. Humans and chimpanzees have coexisted over generations at this site, and chimpanzees have had to cope with many of the same problems that local people have endured, such as war, disease, and increased pressure on the land. Chimpanzee communities across Africa are increasingly exposed to humans and their activities. One hopes that research on chimpanzees at Caiquene-Cadique, along with other neighbouring communities, will help in the design of conservation strategies, especially for great apes inhabiting anthropogenic environments. For any biodiversity conservation strategy to work in human-influenced habitats, the needs of local people as well of those of sympatric wildlife will have to be understood and incorporated.

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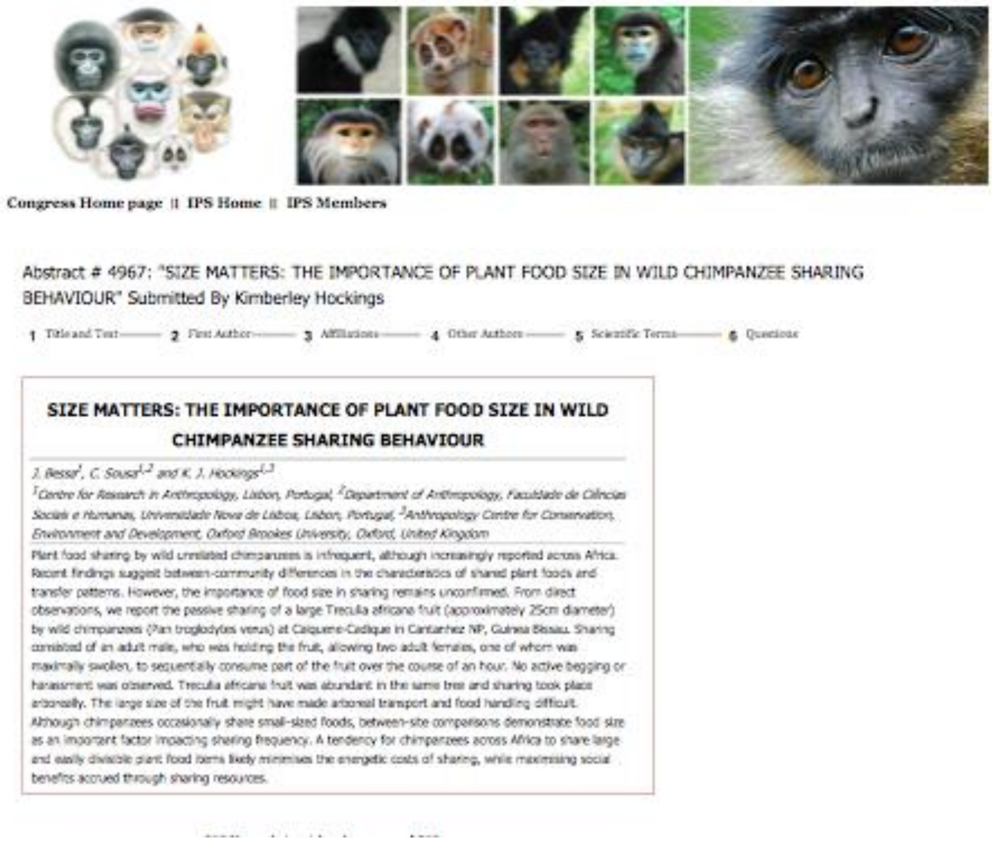
9. Appendices

Appendix A



Abstract # 4967: "SIZE MATTERS: THE IMPORTANCE OF PLANT FOOD SIZE IN WILD CHIMPANZEE SHARING BEHAVIOUR" Submitted By Kimberley Hockings

SIZE MATTERS: THE IMPORTANCE OF PLANT FOOD SIZE IN WILD CHIMPANZEE SHARING BEHAVIOUR

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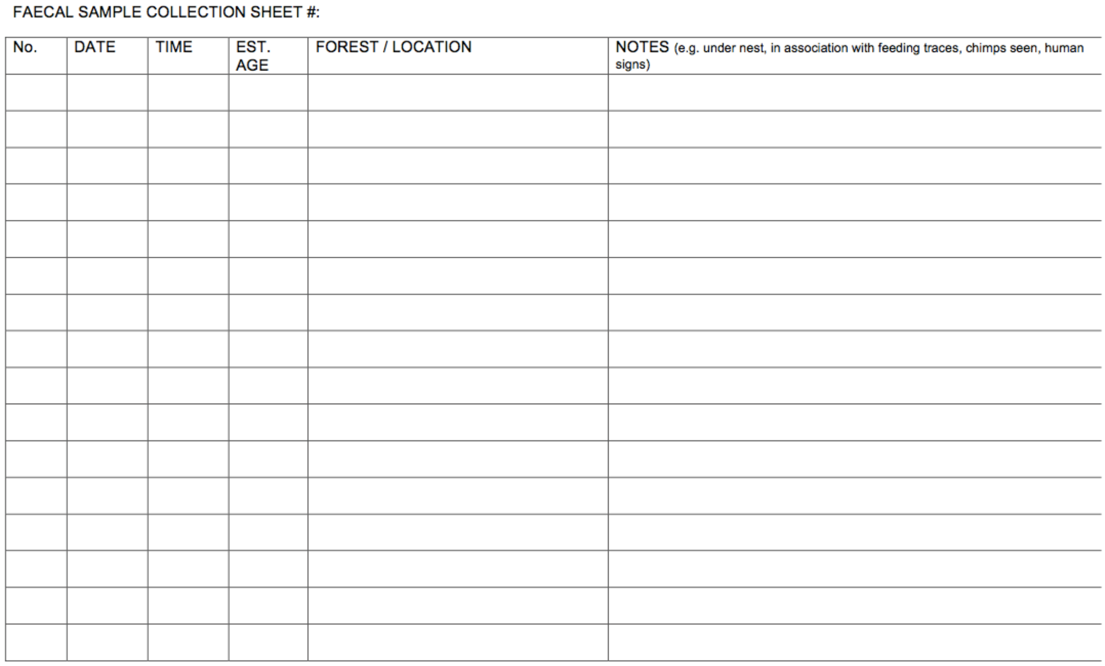
Plant food sharing by wild unrelated chimpanzees is infrequent, although increasingly reported across Africa. Recent findings suggest between-community differences in the characteristics of shared plant foods and transfer patterns. However, the importance of food size in sharing remains unconfirmed. From direct observations, we report the passive sharing of a large Treculia africana fruit (approximately 25cm diameter) by wild chimpanzees (Pan troglodytes verus) at Caiquene-Cadique in Cantanhez NP, Guinea Bissau. Sharing consisted of an adult male, who was holding the fruit, allowing two adult females, one of whom was maximally swollen, to sequentially consume part of the fruit over the course of an hour. No active begging or harassment was observed. Treculia africana fruit was abundant in the same tree and sharing took place arboreally. The large size of the fruit might have made arboreal transport and food handling difficult. Although chimpanzees occasionally share small-sized foods, between-site comparisons demonstrate food size as an important factor impacting sharing frequency. A tendency for chimpanzees across Africa to share large and easily divisible plant food items likely minimises the energetic costs of sharing, while maximising social benefits accrued through sharing resources.

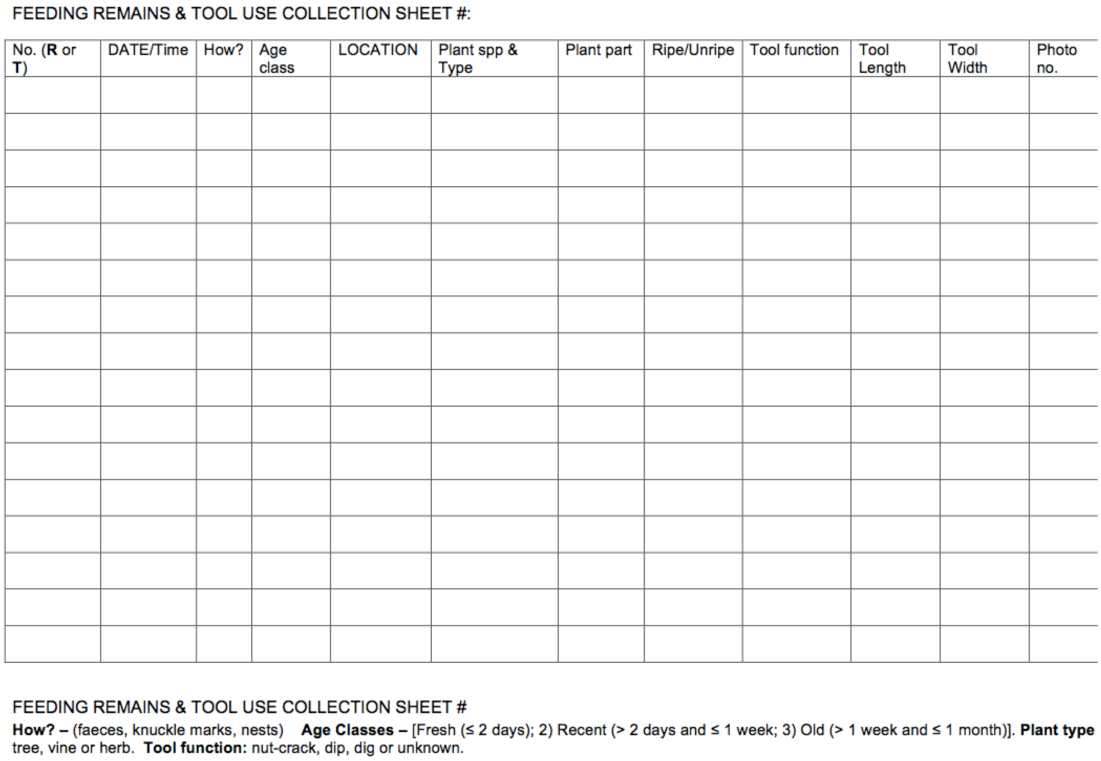
Appendix B1

Data collection sheets for faecal samples and feeding traces



FAECAL SAMPLE COLLECTION SHEET #:

No.	DATE	TIME	EST. AGE	FOREST / LOCATION	NOTES (e.g. under nest, in association with feeding traces, chimps seen, human signs)



FEEDING REMAINS & TOOL USE COLLECTION SHEET #:

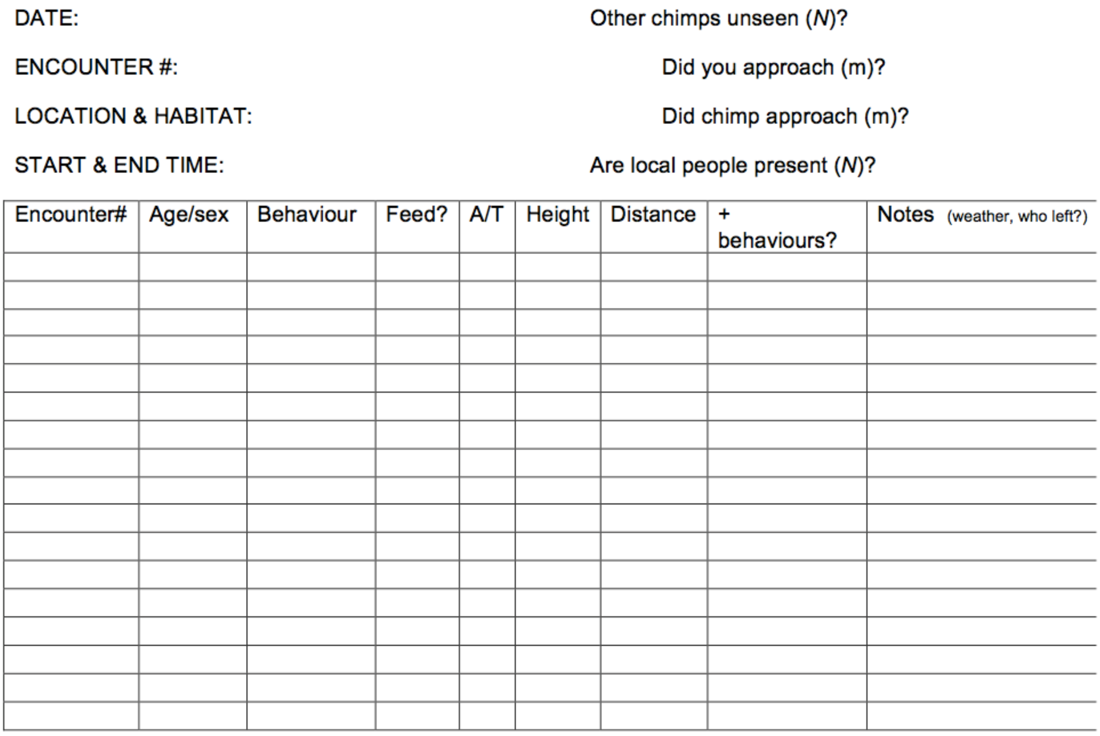
No. (**R** or **T**)	DATE/Time	How?	Age class	LOCATION	Plant spp & Type	Plant part	Ripe/Unripe	Tool function	Tool Length	Tool Width	Photo no.

FEEDING REMAINS & TOOL USE COLLECTION SHEET #

How? – (faeces, knuckle marks, nests) **Age Classes –** [Fresh (≤ 2 days); 2) Recent (> 2 days and ≤ 1 week; 3) Old (> 1 week and ≤ 1 month)]. **Plant type** tree, vine or herb. **Tool function:** nut-crack, dip, dig or unknown.

Appendix B2

Data collection sheets for chimpanzee encounters



DATE:

ENCOUNTER #:

LOCATION & HABITAT:

START & END TIME:

Other chimps unseen (*N*)?

Did you approach (m)?

Did chimp approach (m)?

Are local people present (*N*)?

Encounter#	Age/sex	Behaviour	Feed?	A/T	Height	Distance	+ behaviours?	Notes (weather, who left?)

Appendix C.

Density (i.e. number of individual trees of a species per ha) and relative density (i.e. percentage of total tree density) of all tree species found in the quadrats.

No.	Species	Family - Sub-family	Total	Density (ha)	Relative Density (%)
1	*Pavetta corymbosa*	Rubiaceae	140	70	7,0
2	*Monodora tenuifolia*	Annonaceae	127	63,5	6,4
3	*Terminalia macroptera*	Combretaceae	121	60,5	6,1
4	*Dialium guineense*	Leguminosae / Fabaceae - Caesalpinioideae	97	48,5	4,9
5	*Aedesia glabra*	Compositae	91	45,5	4,6
6	*Elaeis guineensis*	Palmae / Arecaceae	86	43	4,3
7	*Anthostema senegalense*	Euphorbiaceae	84	42	4,2
8	*Synsepalum pobeguinianum*	Sapotaceae	75	37,5	3,8
9	*Malacantha alnifolia*	Sapotaceae	49	24,5	2,5
10	*Erythrina senegalensis*	Leguminosae / Fabaceae - Papilionoideae	40	20	2,0
11	*Antidesma membranaceum*	Euphorbiaceae	36	18	1,8
12	*Ricinodendron heudelotii*	Euphorbiaceae	36	18	1,8
13	*Spondias mombin*	Anacardiaceae	35	17,5	1,8
14	*Lecaniodiscus cupanioides*	Sapindaceae	34	17	1,7
15	*Parinari excelsa*	Chrysobalanaceae	32	16	1,6
16	*Alchornea cordifolia*	Euphorbiaceae	29	14,5	1,5
17	*Ficus sur*	Moraceae	29	14,5	1,5
18	*Xylopia aethiopica*	Annonaceae	28	14	1,4
19	*Smeathmannia pubescens*	Passifloraceae	26	13	1,3
20	*Tabernaemontana africana*	Apocynaceae	26	13	1,3
21	*Anisophyllea laurina*	Rhizophoraceae	25	12,5	1,3
22	*Sterculia tragacantha*	Sterculiaceae	25	12,5	1,3
23	*Diospyros heudelotii*	Ebenaceae	24	12	1,2
24	*Drypetes gilgiana*	Putranjivaceae	20	10	1,0

No.	**Species**	**Family - Sub-family**	**Total**	**Density (ha)**	**Relative Density (%)**
25	*Albizia adianthifolia*	Leguminosae / Fabaceae - Mimosoideae	19	9,5	1,0
26	*Combretum micranthum*	Combretaceae	19	9,5	1,0
27	*Calycobolus heudelotii*	Convolvulaceae	18	9	0,9
28	*Trichilia monadelpha*	Meliaceae	18	9	0,9
29	*Holarrhena floribunda*	Apocynaceae	16	8	0,8
30	*Trichilia prieuriana*	Meliaceae	15	7,5	0,8
31	*Pentaclethra macrophylla*	Leguminosae / Fabaceae - Mimosoideae	14	7	0,7
32	*Neocarya macrophylla*	Chrysobalanaceae	13	6,5	0,7
33	*Treculia africana*	Moraceae	13	6,5	0,7
34	*Uvaria chamae*	Annonaceae	13	6,5	0,7
35	*Vitex doniana*	Labiateae	13	6,5	0,7
36	*Landolphia heudelotii*	Apocynaceae	12	6	0,6
37	*Allophylus africanus*	Sapindaceae	10	5	0,5
38	*Alstonia congensis*	Apocynaceae	10	5	0,5
39	*Cissampelos mucronata*	Menispermaceae	10	5	0,5
40	*Cuviera nigrescens*	Rubiaceae	10	5	0,5
41	*Milicia regia*	Moraceae	10	5	0,5
42	*Phoenix reclinata*	Palmae / Arecaceae	10	5	0,5
43	*Sarcocephalus latifolius*	Rubiaceae	9	4,5	0,5
44	*Sorindeia juglandifolia*	Anacardiaceae	9	4,5	0,5
45	*Trema guineensis*	Ulmaceae	9	4,5	0,5
46	*Borassus aethiopum*	Palmae / Arecaceae	8	4	0,4
47	*Detarium senegalense*	Leguminosae / Fabaceae - Caesalpinioideae	8	4	0,4
48	*Landolphia hirsuta*	Apocynaceae	8	4	0,4
49	*Newbouldia laevis*	Bignoniaceae	8	4	0,4
50	*Strombosia pustulata*	Olacaceae	8	4	0,4

No.	Species	Family - Sub-family	Total	Density (ha)	Relative Density (%)
51	*Ceiba pentandra*	Bombacaceae	7	3,5	0,4
52	*Dichrostachys cinerea*	Leguminosae / Fabaceae - Mimosoideae	7	3,5	0,4
53	*Macrosphyra longistyla*	Rubiaceae	7	3,5	0,4
54	*Ficus sp.*	Moraceae	6	3	0,3
55	*Rauvolfia vomitoria*	Apocynaceae	6	3	0,3
56	*Urena lobata*	Malvaceae	5	2,5	0,3
57	*Albizia ferruginea*	Leguminosae / Fabaceae - Mimosoideae	4	2	0,2
58	*Morinda geminata*	Rubiaceae	4	2	0,2
59	*Piliostigma thonningii*	Leguminosae / Fabaceae - Caesalpinioideae	4	2	0,2
60	*Rothmannia whitfieldii*	Rubiaceae	4	2	0,2
61	*Anthocleista procera*	Loganiaceae	3	1,5	0,2
62	*Bridelia micrantha*	Euphorbiaceae	3	1,5	0,2
63	*Macaranga heterophylla*	Euphorbiaceae	3	1,5	0,2
64	*Mezoneuron benthamianum*	Leguminosae / Fabaceae - Caesalpinioideae	3	1,5	0,2
65	*Mucuna sp.*	Leguminosae / Fabaceae - Papilionoideae	3	1,5	0,2
66	*Ritchiea capparoides*	Capparaceae	3	1,5	0,2
67	*Saba senegalensis*	Apocynaceae	3	1,5	0,2
68	*Salacia senegalensis*	Celastraceae	3	1,5	0,2
69	*Hunteria umbellata*	Apocynaceae	2	1	0,1
70	*Parkia biglobosa*	Leguminosae / Fabaceae - Mimosoideae	2	1	0,1
71	*Annona glabra*	Annonaceae	1	0,5	0,1
72	*Blighia unijugata*	Sapindaceae	1	0,5	0,1
73	*Craterispermum laurinum*	Rubiaceae	1	0,5	0,1
74	*Ficus mucuso*	Moraceae	1	0,5	0,1
75	*Hymenocardia acida*	Euphorbiaceae	1	0,5	0,1
76	*Klainedoxa gabonensis var. oblongifolia*	Irvingiaceae	1	0,5	0,1

No.	**Species**	**Family - Sub-family**	**Total**	**Density (ha)**	**Relative Density (%)**
77	*Mafer phyllanthus*	Euphorbiaceae	1	0,5	0,1
78	*Philenoptera cyanescens*	Leguminosae / Fabaceae-Papilionoideae	1	0,5	0,1
79	*Pterocarpus erinaceus*	Leguminosae / Fabaceae-Papilionoideae	1	0,5	0,1
80	*Tetracera potatoria*	Dilleniaceae	1	0,5	0,1
81	*Vernonia colorata*	Compositae	1	0,5	0,1
82	*Ximenia americana*	Olacaceae	1	0,5	0,1
83	*Unknown*	Unknown	275	137,5	13,8
	Total		1994	997	100,0