



Linking behavioral diversity with genetic and ecological variation in the Nigeria-Cameroon chimpanzee (*Pan troglodytes ellioti*)

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Abwe, E. E. (2018). Linking behavioral diversity with genetic and ecological variation in the Nigeria-Cameroon chimpanzee (*Pan troglodytes ellioti*) [Drexel University].

<https://doi.org/10.17918/D8M65Z>

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Linking behavioral diversity with
genetic and ecological variation in the
Nigeria-Cameroon chimpanzee
(*Pan troglodytes ellioti*)

A Thesis

Submitted to the Faculty

of

Drexel University

by

Ekwoke Enang Abwe

in partial fulfillment of the
requirements for the degree

of

Doctor of Philosophy

March 2018





DREXEL UNIVERSITY

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Dissertation/Thesis Title: Linking behavioral diversity with genetic
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Cameroon chimpanzee (*Pan troglodytes ellioti*)

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Dedication

My dad

Elias Abwe

and

sister

Pastor Belinda Abwe

Acknowledgements

This project was accomplished with the support and encouragement of many people. I am indebted to my committee: Katy Gonder, Bethan Morgan, Mesha Hunter-Brown, Jake Russell and Sean O'Donnell. Thank you for your advice and insightful comments in the design, data analysis and write up of this dissertation.

I am particularly grateful to my advisor Katy Gonder for accepting me as her student and it has been a great privilege to work under her mentorship. I thank Katy for her continuous support through the entirety of this project including visiting me in the field. Katy's advice and support in the design and execution of this project, both in the field and lab, and final write up of this document were invaluable.

I would like to express my sincere gratitude to Bethan Morgan, my mentor for so many years. Among other things, Bethan read through my dissertation chapters and her insightful comments brought this project to fruition. I would also like to acknowledge the unwavering support of James Christie. James and Bethan have always believed in me!

I would love to acknowledge the contributions of Sean O'Donnell, Mike O'Connor, Dana Venditti, Hilton Oyamaguchi, and Matt Mitchell in my data analyses. Sean introduced me to EstimateS which I used to compare plant species richness within and between my study sites. Dana helped me with principal component analyses and factor analyses of mixed data in R, and especially making the PCA and FAMD plots beautiful! Mike, Hilton and Matt provided insightful comments on my general data analyses.

The field part of this project was possible because of contributions from various organizations and people in Cameroon. I am especially grateful to the San Diego Zoo Global –

Ebo Forest Research Project (EFRP) for logistical, material and technical support. The facilities provided by EFRP including transportation, office space and equipment, the Bekob and Njuma Research stations in the Ebo forest, and an army of field assistants made data collection possible. I would like to thank the EFRP field assistants including: Julius Ngwane, Solomon Ngongbia, Lappe Blaise, Celestin Njukang, Wilson Tuka, Stanley Enongene, Jean Melba, Marc Touob, Junior Kibong, Elie Liboho, Jonas Mam and Daniel Batouan. I am also indebted to EFRP staff including Daniel Mfossa, Marcel Ketchen, Christian Mbella, Abwe Enang, Wilson Tuka and Solomon Ngongbia for helping me to macroscopically assess chimpanzee fecal samples for dietary analysis. I am thankful to Josiane Agha for her assistance with data entry. Thank you to Felix Nkumbe, the tireless EFRP driver. Thanks to His Royal Highness Dipita Gaston, president of traditional rulers of communities around the Ebo forest for his dedication to biodiversity conservation and an enabling research environment.

I am especially grateful to Wildlife Conservation Society, Cameroon for logistical and technical support in the Mbam & Djerem National Park (MDNP). I am thankful to Roger Fotso, Bernard Fosso, Eric Tegua, Arielle Noubi, Arouna Forche, Jean Marie Elouna and Noel Yanjeu for facilitating my data collection at Ganga, MDNP. I also wish to express sincere gratitude to Albert Mouna the Conservator of the MDNP, and park rangers. My field data collection at Ganga was possible due a dedicated team of field assistants including Roger Doudjar, Daouda Betare, Thomas Elanga, Missa Jacques, Moise Bello, Eric Tegua, Fabrice Kentatchime, Flaubert Mba, Alvine Dadjo and Ruffin Ambahe. I want to acknowledge the skill and dedication of paddlers who ferried us up and down the Djerem River, braving the rapids and the hippos! I am particularly thankful to Roger, Fabrice, Alvine and Flaubert for leading data collection expeditions

at Ganga while I was in Ebo forest or back at Drexel. I am equally indebted to Fabrice for help with data entry and scanning datasheets, and uploading these alongside photos and videos on the Gonder Lab Dropbox.

Thanks to Barthélemy Tchiengue of the National Herbarium, Cameroon for botanical identification across Ebo forest and MDNP. Botanical inventories and identification were facilitated by Ruffin Ambahe, Marcel Ketchen, Fabrice Kentatchime, Lappe Blaise, Roger Doudjar, Daouda Betare, and Elanga Thomas.

I am grateful to my family for their support. Special thanks to my wife Martha and my boys: Enang, Akwe, Mejene, Nyame and Ekukole for supporting me and enduring my absence during these years. My family in the US Adelley (my mum), Marion, Agnes, Ivo, Theo, Therion and Jelani who made me feel at home away from home. To my family in Cameroon (Stella, Abwe, Ngalame, Etape, Masango, Hubert and Shirley), I thank you for supporting Martha and the boys, and for your continuous prayers and support during this project.

I am also indebted to my friends. I want to express my sincere appreciation to Joe Kujawski and his family for accepting me as a member of their household. Thanks to Miguel and Melissa for weekends spent with them. Thanks to Matt Mitchell and Dana Venditti for always hanging out with me. I also wish to express special gratitude to Martin Cheek for his technical and moral support for so many years. I want to say a special thank you to Bill Konstant for reinvigorating walks through the woods, and his passion for biodiversity conservation. Thanks to Bill for sharing the conservation story and photos of my dad.

I also wish to express my appreciation to past and present members of the Gonder Lab: Matt, Paul, Drew, Heidi, Deme, Miguel, Pat, Dana, Hilton, Janina, Bryan, Steve, Ian and Walker.

I want to sincerely thank the Government of Cameroon, through the Ministry of Forestry and Wildlife (MINFOF), and Ministry of Scientific Research and Innovation (MINRESI) for permission to carry out this research and an enabling research environment.

This research was supported by grants from Leakey Foundation, Primate Conservation Inc. and NSF grant to M. K. Gonder. I am grateful to San Diego Zoo Global (SDZG) for supporting this research, and awards via SDZG from USFWS Great Apes Conservation Fund, the Arcus Foundation and the Margot Marsh Biodiversity Foundation.

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List of Abbreviations and Acronyms

ANOVA – Analysis of variance

BA – Basal area

DBH – Diameter at breast height

DRC – Democratic Republic of Congo

EFRP – Ebo Forest Research Project

ENM – Ecological Niche Model

FAMD – Factorial analysis of mixed data

GGNP – Gashaka Gumti National Park

GIS – Geographic Information System

GPS – Global Positioning System

MDNP – Mbam & Djerem National Park

MINFOF – Ministry of Forestry and Wildlife

MINRESI – Ministry of Scientific Research and Innovation

NGO – Non-Governmental Organization

NSF – National Science Foundation

PCA – Principal component analysis

SD – Standard Deviation

SDZG – San Diego Zoo Global

SNP – Single-nucleotide polymorphism

SPSS – Statistical Package for the Social Sciences

THV – Terrestrial herbaceous vegetation

USFWS – United States Fish and Wildlife Service

WCS – Wildlife Conservation Society

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ABSTRACT

Linking behavioral diversity with
genetic and ecological variation in the
Nigeria-Cameroon chimpanzee
(*Pan troglodytes ellioti*)
Ekwoke Enang Abwe

Advisor: Mary Katherine Gonder, Ph.D.

Tropical rainforests are rich in vertebrates, the result of processes that generate and maintain biological diversity, and low extinction rates under relatively stable climatic conditions. The Gulf of Guinea in Central/West Africa is a biodiversity hotspot with several endemic species, including several primate species. The diversity of endemic species found in this region has been attributed to a complex forest history during the Pleistocene; habitat variation associated with the confluence of the Gulf of Guinea rainforest to the west with the Congo Basin rainforest to the south and drier savanna habitats to the north; and biogeographic barriers including the Cameroon Highlands and riverine barriers, such as the Sanaga River in Central Cameroon. The contributions of the Sanaga River and Cameroon Highlands in promoting species diversification have been examined in some detail, and a growing body of data, suggests that environmental variation, particularly in an ecotone area in southern Cameroon has been important in promoting the diversification of birds, lizards and insects. Little is known about whether ecological variation has contributed to the diversification of endemic mammals across this region.

The chimpanzees of Cameroon present a unique opportunity to investigate how ecological variation contributes to promoting intraspecific divergence in the endemic mammals of the region. In addition to harboring two chimpanzee subspecies (*Pan troglodytes troglodytes* and *P. t. ellioti*), there are two distinct gene pools associated with *P. t. ellioti*. These two gene pools were previously shown to inhabit two significantly different niches – one associated with the mountainous rainforest habitats found in western Cameroon and one associated with the ecotone habitats found in central Cameroon. This thesis explores environmental and ecological differences between rainforest and ecotone habitats at a fine geographic scale, and compares and contrasts chimpanzee socioecology patterns between these habitats. Research was conducted from January 2016 to December 2017 at three study sites to represent a range of environments inhabited by *P. t. ellioti*. I completed surveys for 15 months (January 2016 to March 2017) at two rainforest sites (Njuma and Bekob) in Ebo forest. Njuma was selected for study because it represents relatively undisturbed lowland rainforest, whereas Bekob represents a regenerating human-modified lowland rainforest landscape. Complementary studies were also completed for 24 months (January 2016 to December 2017) at one ecotone site in Mbam & Djerem National Park (Ganga). Quantitative ecological methods were used to characterize habitats and the seasonal availability of fleshy fruits that are important to chimpanzees. Since chimpanzees across the sites are not habituated to humans, I used indirect methods (fecal samples and nests) to investigate chimpanzee diet and nesting patterns.

The first aim of study was to examine whether and how the niches of *P. t. ellioti* in western Cameroon (Njuma and Bekob) differed from the niche occupied by *P. t. ellioti* in central Cameroon (Ganga) at fine geographic scale. The main variables that distinguished the rainforest from the ecotone habitats included rainfall (annual amounts are higher at the rainforest) and the diversity, density and

size of trees (higher at the rainforest than the ecotone). On the other hand, the ecotone had a higher density of lianas and terrestrial herbaceous vegetation. The availability of fleshy fruits was higher at the ecotone, though with marked seasonality compared to the rainforest. At Bekob, there was the prevalence of introduced and secondary forest plant species that I predicted to be important in the socioecology of chimpanzees.

The second aim of the study was to examine how occupying rainforest and ecotone niches impact chimpanzee feeding behavior. The main differences in the dietary ecology of the ecotone and rainforest chimpanzees were in the seasonal variation of fleshy fruits and fibrous foods in their diets. Fleshy fruits were the most important dietary component for rainforest chimpanzees in the dry season, whereas the diet of the ecotone chimpanzees was dominated by fibrous foods. Conversely, in the wet season, the proportion of fleshy fruits was more significant in the diet of the ecotone chimpanzees, while fibrous foods were of more significance for the rainforest chimpanzees. Consistent with other human-modified environments, introduced and secondary forest species including *Elaeis guineensis* and *Musanga cecropioides* were important dietary components for chimpanzees at Bekob, especially during periods of low fleshy fruit availability. Animal consumption, including vertebrates and invertebrates was more significant at Ganga, and was inversely associated with fleshy fruit consumption.

Finally, the third aim of the study was to examine how occupying rainforest and ecotone niches impact chimpanzee nesting behavior. Fruit phenology was an important factor in nesting site selection at the ecotone while rainforest chimpanzees selected steep slopes, hypothesized as an antipredation strategy. Larger nest group sizes were linked to periods of higher fruit availability especially at the Ganga. Chimpanzees across the three sites had site specific preferences for nesting tree species, but

Strombosia grandifolia was commonly preferred across the sites, while nesting in *Elaeis guineensis* was exclusive to chimpanzees at Bekob.

The dietary and nesting patterns of chimpanzees differed considerably between rainforest and ecotone, and may have implications that will improve understanding about why this region is an important area for the genetic diversification of chimpanzees. The ecotone habitat of Ganga is characterized by marked seasonality in fleshy fruit availability and seasonal dietary shifts at the ecotone could imply wider ranging, larger territories and lower levels of gregariousness among chimpanzees. In contrast, the rainforest habitats of Njuma and Bekob are characterized by less pronounced seasonality in fleshy fruits and seasonal dietary shifts. This could reflect smaller territories and more sociality in the rainforest chimpanzee populations. This differentiation in socioecological patterns may be responsible for observed genetic patterns in chimpanzees across this region.

CHAPTER ONE

1. BACKGROUND AND INTRODUCTION

1.1. Tropical forest history and biodiversity

Tropical rainforests are rich in vertebrates, the result of various processes that generate and maintain biological diversity, and low extinction rates under relatively stable climatic conditions (Moritz et al., 2000). Certain areas within tropical Africa are noted for species richness and endemism (Myers, 1988, Myers et al., 2000). The Gulf of Guinea region, for example, is a biodiversity hotspot, harboring multiple endemic species including primates, amphibians, birds, fish and reptiles (Oates et al., 2004). Several hypotheses have been proposed to explain the diversity of vertebrates across this area. On the one hand, diversification by neutral evolutionary processes associated with Pleistocene refugia and separation across biogeographic barriers has been proposed to underpin the diversification of tropical animals (Anthony et al., 2007, Eriksson et al., 2004, Moritz et al., 2000). On the other hand, diversification by natural selection has been proposed to have fueled the adaptation of populations to prevailing local conditions, including occupying ecological gradients (Freedman et al., 2010b, Smith et al., 1997), differences in disease ecology (Locatelli et al., 2014, Locatelli et al., 2016) and anthropogenic changes (Freedman et al., 2010a).

The 'Pleistocene refugia' and 'biogeographic barriers' hypotheses predict that speciation occurs as a result of neutral evolutionary processes (i.e. genetic drift) due to population isolation. The Pleistocene refugia suggests that during maximum glaciation periods that characterized the earth during the Pleistocene, tropical animals were isolated in forest refuges leading to diversification of rainforest taxa (Endler, 1982, Haffer, 1969, Mayr and O'Hara, 1986). Two major

forest biomes in Cameroon (Congo rainforest and Gulf of Guinea rainforest) have been suggested to correspond to Pleistocene refuges (Maley, 1996). These two forest biomes converge in central Cameroon at the Sahel-savanna interface, leading to a mosaic of habitats in what has been termed an 'ecotone' (Smith et al., 1997). For the biogeographic barriers hypothesis, large rivers, mountain ranges and habitat breaks like the Dahomey Gap disrupt gene flow between populations resulting in diversification and speciation (Booth, 1958, Gonder et al., 2006, Mayr and O'Hara, 1986, Moritz et al., 2000). The Cameroon Highlands, Niger River, Cross River and Sanaga River seem to be dispersal barriers to several primate species that are endemic to the area, including the Cross River gorilla (*Gorilla gorilla diehli*) and Preuss's guenon (*Allochrocebus preussi*). Several pairs of subspecies including *P. t. ellioti* and *P. t. troglodytes*, *Cercopithecus erythrotis* and *C. cephus*, *C. nictitans martini* and *C. n. nictitans*, *C. pogonias pogonias* and *C. p. grayi*; and species: *Mandrillus leucophaeus* and *M. sphinx* occur to the north and south respectively of the Sanaga River, Cameroon (Oates et al., 2004, Oates and Nash, 2011).

In contrast to the Pleistocene Refugia and Barrier models that propose that genetic drift is the dominant force that promotes the differentiation of tropical taxa, the ecological gradient hypothesis posits that divergence through natural selection is equally or more important than drift. Specifically, the ecological gradients hypothesis suggests that the diversification of widely-distributed tropical fauna is governed by local adaptation to diverse environmental and ecological conditions. Varying conditions found in forest versus ecotone habitats result in intraspecific differentiation, and eventually speciation (Freedman et al., 2010a, Freedman et al., 2010b, Moritz et al., 2000, Simard et al., 2009, Smith et al., 1997). The rainforest to savanna-

woodland mosaic transition in Cameroon, or central Cameroon ecotone, is associated with the divergence of several taxa including reptiles, birds, and insects (Freedman et al., 2010b, Smith et al., 2011a, Smith et al., 1997), but little is known about whether this ecotone is important in the diversification of mammals that occupy the ecotone. Recent studies have linked the divergence of chimpanzees across Cameroon with the marked environmental gradients across this region (Mitchell et al., 2015b, Sesink Clee et al., 2015).

Increasingly, human activities are fragmenting and isolating forest and ecotone habitats across the Gulf of Guinea, which limit gene flow for primate populations (Bergl et al., 2008, , Morgan et al., 2013), as well as reduce the diversity in habitats that are associated with natural selection in several species (Freedman et al., 2010a). The impact of such anthropogenic alterations to the landscape in modifying the behavior and resource utilization of tropical vertebrates has only recently become a focus of research, and their potential for shaping patterns of intraspecific variation remains largely unexplored. Increasing evidence suggests that human activities in other parts of the world have shaped patterns of intraspecific variation in a wide variety of tropical vertebrates, including birds, orangutans, and several other large mammals (Freedman et al., 2010a, Goossens et al., 2006, Yackulic et al., 2011). However, relatively little is known about how large tropical vertebrates use human-modified landscapes across this region or how resource utilization in these areas differs from that of less-disturbed areas.

1.2. Chimpanzee distribution, phylogenetics and population history

Chimpanzees (*Pan troglodytes*) occupy a wide diversity of habitats across tropical Africa (Caldecott and Miles, 2005, Mittermeier et al., 2013), defined by geographically delimited

subspecies (Gagneux et al., 2001). There are two geographically- and genetically-defined groups: a western African group that includes two subspecies, *P. t. verus* and *P. t. ellioti*, and a central/eastern African group that includes two subspecies, *P. t. troglodytes* and *P. t. schweinfurthii* (Gonder et al., 2006, Gonder et al., 1997, Prado-Martinez et al., 2013, Sudmant et al., 2013). These two groups converge at the Sanaga River in central Cameroon – Figure 1.1. The differentiation of these subspecies has been associated with allopatric speciation governed by neutral evolutionary processes caused by population isolation by riverine barriers (Gonder et al. 1997; Gagneux et al., 2001, Gonder, 2000, Gonder and Disotell, 2006, Gonder et al., 2006, Mitchell et al., 2015a). More recently, differences between these two subspecies have been linked with habitat variation across Cameroon (Mitchell et al., 2015b), which suggests a possible role of local adaptation in the differentiation of these two lineages.

Chimpanzees in Cameroon present a unique opportunity to investigate the processes that generate intraspecific variation, and ultimately, speciation in tropical mammals. Western African and central/eastern African chimpanzee groups converge at the Sanaga River in central Cameroon, which also marks the boundary between the *P. t. ellioti* and *P. t. troglodytes* (Gonder and Disotell, 2006, Mitchell et al., 2015a, Prado-Martinez et al., 2013) – see Figure 2. However, the Sanaga River is not a complete barrier as there is at least one individual per generation exchanged between the two subspecies (Gonder, 2000, Mitchell et al., 2015a). There is further genetic distinction within *P. t. ellioti* itself, with one gene pool associated with the mountainous rainforest in western Cameroon and the other with the ecotone in central Cameroon (Mitchell et al., 2015a). In addition to being separated by the Mbam River – a tributary of the Sanaga River,

the habitats occupied by the distinct *P. t. ellioti* gene pools are different (Mitchell et al., 2015b, Sesink Clee et al., 2015).

1.3. Habitat diversity and chimpanzees

Chimpanzees exhibit marked ecological flexibility across their current range of forested regions of sub-Saharan Africa, (Stumpf, 2011, Watts, 2012), but the importance of this flexibility in the evolution of the species remains unclear. Much of their range in Equatorial Africa is characterized by two annual wet seasons and total annual rainfall in excess of 2000 mm, but other parts of the chimpanzee range receive less than 1000 mm of rainfall annually and experience an extended drought (McGrew et al., 1981). Habitats range from closed-canopy rainforest at the equatorial belt to woodland, gallery forest and savanna towards the tropics (Stumpf, 2011, Van Schaik and Pfannes, 2005). Chimpanzees range from sea level at Loango National Park, Gabon, to as high as 2600 m in the Kahuzi-Biega National Park, Democratic Republic of Congo and Bwindi Impenetrable National Park, Uganda (Basabose, 2005, Head et al., 2011, Stanford and Nkurunungi, 2003). In some parts of their range, chimpanzees live in human-modified or human-dominated landscapes (Beck and Chapman, 2008, Hockings et al., 2009, McLennan, 2013).

1.4. Chimpanzee socioecology

Local adaptation to prevailing environmental conditions can be as important as genetic drift in promoting and maintaining diversification of populations and species (Moritz et al., 2000, Smith et al., 2011b, Smith et al., 1997), but the ways that local adaptation has contributed to the partitioning of diversity in chimpanzees has not been explored. Patterns of chimpanzee

socioecology across Africa illustrate that the species is characterized by a complex variation in behaviors associated with a range of ecological niches (Lambert, 2007, Moore, 1996, Stumpf, 2011, Whiten et al., 1999). In general, chimpanzees live in communities of between 20 and 150 individuals, in which members know each other and defend their communal resources from adjacent communities. These communities have a dynamic fusion-fission temporal social structure – coalescing or splitting into temporal social units that vary in size and composition (Mitani, 2006, Sugiyama, 2004). It has been hypothesized that this type of community structure reduces the cost of group living (Chapman et al., 1994a, Newton-Fisher et al., 2000).

The amount and seasonality of rainfall affects plant diversity and productivity in different habitats, and consequently chimpanzee socioecology (McGrew, 2007, Tutin et al., 1997a, Tutin et al., 1997b, Wrangham et al., 2009, Wrangham, 2005). Chimpanzees are fruit specialists and seek to maximize fruit consumption even when this food type is scarce. Plant phenology is subject to climatic patterns and all habitats witness seasonality in fruit availability. Seasonality in overall fruit production is less pronounced in closed-canopy rainforest habitats and chimpanzees inhabiting them have a diverse fruit-based diet for most of the year (Chapman et al., 1997, Chapman et al., 1994b, Hemingway and Bynum, 2005, Stumpf, 2011, van Schaik and Brockman, 2005). Conversely, drier habitats including ecotones and savannas witness greater seasonality in fruit phenology, and chimpanzees that inhabit them have a smaller range of fruit species in their diet (McGrew et al., 1996, McGrew et al., 2004, Tutin et al., 1991). During periods of fruit scarcity, chimpanzees feed on less preferred food sources including fruit species with asynchronous fruiting patterns, non-fruit plant parts and animal prey (Doran et al., 2002, Hunt

and McGrew, 2002, Knott, 2005, McGrew et al., 1988, Murray et al., 2006, Wrangham et al., 1996).

Differences in habitat and diet influence many aspects of chimpanzee population dynamics and socioecology (Boesch et al., 2002, Chapman et al., 1994a, Stumpf, 2011, Wrangham et al., 1996). Community territories for rainforest chimpanzees are smaller and easier to defend by males in these close-knit systems (Herbinger et al., 2001). Conversely, territories for chimpanzees living in drier habitats are larger, with widely dispersed resources which make them more difficult to defend (Mitani and Rodman, 1979). The temporal and spatial distribution of resources within a community's range affect different aspects of chimpanzee behavioral ecology including population size, ranging patterns and sociality, tool use and nesting ecology (Bogart, 2009, Chapman et al., 1995, Hernandez-Aguilar et al., 2013, Lambert, 2007, Pruetz and Bertolani, 2009, Stumpf, 2011, Yamagiwa and Basabose, 2009). For example, the population density of chimpanzees inhabiting ecotone and savanna habitats is generally lower than at closed-canopy rainforests (Hernandez-Aguilar, 2009, McGrew et al., 1981, Ogawa et al., 2007, Pruetz and Bertolani, 2009). Home ranges vary in size from 7 – 30 km² in rainforests (Chapman and Wrangham, 1993, Herbinger et al., 2001, Morgan et al., 2006, Wrangham et al., 1996), to well over 50 km² in drier habitats (Baldwin et al., 1982, McGrew et al., 1981, Ogawa et al., 2007, Pruetz et al., 2002).

Chimpanzee socioecology patterns have been compared between some long-term study sites and inter-population differences in behaviors have been attributed to ecological variation as well as cultural traditions (Whiten et al., 1999). Efforts have also focused on linking socioecological variation and genetic variation across different chimpanzee subspecies in Africa

(Langergraber et al., 2011, Lycett et al., 2009). These analyses have however been limited to populations of two subspecies: *P. t. verus* and *P. t. schweinfurthii*, which occur at the western and eastern ranges of the species. More recent studies have compared feeding and nesting behavior between populations, reviewing literature from all four subspecies (Hunt and McGrew, 2002, Stumpf, 2011, Tagg et al., 2013). But these comparisons are all based on independent datasets that did not systematically incorporate genetic and ecological variation between populations and how these might influence or coincide with differences in socioecological patterns.

Chimpanzees have a fission-fusion social system in which the size and composition of the social group change as time passes and animals move throughout the environment (Mitani, 2006, Sugiyama, 2004). This fission-fusion fluid social system in chimpanzees differs between communities found in closed-canopy versus those found in savanna habitats due to the spatial and temporal distribution of resources (Boesch et al., 2002, McGrew et al., 1996). For example, at closed-canopy rainforest sites, closely related males form coalitions to defend communal resources from adjacent communities (Stumpf, 2011, Watts and Mitani, 2001). Males in such close-knit communities also have strong genetic affinities (Arandjelovic et al., 2011, Inoue et al., 2008, Langergraber et al., 2007). In ecotones and savannas resources are more dispersed and territories are considerably larger (Hernandez-Aguilar, 2009, McGrew et al., 1981, Pruetz and Bertolani, 2009, Stumpf, 2011) – see Table 1, which makes them more difficult to defend (Mitani and Rodman, 1979). Such differences in habitat and resource availability are expected to produce changes in the structure of chimpanzee communities in marginal habitats (Hernandez-Aguilar, 2009, Moore, 1996, Ogawa et al., 2007, Tutin et al., 1983, Yamagiwa and Basabose,

2009). Consequently, the fission-fusion social system observed in rainforest communities may be very different from the social systems in communities occupying ecotones and savannas (Ogawa et al., 2007, Pruetz and Bertolani, 2009). These observations suggest that adaptations driven by ecological variation might play an important role in promoting conditions favorable to intraspecific differentiation and speciation in chimpanzees. However, what remains unexplored is whether such ‘adaptations’ are correlated with intraspecific genetic differentiation in the species.

1.5. Nigeria-Cameroon chimpanzees

The Nigeria-Cameroon chimpanzee (*P. t. ellioti*) population in Cameroon represents a unique opportunity to examine local adaptation in relation to ecological and genetic variation at a fine geographic scale. Cameroon is unique in that it harbors two of the four recognized chimpanzee subspecies (*P. t. ellioti* and *P. t. troglodytes*), and is also the location where the two main branches of the chimpanzee phylogenetic tree converge with one another. Specifically, they converge at the Sanaga River in central Cameroon (Gonder et al., 2006, Mitchell et al., 2015a). *P. t. troglodytes* occupy habitats south of the Sanaga River, and *P. t. ellioti* is found to the north of the Sanaga River. *P. t. ellioti* is further subdivided into two populations—a population in the mountainous closed-canopy rainforests of western Cameroon and a second that occupies the forest-savanna ecotone of central Cameroon (Mitchell et al., 2015a, Sesink Clee et al., 2015). These two genetically distinct populations occupy significantly different habitats (Sesink Clee et al., 2015), which make them an excellent model for examining whether ecological adaptation might be important in promoting and maintaining divergence between these populations.

Socioecological research on Nigeria-Cameroon chimpanzees remain sparse, particularly in Cameroon (Morgan et al., 2011). Gashaka Gumti National Park (GGNP), Nigeria is a mosaic habitat of woodland, lowland and gallery forest with 4-5 months of drought per year, and studies on chimpanzee socioecology have been ongoing since 2000. The home range and density of chimpanzees at GGNP are estimated at 26 km² and 1.3 individuals/km² respectively (Sommer et al., 2004). The chimpanzees at GGNP have a largely fruit-based diet, but they also harvest arboreal ants and ground-dwelling army ants using tools made from vegetal material, and dip for honey with stick tools (Fowler, 2006, Fowler and Sommer, 2007, Hohmann et al., 2012, Schoening et al., 2007, Sommer et al., 2012). The chimpanzees at Ngel Nyaki Forest Reserve, Nigeria, with a population density estimated at 1.67 individuals/km² (Beck and Chapman, 2008) consume fruits from 52 plant species and figs are an important fallback food (Dutton and Chapman, 2015). The Ngel Nyaki population also engage in subsistence tool use behavior to acquire ants, and honey from stingless beehives (Dutton and Chapman, 2014).

Human activities influence chimpanzee nesting behaviors with terrestrial nests common in areas with less hunting pressure in the Lebialem-Mone landscape in southwest Cameroon (Last and Muh, 2013). Chimpanzees in the Ebo Forest, Cameroon have an interesting tool use repertoire including nut cracking, termite fishing and honey dipping (Abwe and Morgan, 2008, Morgan and Abwe, 2006). The study of the socioecology of different *P. t. ellioti* populations is at its infancy, yet there are marked differences between populations occupying distinct ecological niches (Abwe and Morgan, 2008, Fowler and Sommer, 2007, Morgan and Abwe, 2006, Wrangham, 2006). Nut cracking and termite fishing are restricted to rainforest *P. t. ellioti* in the Ebo forest (Abwe and Morgan, 2008, Morgan and Abwe, 2006), and terrestrial nesting behavior

is limited to rainforest populations (Abwe and Morgan, 2008, Last and Muh, 2013).

Understanding environmental and ecological differences across the Nigeria-Cameroon chimpanzee range, and how genetically distinct local chimpanzee populations exploit different niches may shed light on the proximate processes that contribute to the diversification in many primate species across Cameroon and the Gulf of Guinea region in general. This study was aimed at assessing environmental and ecological variation in habitats occupied by two distinct gene pools of the Nigeria-Cameroon chimpanzee, and to determine how the socioecology of chimpanzees across this region varies as a result of these differences.

1.6. Study sites

1.6.1. Ebo forest

The Ebo forest is located in Littoral Region, Cameroon and extends for more than 1500 km², of which c. 1100 km² is proposed as a national park. The forest harbors one of the most important extant populations of *P. t. ellioti* (Morgan et al., 2011) and is associated with the *P. t. ellioti*-rainforest gene pool (Mitchell et al., 2015a). Annual rainfall at Ebo forest exceeds 2500 mm, and the wet season extends between March and November, peaking in July-August. The forest is characterized by an altitudinal range between 100-1200 m above sea level with open- and closed-canopy semi-deciduous and evergreen lowland and submontane rainforest of the Atlantic forest dominated by Leguminosae (Letouzey, 1985). Two sites (Njuma and Bekob) were selected in Ebo forest based on differences in anthropogenic history and modification.

1.6.1.1. Bekob (human-modified rainforest)

Bekob, in the northeastern part of Ebo forest (Figure 1.2) has a long history of human habitation but was vacated in the late 1950s following civil strife at Cameroon's independence.

Open- and closed-canopy evergreen and semi-deciduous forests characterize abandoned villages and farmland in lower altitude (~500 m above sea level) areas, while higher altitudes (up to 1200 m) harbor evergreen closed-canopy submontane vegetation (Dowsett-Lemaire and Dowsett, 2001, Morgan and Abwe, 2006). The habitat at Bekob is heterogenous with closed-canopy mature submontane vegetation dominated by several species of *Garcinia*, and anthropogenically altered closed- and open-canopy young and old secondary forests and abandoned plantations at lower altitudes. Common upper-canopy species at Bekob are *P. angolensis*, and *Santiria trimera*, while the middle and lower canopies are dominated by *Uapaca guineensis*, *Tabernaemontana crassa*, *Oncoba welwitschii* and *Drypetes* spp.

1.6.1.2. Njuma (near pristine rainforest)

The Njuma area lies to the west of the Ebo River which traverses the forest from north to south (Figure 1.2), and is composed of closed-canopy lowland rainforest. Njuma was selectively logged in the late 1980s – the main indicators of which are tree stumps, abandoned logging roads and evacuation trails (Dowsett-Lemaire and Dowsett, 2001). At higher altitudes (up to 900 m altitude), closed-canopy submontane assemblages are still intact. Common upper-canopy species at Njuma include *Scyphocephalum mannii*, *Desbordesia glaucescens*, and *Pycnanthus angolensis*, while the middle and lower canopies are dominated by *Coula edulis*, and several species of *Diospyros* and *Drypetes*.

The Ebo forest harbors a rich assemblage of diurnal primates including drills (*Mandrillus leucophaeus*), Preuss's red colobus (*Procolobus pennantii preussi*), red-capped mangabeys (*Cercocebus torquatus*), Preuss's monkeys (*Allochrocebus preussi*), chimpanzees (*P. t. ellioti*) and gorillas (*Gorilla gorilla* sp.), and large mammals including elephants (*Loxodonta cyclotis*), red river

hogs (*Potamochoerus porcus*), and duikers (*Cephalophus* spp.) (Morgan et al., 2011, Morgan et al., 2003, Oates et al., 2004, Oates and Nash, 2011). The forest is also noted for its botanical diversity with several plant endemics including *Palisota ebo*, *Ardisia ebo*, *Inversodicraea ebo*, *Talbotiella ebo* and *Gilbertiodendron ebo* being ‘discovered’ and recorded (Cheek and Xanthos, 2012, Cheek et al., 2017, Mackinder et al., 2010, van der Burgt et al., 2015). Poaching and the bushmeat trade, and habitat loss from logging, subsistence-shifting agriculture and agro-industrial plantations are the main conservation threats at Ebo forest; and these are exacerbated by the proximity of the forest to the city of Douala and other major population centers in Cameroon (Morgan et al., 2011, Whytock and Morgan, 2010).

1.6.2. Mbam & Djerem National Park

The Mbam & Djerem National Park (MDNP) straddles the Adamawa, Centre and East Regions of Cameroon and extends over 4165 km². The national park was created in 2000, as an off-shoot of the Chad-Cameroon petroleum pipeline project (Maisels, 2000). The MDNP harbors an important population of *P. t. ellioti* (Morgan et al., 2011) and it is associated with the *P. t. ellioti*-ecotone gene pool (Mitchell et al., 2015a). Annual rainfall at MDNP is ~2000 mm, and the wet season is concentrated between April and October. The dry season drought conditions are exacerbated by the dry Harmattan winds from the Sahara Desert that blow across the area from December through January. The vegetation of the park is composed of closed-canopy rainforest, woodland, gallery forest and savanna mosaics. With a dense network of rivers, riparian forest constitutes a major vegetation class. The vegetation complex here has been described as ecotone: a forest-woodland-savanna mosaic, rich in habitats and species (Maisels, 2005, Smith et al., 1997).

1.6.2.1. Ganga (ecotone)

My research station in the MDNP was at Ganga, which is located to the northeast of the park along the Djerem River. The high closed-canopy habitat at Ganga is dominated by *Pseudospondias microcarpa*, *U. guineensis*, *Parkia* sp., *Berlinia* sp.; while *Hymenocardia lyrata*, *Xylopia aethiopica* and *Vitex doniana* dominate high open-canopy secondary vegetation; and middle and the lower strata are dominated by *Spondianthus preussi* and *Ochna afzelii*. The MDNP harbors 13 primate species including grey-cheeked mangabeys, olive baboons, putty-nosed monkeys, De Brazza's monkeys (*Cercopithecus neglectus*), tantalus monkeys (*Chlorocebus aethiops tantalus*), guereza colobus (*Colobus guereza*), crowned guenons (*Cercopithecus pogonias*) and chimpanzees (*P. t. ellioti*) (Maisels, 2000, Maisels et al., 2007, Morgan et al., 2011). Other large mammals common in the park include elephants (*Loxodonta* sp.), buffalos (*Syncerus caffer*), bongos (*Tragelaphus eurycerus*), red river hogs (*P. porcus*), and duikers (*Cephalophus* spp.) and antelopes (Maisels, 2000). The park and adjacent areas are subject to anthropogenic influence including controlled and illegal annual bushfires, cattle grazing and poaching. In many parts of the park, savanna habitats are being colonized by woodland, a result of the ceased annual bushfires associated with human emigration to more urban settlements along the Yoko-Tibati road (Maisels, 2000, Mitchard et al., 2009).

1.6.3. Dissertation structure

This dissertation is arranged in three main chapters that relate the socioecology of chimpanzees in Cameroon to differences in environmental and ecological conditions across their habitats. In Chapter Two, I expanded on a previous ecological niche modelling study that distinguished three suitable chimpanzee habitats in Cameroon which correspond to the

distributions of the three-distinct chimpanzee genetic pools found in Cameroon: *P. t. troglodytes*-lowland rainforest, *P. t. ellioti*-mountainous rainforest and *P. t. ellioti*-ecotone. The aim of this chapter was to test the hypothesis that habitats occupied by distinct gene pools of the Nigeria-Cameroon chimpanzees (mountainous rainforest versus ecotone) are significantly different at a fine geographic scale. I examined monthly differences and seasonality in rainfall across Mbam & Djerem National Park (ecotone) and Ebo forest (rainforest) over a seven-year period 2010-2016. Furthermore, I assessed habitat structure, and botanical composition and fruit phenology across the ecotone and rainforest habitats. In addition to assessing differences between ecotone and rainforest habitats, I also examined the effects of anthropogenic influence on habitat diversity and productivity at a rainforest site (Bekob).

In chapters Three and Four, I tested the hypothesis that Nigeria-Cameroon chimpanzees occupying difference niches (Chapter Two) have different 'local cultures'. In Chapter Three, I assessed the influence of spatial and temporal distribution of resources across the ecotone and rainforest habitats on the dietary and ranging behavior of chimpanzees across each site. I examined the dietary ecology of chimpanzee in relation to prevailing ecological conditions by comparing dietary breadth in fruits, the proportion of fruit, fibrous food and animal prey in the diet in relation to temporal and spatial availability of fruits. I equally assessed the importance of different resources in the dietary ecology of chimpanzees across the sites including those that play the role of preferred and fallback or filler food resources in near pristine and human-modified habitats. Finally, in Chapter Four, I examined the link between environmental and ecological differences, and ranging behavior using nesting patterns in chimpanzee populations across ecotone and rainforest habitats. Here, I compared the distribution of nesting sites across

the ecotone and rainforest habitats in relation to relief, habitat type and fruit phenology. Nest characteristics including nest group sizes, nest heights, tree species and sizes in which nests were made were compared between sites and seasonally within each site. Finally, in this chapter, nesting tree preferences for each site were assessed by comparing observed and expected tree species use based on the density of each tree species across the habitats, including the influence of anthropogenic modification on nesting tree species preferences.

In Chapter Five, I gave an overview of the question and hypotheses tested in this study. I also developed a synthesis of the major environmental variables that are shared and that differ between the ecotone and rainforest habitats, and how these differences are linked to patterns of chimpanzee socioecology. I related these results of to the socioecology of chimpanzee populations in similar habitats across Africa to place my findings into a broader context. In addition, I highlighted some limitations of this study and future research trends. Finally, I briefly highlighted the conservation status of Nigeria-Cameroon chimpanzees in Cameroon and made recommendations for steps forward to preserve chimpanzees and their unique socioecological heritage in Cameroon.

Table 1: Environmental, ecological and socioecological variation in chimpanzee populations across Africa

Site	Gashaka ¹	Ngel Nyaki ²	Ebo ³	Dja ⁴	Goualougo ⁵	Loango ⁶	Gombe ⁷	Mahale ⁸	Ugalla ⁹	Ngogo ¹⁰	Semliki ¹¹	Budongo ¹²	Kahuzi ¹³	Taj ¹⁴	Bossou ¹⁵	Fongoli ¹⁶	Assirik ¹⁷
Location	Nigeria	Nigeria	Cameroon	Cameroon	Congo Rep	Gabon	Tanzania	Tanzania	Tanzania	Uganda	Uganda	Uganda	DRC	Ivory Coast	Guinea	Senegal	Senegal
Habitat	W, L, G	W, Mt-F	TRF	TRF	TRF	TRF	G, W	G, W	S, W	MF	S, G	TMF	Mt-F, B	TRF	TF	S, W	S, W
Annual Mean Rainfall	1826	>1780		1637	1728	2215	1775	1836	980	1671	1452	1842	1619	1829	2230	900	954
Elevation	300-1000	1400-1600	200-1200		330-600		1137	1040	980-1712	1500	1200	1100	2200	202	550		100-311
Dry season months	5						4	4	5	4	4	3	3	3	3	6	7
Population	>35	11 to 13			54		36-60	45-101	30-35	>140	>29	32-56	22	29-82	16-22	35	>15
Party size	3.7				3.4		4.5	6.1	2	10.3	4.8	5.66	4.4	8.3	4	15	4
Average Home range (km ²)	26	7.5			17.3		4 - 24	7 - 17					10	13-26	15-20	>65	50
Average day range (m)							3450	4825					400	2400	1000		
Number of species eaten		52		80	116	116	103	198		191	45	83	114				43

¹(Sommer et al., 2004)

²(Beck and Chapman, 2008, Dutton and Chapman, 2015)

³(Morgan and Abwe, 2006)

⁴(Deblauwe, 2006)

⁵(Morgan and Sanz, 2006)

⁶(Head et al., 2011)

⁷(Goodall, 1986, Wallis, 1997, Wrangham, 1979, Wrangham and Smuts, 1980)

⁸(Hasegawa and Hiraiwa-Hasegawa, 1983, Nishida et al., 2003)

⁹(Ogawa et al., 2007)

¹⁰(Mitani et al., 2002a, Watts, 1998, Watts and Mitani, 2001)

¹¹(Hunt and McGrew, 2002)

¹²(Newton-Fisher, 1999, Newton-Fisher, 2003)

¹³(Basabose, 2002)

¹⁴(Boesch, 1997, Boesch and Boesch-Achermann, 2000, Herlinger et al., 2001, Lehmann and Boesch, 2004a)

¹⁵(Sugiyama, 1989, Sugiyama, 1994, Sugiyama, 2004, Sugiyama and Koman, 1992)

¹⁶(Pruetz and Bertolani, 2009)

¹⁷(Hunt and McGrew, 2002, McGrew et al., 1988)

Codes:

B: Bambo forest

G: Gallery forest

L: Lowland forest

MF: Moist evergreen forest

Mt-F: Montane forest

R: Riverine forest

S: Savanna

TF: Tropical forest

TRF: Tropical rainforest

W: Woodland

Adapted from Stumpf, 2011.

Figures Chapter One

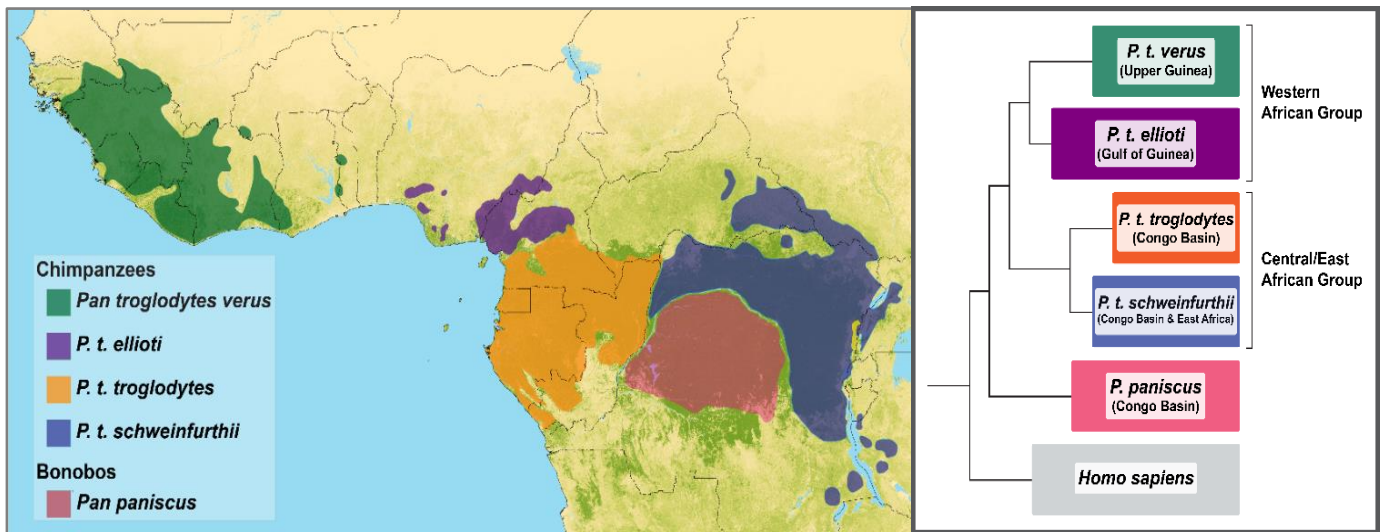


Figure 1.1. Chimpanzee distribution and phylogeny (adapted from Mitchell et al. 2015a)

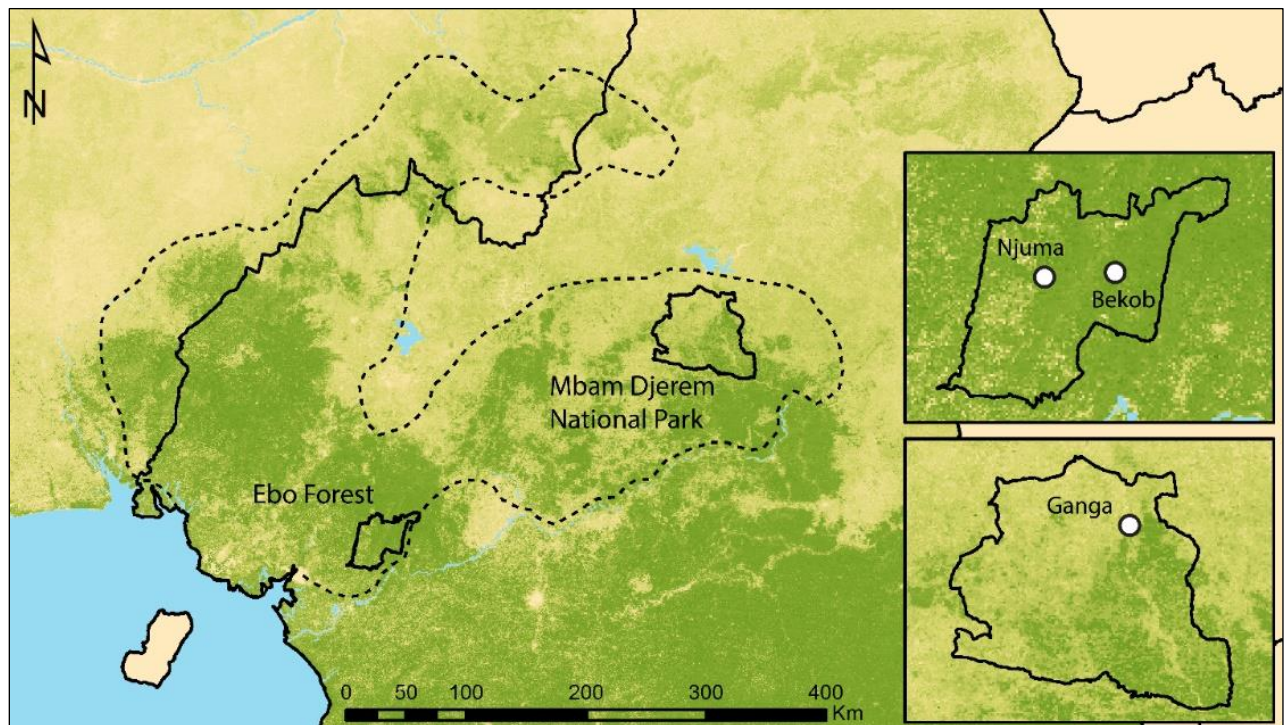


Figure 1.2. Map of study sites – Ebo forest: Bekob (human-modified, rainforest) and Njuma (near pristine, rainforest), and Ganga (ecotone)

CHAPTER TWO

2. ENVIRONMENTAL AND ECOLOGICAL VARIATION ACROSS THE NIGERIA-CAMEROON CHIMPANZEE RANGE: CLIMATE, FOREST STRUCTURE, FLORISTIC DIVERSITY AND FRUIT PHENOLOGY

Abstract

The role of ecology in the speciation of tropical animals, especially of mammals, has been of long-standing interest but evidence to link ecology and intraspecific differentiation remains sparse. The chimpanzees (*Pan troglodytes*) of Cameroon present a unique opportunity to investigate how ecological variation contributes to promoting intraspecific divergence in the endemic mammals of the region. In addition to harboring two chimpanzee subspecies (*Pan t. troglodytes* and *P. t. ellioti*), there are two distinct gene pools associated with *P. t. ellioti*. Previous studies revealed that these two gene pools are found in two different niches – one associated with the mountainous rainforest habitats found in western Cameroon and one associated with ecotone habitats found in central Cameroon. I investigated fine scale environmental and ecological differences between these rainforest and ecotone habitats across this region to assess the ways that they differ from one another at a fine geographic scale to broaden understanding about how the niches of these two population might differ from one another using variables that are relevant to chimpanzees in the local environments, such as fleshy fruit availability. Based on previous ecological niche modelling (ENM) of suitable chimpanzee habitats across this region, I hypothesized that the rainforest habitats (Bekob and Njuma) would be wetter and less seasonal, richer in floristic composition and fleshy fruit availability compared to the ecotone habitat (Ganga). Consistent with the ENM, the ecotone had less rainfall and greater seasonality than the rainforest. Bekob and Njuma had higher plant

species (alpha) diversity compared to Ganga, but beta diversity was higher at Ganga and Njuma than at Bekob. Counter to my prediction, there was greater availability of fleshy fruits at the ecotone than the rainforest. But seasonality in fruit availability was more pronounced at the ecotone, with the dry season associated with low fruit availability. The main variables that distinguished the rainforest from the ecotone chimpanzee habitats based on a principal component analysis included rainfall (annual amounts are higher at the rainforest) and the diversity, density and size of trees (higher at the rainforest than the ecotone). On the other hand, the ecotone had a higher density of lianas and terrestrial herbaceous vegetation. Differences in environmental and ecological conditions, especially seasonality in fleshy fruit availability are known to influence many aspects of chimpanzee socioecology including grouping and ranging patterns, activity budget, and territoriality. Adaptations to seasonal availability of fleshy fruits by populations in distinct habitats may be important in promoting and maintaining genetic diversity in chimpanzees across Cameroon.

2.1. Introduction

Tropical rainforests are rich in vertebrates, the result of various processes that generate and maintain biological diversity and low extinction rates under stable climatic conditions (Moritz et al., 2000). Certain areas within the tropics are noted for species richness and endemism (Myers, 1988, Myers et al., 2000). The Gulf of Guinea region, for example, is a biodiversity hotspot, harboring multiple endemic taxa including primates, amphibians, birds, fish and reptiles (Oates et al., 2004); and plants (Cheek et al., 2001). Several hypotheses have been proposed to explain the diversity of vertebrates across this area. On the one hand, diversification by neutral evolutionary processes associated with Pleistocene refugia and separation across biogeographic

barriers has been proposed to underpin the diversification of tropical animals (Anthony et al., 2007, Eriksson et al., 2004, Moritz et al., 2000). On the other hand, diversification by natural selection has been proposed to have fueled the adaptation of populations to prevailing local conditions, including occupying ecological gradients (Freedman et al., 2010b, Smith et al., 1997), differences in disease ecology (Locatelli et al., 2014, Locatelli et al., 2016) and anthropogenic changes (Freedman et al., 2010a).

Africa harbors two species of chimpanzees: *Pan paniscus* (limited to the south of the Congo River in the Democratic Republic of Congo) and *P. troglodytes* (having wider distribution from Senegal in west to Tanzania in east Africa). The diverse range of *P. troglodytes* is defined by four geographically delimited subspecies including: western (*P. t. verus*), eastern (*P. t. schweinfurthii*), central (*P. t. troglodytes*) and Nigeria-Cameroon (*P. t. ellioti*) chimpanzees (Caldecott and Miles, 2005, Mittermeier et al., 2013). However, the processes that have generated the distribution and diversity of chimpanzees across Africa are largely unexplored. Cameroon is of particular interest in this regard, as it constitutes an area of active chimpanzee speciation (Mitchell et al., 2015a, Mitchell et al., 2015b). In addition to representing the primary boundary between the west African (*P. t. verus* and *P. t. ellioti*) and east/central African (*P. t. troglodytes* and *P. t. schweinfurthii*) chimpanzee groups, the Sanaga River in central Cameroon marks the separation between several sister taxa including *P. t. troglodytes* and *P. t. ellioti* (Gonder et al., 2006, Oates et al., 2004). There is a further genetic distinctiveness found within *P. t. ellioti* – with one gene pool associated with the mountainous rainforest habitats in western Cameroon and the other with the forest-woodland-savanna mosaic in central Cameroon (Mitchell et al., 2015a). Ecological variation, which has been noted to drive diversification for

other vertebrates in this region (Smith et al., 1997), could be as important as forest history and riverine barriers in generating and maintaining the diversification of chimpanzees across Cameroon (Mitchell et al., 2015b). The Sanaga River area in central Cameroon is also associated with the highest human population densities in the central Africa region, and habitat loss and fragmentation are some of the anthropogenic imprints affecting great ape diversification across this area (Bergl et al., 2008, Oates et al., 2004).

Using environmental and ecological variables, a chimpanzee presence dataset, and genetic data from samples collected across Cameroon, Sesink Clee et al. (2015) modelled three suitable habitats for chimpanzees in Cameroon that corresponded to the three gene pools found in the region: *P. t. troglodytes* (lowland rainforest), *P. t. ellioti* (mountainous rainforest) and *P. t. ellioti* (ecotone). The main distinguishing factors between these habitats were forest cover, rainfall and temperature seasonality, and relief (Sesink Clee et al., 2015). Environmental and ecological conditions across the *P. t. troglodytes* range including rainfall, relief and forest cover are fairly homogenous. The *P. t. ellioti* range is characterized by variation in precipitation and temperature seasonality, relief and forest cover between the western rainforest and ecotone habitats (Sesink Clee et al., 2015). However, while niche variation captured through remote sensing is salient and informative, ecological details including forest structure, species richness and fruit phenology that are important to many frugivores including chimpanzees cannot be depicted in such models. Measuring spatio-temporal variation in fruit phenology, terrestrial herbaceous vegetation availability and overall habitat diversity at a very fine geographic scale is particularly important for great apes that have a largely fruit-based diet but rely on other plant

parts and non-plant food resources during periods of fruit scarcity (Anderson et al., 2005, Marshall et al., 2009).

Chimpanzees exist in a wide range of habitats (Basabose, 2004, Bogart and Pruetz, 2008, Chapman et al., 2000, Furuichi and Hashimoto, 2004, Hunt and McGrew, 2002, McLennan, 2010), and several studies have shown that this variation impacts many aspects of their socioecology (Humble and Matsuzawa, 2001, Pruetz et al., 2008, Whiten et al., 1999, Yamakoshi, 1998). What remains unexplored is whether fine scale intra- and inter-specific habitat differentiation correspond with genetic differentiation. Such information is important to understand how and why populations diverge from one another and the processes that underpin local adaptation.

This project aimed to assess environmental and ecological variation including floristic composition, forest structure and fruit phenology across two chimpanzee sites in Cameroon corresponding to the two gene pools in the Nigeria-Cameroon chimpanzee range: Ebo forest (*P. t. ellioti*-rainforest), and MDNP (*P. t. ellioti*-ecotone) at a fine geographic scale. Based on the Ecological Niche Models (ENMs) reported in Sesink Clee et al. (2015), these two chimpanzee habitats are distinct in abiotic and biotic conditions. The Ebo forest and MDNP are important strongholds for Nigeria-Cameroon chimpanzees, together harboring more than 1000 individuals of the most threatened and least studied of the four chimpanzee subspecies (Morgan et al., 2011). Two sites were selected in the Ebo forest (Bekob and Njuma) based on differences in anthropogenic history/modification. To the west, Njuma (near pristine, rainforest) is characterized by closed-canopy rainforest that was selectively logged in the 1980s, Bekob (human-modified, rainforest) to the north-east was inhabited by humans until the late 1950s,

and is characterized by a mosaic of habitats including abandoned farmland, secondary forest and mature mid-altitude habitats. The MDNP research site was Ganga, in the north east of the park (Figure 1.2). Ganga is characterized by a mosaic of forest, woodland and mosaic habitats that occur along the Djerem River and its tributaries.

I specifically tested the hypothesis that *“The niches occupied by the two distinct gene pools of the Nigeria-Cameroon chimpanzee in Cameroon are significantly different at a fine geographic scale as shown by the ENMs at a coarse scale”*. I examined a range of environmental and ecological variables; and based on the ENM I predicted that: 1) the *P. t. ellioti*-ecotone habitat will have less rainfall and greater seasonality compared to the *P. t. ellioti*-rainforest habitats, 2) there would be greater variation in plant species diversity between habitats at the ecotone, 3) plant species diversity will be higher at the rainforest than the ecotone, 4) the diversity of fleshy fruit will be higher at the rainforest than the ecotone, 5) there will be greater seasonality in fruit availability at the ecotone than the rainforest, and 6) introduced and secondary forest species will influence plant species diversity and seasonality in fruit availability at Bekob based on anthropogenic modification.

2.2. Methods

2.2.1. Data collection

2.2.1.1. Climate data

Rainfall data were collected daily at 0700H from January 2010 to December 2016 at two sites in Ebo forest (Bekob and Njuma) using traditional rain gauges by Ebo Forest Research Project. Hobo dataloggers were installed at Bekob and Njuma from 2013 for temperature and humidity records. For MDNP (Ganga), temperature and rainfall data over the same period were

collected from the water-retention dam of the Cameroon Electricity Corporation at Mbakaou, a village at the northern border of the park. For rainfall seasonality, months with <100 mm cumulative rainfall were considered dry, while months with >100 mm cumulative rainfall were considered wet (Willie et al., 2014). The dry season was successive months with <100 mm cumulative rainfall each, while the wet season was successive months with >100 mm cumulative rainfall each.

2.2.1.2. Botanical inventory

In order to assess plant species diversity, at each site I established 10 transects of 2 km length each perpendicular to the main drainage following a fixed bearing: Bekob (270°), Njuma (20°) and Ganga (270°). To minimize vegetation disturbance, I used secateurs to establish transects and installed flagging tape at regular intervals along the transects for direction. Distance-marked flagging tape were located approximately every 25 m, to facilitate orientation along the transects. The total area surveyed for trees/lianas ≥ 10 cm diameter at breast height (DBH) per site was 10 hectares.

2.2.1.2.1. Tree and liana enumeration

All trees and lianas with a DBH ≥ 10 cm within a hypothetical 5 m band (2.5 m on either side of the transect center line) were enumerated (with oil paint), measured (DBH at ~ 1.3 m, using a DBH tape), and identified – Figure 2.1. Where it was not possible to measure DBH, for example, with tall buttress trees, I estimated the diameter to the nearest 5 cm. From the DBH of trees, I calculated the basal area for each tree assuming circular cross-section of trunks (Morgan,

2001). Canopy height and canopy cover were estimated using a densitometer and range finder respectively, taken every 100 m, along the transects beginning at 50 m.

2.2.1.2.2. Terrestrial herbaceous vegetation (THV)

The diversity of THV, which are important to chimpanzees as fallback food (Boesch et al., 2002, Tutin et al., 1997a, Wrangham et al., 1991, Yamakoshi, 2004), was assessed using 4 m² quadrats positioned on alternate sides of each transect at 100 m intervals – Figure 2.1. Each quadrat was 2 x 2 m (corners were marked with flagging tape), and there were 20 quadrats per transect, giving a total area assessed of 800 m² per site. Within each quadrat, species were identified, and the number of species present was noted. Given that chimpanzees feed preferentially on species in the Marantaceae and Zingiberaceae families (Tutin et al., 1991), the presence or absence of species from these families in each quadrat was also noted.

2.2.1.2.3. Botanical identification

Botanical identification in the field was carried out in collaboration with Dr. Barthelemy Tchiengue (National Herbarium, Yaoundé, Cameroon) in August and September 2016 for Njuma and Bekob respectively and during February 2017 for Ganga. Taxonomic classification was based on The Plant List database (<http://www.theplantlist.org/>).

2.2.1.3. Potential fleshy fruit tree species availability

To determine potential plant food species richness across the study sites, the frequency of tree species that could be important to chimpanzees as food sources (based on feeding signs and preliminary macroscopic assessment of feces from each site, and fruit species consumed by chimpanzees across other study sites from literature) was determined from the number of trees

≥10 cm DBH per site. Furthermore, the basal area and stem density of fruit species of consumed preferentially by chimpanzees at each site (based on macroscopic assessment of feces) were assessed (Marshall et al., 2009).

2.2.1.4. Fruit availability – monthly fruitfall measures

Given that chimpanzees are fruit specialists, monthly fruit availability was assessed using fruitfall within a 1 m band along each transect (Furuichi et al., 2001, White, 1994) – Figure 2.1. All fallen fruit known to be eaten by chimpanzees across the three study sites were counted, identified, and photographed. Fruit type (succulent, fleshy-pods, arillate, dehiscent, wind dispersed) as well as evidence of feeding on them by animals were noted (White, 1994).

2.2.2. Principal component analysis for environmental and ecological variables

To investigate the pattern of variation between niches occupied by ecotone and rainforest populations of the Nigeria-Cameroon chimpanzee, I conducted a Principal Component Analysis (PCA) in R with the prcomp package (R version 3.4.3), using variables collected across ten 2 km transects per site at Bekob, Njuma and Ganga. The PCA was geared to bring out variation and patterns in the dataset of correlating habitat variables including annual rainfall, seasonality, tree stem density, liana stem density, number of tree species, mean tree size, and frequency of Marantaceae and Zingiberaceae species in quadrats across Bekob, Njuma and Ganga.

2.2.3. Data analysis

I plotted and compared rainfall data from the three sites and tested monthly rainfall for overall differences in precipitation between the sites. Furthermore, I calculated commonly used measures of habitat and species diversity including the Jaccard Classic index and Shannon-

Weiner diversity index for the rainforest and ecotone using EstimateS, Version 9.1.0 (Colwell, 2016). I used the Jaccard Classic index to determine the degree of differentiation in plant species (beta diversity) between transects across Bekob, Njuma and Ganga (Magurran, 2013). Shannon-Weiner diversity (alpha diversity) values and number of plant species per transect for each site were compared between sites to test for differences in species richness.

The number of stems per hectare (ha^{-1}) and basal area $\text{m}^2 \text{ha}^{-1}$ were calculated for each species per site. Dominant families and species were determined by stem density and basal area. The structure of forests across the three sites were compared in relation to habitat diversity, DBH, stem density, and species richness (McLennan, 2010). Species rarefaction curves were generated to compare species richness between sites, based on the number of individuals sampled across each site. Fruitfall for important species in the diet of chimpanzees across the sites was expressed in density of fallen fruits per hectare. In addition to inter-site fruitfall comparisons, the availability of fruit within each site was compared between the wet and dry seasons.

Nonparametric Kruskal-Wallis one-way ANOVA analyses were used to test for overall differences between the sites, and significant values were adjusted by the Bonferroni correction. Mann-Whitney U tests were used to test for seasonal differences in fruit availability within each site. Data analyses were two tailed, 0.05 significance and carried out using SPSS (IBM SPSS Statistics 24).

2.3. Results

2.3.1. Climate

2.3.1.1. Temperature and rainfall

The Hobo temperature dataloggers deployed at Bekob and Njuma malfunctioned. But analyses of temperature data between 2013 and 2015 across the ecotone and rainforest sites by Ley and her colleagues using Hobo dataloggers show that mean minimum temperature at Njuma (rainforest) was 22 °C and mean maximum temperature was 26 °C. At Miyere (~20 km from Ganga), mean minimum temperature was 19 °C and mean maximum temperature was 23 °C. Monthly temperature fluctuation was 4 °C and highest mean temperatures were associated with the dry season at both sites (Ley et al., in press).

Mean monthly rainfall at the rainforest sites was $194.683 \pm \text{SD } 139.229$ mm (N = 84, Range: 0-692.1 mm) for Bekob and $261.317 \pm \text{SD } 192.147$ mm (N = 84, Range: 0-832.9 mm) for Njuma. At Ganga, mean monthly rainfall was $181.124 \pm \text{SD } 150.895$ mm (N = 84, Range: 0-504.0 mm). There was a difference in mean monthly rainfall between the rainforest and ecotone sites (Kruskal-Wallis: N = 252, $\chi^2 = 8.410$, df = 2, P = 0.015). Mean monthly rainfall was lower at Ganga than Njuma (N = 168, Z = -2.767, P = 0.017). There was no significant difference between the two rainforest sites (P = 0.098), and between Ganga and Bekob – Figure 2.2.

The rainfall regime was similar between the ecotone and rainforest, with one annual dry and wet season (Figure 2.3). The driest months were December to January while rainfall peaked between July and October. The dry season was slightly longer at the ecotone (late November to early March), while at the rainforest, it extended from late November to mid-February. In addition, because of its northernmost location, the annual dry Harmattan winds from the Sahara

Desert that blow through this area from December through January may exacerbate drought at the ecotone more than the mountainous rainforest in Ebo forest.

2.3.2. Botanical enumeration

Across the three sites, 15,407 individual trees and lianas (≥ 10 cm DBH) were sampled in 30 hectares, comprising at least 473 species, 262 genera, in 65 families.

At Bekob, 5482 trees (including 70 lianas) were sampled consisting of at least 301 identified species, 192 genera, in 62 families (Appendix 2.7). Because it was not possible to confidently distinguish liana leaves in high and dense tree canopies for identification across the three sites, this group of plants was categorized as 'liana', irrespective of species. There were 405 trees (excluding lianas) that could not be identified to species/genus level, and 262 could not be identified to family level.

At Njuma 5017 stems (including 63 lianas) were sampled with at least 306 species, 184 genera, in 54 families (Appendix 2.8). There were 288 trees (excluding lianas) that could not be identified to species/genus level, and 188 could not be identified to family level.

At Ganga, 4908 stems (including 170 lianas) were sampled comprising at least 184 species, 126 genera, in 42 families (Appendix 2.9). Of these, 235 trees (excluding lianas) could not be identified to species/genus level, and 202 could not be identified to family level.

2.3.3. Forest structure

2.3.3.1. Diameter at breast height

The mean DBH of trees and lianas at the sites were: $22.581 \pm \text{SD } 15.738$ cm ($N = 5446$, range: 10-131 cm) for Bekob, $27.437 \pm \text{SD } 23.426$ cm ($N = 5008$, range: 10-200 cm) Njuma and

22.543 $\pm$ SD 16.495 cm (N = 4906, range: 10-180 cm) for Ganga. Mean tree sizes were different between the sites (N = 15361, $X^2 = 108.584$, df = 2, $P < 0.001$), with Njuma trees significantly larger than the Bekob ($Z = -8.353$, $P < 0.001$), and Ganga ($Z = -9.608$, $P < 0.001$). There was no significant difference in mean tree diameters between Bekob and Ganga ($Z = 1.497$, $P = 0.807$). However, the ecotone and rainforest had a similar tree size structure with a predominance of trees between 10-19 cm DBH range, and trees in the 20-29 cm DBH range were common. But Njuma had more tree stems > 60 cm than either the Bekob or the Ganga (Figure 2.4).

2.3.3.2. Basal area

The basal area was 323.87 m² ha⁻¹ for Bekob (N = 5446), 511.641 m² ha⁻¹ for rainforest-Njuma (N = 5008), and 300.479 m² ha⁻¹ for Ganga (N = 4906). Mean basal area per tree across the sites were 0.05907 m² ha⁻¹ for Bekob, 0.10218 m² ha⁻¹ for Njuma and 0.06122 m² ha⁻¹ for Ganga. There was a significant difference in the mean basal area between the three sites (N = 15360, ($X^2 = 109.001$, df = 2, $P < 0.001$), Njuma was larger than Bekob ($Z = -8.371$, $P < 0.001$) and larger than the Ganga ($Z = -9.625$, $P < 0.001$). There was no significant difference between Bekob and Ganga ($Z = 1.497$, $P = 0.403$). The three top tree species for the Njuma including *Scyphocephalum mannii* (70 stems), *Pycnanthus angolensis* (87 stems) and *Desbordesia glaucescens* (92 stems) had a total basal area of 14.796 m² ha⁻¹ compared to 6.149 m² ha⁻¹ for 493 stems in the Bekob and 6.941 m² ha⁻¹ for 1075 stems for the Ganga.

2.3.3.3. Stem density

The stem density for trees and lianas ≥ 10 DBH for Bekob was 548 stems per hectare, 501 stems/hectare for Njuma and 490 stems/hectare at Ganga. The mean number of stems per

species was $18.21 \pm \text{SD } 48.498$ ($N = 301$) for Bekob, $16.40 \pm \text{SD } 41.631$ ($N = 306$) for Njuma and $26.67 \pm \text{SD } 67.018$ ($N = 184$) for Ganga. There was no significant difference between sites on species-stem density ($N = 791$, $X^2 = 1.403$, $df = 2$, $P = 0.496$). But at each site, some species were more common. For example, at Bekob, *Tabernaemontana crassa*, *Drypetes* sp. and *Cola* sp. comprised 18.3% of the total stem density of the trees and lianas while at Njuma, *Diospyros* sp., *Drypetes* sp. and *Diogoia zenkeri* made up 18.4% of the stem density. At Ganga *Hymenocardia lyrata*, *Xylopia aethiopica* and *Spondianthus preussii* made up 25.1% of the stem density (Table 2.5). For lianas, Ganga had a density of 17.0 stems ha^{-1} (3.5% of total stem density), Bekob 7.0 stems ha^{-1} (1.3% of total stem density) and Njuma 6.2 stems ha^{-1} (1.2% of total stem density) (Table 2.8). For the 10 most common species at each site, the rainforest sites shared four species (*Cola* sp., *Strombosia grandifolia*, *T. crassa* and *Drypetes* sp.) and Bekob shared *U. guineensis* with Ganga. There was no species overlap between Njuma and Ganga for the most common species (Table 2.7).

2.3.3.4. Family composition

There were 62 families at Bekob, 54 at the Njuma and 42 at the Ganga. At each site, the habitat was dominated by a few families in terms of basal area and number of species. The most important families at Bekob in terms of basal area were Myristicaceae ($37.86 \text{ m}^2 \text{ ha}^{-1}$), Leguminosae ($31.96 \text{ m}^2 \text{ ha}^{-1}$) and Burseraceae ($23.58 \text{ m}^2 \text{ ha}^{-1}$). In terms of number of species in dominant families, Leguminosae (34), Euphorbiaceae (22) and Malvaceae (17) were the most important. At Njuma for the ten dominant families, Myristicaceae with four species had the largest basal area ($135.590 \text{ m}^2 \text{ ha}^{-1}$). Leguminosae ($67.51 \text{ m}^2 \text{ ha}^{-1}$) with 50 species was most significant in terms of number of species, followed by Clusiaceae (20 species) and Euphorbiaceae

(17 species). Leguminosae ($77.744 \text{ m}^2 \text{ ha}^{-1}$), Phyllanthaceae ($54.079 \text{ m}^2 \text{ ha}^{-1}$) and Annonaceae ($24.417 \text{ m}^2 \text{ ha}^{-1}$) were the most important families at the ecotone site in basal area, and Leguminosae (29 species) was the most represented in species. The ten top families in the Bekob constituted 63.9% of the total basal area, 76.9% at Njuma and 82.8% at Ganga (Table 2.6).

2.3.3.5. Species composition

There were 301 and 306 species at the two rainforest sites of Bekob and Njuma respectively and 184 species for Ganga (Appendices 2.7, 2.8 and 2.9). But at each site of a few tree species were dominant in terms of stem count and basal area (Table 2.7). Among the ten top species at Bekob in terms of basal area, *P. angolensis* ($28.822 \text{ m}^2 \text{ ha}^{-1}$), *Santiria trimera* ($18.906 \text{ m}^2 \text{ ha}^{-1}$) and *Drypetes* sp. ($13.763 \text{ m}^2 \text{ ha}^{-1}$) were the most represented. But the most represented in terms of stem density were *T. crassa* (476), *Drypetes* sp. (297), *Cola* sp. (230), *Garcinia conrauana* (185) and *U. guineensis* (155). At Njuma, *S. mannii* ($67.82 \text{ m}^2 \text{ ha}^{-1}$), *P. angolensis* ($47.25 \text{ m}^2 \text{ ha}^{-1}$) and *D. glaucescens* ($32.89 \text{ m}^2 \text{ ha}^{-1}$) dominated basal area while *Diospyros* sp. (338), *Drypetes* sp. (306), *Strombosia* sp. (200), *D. glaucescens* (92) and *P. angolensis* (87) had the most stems. Among the ten most important species at Ganga, *Berlinia* sp. ($30.29 \text{ m}^2 \text{ ha}^{-1}$), *X. aethiopica* ($23.38 \text{ m}^2 \text{ ha}^{-1}$), *H. lyrata* ($15.73 \text{ m}^2 \text{ ha}^{-1}$), *U. guineensis* ($12.08 \text{ m}^2 \text{ ha}^{-1}$) and *Vitex doniana* ($10.77 \text{ m}^2 \text{ ha}^{-1}$) were the dominant in basal area while *H. lyrata* (573), *X. aethiopica* (374), *S. preussii* (288), *U. guineensis* (194) and *U. togoensis* (153) had the most stems. Overlap in commonest species between the sites was minimal. The two rainforest sites shared *P. angolensis*, while Bekob and Ganga shared *U. guineensis*.

2.3.3.6. Canopy cover

There was no significant difference between the three sites in mean percentage canopy cover ($N = 176$, $X^2 = 5.662$, $df = 2$, $P = 0.059$). Average percentage canopy cover at the sites was ($73.83 \pm SD 13.850\%$ ($N = 60$, Bekob), $77.59 \pm 9.770\%$ ($N = 56$, Njuma) and $69.42 \pm SD 18.642\%$ ($N = 60$, Ganga).

2.3.3.7. Canopy height

Mean canopy heights across the three sites were $22.0 \pm SD 5.909$ m ($N = 60$) for Bekob and $29.21 \pm SD 9.991$ m ($N = 57$) for Njuma, and $17.25 \pm SD 7.670$ m ($N = 60$) for Ganga. Mean tree canopy heights varied significantly across the sites ($N = 177$, $X^2 = 42.224$, $df = 2$, $P < 0.001$), with Njuma higher than Bekob ($Z = -3.541$, $P = 0.001$), and Ganga ($Z = -6.493$, $P < 0.001$) and Bekob was higher than Ganga ($Z = 2.991$, $P = 0.008$).

2.3.4. Species richness and variation between sites

The rainforest sites (Bekob and Njuma) had higher species richness than the Ganga with 301 and 306 species for Bekob and Njuma respectively while Ganga had 184 species (Appendices 2.7, 2.8, and 2.9). The rate of new species encountered at each site with increasing number of sampled individuals was higher and similar for rainforest sites than the ecotone (Figure 2.5).

2.3.4.1. Beta diversity

The mean Jaccard Classic indices across Bekob, Njuma and Ganga were 0.371 ± 0.04 ($N = 45$), 0.405 ± 0.032 ($N = 45$) and 0.438 ± 0.061 ($N = 45$) respectively. There was a significant difference in species evenness between transects across the three sites ($N = 135$, $X^2 = 34.997$, $df = 2$, $P < 0.001$). There was more variation in species between transects at Ganga than Bekob ($Z =$

-5.882, $P < 0.001$), and Njuma and Bekob ($Z = -3.489$, $P = 0.001$). There was no significant difference between Njuma and Ganga ($Z = 2.393$, $P = 0.050$) - Figure 2.6.

2.3.4.2. Alpha diversity

The Shannon-Weiner diversity index (H') for the rainforest sites were 4.85 and 5.08 for Bekob and Njuma respectively, and 4.83 Ganga. Mean Shannon-Weiner diversity indices comparisons for all 10 transects per site showed significant differences between the ecotone and rainforest sites ($N = 30$, $X^2 = 20.354$, $df = 2$, $P < 0.001$). Both Njuma ($Z = -4.307$, $P < 0.001$) and Bekob ($Z = 3.316$, $P = 0.003$) had higher species richness than Ganga. There was no difference in species richness between the two rainforest sites (Figure 2.7).

Similarly, comparisons of the number of tree species per transect across the sites showed significant differences between the rainforest and ecotone habitats ($N = 30$, $X^2 = 20.046$, $df = 2$, $P < 0.001$). Njuma was richer in species than Ganga ($Z = -4.211$, $P < 0.001$), and Bekob than Ganga ($Z = 3.422$, $P = 0.002$), but there was no difference between the two rainforest sites (Figure 2.8). Greater species richness could be an indication of more potential resources for chimpanzees at the rainforests than the ecotone site.

2.3.4.3. Species overlap and similarity between sites

Some tree species were common to the three sites. But there was more species overlap between rainforest sites (189 common species) than with either Bekob and Ganga (112), or Njuma and Ganga (100) – Table 2.1. Many common species overlapped between the rainforest and ecotone including *U. guineensis*, *T. crassa*, *P. angolensis*, and *Milicia excelsa* while less common species like *Coula edulis*, *Crateranthus cameroonensis*, *Medusandra mpomniana*

overlapped between the rainforest sites. On the other hand, there was limited overlap in rare species between the sites, for example *Hoplostigma pierreanum* (Bekob), *Podocarpus latifolius* (Njuma) and *Celtis milbraedii* (Ganga) were restricted to each site.

2.3.5. Potential chimpanzee food species

Based on feeding sign observations and preliminary fecal sample assessment at the ecotone and rainforest sites, as well as foods consumed by chimpanzees at other study sites compiled from literature, there were at least 136 potential chimpanzee food plant tree/liana species of ≥ 10 cm DBH across the three sites.

2.3.5.1. Stem density of potential chimpanzee food resources

Bekob had 93 potential fruit tree species, with a density of 9.3 species per hectare, Njuma had 98 species (9.8 species per hectare) and Ganga had 71 (7.1 species per hectare). There was no difference in the stem density of potential food plants between the sites ($N = 262$, $\chi^2 = 0.595$, $df = 2$, $P = 0.743$).

2.3.5.2. Basal area of potential chimpanzee food resources

The mean basal area for potential food plants was similar across the three sites ($N = 262$, $\chi^2 = 1.008$, $df = 2$, $P = 0.604$). The basal area of potential food plant species across the three sites were: $167.461 \text{ m}^2 \text{ ha}^{-1}$ ($N = 2580$) for Bekob, $209.72 \text{ m}^2 \text{ ha}^{-1}$ ($N = 1879$) for Njuma and $148.248 \text{ m}^2 \text{ ha}^{-1}$ ($N = 2086$) for Ganga.

2.3.5.3. Occurrence of species commonly consumed by chimpanzees

Chimpanzees show preference for fruits from some plant species, consuming them more than other species that fruit synchronously (Newton-Fisher, 1999, Wrangham et al., 1996). I assessed the occurrence (stem density and basal area) of the 12 most important species in the diet of each community across the ecotone and rainforest sites based on feeding signs and preliminary macroscopic fecal sample assessments (Table 2.8). Species that were common across the ecotone and rainforest sites included liana (*Landolphia* spp.), *Ficus* spp., *Pseudospondias microcarpa* and *P. longifolia*, and *Uapaca guineensis*. Common species between the Bekob and Njuma included *Pycnanthus angolensis*, *Antrocaryon klaineianum*, *Musanga cecropioides* (umbrella tree) and *Grewia coriacea*, while *Canarium schweinfurthii* was common between Bekob and Ganga.

2.3.5.3.1. Stem density of the 12 top consumed foods per site

The mean stem density of the 12 top fruit plant species at the rainforest sites were: $4.66 \pm \text{SD } 4.889 \text{ stems ha}^{-1}$ ($N = 559$, range: 3-155) for Bekob and $2.592 \pm \text{SD } 2.911 \text{ stems ha}^{-1}$ ($N = 311$, range: 2-87) for Njuma, and for Ganga it was $8.35 \pm \text{SD } 6.587 \text{ stems ha}^{-1}$ ($N = 1002$, range: 9-194). There were differences between the sites in the stem density of 12 top important plant food species ($N = 36$, $\chi^2 = 7.406$, $df = 2$, $P = 0.025$). Specifically, the density was significantly higher at Ganga than the Njuma ($Z = 2.714$, $P = 0.020$), while there was no significant difference either between the Ganga and Bekob ($P = 0.377$), nor between the two rainforest sites. Ganga had a higher density of lianas (3.5% of the total stem density at the site) than either Bekob (1.3%) or Njuma (1.2%).

2.3.5.3.2. Basal area of the 12 top consumed foods per site

The mean basal area by species for the 12 most important foods consumed by chimpanzees across the three was similar ($N = 36$, $X^2 = 2.723$, $df = 2$, $P = 0.256$). The average mean basal area by species at the rainforest sites were $6.345 \pm SD 8.931 \text{ m}^2 \text{ ha}^{-1}$ for Bekob and $6.124 \pm SD 13.170 \text{ m}^2 \text{ ha}^{-1}$ for Njuma, while Ganga had $5.951 \pm SD 4.239 \text{ m}^2 \text{ ha}^{-1}$.

2.3.6. Terrestrial herbaceous vegetation composition

The mean number of THV species per quadrat across the rainforest was $5.39 \pm SD 1.683$ ($N = 200$, range: 0-11) for Bekob, $5.16 \pm SD 2.259$ ($N = 197$, range: 0-14) for Njuma), and for Ganga $6.73 \pm SD 2.012$ ($N = 200$, range: 0-12). The diversity in THV species was different between the ecotone and rainforest sites ($N = 597$, $X^2 = 74.341$, $df = 2$, $P < 0.001$). The Ganga was more diverse than Njuma ($Z = 7.847$, $P < 0.001$) and Bekob ($Z = -7.007$, $P < 0.001$) and there was no significant difference between the two rainforest sites.

Marantaceae and Zingiberaceae are two important families on which chimpanzees depend on for THV (Tutin et al., 1991). Across the sites, 11 (5.5%) quadrats in Bekob, 14 (7.1%) in Njuma and 88 (44%) at Ganga contained Marantaceae species while 17 (8.5%) quadrats in Bekob, 3 (1.5%) at Njuma and 55 (27.5%) at Ganga contained Zingiberaceae species. The frequency and diversity of Marantaceae and Zingiberaceae species was higher at the ecotone than the two rainforest sites.

2.3.7. Fruit availability of most consumed species – fruitfall

The mean density of fruitfall for important fruits in the diet of chimpanzees at Bekob was $20.39 \pm 35.375 \text{ fruits ha}^{-1}$ (dry season: 14.58 ± 30.273 , and wet season: $25.71 \pm 40.06 \text{ fruits ha}^{-1}$) and for

Njuma 8.92 ± 11.80 fruits ha^{-1} (dry season: 3.4 ± 4.19 , and wet season: 12.38 ± 13.73 fruits ha^{-1}). For Ganga, the mean density was 55.34 ± 65.413 fruits ha^{-1} (dry season: 23.70 ± 37.51 , and wet season: 73.80 ± 72.28 fruits ha^{-1}). There was a significant difference in fruit availability based on fruitfall across the sites (Kruskal-Wallis: $N = 68$, $X^2 = 13.252$, $df = 2$, $P = 0.001$). The density of fruitfall was higher at Ganga than Njuma ($Z = 3.553$, $P < 0.001$), Ganga than Bekob ($Z = -2.653$, $P = 0.024$) and there was no difference between the two rainforest sites (Figure 2.9).

There was no seasonal difference in fruit availability at Bekob ($N = 23$, Mann-Whitney U test: $Z = 89.00$, $P = 0.169$) – Figure 2.10. The density of fruits was higher in the wet than the dry season at Njuma ($N = 26$, Mann-Whitney U test: $Z = 126.500$, $P = 0.012$) – Figure 2.11 and Ganga ($N = 19$, Mann-Whitney U test: $Z = 72.000$, $P = 0.010$) – Figure 2.12. Some common dry season species at Bekob were *A. klaineum*, *Elaeis guineensis*, *Pseudospondias longifolia*, *Pycnanthus angolensis*, *U. guineensis*, and *Ficus* spp. In the wet season there was *Canarium schweinfurthii*, *A. klaineum*, *E. guineensis*, *Landolphia* sp., *Uapaca* sp., *U. guineensis*, and *P. angolensis*. Dry season species at Njuma included *A. klaineum*, *U. guineensis*, and *P. angolensis*. In the wet season, common species were *Grewia coriacea*, *P. angolensis*, *C. edulis*, *Uapaca* sp., *U. guineensis*, *Landolphia* spp. and *P. longifolia*. Dry season species at Ganga included *U. guineensis* and *Ficus* spp. In the wet season *Landolphia* sp., *Saba* sp., *Synsepalum* sp., *Myrianthus arboreus*, *Olax subscorpioidea*, *P. angolensis*, *Pseudospondias microcarpa*, and *Ficus* spp. were common.

2.3.8. Principal component analysis: environmental and ecological variables distinguishing Nigeria-Cameroon chimpanzee habitats

The PC1 and PC2 accounted for 77.9% of the variation between the sites - Figure 2.13 and Appendix 2.10. In PC1, annual rainfall was one of the main variables that separated the habitats at Njuma and Ganga. Annual rainfall volume was higher at Njuma than Ganga, while Bekob was intermediate. Mean tree size accounted for major habitat characteristic separation between Bekob, Njuma and Ganga. The size of trees at Njuma was significantly larger and separated this rainforest site from Ganga, while Bekob was intermediate. Tree stem density was higher at Bekob and distinguished this human-modified rainforest site from Njuma (pristine rainforest) and Ganga (ecotone).

Tree species diversity was another variable that separated the habitats at Bekob, Njuma and Ganga. The number of tree species at Njuma and Bekob was higher than at Ganga. The stem density of lianas distinguished the habitat at Ganga from Bekob and Njuma. The stem density of lianas was significantly higher at Ganga but was less significant at Bekob and Njuma. It was however not possible to assess the diversity of lianas, since their leaves cannot be easily distinguished in dense forest canopies. The frequency of THV (Marantaceae and Zingiberaceae) in quadrats in PC1 was also a significant variable that distinguished between the habitats at Ganga, Bekob and Njuma. The high frequency of THV in quadrats was an important variable that characterized the habitat at Ganga but was less significant at Bekob and Njuma.

2.4. Discussion

This paper examined the specific abiotic and biotic conditions predicted to vary from ENM and niche tests reported by Sesink Clee et al. (2015) at a fine geographic scale. I compared environmental and ecological variables across Ebo forest and MDNP that correspond to the two distinct gene pools of the Nigeria-Cameroon chimpanzee in Cameroon in the rainforest and ecotone respectively. I further examined differences between two rainforest sites in Ebo forest that contrasted in the level of anthropogenic modification. My major predictions included higher rainfall, plant species diversity, and fruit phenology at the rainforest sites compared to the ecotone. In addition, I expected that the ecotone would have greater seasonality in rainfall and this, in addition to riverine forests would be linked to greater habitat diversity at the site. This knowledge is salient in understanding whether habitats in which distinct chimpanzee gene pools occur are significantly different from one another, and for examining how local variation in population socioecological traits (feeding and nesting behavior) correspond with intraspecific divergence.

Consistent with the prediction, monthly rainfall volumes were lower at Ganga (the *P. t. ellioti*-ecotone site) compared to the *P. t. ellioti*-rainforest sites (Njuma and Bekob), but the rainfall pattern across the year was similar, with all sites characterized by one dry and one wet season. The ENMs predicted higher precipitation at *P. t. ellioti*-rainforest compared to *P. t. ellioti*-ecotone based on remote sensing data (Sesink Clee et al., 2015), which was supported by the results of this detailed assessment. The PCA revealed that annual rainfall was the main distinguishing variable between these ecotone and rainforest sites. Similar to the ENMs and niche-comparison tests (Sesink Clee et al., 2015), there was greater seasonality at *P. t. ellioti*-ecotone habitat

(Ganga) compared to *P. t. ellioti*-rainforest habitats at Njuma or Bekob. Njuma and Bekob had three months of dry season compared to four-five months at Ganga. The *P. t. ellioti* habitat at GGNP, Nigeria, has a similar rainfall pattern as Ganga (MDNP) with four-five months of drought (Hohmann et al., 2012, Sommer et al., 2004). With a wide geographic range across tropical Africa, chimpanzee habitats are characterized by differences in rainfall volume and seasonality (Stumpf, 2011). The more equatorial habitats witness greater amounts of rainfall with less marked seasonality (Chapman et al., 1997, Chapman et al., 1994b, Hemingway and Bynum, 2005, Stumpf, 2011, van Schaik and Brockman, 2005). More tropical habitats are associated with lower annual rainfall and longer drought periods compared to equatorial habitats (Hunt and McGrew, 2002, McGrew et al., 2004, McGrew et al., 1996, Pruetz and Bertolani, 2009, Tutin et al., 1991).

Equatorial habitats that experience higher precipitation have high plant species diversity and produce large fruit crops for most of the year and chimpanzee populations that inhabit them have a diverse and consistent fruit-based diet (Chapman et al., 1997, Chapman et al., 1994b, Hemingway and Bynum, 2005, Stumpf, 2011, van Schaik and Brockman, 2005, Watts et al., 2012a). Conversely, lower rainfall and/or greater seasonality in ecotone and savanna habitats results in lower plant diversity, and greater seasonality in fruit availability. Chimpanzee populations in such habitats have lower dietary diversity in fleshy fruits (Dutton and Chapman, 2015, Fowler, 2006, McGrew et al., 1988). In addition, chimpanzee populations in such habitats are known to adopt strategies to mitigate seasonal fruit scarcity including feeding on fallback fruits, ranging wider and in smaller parties, and dietary shifts to non-fruit food sources compared to chimpanzees at resource-rich sites with lower seasonality in fruit availability (Doran et al.,

2002, Hunt and McGrew, 2002, Knott, 2005, McGrew et al., 1988, Murray et al., 2006, Pruetz and Bertolani, 2009, Wrangham et al., 1996).

Differences in habitat diversity between the ecotone and rainforest in general were generally consistent with the ENMs (Sesink Clee et al., 2015). As predicted, there was greater diversity in species between habitats at the ecotone compared to the rainforest. Between the rainforest sites, there was greater species diversity between habitats at Njuma than Bekob (human-modified site). Variation in species between habitats at Ganga could be linked to climatic conditions and anthropogenic modification including annual bushfires (Mitchard et al., 2009). Ganga was comprised of closed-canopy mature forest along seasonally flooded plains bordering the Djerem River and its tributaries, low closed-canopy old secondary forest dominated by *Myrianthus arboreus*, high and low open-canopy secondary and colonizing forests, and open savanna. Species variation within habitats at Bekob and Njuma could be linked to the altitudinal range, spanning lowland and submontane vegetation classes. Variation in relief between rainforest and ecotone habitats was one of the distinguishing variables across *P. t. ellioti* range in the EMNs (Sesink Clee et al., 2015). Though this variable was not directly quantified in this study, the altitudinal range at Njuma was ~100-900 m and at Bekob ~500-1200 m. At Ganga, there was less altitudinal variation (~700-900 m). Relics of the recent anthropogenic history at the Bekob included the prevalence of introduced and secondary forest species at lower altitudes. Closed- and open-canopy vegetation at these low altitude areas include *Musanga cecropioides* (umbrella tree) and other forest pioneer species, while *E. guineensis*, *Dacryodes edulis*, *Psidium guajava* and other farm species are common in abandoned farmland. The high-altitude areas are intact with closed-canopy vegetation characterized by submontane species dominated by *Garcinia*. Njuma is

composed of more homogenous high closed-canopy vegetation ranging from lowland to submontane forests. The overall structure of the lowland vegetation at this site has not been greatly altered by the selective logging that occurred there in the 1980s.

Habitat diversity is a function of environmental and ecological conditions including precipitation (Chapman et al., 2004, Hohmann et al., 2012), relief (Nkurunungi et al., 2004, Proctor et al., 2007), soil moisture (Marshall et al., 2009) and the degree of anthropogenic influence (Arnhem et al., 2007, Chapman et al., 2000). Habitat heterogeneity can be advantageous to primates when the different categories are species-rich, and species therein have asynchronous fruiting patterns, that will reduce seasonality in food availability (Basabose, 2005, Mulavwa et al., 2010). At Ganga, closed canopy habitats are associated with lowland rainforest species including *Pseudospondias microcarpa*, *U. guineensis*, *Canarium schweinfurthii*, while open- and closed-canopy secondary and colonizing habitats are rich in various species of *Landolphia*, *Saba* and *Ficus*. These plant species are all important for the dietary ecology of chimpanzees. At Bekob, secondary forest habitats harbor several species including *Musanga cecropioides* (umbrella tree) and *Elaeis guineensis* (oil palm tree), that chimpanzees feed on. Many chimpanzee populations use different habitats alternately depending on resource availability in each vegetation type (Basabose, 2005, Furuichi et al., 2001, Mulavwa et al., 2010). But where habitat diversity is characterized by species-deficient classes, chimpanzees are subjected to greater socioecological costs (Hunt and McGrew, 2002, Pruetz and Bertolani, 2009).

Tree size and basal area were more important at Njuma than either Bekob or Ganga. However, tree stem density was higher at Bekob than at Njuma and Ganga. These differences could be attributed to the degree of habitat alteration. Most of the vegetation at Bekob is young

with smaller trees, and at various levels of ecological succession due to recent anthropogenic modification. Lower stem density and basal area at Ganga could be attributed to climatic conditions and anthropogenic influence including annual bushfires.

As predicted, there was higher tree species diversity at the rainforest sites than at the ecotone site, and specifically, the PCA distinguished the ecotone and rainforest habitats based on tree species richness. Tree species richness was an important contributor to the uniqueness of the rainforest habitats, but was less significant at the ecotone site. Differences in tree species composition could be attributed to climatic, altitudinal variation and anthropogenic influence. Climatic conditions at the rainforest sites were less variable than at the ecotone site, and wider altitudinal range at the rainforest sites supports both lowland and submontane plant species. Environmental conditions at Ganga are akin to GGNP, Nigeria and tree species richness between the two sites is similar (Fowler, 2006). The Dja Reserve, Cameroon, a lowland rainforest in the Congo Basin has similar species richness as the rainforest sites, dominated by Leguminosae (Sonké and Couvreur, 2014). Diets of chimpanzees at sites with higher plant species diversity are more diverse (Watts et al., 2012a) than at sites with lower diversity (Chancellor et al., 2012, Hunt and McGrew, 2002, Stanford and Nkurunungi, 2003). Such diversity in species richness and diets have also been noted for Sumatran and Bornean orangutans, Indonesia (Marshall et al., 2009). The main differences in species composition between the rainforest sites of Bekob and Njuma pertained to introduced and secondary forest species, the result of anthropogenic modification. Some of these species including *Elaeis guineensis* (oil palm) *Musanga cecropioides* (umbrella tree), *Psidium guajava* (guava) and *Dacryodes edulis* produce fruits on which chimpanzees feed and could be important in the socioecology of the species.

The density of lianas varied between the ecotone and rainforest habitats and was one of the main variables that distinguished these habitat types in the PCA. The density of lianas was higher in at Ganga, which distinguished it from both Njuma and Bekob. However, it was not possible assess the diversity of lianas across the sites during this study. But from the diversity of fruitfall present at Ganga that were not from trees, I can infer that the diversity and fruit phenology of lianas was higher at the ecotone than the rainforest sites. Many lianas including *Landolphia* spp. and *Saba* spp. are important food sources for chimpanzee populations (Moscovice et al., 2007, Piel et al., 2017). The frequency and diversity of terrestrial herbs in the Marantaceae and Zingiberaceae families varied between the ecotone and rainforest habitats. From the PCA, the frequency of THV encountered in quadrats along transects was more important at the ecotone, and distinguished this habitat from the rainforest habitats where THV was less significant. The quality and quantity of THV is important in chimpanzee socioecology, as herbs function as fallback food resources for chimpanzees during periods of fruit scarcity (Boesch et al., 2002, Yamakoshi, 2004, Tutin et al., 1997a).

The fourth prediction of higher fruit availability from fruitfall at the rainforest compared to the ecotone was not supported. Potential fruit trees and fruit production varied spatially and temporarily across the sites. There was a higher density of stems and fruit availability for common species that are important to the diet of chimpanzees at the ecotone than the rainforest sites. Other things being equal, chimpanzees at the ecotone should encounter more important fruit species at lower ranging cost than at the rainforest. Fruit production by trees and lianas at GGNP, a *P. t. ellioti* ecotone site in Nigeria was higher than at the Salonga, a *P. paniscus* rainforest site in DR Congo (Hohmann et al., 2012). Higher fruit availability at the ecotone could

be linked to swamps along the main rivers and higher irradiance. The flood zone of the Djerem River and its seasonal tributaries irrigate swamps that store moisture which may tamper the effects of the long drought period at the ecotone. These swamps could also be very fertile due to alluvial deposits from annual floods, but this was not tested. Soil-rich swamps at Sumatra and Borneo, Indonesia support a diverse and highly productive flora (Marshall et al., 2009). In addition, open habitats characteristic of the ecotone site may benefit from higher irradiance, providing for greater fruit ripening in upper and lower canopy species. These habitat types are rich in fruits from both trees and lianas. Open and closed habitats at the ecotone support a wider diversity of terrestrial herbaceous vegetation, including Marantaceae and Zingiberaceae species compared to the rainforest. The quantity and quality of THV plays major role in the diet of chimpanzee populations and affects group dynamics (Marshall and Wrangham, 2007, Tutin et al., 1991, Wrangham, 1986, Wrangham et al., 1998).

However, consistent with the fifth prediction, there was more marked seasonality in fruit availability at the ecotone site compared to the rainforest sites. The wet season at Ganga was associated with higher fruit availability with many tree and liana species fruiting synchronously. Conversely, fruit availability in the dry season at Ganga was limited to a couple of species which had asynchronous fruiting patterns. There was less marked seasonality in fruit availability at Bekob and Njuma, where many species produced fruits synchronously during the dry and wet seasons, including species that fruited asynchronously. At Bekob, *E. guineensis* (oil palm), *Musanga cecropioides* (umbrella tree) and other secondary forest plant species produced fruits asynchronously in the wet and dry seasons.

Chimpanzees are fruit specialists and their socioecology is largely influenced by the spatial and temporal availability of ripe fruits (Anderson et al., 2002, Mitani et al., 2002b). Given the greater seasonality in fruit availability, the chimpanzee communities at the ecotone may be subjected to greater seasonal shifts in dietary component of fleshy fruits compared to the rainforest. The consumption of fallback food resources including THV may be more frequent and consistent at the ecotone than the rainforest sites, especially during the dry season. Low availability and/or patchy distribution of food resources increase ranging and grouping costs (Chapman et al., 1995, Wrangham et al., 1996), and chimpanzees at the ecotone may be subjected to wider ranging and less cohesion during the dry season geared at reducing intra-group feeding competition. Though social factors like the presence of estrous females influence grouping patterns, fruit availability remains a dominant grouping factor as even the reproductive cycles in female chimpanzees have been linked to seasonality in fruit availability (Anderson et al., 2002, Mitani et al., 2002a, Wallis, 1995). Low fruit availability was associated with lower rates of gregariousness in Nigeria-Cameroon chimpanzees at GGNP, Nigeria (Hohmann et al., 2012). All other things being equal, foraging parties are expected to be smaller at the ecotone during the dry season. The chimpanzee population at the rainforest and especially the Bekob may witness less seasonality in dietary breath as they consume fruit species from abandoned farmland and secondary forest species.

The factors that accounted for significant variation between the ecotone and rainforest *P. t. ellioti* habitats were rainfall and the structure of the forest including tree species and stem densities, THV and lianas. The diversity of tree species and density of tree stems was higher at the rainforest than the ecotone. Conversely, the density of lianas and THV (Marantaceae and

Zingiberaceae) was higher at the ecotone than the rainforest. These results confirm the diversity of habitats across the chimpanzee range in Cameroon and especially the distinctiveness of habitats associated with the different gene pools of the Nigeria-Cameroon chimpanzee (Mitchell et al., 2015b). It was however difficult to ascertain the optimal habitat for *P. t. ellioti* from these results given the uniqueness of the ecotone and rainforest habitats. Differences in environmental conditions including rainfall seasonality, and ecological conditions including botanical composition, structure and phenology influence patterns of chimpanzee socioecology (Potts et al., 2011). The grouping patterns between eastern and western chimpanzees are different, with the latter more akin to bonobos (Stumpf, 2011). The basis of such differences is attributed to seasonality in resource availability including fruits and THV. While eastern chimpanzee groups are male-bonded (Wrangham and Smuts, 1980), western chimpanzees are bisexually-bonded (Boesch, 1996) and bonobos are female-bonded (Stanford, 1998). But intra-community social relationships in central and Nigeria-Cameroon chimpanzees are unknown (Stumpf, 2011).

Differences in habitat structure and resource availability are expected to affect the community structure of chimpanzees including but not limited to party sizes and composition, activity budget, sociality and territoriality (Anderson et al., 2002, Herbinger et al., 2001, Hernandez-Aguilar, 2009, Moore, 1996, Ogawa et al., 2007, Tutin et al., 1983, Yamagiwa and Basabose, 2009). Understanding how local chimpanzee populations adapt to distinct ecological conditions across an active speciation zone can help us in understanding hominin evolutionary patterns across diverse landscapes across Africa.

Tables Chapter Two

Table 2.1. Shared species and similarity statistics: Bekob (1), Njuma (2) Ganga (3)

First Sample	Second Sample	Sobs First Sample	Sobs Second Sample	Shared Species Observed	ACE First Sample	ACE Second Sample	Chao Shared Estimated	Jaccard Classic	Sorensen Classic	Chao-Jaccard-Raw Abundance-based	Chao-Jaccard-Est Abundance-based	Chao-Sorensen-Raw Abundance-based	Chao-Sorensen-Est Abundance-based
1	2	301	306	189	368.876	372.5	219.852	0.452	0.623	0.829	0.874	0.907	0.933
1	3	301	184	112	368.876	225.17	123.788	0.3	0.462	0.421	0.49	0.592	0.658
2	3	306	184	100	372.5	225.17	124.586	0.256	0.408	0.406	0.444	0.578	0.615

Table 2.2. Stem densities of the ten most common tree species in the rainforest and ecotone

Human-modified rainforest-Bekob		Rainforest-Njuma		Ecotone-Ganga	
Species	Stem density	Species	Stem density	Species	Stem density
<i>Tabernaemontana crassa</i>	47.6	<i>Diospyros</i> sp.	33.8	<i>Hymenocardia lyrata</i>	57.3
<i>Drypetes</i> sp.	29.7	<i>Drypetes</i> sp.	30.6	<i>Xylopia aethiopica</i>	37.4
<i>Cola</i> sp.	23	<i>Diogoia zenkeri</i>	29.8	<i>Spondianthus preussii</i>	28.8
<i>Garcinia conrauana</i>	18.5	<i>Strombosia</i> sp.	20	<i>Ochna afzelii</i>	24.2
<i>Strombosia grandifolia</i>	16.6	<i>Diospyros bipidensis</i>	16.8	<i>U. guineensis</i>	19.4
<i>Oncoba welwitschii</i>	16.4	<i>Anisophyllea</i> sp.	13.9	Liana	17
<i>Uapaca guineensis</i>	15.5	<i>Cola</i> sp.	13.1	<i>Vitex doniana</i>	15.6
<i>Strombosia</i> sp.	14.2	<i>S. grandifolia</i>	11.5	<i>Holarrhena floribunda</i>	15.4
<i>Vitex grandifolia</i>	13.8	<i>T. crassa</i>	11	<i>Lannea acida</i>	15.3
<i>Pycnanthus angolensis</i>	11.2	<i>Desbordesia glaucescens</i>	9.2	<i>Uapaca</i> sp.	15.3
All others	341.7	All others	321.1	All others	245.1

Table 2.3. Most important families by basal area per hectare across the three sites

Human-modified rainforest-Bekob			Rainforest-Njuma			Ecotone-Ganga		
Family	BA/m ²	#Species	Family	BA/m ²	#Stems	Family	BA/m ²	#Species
Myristicaceae	37.86	4	Myristicaceae	135.59	4	Leguminosae	77.74	29
Leguminosae	31.96	34	Leguminosae	67.51	50	Phyllanthaceae	54.07	11
Burseraceae	23.58	3	Olacaceae	53.47	16	Annonaceae	24.41	7
Malvaceae	21.55	17	Irvingiaceae	49.99	6	Sapotaceae	17.67	8
Olacaceae	18.06	14	Putranjivaceae	19.25	6	Anacardiaceae	17.46	5
Apocynaceae	16.03	7	Euphorbiaceae	14.42	17	Malvaceae	16.76	11
Phyllanthaceae	14.76	7	Apocynaceae	15.06	9	Moraceae	14.49	10
Putranjivaceae	14.41	4	Ebenaceae	14.13	6	Lamiaceae	12.03	2
Clusiaceae	13.54	10	Phyllanthaceae	11.93	12	Apocynaceae	7.21	6
Euphorbiaceae	10.30	22	Clusiaceae	11.21	20	Burseraceae	6.99	2
All others	116.64	179	All others	118.27	156	All others	51.58	93

Table 2.4. Most important tree species in terms of basal area across the three sites

Human-modified rainforest-Bekob			Rainforest-Njuma			Ecotone-Ganga		
Species	BA/m ²	#Stems	Species	BA/m ²	#Stems	Species	BA/m ²	#Stems
<i>P. angolensis</i>	28.822	112	<i>S. mannii</i>	67.820	70	<i>Berlinia</i> sp.	30.299	128
<i>Santiria trimera</i>	18.906	84	<i>P. angolensis</i>	47.251	87	<i>X. aethiopica</i>	23.383	374
<i>Drypetes</i> sp.	13.763	297	<i>D. glaucescens</i>	32.891	92	<i>H. lyrata</i>	15.732	573
<i>U. guineensis</i>	11.338	155	<i>Drypetes</i> sp.	15.863	306	<i>U. guineensis</i>	12.080	194
<i>Cola</i> sp.	10.353	230	<i>Brachystegia cynometroides</i>	12.661	33	<i>Uapaca togoensis</i>	11.848	153
<i>T. crassa</i>	8.972	476	<i>Coelocaryon preussii</i>	12.027	41	<i>Vitex doniana</i>	10.776	156
<i>Vitex grandifolia</i>	8.008	138	<i>Strombosia</i> sp.	11.821	200	<i>S. preussii</i>	9.983	288
<i>Margaritaria discoidea</i>	6.519	94	<i>Coula edulis</i>	10.904	59	<i>Parkia</i> sp.	9.340	116
<i>Oncoba welwitschii</i>	5.828	164	<i>Alstonia boonei</i>	10.667	24	<i>P. microcarpa</i>	9.338	31
<i>Garcinia conrauana</i>	5.761	185	<i>Diospyros</i> sp.	10.353	338	<i>Milicia excelsa</i>	7.274	38
All others	205.582	3533	All others	279.524	3778	All others	160.703	2857

Table 2.5: 12 most important chimpanzee plant food species consumed per site

Human-modified rainforest- Bekob				Rainforest-Njuma				Ecotone-Ganga			
Species	Stems	% of total stems at site	BA/m ²	Species	Stems	% of total stems at site	BA/m ²	Species	Stems	% of total stems at site	BA/m ²
<i>Uapaca guineensis</i>	155	2.83	11.34	<i>P. angolensis</i>	87	1.74	47.25	<i>U. guineensis</i>	194	3.95	12.08
<i>Pycnanthus angolensis</i>	112	2.04	28.82	Liana	62	1.24	0.99	Liana	170	3.46	2.33
<i>Santiria trimera</i>	84	1.53	18.91	<i>U. guineensis</i>	55	1.10	7.85	<i>Vitex doniana</i>	156	3.18	10.78
Liana	70	1.28	1.22	<i>S. trimera</i>	43	0.86	5.79	<i>Uapaca</i> sp.	153	3.12	11.85
<i>Grewia coriacea</i>	40	0.73	2.46	<i>G. coriacea</i>	30	0.60	0.99	<i>Olex subscorpioidea</i>	76	1.55	1.38
<i>Elaeis guineensis</i>	33	0.60	3.64	<i>M. cecropioides</i>	8	0.16	3.99	<i>Synsepalum</i> sp.	72	1.47	2.99
<i>Pseudospondias longifolia</i>	28	0.51	3.27	<i>Cleistopholis patens</i>	6	0.12	0.27	<i>Myrianthus arboreus</i>	44	0.90	2.42
<i>Ficus</i> sp.	12	0.22	3.07	<i>Ficus</i> spp.	6	0.12	1.42	<i>Milicia excelsa</i>	38	0.77	7.27
<i>Uapaca</i> sp.	10	0.18	0.94	<i>Nuclea diderrichii</i>	6	0.12	2.66	<i>Pseudospondias microcarpa</i>	31	0.63	9.34
<i>Musanga cecropioides</i>	9	0.16	0.60	<i>Keayodendron bridelioides</i>	4	0.08	0.44	<i>Tricalysia</i> sp.	31	0.63	0.40
<i>Canarium schweinfurthii</i>	3	0.05	1.11	<i>Antiaris africana</i>	2	0.04	1.78	<i>C. schweinfurthii</i>	28	0.57	6.28
<i>Antrocaryon klaineianum</i>	3	0.05	0.77	<i>Pseudospondias longifolia</i>	2	0.04	0.07	<i>Ficus</i> spp.	9	0.18	4.31
	559	10.20	76.15		311	6.21	73.50		1002	20.42	71.42

Figures Chapter Two

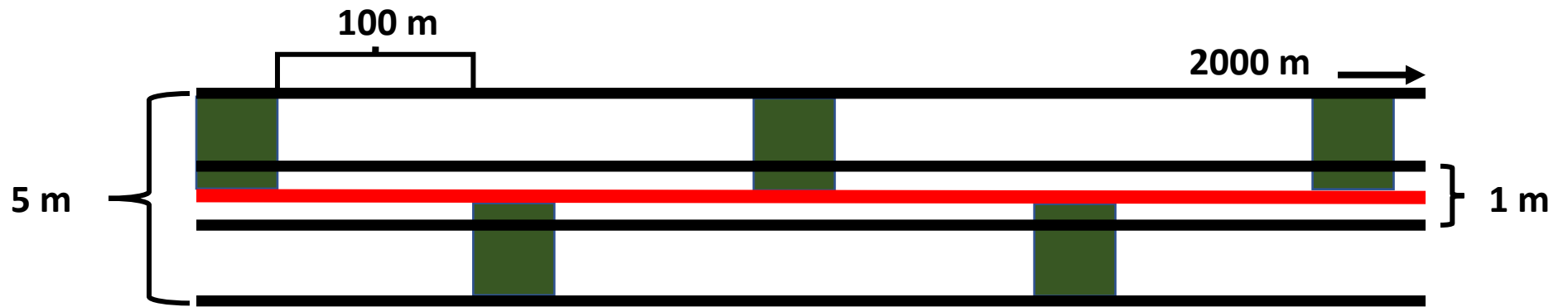
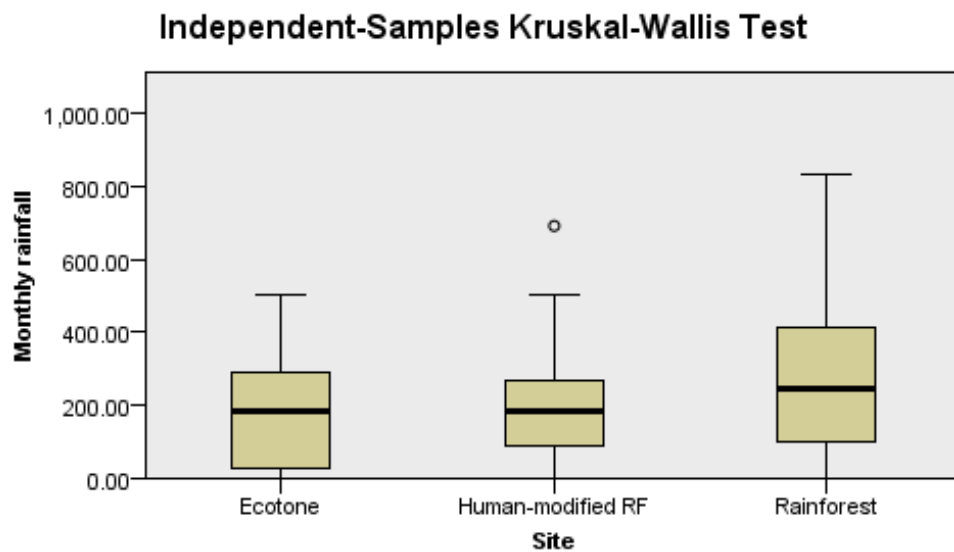


Figure 2.1. Lay out of transects: 2 km length per transect (transect center-line – red), 5 m band for the enumeration, identification and marking of trees and lianas ≥ 10 cm DBH, 1 m band for monthly fruitfall assessment, and 4 m² quadrats at 100 m intervals on alternate sides of the transect center line for THV assessment.



Total N	252
Test Statistic	8.410
Degrees of Freedom	2
Asymptotic Sig. (2-sided test)	.015

1. The test statistic is adjusted for ties.

Figure 2.2. Mean monthly rainfall variation for ecotone-Ganga, human-modified rainforest-Bekob and rainforest-Njuma between January 2010 and December 2016

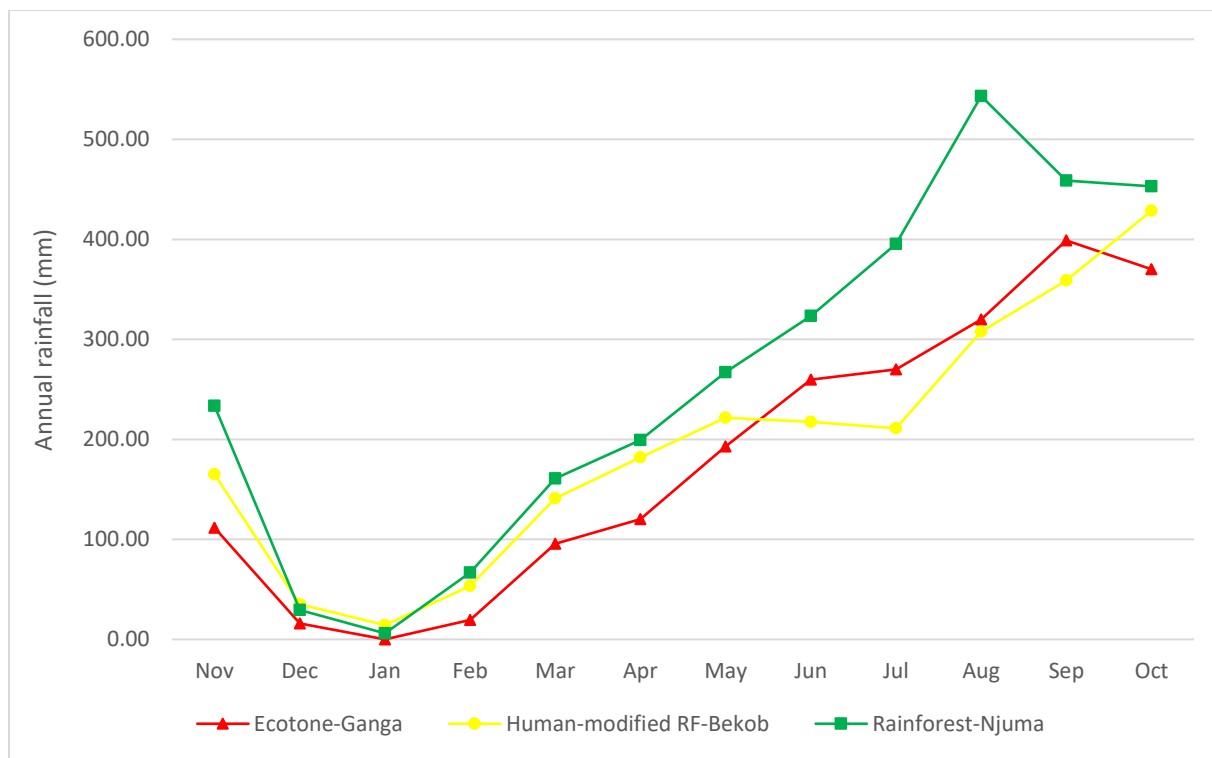


Figure 2.3. Mean monthly rainfall graph (2010-2016) for Ganga, Bekob and Njuma

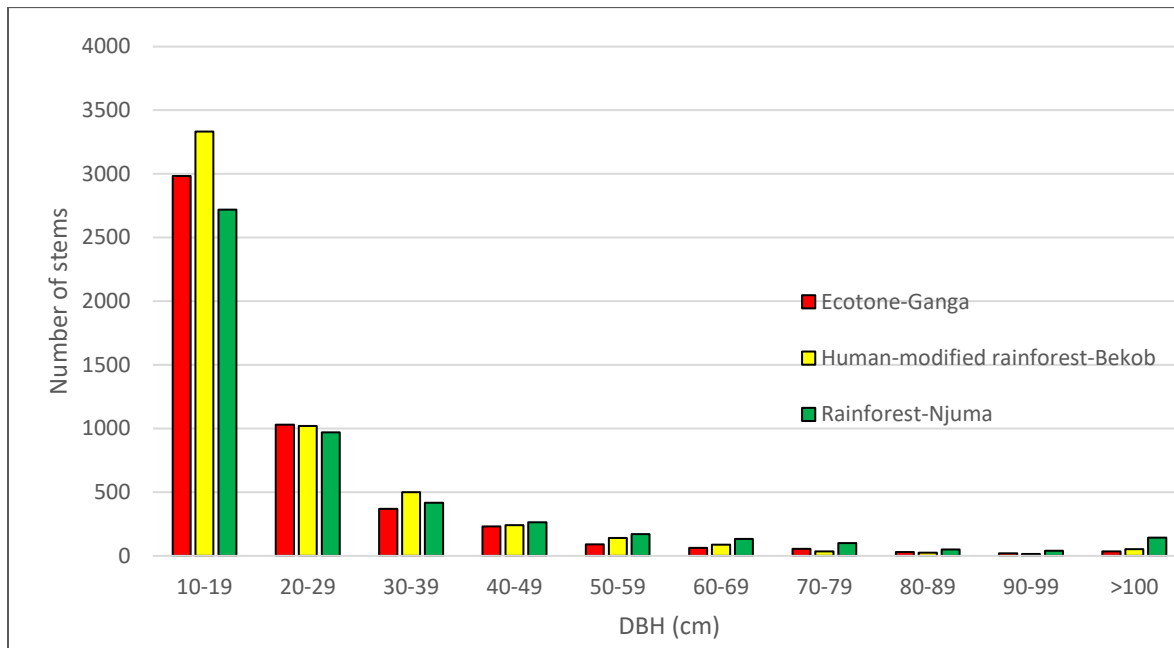


Figure 2.4. Distribution of trees by DBH classes across the ecotone and rainforest sites

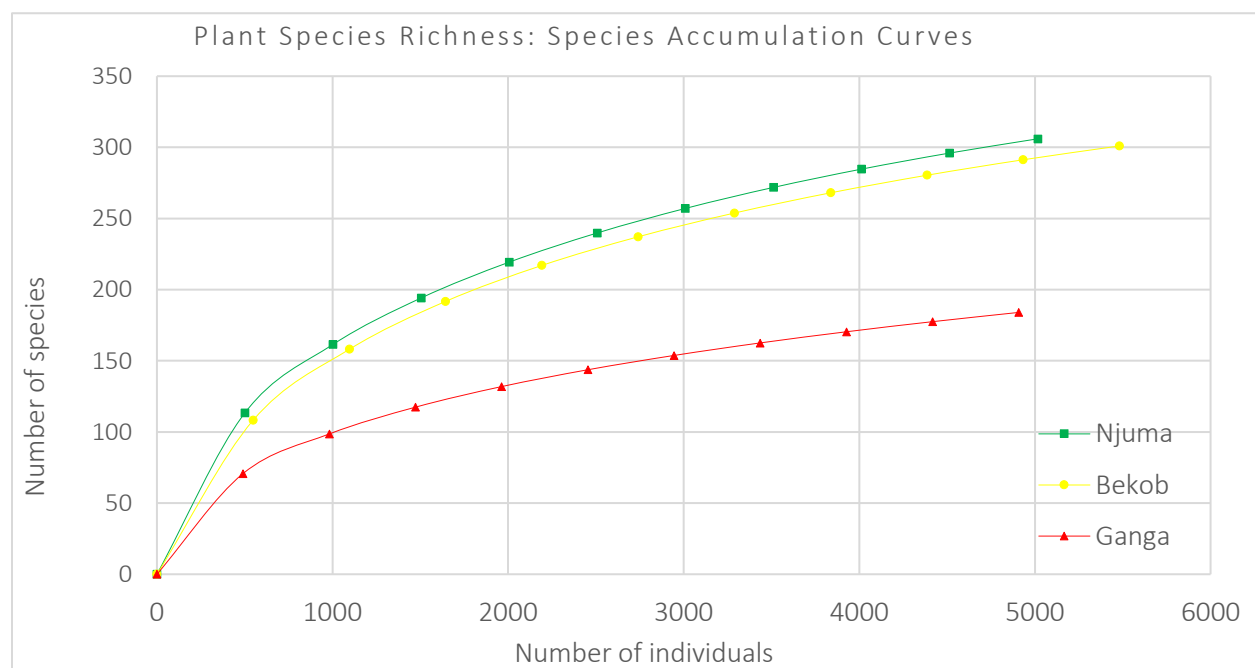
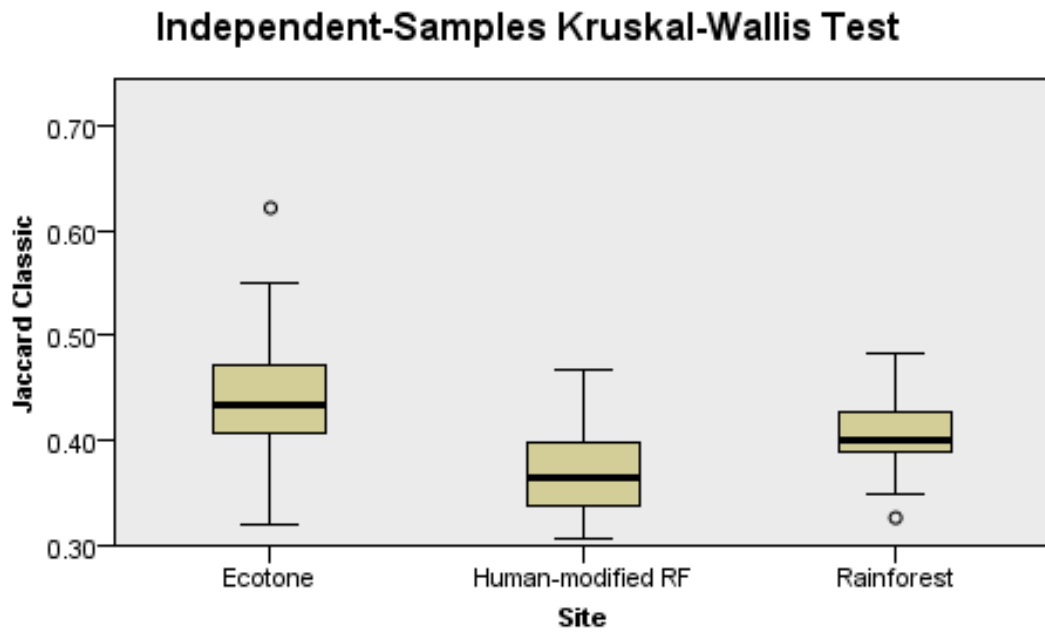


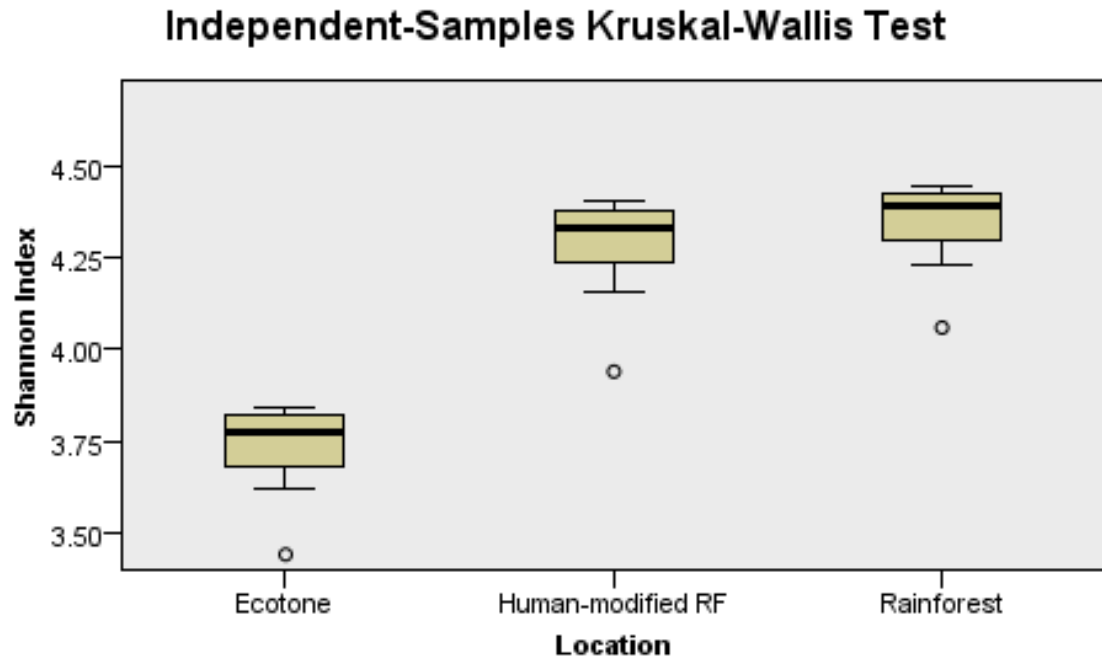
Figure 2.5. Species accumulation curves of trees ≥ 10 cm DBH in Bekob, Njuma and Ganga. Curves are based on species occurrence in 10 transects (2000 x 5m, each) per site. Larger sample sizes would have been more representative



Total N	135
Test Statistic	34.997
Degrees of Freedom	2
Asymptotic Sig. (2-sided test)	.000

1. The test statistic is adjusted for ties.

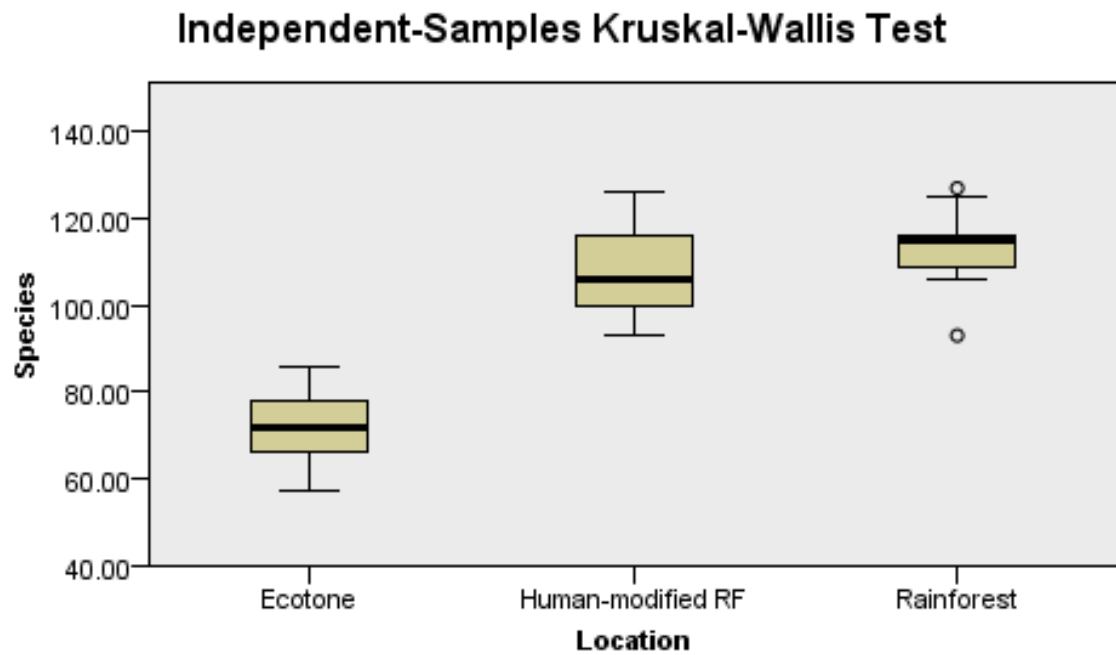
Figure 2.6. Variation in spatial composition in plant species between transects at Bekob, Njuma and Ganga



Total N	30
Test Statistic	20.354
Degrees of Freedom	2
Asymptotic Sig. (2-sided test)	.000

1. The test statistic is adjusted for ties.

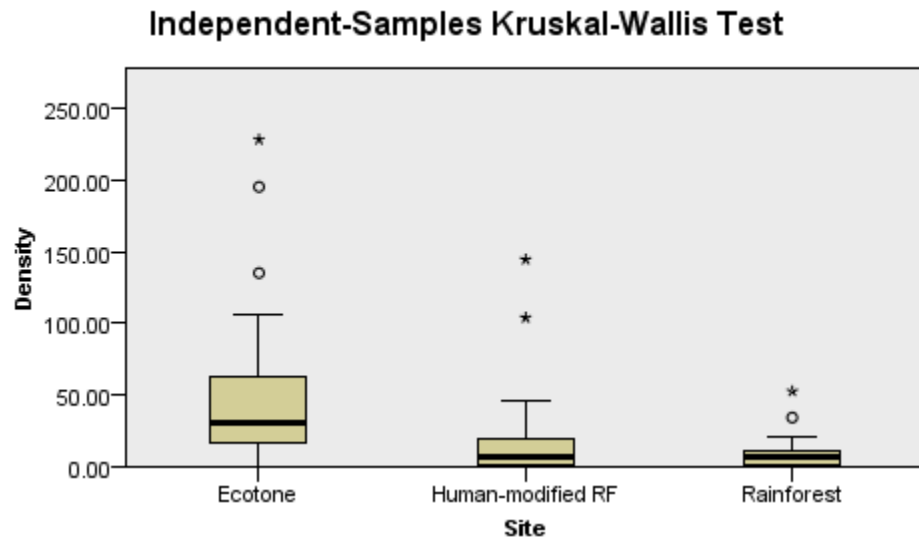
Figure 2.7. Mean Shannon-Weiner diversity between transects across the ecotone-Ganga, human-modified rainforest-Bekob, and rainforest-Njuma



Total N	30
Test Statistic	20.046
Degrees of Freedom	2
Asymptotic Sig. (2-sided test)	.000

1. The test statistic is adjusted for ties.

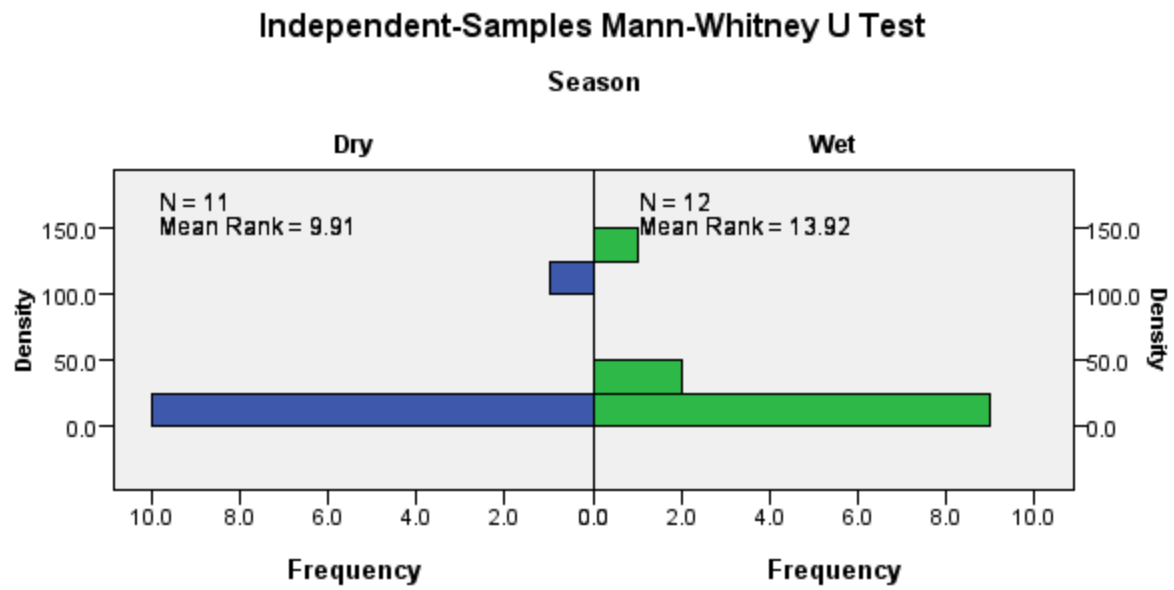
Figure 2.8. Mean species richness variation between transects at Bekob, Ganga and Njuma



Total N	68
Test Statistic	13.252
Degrees of Freedom	2
Asymptotic Sig. (2-sided test)	.001

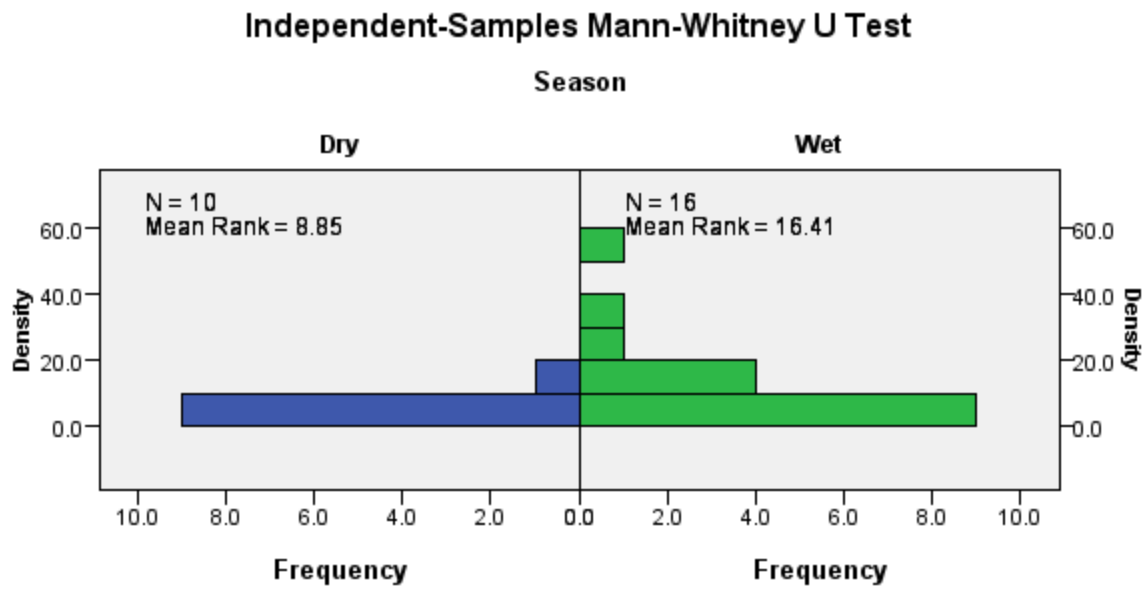
1. The test statistic is adjusted for ties.

Figure 2.9. Fruitfall variation for the most consumed fruit species at Ganga (ecotone), Bekob (human-modified rainforest) and Njuma (rainforest)



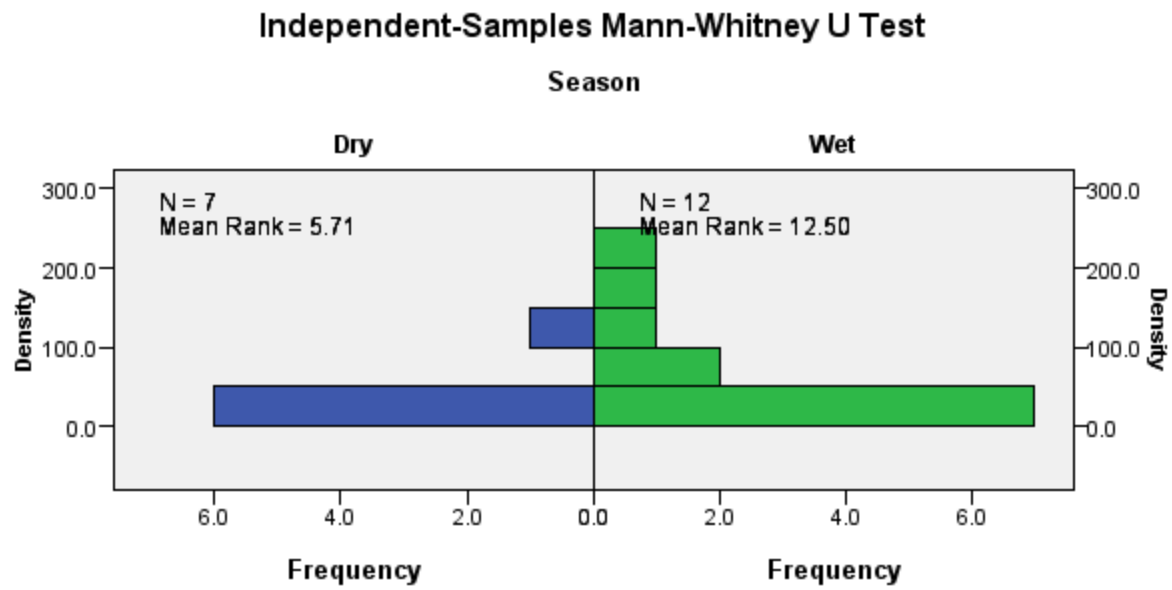
Total N	23
Mann-Whitney U	89.000
Wilcoxon W	167.000
Test Statistic	89.000
Standard Error	16.232
Standardized Test Statistic	1.417
Asymptotic Sig. (2-sided test)	.156
Exact Sig. (2-sided test)	.169

Figure 2.10. Seasonality in fruit availability for the 12 most consumed fruit species at Bekob



Total N	26
Mann-Whitney U	126.500
Wilcoxon W	262.500
Test Statistic	126.500
Standard Error	18.964
Standardized Test Statistic	2.452
Asymptotic Sig. (2-sided test)	.014
Exact Sig. (2-sided test)	.012

Figure 2.11. Seasonality in fruit availability for the 12 most consumed fruit species at Njuma



Total N	19
Mann-Whitney U	72.000
Wilcoxon W	150.000
Test Statistic	72.000
Standard Error	11.832
Standardized Test Statistic	2.535
Asymptotic Sig. (2-sided test)	.011
Exact Sig. (2-sided test)	.010

Figure 2.12. Seasonality in fruit availability for the 12 most consumed fruit species at Ganga

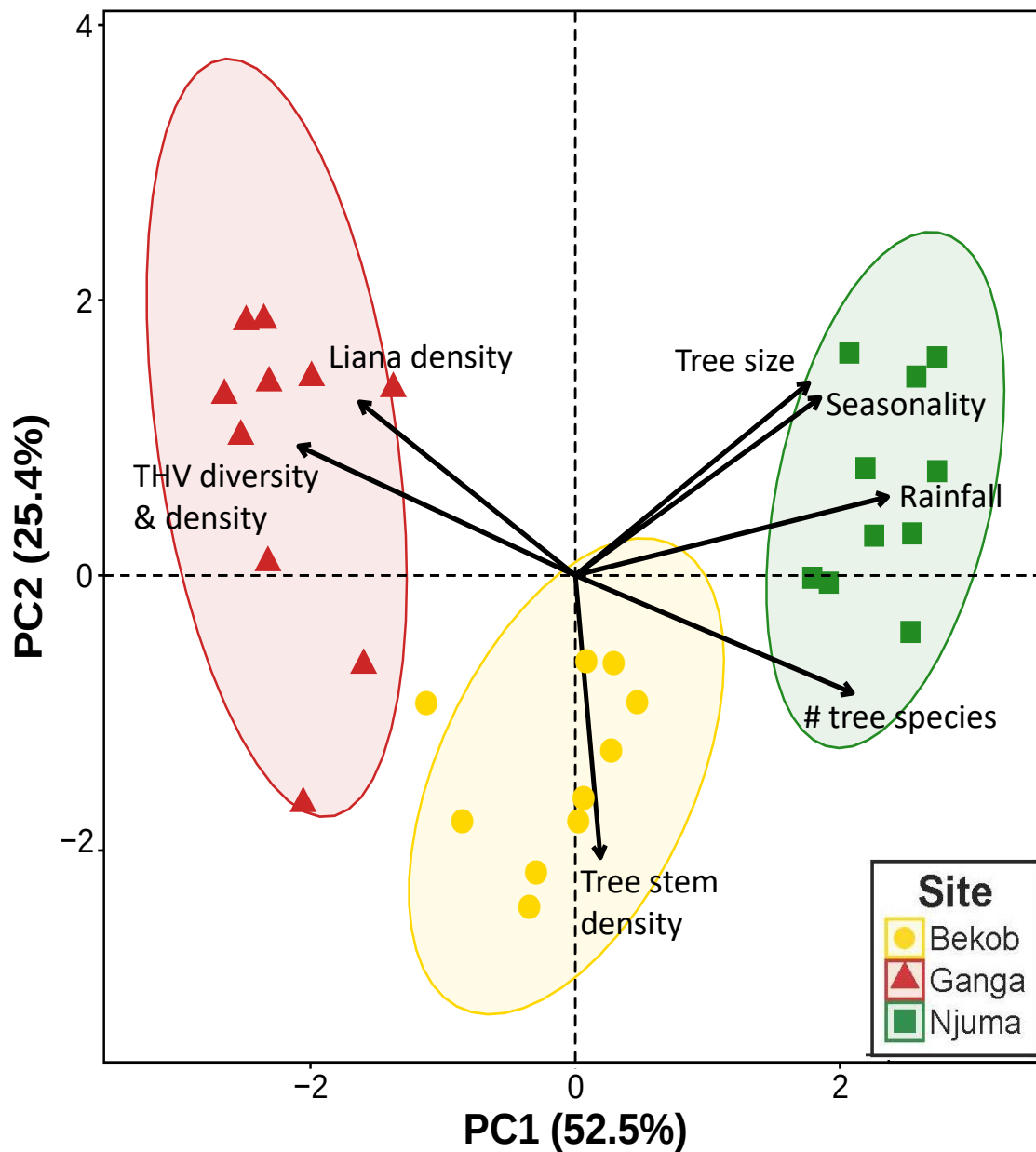


Figure 2.13. Principal component analysis (PCA). PCA generated based on environmental and botanical variables along ten 2 km long transects at ecotone and rainforest chimpanzee habitats. Samples are color-coded by site: (1) circle – Bekob (human-modified rainforest), (2) square – Njuma (pristine rainforest) and (3) triangle – Ganga (ecotone).

CHAPTER THREE

3. DIETARY ECOLOGY OF NIGERIA-CAMEROON CHIMPANZEES (*Pan troglodytes ellioti*) ACROSS RAINFOREST AND ECOTONE HABITATS IN CAMEROON

Abstract

The relationships between chimpanzee (*Pan troglodytes*) socioecology and the diversity of habitats the species occupies across forested regions of tropical Africa is a topic of enduring interest. The factors that underpin this diversity remain largely unexplored, and especially regarding whether these factors contribute to the evolution of chimpanzee populations. The chimpanzees of Cameroon represent a unique opportunity to address this issue. Cameroon is home to two chimpanzee subspecies, *P. t. ellioti* and *P. t. troglodytes*, that form the major branch point of the chimpanzee phylogenetic tree. In addition, the genetic history of these two subspecies have been tied to environmental variation across this region, and niche differentiation has been important in shaping recent patterns of genetic diversification in the Nigeria-Cameroon chimpanzee (*P. t. ellioti*). This subspecies can be further subdivided into two gene pools that occupy distinctive habitats, one deme is found in the mountainous forests of western Cameroon while the other deme is found in an ecotone in central Cameroon. Chimpanzees are fruit specialists and their responses to the spatial and temporal distribution of fruits across different habitats underlie many aspects of their socioecology. Such local socioecological differentiation may promote genetic diversification of chimpanzee populations inhabiting distinct environments across the Gulf of Guinea region. Thus, I hypothesized that environmental and ecological differences between the habitats occupied by chimpanzees belonging to each of these demes may promote variation in chimpanzee feeding ecology across

Cameroon, which may in turn contribute to observed pattern of the genetic differentiation between chimpanzee populations in the region.

I used macroscopic fecal sample assessment to investigate dietary variation in *P. t. ellioti* in Ebo forest (rainforest) and Mbam & Djerem National Park (ecotone) in relation to fruit availability measured through monthly fruitfall. Ecological and behavioral data were collected simultaneously across the sites between January 2016 to December 2017. I further conducted Principal Component Analyses (PCA) on the content of feces from across the ecotone and rainforest sites, to determine the variables that account for dietary variation between the ecotone and rainforest chimpanzee populations. Fecal samples collected during the dry and wet seasons were analyzed separately for seasonal patterns.

The ecotone was richer in fleshy fruit availability, but also had greater seasonality in fruit availability compared to the rainforest. Annually, dietary diversity in fleshy fruits was higher for chimpanzees at Bekob and Njuma than Ganga. The main differences in the dietary ecology chimpanzees at Bekob and Njuma (rainforest), and Ganga (ecotone) were in the seasonal variation of fleshy fruits and fibrous foods in their respective diets. Fleshy fruits were the most important dietary component for chimpanzees at Bekob and Njuma in the dry season, whereas the diet of chimpanzees at Ganga was dominated by fibrous foods. Conversely, in the wet season, the proportion of fleshy fruits was more significant in the diet of the Ganga chimpanzees, while fibrous foods were of more significance for the chimpanzees at Bekob and Njuma. Animal consumption, including vertebrates and invertebrates was more significant at Ganga, and was inversely associated with fleshy fruit consumption. The chimpanzees at Bekob incorporated more fruits from introduced and secondary forest plant species in their diet especially during periods of fleshy fruit scarcity compared to chimpanzees at Njuma. Collectively

these observations suggest a positive role for habitat diversity and differences in feeding ecology in the evolution of chimpanzee populations.

3.1. Introduction

With a wide geographic distribution across diverse habitats in Africa (Caldecott and Miles, 2005, Mittermeier et al., 2013), chimpanzees are undoubtedly one of the most ecologically flexible primate species (Stumpf, 2011). Studies of chimpanzee socioecology across Africa illustrate that the species is characterized by a complex variation in behaviors associated with a range of ecological habitats (Fowler and Sommer, 2007, Furuichi et al., 2001, Hockings et al., 2009, Lambert, 2007, Moore, 1996, Stumpf, 2011, Whiten et al., 1999). Chimpanzees are frugivorous, striving to maintain a largely fruit-based diet even during periods of fruit scarcity irrespective of their habitat (Hunt and McGrew, 2002, Tutin et al., 1997a, Wrangham et al., 1991). In addition to the consumption of fruits, non-fruit plant parts including leaf, flower, pith, bark and root; and vertebrates and invertebrates also constitute regular components of chimpanzee diets (Dutton and Chapman, 2015, Fowler and Sommer, 2007, Morgan and Sanz, 2006, Potts et al., 2011, Pruett, 2006). However, depending on the habitat, there are noticeable seasonal differences in the composition of chimpanzee diets in terms of species preferences, diversity of species ingested as well as the proportions of fruit, non-fruit plant parts and animal prey in the diet (Hunt and McGrew, 2002, Stumpf, 2011). Generally, differences in feeding behaviors between populations have been attributed to ecological variation (Stumpf, 2011) and cultural traditions (Boesch et al., 1994, Whiten et al., 1999, Yamakoshi, 1998).

The spatial and temporal distribution of food resources determine many key aspects of chimpanzee socioecology (Wrangham, 1977). Several factors including rainfall seasonality, soil

characteristics, irradiance, and human disturbance affect habitat composition and productivity, and consequently the behavioral ecology of primates that inhabit them (Chapman et al., 2000, Hockings et al., 2012, Marshall et al., 2009, McGrew, 2007, Potts et al., 2009, Tutin et al., 1997b, Wrangham et al., 2009, Wrangham, 2005). In general, equatorial lowland rainforest and other closed-canopy habitats have greater biomass and fruit/food productivity than more open and savanna habitats (Hunt and McGrew, 2002, Potts et al., 2009, Potts et al., 2011, Pruetz and Bertolani, 2009). Equatorial lowland habitats also tend to be richer in species diversity and productivity than higher altitude habitats (Basabose, 2002, Basabose, 2004, Nkurunungi et al., 2004); and more moist habitats including swamps tend to have higher productivity than adjacent dry areas (Marshall et al., 2009). As a result, chimpanzees in closed-canopy rainforest habitats have a more diverse and consistent fruit-based diet for most of the year (Chapman et al., 1997, Chapman et al., 1994b, Hemingway and Bynum, 2005, Stumpf, 2011, van Schaik and Brockman, 2005, Watts et al., 2012a) than populations at drier habitats including ecotone and savanna which experience greater seasonality in fleshy fruit availability (Hunt and McGrew, 2002, McGrew et al., 2004, McGrew et al., 1996, Pruetz and Bertolani, 2009). Chimpanzees in ecotone and savanna habitats incorporate more fallback foods in their diet (Marshall and Wrangham, 2007, Tutin et al., 1991) especially during extended periods of fruit scarcity (Doran et al., 2002, Hunt and McGrew, 2002, Knott, 2005, McGrew et al., 1988, Murray et al., 2006, Pruetz and Bertolani, 2009, Wrangham et al., 1996). The dietary diversity of montane chimpanzee populations is lower than that of lowland rainforest populations (Chancellor et al., 2012, Stanford and Nkurunungi, 2003). The availability of natural food sources is also influenced by anthropogenic modification of natural habitats, and chimpanzees living in human-dominated landscapes supplement wild food diets with cultivars (Hockings et al., 2009, McLennan, 2013)

while secondary forest species are important food sources for populations at human-modified sites (Carvalho et al., 2015a, Furuichi et al., 2001, Yamakoshi, 1998).

Chimpanzees spend more than 60% of their foraging time on fruits (Bogart and Pruett, 2011, Morgan and Sanz, 2006, Newton-Fisher, 1999, Tutin et al., 1997a, Watts et al., 2012a, Wrangham et al., 1996). Fruit remains including seed, fiber and tegument constitute more than 50% of dietary composition (Dutton and Chapman, 2015, Head et al., 2011, Moscovice et al., 2007, Stanford and Nkurunungi, 2003, Tutin and Fernandez, 1985, Yamagiwa and Basabose, 2006). But there are site-specific preferences for some fruit species (Basabose, 2002, Newton-Fisher, 1999, Potts et al., 2011, Watts et al., 2012a, Wrangham et al., 1996). Preferred foods are resources that are consumed disproportionately more than other resources that may occur across the habitat at the same frequency (Marshall and Wrangham, 2007).

All habitats experience seasonality in plant phenology, and fruit availability varies seasonally and sometimes interannually (Chapman et al., 2005, Marshall et al., 2009, Tutin et al., 1997a, Tweheyo and Lye, 2003), thereby affecting chimpanzee feeding ecology and habitat use. Chimpanzees generally respond to periods of fruit scarcity by increasing their daily ranges to maximize fruit consumption (Wrangham et al., 1996), spending more time feeding, reducing party size, consuming less preferred fruit species that have asynchronous fruiting patterns, feeding on non-fruit plant parts (Tutin et al., 1991, Wrangham et al., 1996, Yamakoshi, 1998), or employing tools to attain food sources that cannot be accessed otherwise (Doran, 1997, Tutin et al., 1997a, Yamakoshi, 1998). Resources used as fallback foods vary between populations (Tutin et al., 1997a). For example, figs are considered a fallback food resource for several chimpanzee populations (Wrangham et al., 1991, Wrangham et al., 1993). But figs are also considered a preferred food resource at other sites (Basabose, 2002, Carvalho et al., 2015a, Dutton and

Chapman, 2015, Newton-Fisher, 1999, Yamakoshi, 1998). Apart from fruits, chimpanzees also consume non-fruit plant parts, including leaves, pith, bark, and cambium (Morgan and Sanz, 2006, Tutin et al., 1991, Yamagiwa and Basabose, 2009). The consumption of terrestrial herbs especially of the Zingiberaceae and Marantaceae families is widely associated with fruit scarcity (Basabose, 2002, Tutin et al., 1991, Wrangham et al., 1998).

In addition to these plant forms, chimpanzees also consume vertebrates and invertebrates including several species of ants, termites, bees/honey, larvae, birds, eggs, crabs, other primates and mammals (Boesch and Boesch, 1989, Bogart and Pruett, 2008, Deblauwe, 2009, Humle and Matsuzawa, 2001, Humle and Matsuzawa, 2002, Mitani and Watts, 2001, Sanz et al., 2004, Stanford et al., 1994). Many of these food sources are acquired using tools, and tool use behavior has been hypothesized as an innovation by chimpanzees to overcome food scarcity in certain habitats (Yamagiwa and Basabose, 2009, Yamakoshi, 1998).

The Gulf of Guinea is a biodiversity hotspot harboring many endemic species of plants and animals including primates (Oates et al., 2004). A range of mechanisms have been proposed to generate this rich diversity. Most hypotheses propose that genetic drift is responsible for speciation brought about by separation into Pleistocene Refuges or separation across biogeographic boundaries (Anthony et al., 2007, Eriksson et al., 2004, Moritz et al., 2000). The potential role(s) of local adaptation by natural selection has only recently come to be appreciated as an important factor underpinning speciation and intraspecific differentiation (Cheek et al., 2001, Smith et al., 2011b, Smith et al., 1997, Freedman et al., 2010a). One such example are the chimpanzees of Cameroon. The ranges of *P. t. troglodytes* and *P. t. ellioti* converge at the Sanaga River, and until recently, the separation of these subspecies was proposed to have been the result of genetic drift brought about by the separation from one

another at the Sanaga (Gonder et al. 1997; Gagneux et al., 2001, Gonder, 2000, Gonder and Disotell, 2006, Gonder et al., 2006, Mitchell et al., 2015a). However, Mitchell et al. (2015b) showed that environmental variation has been important in the separation of these populations under an isolation-with-migration population structure. These observations suggest that local adaptation likely plays a role in promoting the differences between these two subspecies. Furthermore, additional evidence suggests that environmental variation also plays a role in separating *P. t. ellioti* into two gene pools – one found in the mountainous rainforests of western Cameroon and another population found in an ecotone covering much of central Cameroon (Mitchell et al., 2015b, Sesink Clee et al., 2015). Understanding the relationship between genetic, ecological and socioecological variation in chimpanzees at an active diversification zone can be important in understanding evolutionary patterns of several other vertebrates across this area. However, the socio-ecology of chimpanzees across this region remains largely unexplored (Morgan et al., 2011).

Even though the study of *P. t. ellioti* socioecology is nascent, current evidence suggests that there are marked differences in dietary behaviors between populations occupying different ecological niches (Abwe and Morgan, 2008, Fowler and Sommer, 2007, Morgan and Abwe, 2006, Wrangham, 2006). At Ngel Nyaki Forest Reserve, a small reserve located in the Cameroon Highlands in eastern Nigeria a small of population of *P. t. ellioti* consume various plant parts from at least 52 plant species and incorporate small mammals, ants and honey in their diet (Dutton and Chapman, 2014, Dutton and Chapman, 2015). At GGNP, which is located in eastern Nigeria along the border shared with Cameroon near Ngel Nyaki, chimpanzees also have a fruit-based diet and are involved in subsistence tool use to acquire terrestrial and arboreal ants, as well as honey (Fowler and Sommer, 2007, Hohmann et al., 2012, Schoening et al., 2007, Sommer et al.,

2012, Sommer et al., 2017). At Ebo forest, Cameroon chimpanzees similarly have a subsistence tool use repertoire for termite fishing and honey dipping, as well as nut cracking (Abwe and Morgan, 2008, Morgan and Abwe, 2006); and hunt monkeys (Morgan et al., 2012), which appears to be absent elsewhere within the range of the subspecies this far (Fowler and Sommer, 2007, Morgan and Abwe, 2006, Wrangham, 2006).

Comparative chimpanzee dietary studies have generally focused on variation between rainforest and ecotone-savanna populations (Hohmann et al., 2012, Hunt and McGrew, 2002, Stumpf, 2011) or variation between adjacent communities (Humle, 2003, Potts et al., 2011). No previous study has spanned an active diversification zone within and between subspecies making it difficult to directly address the hypothesis whether socioecological differences in populations inhabiting distinct niches contribute to promoting the genetic divergence of chimpanzees.

This project aimed to assess the dietary ecology in relation to ecological variation within and between three chimpanzee sites in Cameroon corresponding to the two gene pools present in the subspecies. Previous studies have shown that the two chimpanzee gene pools identified in the Nigeria-Cameroon chimpanzee are associated with environmental variation (Mitchell et al., 2015b) and they occupy different niches. In this study, I addressed whether these differences result in significant differences in their dietary ecology. In order to complete the study, I used chimpanzee feces collected opportunistically at nesting and feeding sites, and trails; and circumstantial evidence at feeding sites to assess monthly and seasonal variation in the composition (number of species consumed, and the proportion of fruit, non-fruit plant part and animal prey) of chimpanzee diets in relation to fruit availability measured through monthly fruitfall across the three sites. Based on the ecological and environmental differences across the sites, I predicted that 1) dietary diversity in fruit species would be higher at the rainforest than

the ecotone, 2) there would be more pronounced seasonal shifts in the dietary components including fleshy fruits and fibrous foods at the ecotone than at the rainforest, and 3) secondary forest fruit species would be important dietary items at the Bekob.

3.2. Methods

3.2.1. Study sites

Ebo forest and MDNP are important strongholds for the Nigeria-Cameroon chimpanzee, together harboring more than 1000 individuals of the most threatened and least studied of the four chimpanzee subspecies (Morgan et al., 2011). Two sites were selected in the Ebo forest based on differences in the level of anthropogenic history (hereafter human-modified rainforest: Bekob and near-pristine rainforest: Njuma). To the west, Njuma is characterized by closed-canopy rainforest that was selectively logged in the 1980s. To the north-east, Bekob inhabited until the late 1950s is characterized by a mosaic of habitats including abandoned farmland, secondary and mature submontane forests. The MDNP site (Ganga) is located in the north east of the park, and is characterized by a mosaic of habitats including high and low closed-canopy gallery forests, and high and low open-canopy secondary and colonizing forests, and savanna.

Data were collected monthly across Bekob and Njuma (Ebo forest) between January 2016 to March 2017. At Ganga (MDNP), monthly data collection was between January 2016 to December 2017. Data were collected simultaneously across the sites between January 2016 to March 2017 (detailed site descriptions in Chapter One, Section 1.6).

3.2.1.1. Sampling

To assess botanical diversity and fruit availability, at each of the three sites, I established 10 straight-line transects of 2 km length each perpendicular to the main drainage, following a

fixed bearing: Bekob (270°), Njuma (20°) and Ganga (270°). To minimize vegetation disturbance (so animals and poachers do not adopt transects as trails), I used secateurs to establish transects and installed flagging tape at regular intervals along the transects for direction. All trees and lianas with a diameter at breast height (DBH) ≥ 10 cm within a 5 m band (2.5 m on either side of the transect center-line) were enumerated (with oil paint), DBH measured at about 1.3 height, and identified – Figure 2.1. Where it was not possible to measure DBH, for example, tall buttress trees, the diameter was estimated to the nearest 5 cm. Botanical identification in the field was carried out in collaboration with Dr. Barthelemy Tchiengue (National Herbarium, Yaoundé, Cameroon) in August and September 2016 for Njuma and Bekob respectively and during February 2017 for Ganga. Taxonomic classification was based on The Plant List database (<http://www.theplantlist.org/>).

3.2.1.2. Terrestrial herbaceous vegetation

The diversity of terrestrial herbaceous vegetation (THV) was assessed using 4 m² quadrats positioned on alternate sides of each transect at 100 m intervals (Morgan, 2001) – Figure 2.1. Each quadrat was 2 x 2 m (corners were marked with flagging tape), and there were 20 quadrats per transect, giving a total area assessed of 800 m² per site. In each quadrat, THV species were identified, and the number of species present was noted. Given that chimpanzees preferentially feed on THV species in the Marantaceae and Zingiberaceae families (Tutin et al., 1991), the presence or absence of these in each quadrat was also noted.

3.2.1.3. Fruitfall assessment

Monthly fruit availability was assessed using fruitfall on a 1 m band along each transect (Furuichi et al., 2001, White, 1994) – Figure 2.1. All fallen fruit known to be eaten by

chimpanzees across the sites were identified, counted, and photographed, then cleared off the trail. Fruit type (succulent, fleshy-pods, arillate, dehiscent and wind dispersed) as well as evidence of feeding on them by animals were noted (White, 1994). From preliminary assessment of feces across the rainforest and ecotone sites, I determined the 12 most important fruit species in the diet of the study chimpanzee populations. Monthly fruitfall for these species per site was expressed in density per hectare across each site.

3.2.1.4. Other primates, large mammals, termite, ant and honeybee colonies

The density of termite mounds, ant nests, and bee hives were noted within a 5 m band along transects across the three sites. Colonies of foraging or migrating termites and ants were also noted monthly along transects. All mammal observations including direct sightings and vocalizations were also recorded.

3.2.1.5. Chimpanzee activity sites

I tracked chimpanzee vocalizations to locate activity sites in order to observe opportunistic behaviors whenever it was possible. However, whenever I sighted chimpanzees, I limited observation time to avoid groups becoming habituated to my presence, as hunting is prevalent across the study sites. Whenever an activity site was observed along straight line transects or reconnaissance transects (recces), I marked and revisited the site to ascertain the regularity of the behavior. Visiting activity sites was important to gather direct and circumstantial evidence of chimpanzee feeding ecology and subsistence tool use behaviors including termite fishing, ant dipping, honey dipping and nut cracking.

3.2.2. Fecal sample collection and processing

I collected fresh chimpanzee feces (not <2 days old) for dietary assessment opportunistically at feeding and nesting sites, and trails during monthly transect and recce walks. These samples were collected in plastic bags and labelled with date, site and geographic coordinates. All samples were weighed using a scale and washed in a 1 mm mesh sieve in flowing water to remove the matrix, then the remains were dried in an oven (McGrew et al., 2009) and lodged in a labelled plastic bag.

3.2.2.1. Macroscopic assessment of fecal samples

Once dried, the content of each feces was sorted into different categories, including fruit remains (seeds, fruit-fiber and tegument), non-fruit plant material (leaves, fiber, and bark) – hereafter fibrous food, and animal remains (chitinous parts of ants and termites, fur and bones of vertebrates, and egg shells). The seeds in each feces were identified to determine the number of species ingested. I assessed the proportion of food components (fruit remains, fibrous food and animal prey) to the total volume of the dried sample (McLennan, 2013, Yamagiwa and Basabose, 2006). I counted all seeds >0.5 cm diameter and assessed the percentage volume of each species ingested in relation to the entire sample. For species with seeds <0.5 cm diameter, the volume of each per fecal sample was assessed and expressed as percentage of the volume of the sample. Finally, fibrous food and animal prey in samples were estimated in relation to the total volume of each sample and expressed as a percentage volume (McGrew et al., 2009, McLennan, 2013).

3.2.2.2. Chimpanzee preferred and fallback food resources

Fruit species that were present in $\geq 50\%$ of the fecal samples in any given month and/or accounted for $\geq 50\%$ of monthly fruit consumption volume for each population across the three sites were considered preferred (Hohmann et al., 2012, Piel et al., 2017, Pruetz, 2006). Fallback foods were resources whose consumption was inversely associated with preferred fruit consumption, and these were particularly important for each population during periods of fruit scarcity (Basabose, 2002).

3.2.2.3. Species identification

I identified most of the seeds to either species or genus levels, and when identification was not possible, I coded unidentified seeds and used the codes consistently whenever the same seeds were observed in subsequent samples. Since it was usually not possible to macroscopically determine the plant species from which leaf, bark, and pith in the feces were derived, these were all categorized as fibrous food. It was also not possible to authoritatively determine vertebrate and invertebrate species in feces macroscopically. For the former, fur, bone, and teeth were generally attributed to mammals; and for the latter tools at termite mounds, ant nests and beehives were used to infer insect species consumed.

3.2.3. Data analysis

Nonparametric tests were used to evaluate patterns of seasonal variation in diet composition within and between the three sites, as the data were not normally distributed. Mann-Whitney U Tests were used to compare seasonality in feeding patterns within sites, and Kruskal-Wallis one-way ANOVA analyses were used to test for overall differences between the sites, and significant values were adjusted for multiple comparisons with a Bonferroni correction.

Pearson R tests were used to determine the association between dietary components, and between diet composition and fruit availability. All tests were two-tailed, with a 0.05 significance and were performed in SPSS (IBM SPSS Statistics 24).

3.2.4. Principal component analysis for variation in dietary patterns between the ecotone and rainforest chimpanzee populations

To investigate the variation in feeding ecology between Nigeria-Cameroon chimpanzee populations occupying distinct niches, I conducted a PCA in R with the prcomp package (R version 3.4.3), on feeding habits based on remnants of food components in chimpanzee feces across Bekob, Njuma and Ganga. The PCA was geared to bring out variation and patterns in the dataset of correlating components of fecal samples from Bekob, Njuma and Ganga including: number of fruit species in sample, volume of fruits in sample, volume of fiber, volume of seeds >5 mm, and the number of seeds >5 mm. To account for seasonality, I analyzed 265 fecal samples (Bekob:56, Njuma:95, Ganga: 114) collected in the dry (December-February) and 337 fecal samples (Bekob:122, Njuma:90, Ganga:125) from the wet (May-September) seasons separately.

3.3. Results

3.3.1. Fruit availability from monthly fruitfall

The mean density of fruitfall for important fruits in the diet of chimpanzees at Bekob was 20.39 ± 35.375 fruits ha^{-1} (dry season: 14.58 ± 30.273 , and wet season: 25.71 ± 40.06 fruits ha^{-1}) and for Njuma 8.92 ± 11.80 fruits ha^{-1} (dry season: 3.4 ± 4.19 , and wet season: 12.38 ± 13.73 fruits ha^{-1}). For Ganga, the mean density was 55.34 ± 65.413 fruits ha^{-1} (dry season: 23.70 ± 37.51 , and wet season: 73.80 ± 72.28 fruits ha^{-1}). There was a significant difference in fruit

availability based on fruitfall across the sites (Kruskal-Wallis: $N = 68$, $X^2 = 13.252$, $df = 2$, $P = 0.001$). The density of fruitfall was higher at Ganga than Njuma ($Z = 3.553$, $P < 0.001$), Ganga than Bekob ($Z = -2.653$, $P = 0.024$) and there was no difference between the two rainforest sites (Figure 2.9). There was no seasonal difference in fruit availability at Bekob ($N = 23$, Mann-Whitney U test: $Z = 89.00$, $P = 0.169$). The density of fruits was higher in the wet than the dry season at Njuma ($N = 26$, Mann-Whitney U test: $Z = 126.500$, $P = 0.012$) and Ganga ($N = 19$, Mann-Whitney U test: $Z = 72.000$, $P = 0.010$) (Figure 2.9).

Ganga had a higher frequency and diversity of THV in Marantaceae and Zingiberaceae families than Bekob and Njuma. Details on seasonal availability of fruits and THV in Bekob, Njuma and Ganga are found in Chapter Two: Section 2.3.8.1.

3.3.2. Presence of other primates, large mammals, termite, ant and honeybee colonies

The encounter rate of other primates was <0.5 group per day at the rainforest sites whereas at the ecotone sites it was >1 group per day. Common diurnal primates at Ganga included: grey-cheeked mangabey (*Lophocebus albigena*), crowned guenon (*Cercopithecus pogonias*), putty-nosed monkey (*C. nictitans*), guereza colobus (*Colobus guereza*), and baboons (*Papio anubis*). At Bekob and Njuma, common diurnal primates included putty-nosed monkey (*C. nictitans*), Preuss's guenon (*Allochrocebus preussi*), red-eared monkey (*C. erythrotis*), red-capped mangabey (*Cercocebus torquatus*), crowned guenon (*C. pogonias*) and drills (*Mandrillus leucophaeus*). Elephant (*Loxodonta cyclotis*) signs including dung and prints were common at Ganga (> 1 per hectare), less common at Bekob (<1 per hectare) and rare at Njuma.

The density of active termite (*Macrotermes* sp.) mounds in the rainforest sites was 1.9 and 0.5 mounds per hectare for Bekob and Njuma respectively, and for Ganga it was 3.8 mounds

per hectare. Black ant (*Pachycondyla* sp.) nests occurred at a density of 8.2 nests per hectare at Ganga, but were not observed at the rainforest sites. Foraging and migrating parties of army ants and termites were not systematically recorded, but encounter rates were higher at the ecotone than the rainforest sites.

3.3.3. Inter-site comparison of dietary diversity and composition

Between January 2016 and March 2017, I collected 30 chimpanzee fecal samples at Bekob and 62 samples at Njuma opportunistically from nesting and feeding sites. At Ganga, I collected 341 fecal samples between January 2016 and December 2017. Because of the small sample sizes for the two rainforest sites, 240 and 184 fecal samples collected opportunistically between 2005 and 2015 were included in the dietary analysis for Bekob and Njuma respectively.

3.3.3.1. Diversity of dietary fruit species

The number of fruit species consumed by chimpanzees based on macroscopic fecal analysis and feeding signs were 59 and 63 species for Bekob and Njuma respectively, and 53 for the Ganga – Tables: 3.1, 3.3 and 3.5. At Bekob, 268 (99.3%) of the 270 fecal samples assessed contained one or more fruit species, 99.6% (N = 256) for Njuma, and 97.1% (N = 341) for Ganga.

The average number of fruit species per fecal sample was $2.46 \pm \text{SD } 1.309$ (range 0-7) and $2.36 \pm \text{SD } 1.294$ (range 0-9) fruits for Bekob and Njuma respectively, and $1.92 \pm \text{SD } 1.106$ (range 0-5) for Ganga. There was a significant difference between the rainforest and ecotone populations in the mean number of species per fecal sample (Kruskal-Wallis: $N = 867$, $X^2 = 29.869$, $df = 2$, $P < 0.001$). Specifically, there was a higher mean number of fruit species per fecal sample at Bekob than Ganga ($Z = 5.105$, $P < 0.001$), Njuma than Ganga ($Z = -3.979$, $P < 0.001$), while there was no difference between Bekob and Njuma (Figure 3.1).

3.3.3.2. Seasonality in the number of species consumed

The mean number of fruit species consumed at the Bekob was higher in the wet season than the dry season (Mann-Whitney U test: $N_1 = 115$, $N_2 = 155$, $Z = -3.897$, $P < 0.001$), while there was no marked seasonality in the number of fruit species per fecal sample at Njuma (Mann-Whitney U test : $N_1 = 95$, $N_2 = 161$, $Z = -0.856$, $P = 0.392$) and Ganga (Mann-Whitney U test : $N_1 = 188$, $N_2 = 153$, $Z = -0.665$, $P = 0.506$). These results are detailed in Appendices 3.1, 3.2, 3.3.

3.3.3.3. Relationship between fruit availability and fruit consumption

At Ganga, there was a positive and significant correlation between fruit species availability and the volume of the species represented in chimpanzee fecal samples ($N = 21$, Pearson R: 0.445, $P = 0.043$) – Figure 3.2. It was not possible to correlate species availability and consumption for Bekob and Njuma as most of the fecal samples were collected before the fruit availability assessment.

3.3.3.4. Preferred fruit species by chimpanzees across the three sites

At Bekob, *Landolphia* spp., *Antrocaryon klaineum*, *Uapaca guineensis*, *Santiria trimera*, *Ficus* spp., *Pycnanthus angolensis*, *Cleistopholis patens* and *Musanga cecropioides* were present in $\geq 50\%$ of samples in months they were consumed (Table 3.1); and *Landolphia* spp., *U. guineensis* and *S. trimera* represented $\geq 50\%$ monthly fruit consumption volume in some months (Table 3.2).

At Njuma, *A. klaineum*, *U. guineensis*, *Grewia coriacea*, *P. angolensis* and *Landolphia* spp. were present in $\geq 50\%$ of samples (Table 3.3); and *G. coriacea*, *P. angolensis* and *Landolphia* spp. represented $\geq 50\%$ monthly fruit consumption volume in some months (3.4).

At Ganga, *U. guineensis*, *Pseudospondias microcarpa*, *Myrianthus arboreus*, *Landolphia* spp., *Aframomum* spp., *Canarium schweinfurthii*, Unidentified #26, Unidentified #33 and Unidentified # 34 were present in $\geq 50\%$ of samples in months they were consumed (Table 3.5). And species with a monthly consumption volume of $\geq 50\%$ included *U. guineensis*, *G. coriacea*, *M. arboreus*, *Landolphia* spp., Unidentified #26 and Unidentified #34 (Table 3.6). Across the ecotone and rainforest, *Landolphia* spp. and *U. guineensis* were common preferred fruits.

3.3.3.5. Fallback fruit species

Some species with asynchronous fruiting patterns or those that produced fruits during the dry season, associated with fruit scarcity across the ecotone and rainforest were important in the diets of chimpanzees. At Bekob, *A. klaineana*, *U. guineensis*, *Ficus* spp. and *Keayodendron bridelioides* were important dry season fruits. In addition, at this site, *Musanga cecropioides* (umbrella tree) and *Elaeis guineensis* (oil palm) were consumed at for eight and six months respectively, including during the dry season. At Njuma, *A. klaineana*, *K. bridelioides*, *Antiaris toxicaria* and *Ficus* spp. were important for chimpanzees during the dry season. Finally, at Ganga, *U. guineensis*, *Ficus* spp. and three unidentified species were important fruit sources for chimpanzees at this site during the dry season. Some of these species were present in $\geq 50\%$ of samples and/or represented $\geq 50\%$ fruit consumption volume for given months, and were thus also preferred. But they fulfilled the role of fallback foods because they were associated with seasonal fruit scarcity across the various sites. *Ficus* spp. and *U. guineensis* were common fallback food sources during the dry season across the ecotone and rainforest.

3.3.3.6. Feeding signs on other fruit species

Signs at feeding sites were used to ascertain the consumption of some fruit species that could not be discerned from macroscopic fecal analysis. It was however not possible to determine the frequency at which these species were consumed based on the opportunistic nature of the observations. There were feeding signs on fruits of *Irvingia gabonensis* at the Njuma and Ganga. In addition, the chimpanzees at Ganga cracked the seeds of *I. gabonensis* after eating the fruit to consume the nuts. But the cracking of the seeds was not associated with tools (Figure 3.3). Fruits of *Milicia excelsa* were consumed across the three sites. At the rainforest sites, chimpanzees consumed nuts of *Coula edulis* that were cracked using stone and wooden hammers (Abwe, 2010).

3.3.3.7. Dietary variation between Bekob and Njuma chimpanzee populations

The main dietary components including proportion, diversity and seasonality in fruit, fiber and animal remains for chimpanzees at Bekob and Njuma were relatively similar (Figures 3.12 and 3.13). At both sites, *Landolphia* spp. *A. klaineana*, *S. trimera*, *U. guineensis*, *C. patens*, *K. bridelioides*, *P. angolensis* and *C. dinkalgei* were fleshy fruit species consumed. In addition, there were similarities between the two populations in fallback fruit species consumed including *Ficus* spp. and *M. cecropioides*. However, the chimpanzees at Bekob consumed fruits of *E. guineensis* which was not observed in the diet of chimpanzees at Njuma. Remains of *E. guineensis* fruits were present in ~15% of fecal samples at Bekob, and the species were consumed for several months including periods of scarce fleshy food availability. *Elaeis guineensis* was common in abandoned plantations and secondary forest at Bekob and could be important fallback food

resource for chimpanzees at this site compared to chimpanzees at Njuma, where the species was rare.

3.3.3.8. Proportion of fruit remains in the fecal samples

There was a significant variation in the proportion of fruits in the diets of rainforest and ecotone chimpanzees (Kruskal-Wallis: $N = 867$, $X^2 = 22.110$, $df = 2$, $P < 0.001$). Fruit proportion in chimpanzee diets was higher at Njuma than Ganga ($Z = -4.067$, $P < 0.001$), Bekob than Ganga ($Z = -3.895$, $P < 0.001$) and there was no difference between rainforest sites (Figure 3.4). The mean percentage of fruit remains (seed, fruit-fiber and tegument) composing chimpanzee feces at the rainforest was $86.463 \pm SD 22.299\%$ ($N = 270$) and $88.25 \pm SD 19.243\%$ ($N = 256$) Bekob and Njuma sites respectively, and $74.79 \pm SD 34.341\%$ ($N = 341$) for the Ganga.

3.3.3.9. Seasonality in proportion of fruit components in the diet

There was a significant difference in the seasonal proportion of fruits in the diets of chimpanzees at Ganga (Mann-Whitney U test: $N_1 = 188$, $N_2 = 153$, $Z = -8.991$, $P < 0.001$) and Bekob (Mann-Whitney U test: $N_1 = 115$, $N_2 = 155$, $Z = -2.175$, $P = 0.030$). At both sites, the wet season proportion of fruit consumption was higher than in the dry season. At Njuma on the other hand, there was no marked seasonality in the proportion of fruit components in the diet (Mann-Whitney U test: $N_1 = 95$, $N_2 = 161$, $Z = -1.750$, $P = 0.080$) – see Appendices 3.4, 3.5, and 3.6.

3.3.3.10. Proportion of fibrous food in chimpanzee diets

There was no significant difference in the mean proportion of fibrous food in chimpanzee diets across the rainforest and ecotone chimpanzee populations (Kruskal-Wallis: $N = 867$, $X^2 = 4.692$, $df = 2$, $P = 0.094$) – see Appendix 3.7. At Bekob, 129 (47.8%) of the 270 fecal samples

assessed contained fibrous food remains, 50.4% (N = 256) for Njuma, and 46.6% (N = 341) for Ganga. The mean proportion of fibrous food remains in the diet of chimpanzees was $12.98 \pm \text{SD } 21.246\%$ and $11.104 \pm \text{SD } 18.18\%$ for rainforest sites Bekob and Njuma respectively, and $21.58 \pm \text{SD } 32.275\%$ for Ganga.

3.3.3.11. Seasonality in the consumption of fibrous foods

Across the ecotone and rainforest, the consumption of fibrous food was higher in the dry than the wet season. But the significance of this seasonality was higher at the ecotone (Mann-Whitney U test: N = 188, N = 153, Z = -10.124, P < 0.001) than the rainforest sites: Njuma (Mann-Whitney U test: N₁ = 95, N₂ = 161, Z = -2.093, P = 0.036) and Bekob (Mann-Whitney U test: N₁ = 115, N₂ = 155, Z = -1.990, P = 0.047) – see Appendices 3.8, 3.9 and 3.10.

3.3.3.12. Terrestrial herbaceous vegetation (THV) species consumed

From evidence at feeding sites, stems and leaves of *Aframomum* sp. (Figure 3.5) and Marantaceae sp. (Figure 3.6) were consumed by chimpanzees across the rainforest and ecotone. In addition, *Palisota ambigua* (Commelinaceae) stems (Figure 3.7) were consumed at the ecotone. Fruits of *Aframomum* spp. and Marantaceae spp. was also observed in fecal samples from across the sites. Swallowed leaves from undetermined species were also observed in fecal samples from Bekob and Ganga (Figure 3.8).

3.3.3.13. Animal consumption

At Bekob, 26 (9.6%) of the 270 fecal samples contained remains of vertebrates and invertebrates, 28 (10.9%) samples (N = 256) for Njuma and 126 (36.9%) samples (N = 341) at Ganga. The mean percentages of animal parts in diet of chimpanzees from fecal at the rainforest

sites were $0.547 \pm \text{SD } 4.525\%$ and $0.765 \pm \text{SD } 4.312\%$ for Bekob and Njuma respectively, and $3.605 \pm \text{SD } 11.755\%$ for Ganga. There was a significant difference between the ecotone and rainforest populations in the mean proportion of animal remains in feces (Kruskal-Wallis: $X^2 = 94.952$, $df = 2$, $P < 0.001$). The consumption of vertebrates and invertebrates was significantly higher at Ganga than Bekob ($Z = -8.580$, $P < 0.001$) and Njuma ($Z = 7.890$, $P < 0.001$), and there was no difference between Bekob and Njuma.

There were no seasonal differences across the ecotone and rainforest sites in the consumption of vertebrates and invertebrates – see Appendices 3.11, 3.12 and 3.13. And across the three sites, animal prey consumption was inversely correlated with fruit consumption (Bekob: Pearson $R = -0.327$, $P < 0.001$, Njuma: $R = -0.350$, $P < 0.001$ and Ganga: $R = -0.341$, $P < 0.001$).

3.3.3.13.1. Invertebrate species consumed

Tools abandoned by chimpanzees at termite mounds, ant nests and honey hives were used to infer species of insects consumed across the sites. Tools were associated with army ants (*Dorylus nigricans*) and termites (*Macrotermes* sp.) across the ecotone and rainforest sites. In addition, at the ecotone site, carpenter ants (*Camponotus brutus*) and *Pachycondyla* sp. were also consumed. Tools were also associated with stingless bee hives (*Meliponini* sp.) – Figure 3.9 - at Bekob and Ganga, but there was no discernible evidence of bees or beeswax in chimpanzee fecal samples from either site.

3.3.3.13.2. Vertebrate species consumed

There were no direct observations of hunting other primates or mammals at either the ecotone or rainforest sites during the study period. But at the ecotone, a black and yellow, and

black and white color tufts of hair in two chimpanzee feces could be attributed to a crowned guenon (*Cercopithecus pogonias*) and guereza colobus (*Colobus guereza*) respectively (3.10), while another fecal sample contained bones of a primate hand (Figure 3.11). Also, in March 2016, we came across three chimpanzees in a tree with a baby duiker which they dropped while fleeing after noticing us. On inspection, the duiker was freshly killed, and the chimpanzees had started eating it. Mammalian fur and bones were also recorded in fecal samples from the rainforest sites. In addition, at Njuma where chimpanzees are sympatric with Preuss's red colobus, an attempted capture of a red colobus monkey by a group of chimpanzees was observed in 2011 (Morgan et al., 2012).

3.3.4. Principal component analysis: dietary variation between Bekob, Njuma and Ganga based on remains in fecal samples in the dry and wet seasons

From the PCAs of fecal samples from the dry and wet seasons, the ecotone and rainforest chimpanzees were clearly separated in seasonal consumption of fleshy fruits – Figures 3.12 and 3.13, and Appendices 3.14 and 3.15. In the dry season, PC1 and PC2 accounted for >62% of dietary variation, and remains of fleshy fruits in fecal samples in PC1 (55%) were the main dietary component at Bekob and Njuma, and distinguished these populations from the chimpanzees at Ganga where fleshy fruit consumption was less significant in the dry season. In the wet season, PC1 and PC2 accounted for 63% of dietary variation and fleshy fruit remains in fecal samples PC1 (58%) separated between chimpanzees at Ganga, and Bekob and Njuma. The proportion of fleshy fruit remains in fecal samples was more important at Ganga than either Bekob or Njuma in the wet season.

Fibrous food remains in fecal samples in PC1 (54%) was the main variable that separated Ganga chimpanzees from those at Bekob and Njuma in the dry season. Fibrous food was the

main food component in Ganga chimpanzee diet in the dry season, but was not significant for Bekob and Njuma chimpanzee diets. In the wet season, PC1 and PC2 accounted for 63% of dietary variation, and fibrous food remains in PC1 (55%) distinguished the rainforest and ecotone chimpanzee populations. Fibrous food was significantly important at Bekob and Njuma, and less significant at Ganga during the wet season.

3.4. Discussion

Habitats occupied by distinct gene pools of *P. t. ellioti* across Cameroon are different environmentally and ecologically (Mitchell et al., 2015b, Sesink Clee et al., 2015, Chapter Two). As described in Chapter Two, the *P. t. ellioti*-rainforest sites are characterized by high rainfall associated with low seasonality, high botanical diversity and low seasonality in fruit availability. In addition, habitats at Bekob both harbor primary and secondary forests fruit species, as well as introduced species. Variation in relief between rainforest and ecotone habitats was one of the distinguishing variables across *P. t. ellioti* range in the EMNs (Sesink Clee et al., 2015). Though this variable was not directly quantified in this study, the altitudinal range at Njuma was ~100-900 m and at Bekob ~500-1200 m. At Ganga, there was less altitudinal variation (~700-900 m). On the other hand, at Ganga, the *P. t. ellioti*-ecotone site, there is greater seasonality in rainfall compared to the rainforest sites. These environmental conditions are reflected in ecological conditions at the ecotone: wide diversity in habitats, low species diversity and greater seasonality in fruit availability compared to the rainforest. Even though other ecological factors may be important, fruit availability plays a key role in chimpanzee socioecology (Anderson et al., 2002, Boesch, 1996, Mitani et al., 2002a, Stanford, 1998, Stumpf, 2011, Wallis, 1995, Wrangham

and Smuts, 1980). I assessed dietary patterns in rainforest and ecotone chimpanzee populations across Cameroon in relation to spatial and temporal availability of food resources.

Fruits were the most important dietary component of chimpanzees at all sites, which lends support to the widespread finding that frugivorous diet is a species-typical feature of chimpanzees. As predicted, fruit species diversity in chimpanzee diets at the rainforest was higher than at the ecotone. Despite the greater diversity and availability of fruits in the wet season at the ecotone, dietary diversity in fleshy fruits did not differ from that of the dry season. This could imply that chimpanzees at the ecotone maximized fruit consumption by having a larger home range that includes many different habitats during the dry season, but smaller home ranges during the wet season. Addressing this question, however, is beyond the scope of this study. From the PCA of food components from chimpanzee fecal samples collected across the ecotone and rainforest, variation in the seasonality of fleshy fruit consumption was one of the main axes of differentiation in the dietary ecology of *P. t. ellioti* in ecotone and rainforest habitats. During the dry season, fleshy fruits were the main component of rainforest chimpanzee diets, but were less significant for the chimpanzees at the ecotone. Conversely, in the wet season, fleshy fruits were the most important dietary item at the ecotone, and this separated them from rainforest chimpanzees for which fleshy fruits had less significance.

Low availability and patchy distribution of food resources increase grouping costs (Chapman et al., 1995, Wrangham et al., 1996), and chimpanzee groups in the ecotone (with pronounced seasonality fruit availability) may be smaller during the dry season geared at reducing intra-group feeding competition. Even though other factors like presence of estrous females influence chimpanzee sociality, fruit availability is key, as even reproductive cycles in female chimpanzees have been linked to seasonality in fruit availability (Anderson et al., 2002,

Mitani et al., 2002a, Wallis, 1995). Low fruit availability was also associated with lower rates of gregariousness in Nigeria-Cameroon chimpanzees at GGNP, Nigeria (Hohmann et al., 2012). During the wet season when fruits were abundant and clumped in distribution, the ecotone population preferentially selected some species. Such dietary patterns are common at other populations that exhibit marked seasonality in resource availability including Kibale, Uganda and Mahale, Tanzania (Chapman et al., 1995, Itoh and Nishida, 2007). Many chimpanzee populations show preferences for different fruit species and dietary diversity at many sites is not positively correlated with the diversity of available fruit species including Rubondo, Tanzania; Bwindi and Kibale, Uganda; and Kahuzi-Biega, DR Congo (Moscovice et al., 2007, Stanford and Nkurunungi, 2003, Watts et al., 2012a, Wrangham et al., 1998, Yamagiwa and Basabose, 2009).

The rainforest and ecotone populations also differed in nut processing and consumption. At the rainforest sites, chimpanzees regularly cracked seeds of *Coula edulis* (African walnut tree) using stone and wooden hammers (Abwe, 2010, Morgan and Abwe, 2006). This behavior was more common at Njuma which has a higher density of *C. edulis* trees (Abwe, 2010). In addition to *C. edulis*, other tree species whose seeds are cracked at other chimpanzee sites in west Africa including *Panda oleosa*, *Parinari excelsa*, and *Elaeis guineensis* (Anderson et al., 1983, Boesch and Boesch, 1983, Humle, 2003) are common at the rainforest sites but there was no evidence that the seeds were cracked to eat the nuts. Chimpanzees at the ecotone site fed on nuts of *Irvingia gabonensis* after feeding on the pulp, but there was no evidence that the cracking of the seeds was associated with tools. At the ecotone site, some species producing nuts cracked by chimpanzees at other sites including *Detarium microcarpa* (Whitesides, 1985) and *Parinari excelsa* were common, and *Elaeis guineensis* was present but rare. But there was no evidence of chimpanzees feeding on the fruits or cracking their nuts using tools.

At the ecotone site and rainforest sites, many tree species fruited synchronously during the wet season and the period was associated with higher proportion of fruits in the diet compared to the dry season. In the dry season, *Ficus* spp. and *U. guineensis* were important fruit components in the diet that was dominated by fibrous foods for both the ecotone and rainforest populations, and could function as fallback food resources for these populations. The dietary diversity of chimpanzees at rainforest and drier habitats across Africa with similar habitats mirrors the results in this study (Table 3.7). In general, the fruit diets of chimpanzees in rainforest habitats are more diverse than in ecotone and savanna habitats (Hunt and McGrew, 2002, Pruetz, 2006, Stumpf, 2011). Figs are widely consumed as fallback food sources across many sites, but they are also preferred at some sites (Basabose, 2002, Chancellor et al., 2012, Dutton and Chapman, 2015, Tweheyo and Lye, 2003, Wrangham et al., 1993). The frequency and productivity of filler or fallback food sources are important in chimpanzee population growth and maintenance (Potts et al., 2009, Potts et al., 2011, Tweheyo and Lye, 2003). Chimpanzees at human-modified sites incorporate cultivars in their diets especially when wild fruits are scarce (Hockings et al., 2012, McLennan, 2013). But many populations depend on terrestrial herbs and other non-fruit plant parts during periods of fruits scarcity (Tutin and Fernandez, 1993, Wrangham et al., 1996, Yamagiwa and Basabose, 2009).

Dietary shifts can take the form of an increase or decrease in the number of species consumed, or a switch between food categories (Lambert and Rothman, 2015, Wrangham et al., 1998). Based on the PCA, variation in the seasonal significance of fibrous food consumption distinguished the ecotone chimpanzees from those at the rainforest sites. In the dry season, the proportion of fibrous food in the diet of ecotone chimpanzees was important, and distinguished this population from their rainforest counterparts where fibrous food consumption was less

significant in the dry season. Conversely, in the wet season, fibrous food consumption was more important for the rainforest chimpanzees, and less significant for chimpanzees at the ecotone. Terrestrial herbs are important food components for chimpanzees at other sites especially during periods of fruit scarcity (Tutin et al., 1991, Wrangham et al., 1993, Wrangham et al., 1996). While most populations increase the consumption of THV during lean fruit periods (Chancellor et al., 2012, Tutin et al., 1991, Wrangham et al., 1993), the consumption is less marked in other populations either because of low availability (Head et al., 2011, Morgan, 2001), the presence of asynchronous fruit species (Tweheyo and Lye, 2003, Watts et al., 2012a), or the raiding of human gardens and fields (Bessa et al., 2015, Chancellor et al., 2012, Hockings et al., 2009, Hockings et al., 2012, McLennan, 2013). The ecotone site had a higher frequency and diversity of Marantaceae and Zingiberaceae.

Overall, the dietary patterns of rainforest chimpanzees at Bekob and Njuma were similar, including the diversity of fleshy fruit species, proportion of fruit and fiber in the diet as well seasonal variation in fruit and fiber consumption. However, the two sites were distinguished by the consumption of introduced species especially *E. guineensis* (oil palm) which served as a fallback food resource at Bekob but was absent in the diet of chimpanzees at Njuma. In addition to *E. guineensis*, other introduced and secondary forest species that are consumed by other chimpanzee populations including *Musanga cecropioides*, *Psidium guajava* and *Dacryodes edulis* occur in abandoned plantations and secondary forests at Bekob. Dependence on secondary forest species is also characteristic of the chimpanzees at Bossou, Guinea (Yamakoshi, 1998), Kalinzu, Uganda (Furuichi et al., 2001), Lagoas de Cufada Natural Park, Guinea-Bissau (Carvalho et al., 2015a) and Cantanhez National Park, Guinea-Bissau (Bessa et al., 2015).

The proportion of animals including insects and mammals in the fecal samples of the ecotone chimpanzees was important in distinguishing it from the rainforest sites at Bekob and Njuma, where animal consumption was lower through the year. The higher proportion of animal prey consumption at Ganga could be a function of greater seasonality in fruit availability and/or the greater availability of potential animal prey including termites, ants, other primates and mammals. At the rainforest sites, the prevalence of hunting with shotguns has resulted to a decline in monkeys and duikers (Fa et al., 2006, Whytock and Morgan, 2010), and might have reduced rates of mammal prey consumption by chimpanzees to opportunistic events.

Significant rates of insect prey consumption have been observed at sites with marked seasonality in fruit availability including termites at Fongoli, Senegal (Bogart and Pruetz, 2008, Pruetz, 2006) and ants at GGNP, Nigeria (Fowler and Sommer, 2007, Schoening et al., 2007, Sommer et al., 2017). At some rainforest sites, the quantity of insect prey consumed, and time spent on insect prey fishing is also important (Deblauwe, 2009, Deblauwe and Janssens, 2008, Sanz and Morgan, 2007), while at other sites insect prey consumption could be considered as a 'snack' (Chancellor et al., 2012).

Invertebrate species consumed and methods of acquiring them vary between sites (Boesch et al., 2009, Deblauwe et al., 2006, Deblauwe and Janssens, 2008, Humle and Matsuzawa, 2002, Sanz et al., 2004). Termite fishing, which is common at Njuma, Bekob and Ganga, has not been recorded at the two *P. t. ellioti* sites in Nigeria (Ngel Nyaki and GGNP) where the socioecology of the subspecies has been under investigation for several years (Dutton and Chapman, 2015, Fowler and Sommer, 2007). Central chimpanzees (*P. t. troglodytes*) in lowland Congolian rainforest south of the Sanaga River also feed on various species of ants and termites with the aid of tools (Deblauwe et al., 2006, Deblauwe and Janssens, 2008).

Meat eating is common across chimpanzee populations, and different species are targeted at different sites (Boesch and Boesch, 1989, Mitani and Watts, 2001, Pruetz and Bertolani, 2007, Stanford et al., 1994). Animal prey including insects and mammals are rich in proteins, amino acids and fats (Berenbaum, 1996, Deblauwe and Janssens, 2008, Lambert and Rothman, 2015). The consumption of vertebrates and invertebrates could provide high value nutrients to supplement lower nutritional gains from fibrous plant parts widely consumed during periods of low fruit availability, especially in savanna and ecotone habitats (Bogart and Pruetz, 2008, Fowler and Sommer, 2007). The consumption of vertebrates and invertebrates was higher at the ecotone than the rainforest, and was inversely correlated with fruit consumption. This could either serve as a fallback food strategy or geared at supplementing the lower nutrients in fibrous foods in the dry season.

Environmental and ecological conditions between Ganga and the sites at Ebo forest (Njuma and Bekob) are markedly different, and lead to differences in the feeding ecology of the chimpanzee communities at each study site. As fruit specialists, chimpanzees seek to maximize fruit consumption irrespective of their habitat (Tutin et al., 1991, Wrangham et al., 1998). This affects other aspects of their socioecology including ranging patterns, sociality and territoriality (Herbinger et al., 2001, Hernandez-Aguilar, 2009, Moore, 1996, Ogawa et al., 2007, Tutin et al., 1991, Wrangham et al., 1998, Yamagiwa and Basabose, 2009). Dietary patterns reflect adaptations to local ecological conditions and could be useful in our understanding of chimpanzee habitat use, ranging and grouping dynamics. These dynamics, on the other hand, may result in varying levels of affiliation between community members under distinct ecological conditions, that may be important in observed gene patterning across this region (Mitchell et al. in review). Chimpanzees adopt several strategies to cope with spatial and temporal fruit

availability including ranging wider (Pruetz and Bertolani, 2009), and in smaller parties (Ogawa et al., 2007). There are costs associated with such adaptations including higher travel costs over larger territories and weaker affiliations between community members. Western chimpanzee and bonobo communities are more cohesive compared to eastern chimpanzee communities, and this has been attributed to seasonal variation in food availability (Boesch, 1996, Stanford, 1998, Wrangham and Smuts, 1980). Grouping patterns in central and Nigeria-Cameroon chimpanzees are unexplored (Stumpf, 2011). But a recent study found that *P. t. ellioti* males from rainforest habitats are more closely related to one another than *P. t. ellioti* males from ecotone habitats, and these genetic differences are hypothesized to be the result of socioecological responses to different ecological and environmental conditions in rainforests versus ecotones (Mitchell et al., in review). Smaller territories and asynchronous fruiting species are crucial for chimpanzee community cohesion (Herbinger et al., 2001, Potts et al., 2011, Tweheyo and Lye, 2003, Watts et al., 2012b). Males in such close-knit communities are closely related (Arandjelovic et al., 2011, Inoue et al., 2008, Langergraber et al., 2007). Conversely, habitats with marked seasonality are associated with larger territories and dispersed resources that may be difficult to defend, and bonds between community members may be weaker because of costs associated with wider ranging patterns (Hernandez-Aguilar, 2009, McGrew et al., 1981, Pruetz and Bertolani, 2009). More pronounced seasonality in the availability of fleshy fruits and greater shifts in fleshy fruit consumption at the ecotone, could imply that the chimpanzees at this site are subjected to wider ranging albeit seasonally. Less seasonality in fleshy fruit availability at the rainforest could on the other hand reflect more stable associations in chimpanzee grouping patterns compared the ecotone, where smaller parties might be associated with periods of marked fleshy fruit scarcity.

In summary, seasonal variation in the importance of fleshy fruits versus fibrous foods were the main distinguishing factors in the dietary ecology of *P. t. ellioti* populations in rainforests versus ecotone. The ecotone chimpanzee population relied heavily on fleshy fruits in the wet season, which coincided with high fruit availability across their habitat. During the dry season, during which fleshy fruit availability was low, the ecotone chimpanzees shifted to the consumption of THV which represented the main fallback food at this site. At the rainforest, the consumption of fleshy fruits was important during the dry and the wet seasons, but THV consumption was more pronounced in the wet season. The dietary behavior of the ecotone and rainforest populations is linked to local ecological conditions. Fruit availability especially from lianas is high in the wet season at the ecotone, while the abundant and diverse THV is available when fleshy fruits are scarce. Seasonality in fruit availability is less pronounced at the rainforest, but the higher proportion of fibrous foods in fecal samples from chimpanzee in Bekob and Njuma during the wet season can be associated to low fruit availability. Differentiation in socioecological patterns linked to habitat variation could be important in local adaptation, and in the intraspecific variation seen between the ecotone and rainforest chimpanzee populations.

The habitats harboring *P. t. ellioti*-ecotone and *P. t. ellioti*-rainforest are unique environmentally and ecologically. The distinct *P. t. ellioti* populations exhibit unique dietary preferences and cultures, as measured by tool use. Understanding the socioecological requirements of distinct populations of the most threatened chimpanzee subspecies will be important to conserve not only the population, but also genetic and socio-cultural diversity in the Nigeria-Cameroon chimpanzee and chimpanzee species as a whole.

Table 3.1. Monthly percentage of each fruit species presence in fecal samples at Bekob

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	# months with ≥50%
Number of samples	21	33	58	18	35	20	43	12	13	5	11	4	
<i>Landolphia</i> sp. 1		9.1		5.5				100	53.8	60	36.4		3
<i>Antrocaryon klaineianum</i>	85.7	27.3	8.6	11.1						20	18.2	75	2
<i>Antiaris toxicaria</i>	47.6	27.3	12.1			5.3							0
<i>Uapaca guineensis</i>	85.7	36.4	58.6	5.5			2.3					75	3
<i>Pseudospondias longifolia</i>		12.1	43.1	38.9	5.7					20			0
<i>Grewia coriacea</i>			5.2	5.5	28.6	10.5	2.3		7.7		27.3		0
<i>Santiria trimera</i>		6.1			5.7	73.9	69.8	25					2
<i>Uapaca</i> sp.		9.1	15.5		17.1	15.8	23.6			20	9.1		0
<i>Elaeis guineensis</i>		6.1	43.1	33.33	14.3	10.5				20			0
<i>Ficus</i> spp.	23.8	18.2	20.7	33.33	28.6	10.5	4.6		7.7		27.3	50	1
<i>Pycnanthus angolensis</i>		3	10.3	55.5	68.6	10.5				20			2
<i>Duboscia macrocarpa</i>			5.2	5.5	2.9								0
Unidentified #32			5.2		5.7								0
<i>Aframomum</i> sp. 1		3	5.2			5.3	2.3	33.3	15.4		9.1	25	0
<i>Oncoba welwitschii</i>				11.1			4.6						0
Unidentified #28						5.3	2.3	33.3					0
<i>Treculia</i> sp.							2.3	2.8					0
Unidentified - white seeds								2.8					0
<i>Klainedoxa gabonensis</i>							2.3						0
<i>Musanga cecropioides</i>	76.2	9.1	36.2	44.4	60	31.6	30.2		15.4				2
<i>Mammea africana</i>			5.2	11.1	5.7	5.3			23.1				0
Unidentified small seeds					2.8						9.1		0
Unidentified rough seeds								2.8					0
Unidentified-landolphia-like		9.1	36.2	5.5			2.3						0
<i>Nuclea diderrichii</i>		9.1	5.2	5.5	2.8								0
<i>Annickia chloranta</i>							7						0
<i>Drypetes</i> sp.					2.8	15.8	2.3	2.8					0
<i>Antidesma</i> sp.				11.1	28.6	10.5							0

<i>Cleistopholis patens</i>					57.1								1
<i>Tabernaemontana crassa</i>						5.3							0
<i>Keayodendron bridelioides</i>		12.1	8.6										0
<i>Ricinodendron heudoletii</i>											25		0
Unidentified #12								7.7					0
<i>Cissus dinklagei</i>				11.1	8.6			7.7		18.2			0
<i>Monodora myristica</i>	4.8												0
Unidentified - brown		3			2.8								0
<i>Lecaniodiscus</i> sp.				5.5									0
Unidentified #1							2.3						0
Unidentified #2									20				0
Unidentified #3									20				0
Unidentified #4										9.1			0
Unidentified #5										9.1			0
Unidentified #6								7.7					0
Unidentified D28										9.1			0
Unidentified D31	4.8												0
Unidentified #7								7.7					0
Unidentified D33								7.7					0
Unidentified D19								7.7					0
Unidentified D34								7.7					0
Unidentified D29								7.7					0
Unidentified #8	4.8												0
Unidentified #9	4.8												0
Unidentified #10	4.8												0
Unidentified #11	4.8												0
<i>Canarium schweinfurthii</i>	4.8												0
Unidentified D5			10.4										0
Unidentified D1			5.2										0
Unidentified D14					2.8								0
<i>Trichoscypha</i> sp.						5.3							0

Bold figures represent species that were present in $\geq 50\%$ of the samples in a month

Table 3.2. Monthly percentage consumption (volume) of fruit species in relation to other fruit species consumed at Bekob

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	# months with ≥50%
Number of samples	21	33	58	18	35	20	43	12	13	5	11	4	
<i>Landolphia</i> sp. 1		0.3		0.4				75.6	49.1	63.1	39		2
<i>Antrocaryon klaineum</i>	26.5	16.5	3	0.9						10.8	23.7	27.7	0
<i>Antiaris toxicaria</i>	1.9	21.2	2.3			0.3							0
<i>Uapaca guineensis</i>	59.1	15	29	0.4			2.6					52.3	2
<i>Pseudospondias longifolia</i>		0.9	5.3	1.8	0.2					1			0
<i>Grewia coriacea</i>				1.6	18.4	6.1	2.6		8.5		25.5		0
<i>Santiria trimera</i>		1.1			2.4	58.4	67.7	11.2					2
<i>Uapaca</i> sp.		4.6	3.8		2.8	8.9	13			16.1	4.4		0
<i>Elaeis guineensis</i>		1.6	8.6	8.5	2.1	1.6				3.6			0
<i>Ficus</i> spp.	5.2	11.4	9	24.7	13.1	1.9	1.2		0.1		2.7	17.1	0
<i>Pycnanthus angolensis</i>		0.6	1.1	29.1	26.3	2.7				1.1			0
<i>Duboscia macrocarpa</i>			0.5	0.1									0
Unidentified #32			0.5										0
<i>Aframomum</i> sp. 1		0.1	0.5			0.2	0.9	0.9	0.4			0.1	0
<i>Oncoba welwitschii</i>				0.3			2.6						0
Unidentified #28							1.2	4.3					0
<i>Treculia</i> sp.							0.2	5.2					0
Unidentified - white seeds								2.7					0
<i>Klainedoxa gabonensis</i>							0.1						0
<i>Musanga cecropioides</i>	7	7.3	19.7	14	26.8	10	5.1		10.1				0
<i>Mammea africana</i>			0.8	7.2	0.8	1.1			18				0
Unidentified small seeds													0
Unidentified rough seeds								0.1					0
Unidentified-landolphia-like		0.6	4.3	1.8			0.3						0
<i>Nuclea diderrichii</i>		4.1	0.6	6	1.9								0
<i>Annickia chloranta</i>							1.1						0
<i>Drypetes</i> sp.						3.5	1.1						0

<i>Antidesma</i> sp.				0.1	1.5	5.3							0
<i>Cleistopholis patens</i>					0.5								0
<i>Keayodendron bridelioides</i>		14.6	8.7										0
<i>Ricinodendron heudoletii</i>											2.8		0
Unidentified #12								0.2					0
<i>Cissus dinklagei</i>				1	0.2			0.2		3.5			0
<i>Monodora myristica</i>													0
Unidentified - brown					0.9								0
<i>Lecaniodiscus</i> sp.				1.9									0
Unidentified #1							0.3						0
Unidentified #2									1.1				0
Unidentified #3									3.2				0
Unidentified #4										0.1			0
Unidentified #6								0.9					0
Unidentified D28										1.1			0
Unidentified D31	0.2												0
Unidentified #7								3.9					0
Unidentified D33								0.1					0
Unidentified D19								1.5					0
Unidentified D34								6.9					0
Unidentified D29								0.1					0
<i>Canarium schweinfurthii</i>	0.1												0
Unidentified D5			1.7										0
Unidentified D1			0.6										0

Bold figures represent species that were present in ≥50% of the samples in a month

Table 3.3. Monthly percentage of each fruit species presence in fecal samples at Njuma													
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	# months with ≥50%
Number of samples	39	28	8	38	21	11	34	9	17	11	17	28	0
<i>Antrocaryon klaineum</i>	61.5	14.3				10				27.3	82.4	78.6	3
<i>Uapaca guineensis</i>	28.2		25								11.8	53.6	1
<i>Uapaca</i> sp.					4.8	20							0
<i>Grewia coriacea</i>			25						35.3	63.6			1
<i>Keayodendron bridelioides</i>	20.5		12.5	2.6		10				18.2	47.1	46.4	2
<i>Pycnanthus angolensis</i>	2.6	39.2		84.2	76.2	20	2.9		5.9				0
<i>Chrysanthus</i> sp.				2.6									0
<i>Oncoba welwitschii</i>				2.6									0
<i>Staudtia kamerunensis</i>				7.9	23.8								0
<i>Tabernaemontana crassa</i>	2.6						11.8						0
<i>Pseudospondias longifolia</i>	10.3	3.6	12.5	31.6	4.8								0
<i>Cleistopholis patens</i>				15.8	42.9	10						3.6	0
<i>Santiria trimera</i>			12.5		4.8	40	17.6	11.1					0
<i>Antiaris toxicaria</i>	48.7	39.2	12.5	2.6		10						28.6	0
<i>Cissus dinklagei</i>	2.6	39.2	25	18.4	9.5				5.9		11.8		0
<i>Landolphia</i> sp. 1				10.5	28.6		76.5	88.9	27.3	27.3			2
<i>Landolphia</i> sp. 2													0
<i>Vitex grandifolia</i>										9.1			0
<i>Ficus</i> spp.	15.4	25	25	10.5	23.8		2.9				29.4	46.4	0
Unidentified #27										45.5			0
Unidentified #31					4.8								0
<i>Duboscia macrocarpa</i>					9.5								0
<i>Landolphia</i> sp. 3				2.6									0
<i>Discoglyprena</i> sp.	2.6						2.9						0
Unidentified - blk wt tip		3.6		2.6	4.8								0
<i>Aframomum</i> sp. #1	2.6						2.9						0
<i>Aframomum</i> sp. #2	5.1						5.9		11.8		23.5	7.1	0

<i>Marantochloa</i> sp.						10					11.8		0
<i>Musanga cecropioides</i>	2.6	28.6		28.9	33.3	10	5.9		5.9		5.9		0
<i>Mammea africana</i>				15.8	14.3	10	2.9		23.5				0
Unidentified #1											5.9		0
Unidentified #2									5.9		5.9		0
Unidentified #3		3.6				20			11.8				0
<i>Drypetes</i> sp.	2.6		12.5	7.9	4.8	10	5.9						0
Unidentified - cotton					4.8		2.9						0
<i>Antidesma</i> sp.				18.4	28.6								0
<i>Strombosiopsis</i> sp.		3.6											0
Unidentified #4				2.6		10	5.9						0
Unidentified #5						10	2.9						0
<i>Nuclea diderrichii</i>	2.6	21.4	12.5	13.2	14.3								0
<i>Strombosia</i> sp.		3.6				10							0
Unidentified #6						10							0
Marantaceae sp.							2.9						0
<i>Trichoscypha</i> sp.						40							0
<i>Treculia</i> sp.						30	5.9						0
<i>Canarium schweinfurthii</i>							2.9		11.8				0
Unidentified #7							2.9						0
Unidentified brown											7.1		0
Unidentified D25									5.9				0
<i>Myrianthus arboreus</i>									5.9				0
Unidentified D29							2.9		5.9				0
Unidentified #8							2.9						0
Unidentified D34									5.9				0
Unidentified D36									5.9				0
Unidentified D30								11.1					0
<i>Elaeis guineensis</i>			12.5										0
<i>Tricalysia</i> sp.			12.5			10	8.2						0
<i>Annickia chloranta</i>						10							0
Unidentified D20	2.6												0

<i>Coula edulis</i>								X					0
<i>Irvingia gabonensis</i>							X						0
<i>Milicia excelsa</i>		X											0

Bold figures represent species that were present in ≥50% of the samples in a month

Table 3.4. Monthly percentage consumption (volume) of fruit species in relation to other fruit species consumed at Njuma													
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	# months with ≥50%
Number of samples	39	28	8	38	21	11	34	9	17	11	17	28	0
<i>Antrocaryon klaineianum</i>	48.1	4.3				7.1				21.9	59.3	43.8	1
<i>Uapaca guineensis</i>	6.1		12.6								0.6	7.6	0
<i>Uapaca</i> sp.					1.3	10.6							0
<i>Grewia coriacea</i>			18.6						41.4	60.7			1
<i>Keayodendron bridelioides</i>	9		14.6	2.6		3.4				14.4	32.7	25.2	0
<i>Pycnanthus angolensis</i>	0.3	30		54.1	40.6	8.1	0.1		4.6				1
<i>Chrysanthus</i> sp.				0.1									0
<i>Oncoba welwitschii</i>													0
<i>Staudtia kamerunensis</i>				2.6	2.2								0
<i>Tabernaemontana crassa</i>	0.2						3.8						0
<i>Pseudospondias longifolia</i>	0.3	0.1	0.6	5.8	0.1								0
<i>Cleistopholis patens</i>				2	7	8						0.3	0
<i>Santiria trimera</i>			10.5		2.2	6.5	8.3	11.3					0
<i>Antiaris toxicaria</i>	21.9	17.6	5.8			11.6						4.6	0
<i>Cissus dinklagei</i>	0.7	5.4	3.5	3.6	0.2				0.5		0.1		0
<i>Landolphia</i> sp. 1				3.7	4.6		67.7	88.7	9	0.7			2
<i>Landolphia</i> sp. 2													0
<i>Vitex grandifolia</i>										0.1			0
<i>Ficus</i> spp.	7.6	9.8	9.3	1.8	13.6		1.1				5.3	17.5	0
Unidentified #27										2.2			0
Unidentified #31					2.5								0
<i>Duboscia macrocarpa</i>													0

<i>Landolphia</i> sp. 3													0
<i>Discoglyprena</i> sp.	0.4						0.1						0
Unidentified - blk wt tip		0.2		1	1.5								0
<i>Aframomum</i> sp. #1							0.1						0
<i>Aframomum</i> sp. #2							0.2		0.3		0.2	0.5	0
<i>Marantochloa</i> sp.													0
<i>Musanga cecropioides</i>	0.3	12.8		9.7	11.5	0.7	0.8		1.2		1.5		0
<i>Mammea africana</i>				4.7	4.3	3.5	0.4		11.4				0
Unidentified #1											0.1		0
Unidentified #2									7.1		0.2		0
Unidentified #3		0.3				7			7.1				0
<i>Drypetes</i> sp.	2.1		14.4	0.3	0.1	8.2	4						0
Unidentified - cotton					0.9		2.5						0
<i>Antidesma</i> sp.				1.1	0.7								0
<i>Strombosiopsis</i> sp.		1.8											0
Unidentified #4				0.4		0.3	2.6						0
Unidentified #5						0.2	0.2						0
<i>Nuclea diderrichii</i>	2.8	17.5	5.8	6.5	6.7								0
<i>Strombosia</i> sp.		0.2				0.1							0
Unidentified #6						5.2							0
Marantaceae sp.							0.1						0
<i>Trichoscypha</i> sp.						13.3							0
<i>Treculia</i> sp.						6	0.6						0
<i>Canarium schweinfurthii</i>							0.6		7.2				0
Unidentified #7							0.7						0
Unidentified brown											0.5		0
Unidentified D25									1.4				0
<i>Myrianthus arboreus</i>									1.8				0
Unidentified D29							1.1		5.8				0
Unidentified #8							3.1						0
Unidentified D34									0.9				0
Unidentified D36									0.5				0

Unidentified D30																						0
<i>Elaeis guineensis</i>						2.5																0
<i>Tricalysia</i> sp.						1.8				0.1	1.9											0
<i>Annickia chloranta</i>										0.1												0
Unidentified D20	0.2																					0
<i>Coula edulis</i>																						0
<i>Irvingia gabonensis</i>																						0
<i>Milicia excelsa</i>																						0

Bold figures represent species that were present in $\geq 50\%$ of the samples in a month

Table 3.5. Monthly percentage of each fruit species presence in fecal samples at Ganga

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	# months with $\geq 50\%$
Number of samples	30	20	32	15	10	32	23	39	5	13	41	4	49	11	1	0	0	7	2	2	6	
<i>Uapaca guineensis</i>	53	80	75		30																	3
<i>Pseudospondias microcarpa</i>			65	73	60	9												43	50			4
<i>Grewia</i> sp.		5						3	20	54												1
<i>Synsepalum</i> sp.			56	13																		1
<i>Olax subscorpioidea</i>		5	6	13																		0
<i>Myrianthus arboreus</i>					10	16	13	10		8								29	50	100		2
<i>Landolphia</i> sp. 1					80	100	100	74	40	23								100	50	50	100	7
<i>Landolphia</i> sp. 2						16	22	46	60	31												1
<i>Landolphia</i> sp. 3						6	9															0
<i>Saba</i> sp.					30																	0
<i>Antidesma</i> sp.				7	10										18							0
<i>Aframomum</i> sp. 1							4	5			49	67		9								1
<i>Aframomum</i> sp. 2	3										5		12									0
<i>Monodora</i> sp.			3			3																0
Marantaceae sp.													2	9								0
<i>Monanthes congolensis</i>					30	3																0
<i>Uapaca togoensis</i>				20	20	3																0

<i>Staudtia kamerunensis</i>						3																0
Unidentified 7	3					6					7	33	12									0
Unidentified 8						3																0
Unidentified 9						3																0
<i>Drypetes</i> sp.							26	5					12									0
Unidentified #11							4															0
Unidentified #12								3														0
Unidentified #13								3														0
Unidentified #14				7				23														0
Unidentified #16								3		8												0
<i>Vitellaria paradoxa</i>				33									2									0
Unidentified #19										8												0
<i>Duguetia</i> sp.								3		8	20											0
Unidentified #21										2												0
<i>Aframomum</i> sp. 3										10												0
Unidentified #24										8	5											0
Unidentified #26												33	84									1
Unidentified #27													4									0
Unidentified #29														18								0
Unidentified #30														18								0
Unidentified #32														9								0
Unidentified #33	57	20	3	7							93	100	10									3
Unidentified #34	40	10									90	100										2
<i>Canarium schweinfurthii</i>						3		10	60	31												1
<i>Pycnanthus angolensis</i>									10													0
<i>Lannea welwitschii</i>				7									6	27								0
<i>Vitex doniana</i>				7						23												0
<i>Vitex</i> sp.										15												0
<i>Ricinodendron heudoletii</i>										15												0
<i>Ficus</i> spp.	10	15	43	7							2	33	4									0
<i>Musanga cecropioides</i>								5														0
Sapindaceae sp.														9				14				0

<i>Milicia excelsa</i>		X	X											X	X								0
Unidentified liana	X	X												X	X								0
<i>Irvingia gabonensis</i>															X								0

Bold figures represent species that were present in $\geq 50\%$ of the samples in a month

Table 3.6. Monthly percentage consumption (volume) of fruit species in relation to other fruit species consumed at Ganga																						
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	# months with $\geq 50\%$
Number of samples	30	20	32	15	10	32	23	39	5	13	41	4	49	11	1	0	0	7	2	2	6	
<i>Uapaca guineensis</i>	26	79	41		11																	1
<i>Pseudospondias microcarpa</i>			21	54	20	3												14	8			1
<i>Grewia</i> sp.		0						0	12	56												1
<i>Synsepalum</i> sp.			14	1																		0
<i>Olax subscorpioidea</i>		0	2	1																		0
<i>Myrianthus arboreus</i>					6	5	2	1		1									38	58		1
<i>Landolphia</i> sp. 1					48	90	96	93	71	6								86	55	43	100	7
<i>Saba</i> sp.					4																	0
<i>Antidesma</i> sp.				6	7										5							0
<i>Aframomum</i> sp. 1							0	0			2	1		0								0
<i>Aframomum</i> sp. 2	0	0											0									0
<i>Monodora</i> sp.			0			0																0
Marantaceae sp.													0	2								0
<i>Monanthotaxis congoensis</i>					1	0																0
<i>Uapaca togoensis</i>				12	3	0																0
<i>Staudtia kamerunensis</i>						1																0
Unidentified #7	0					0					0	2	0									0
Unidentified #8						0																0
Unidentified #9						0																0
<i>Drypetes</i> sp.							1	0					0									0
Unidentified #11							0															0
Unidentified #12								0														0

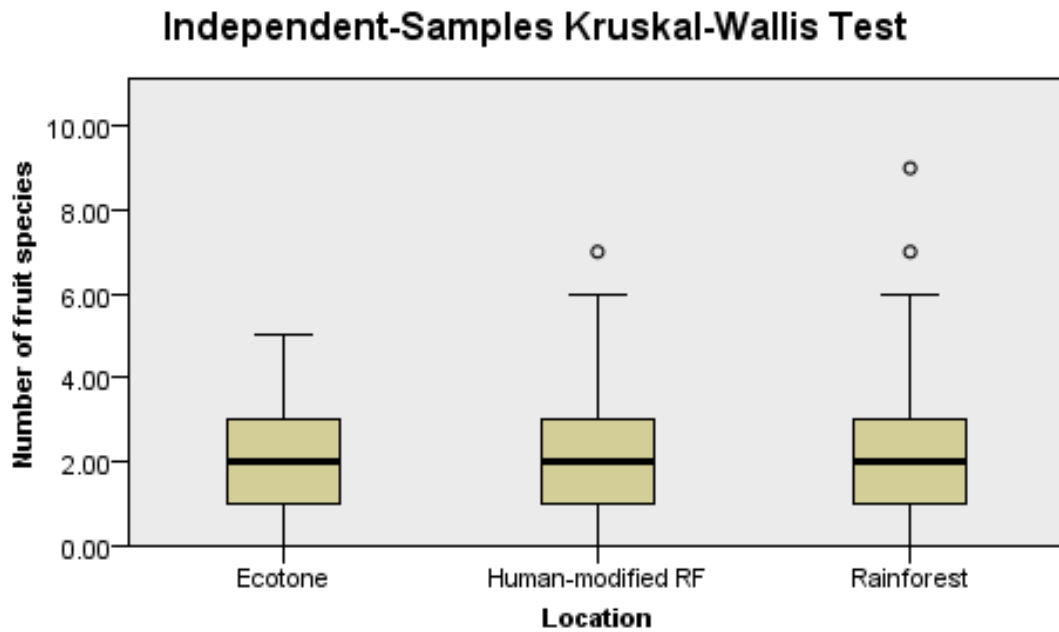
Unidentified #13							0														0
Unidentified #14				0			4														0
Unidentified #16							0		9												0
<i>Vitellaria paradoxa</i>				18								0									0
Unidentified #19																					0
<i>Duguetia</i> sp.							0		1	1											0
Unidentified #21																					0
<i>Aframomum</i> sp. 3							0														0
Unidentified #24									0	1											0
Unidentified #26												70	5								1
Unidentified #27												0									0
Unidentified #29													7								0
Unidentified #30													4								0
Unidentified #32													2								0
Unidentified #33	38	15	7								29	37	12								0
Unidentified #34	28	1									65	31									1
<i>Canarium schweinfurthii</i>						0		1	17	23											0
<i>Pycnanthus angolensis</i>									0												0
<i>Lannea welwitschii</i>													3	2							0
<i>Vitex doniana</i>				1																	0
<i>Vitex</i> sp.										4											0
<i>Ricinodendron heudoletii</i>										1											0
<i>Ficus</i> spp.	8	6	14	7			1				2	30	14	73							1
<i>Musanga cecropioides</i>							1														0
Sapindaceae sp.													0				0				0

Bold figures represent species that were present in $\geq 50\%$ of the samples in a month

Table 3.7. Dietary patterns based on fecal sample assessment - comparisons across chimpanzee study sites

Study site	Subspecies	samples with fruit (%) (n)	Number of fruit species per sample	Percentage of fruit in diet	Percentage of fiber in diet	Number of fruit species	Percentage of animal parts in diet	Leaf swallowing	Reference
Bekob, Cameroon	<i>P. t. ellioti</i>	99.3 (270)	2.5±1.3	86.5±22.3	13.0±21.2	59	0.5±4.5	+	This study
Njuma, Cameroon	<i>P. t. ellioti</i>	99.6 (246)	2.4±1.3	88.2±19.2	11.1±18.2	63	0.8±4.3		This study
Ganga, Cameroon	<i>P. t. ellioti</i>	97.1 (341)	1.9±1.1	74.8±34.3	21.6±32.3	47	3.6±11.7	+	This study
Ngel Nyaki, Nigeria	<i>P. t. ellioti</i>	98.8 (495)		91	9	52			(Dutton and Chapman, 2015)
Dja Reserve, Cameroon	<i>P. t. troglodytes</i>	100 (135)	3.3	80	15.3	80			(Deblauwe, 2009)
Lope Forest Reserve, Gabon	<i>P. t. troglodytes</i>			62.6	18.1	114	9.3		(Tutin et al., 1997a)
Loango National Park, Gabon	<i>P. t. troglodytes</i>	92 (390)	2	89		97			(Head et al., 2011)
Fongoli, Senegal	<i>P. t. verus</i>	(1007)		62.5	32.5	47	5		(Pruetz, 2006)
Cantanhez, Guinea Bissau	<i>P. t. verus</i>	97.9 (377)	2.4±0.05	64.3	35.7	53			(Bessa et al., 2015)
Lagoas de Cufadas NP, Guinea Bissau	<i>P. t. verus</i>	(210)		71.9±0.9	27±0.6	31			(Carvalho et al., 2015a)
Kahuzi-Beiga, DR Congo	<i>P. t. schweinfurthii</i>	99 (7212)				66		+	(Basabose, 2002)
Gishwati, Rwanda	<i>P. t. schweinfurthii</i>	(1381)	2.5±1.2	58±36	40±35	23	7		(Chancellor et al., 2012)
Rubondo, Tanzania	<i>P. t. schweinfurthii</i>	93.5 (147)				46			(Moscovice et al., 2007)
Bwindi NP, Uganda	<i>P. t. schweinfurthii</i>	98.4 (187)	2.05	64.6		30	9.1		(Stanford and Nkurunungi, 2003)
Semliki, Uganda	<i>P. t. schweinfurthii</i>	(72)		54	42	18			(Hunt and McGrew, 2002)
Bulindi, Uganda	<i>P. t. schweinfurthii</i>	99.9 (1436)	3.8	81.6		63		+	(McLennan, 2013)

Leaf swallowing (+) indicates behavior present at site



Total N	867
Test Statistic	29.869
Degrees of Freedom	2
Asymptotic Sig. (2-sided test)	.000

1. The test statistic is adjusted for ties.

Figure 3.1. Annual variation in mean number of fruit species per fecal sample across the ecotone and rainforest sites

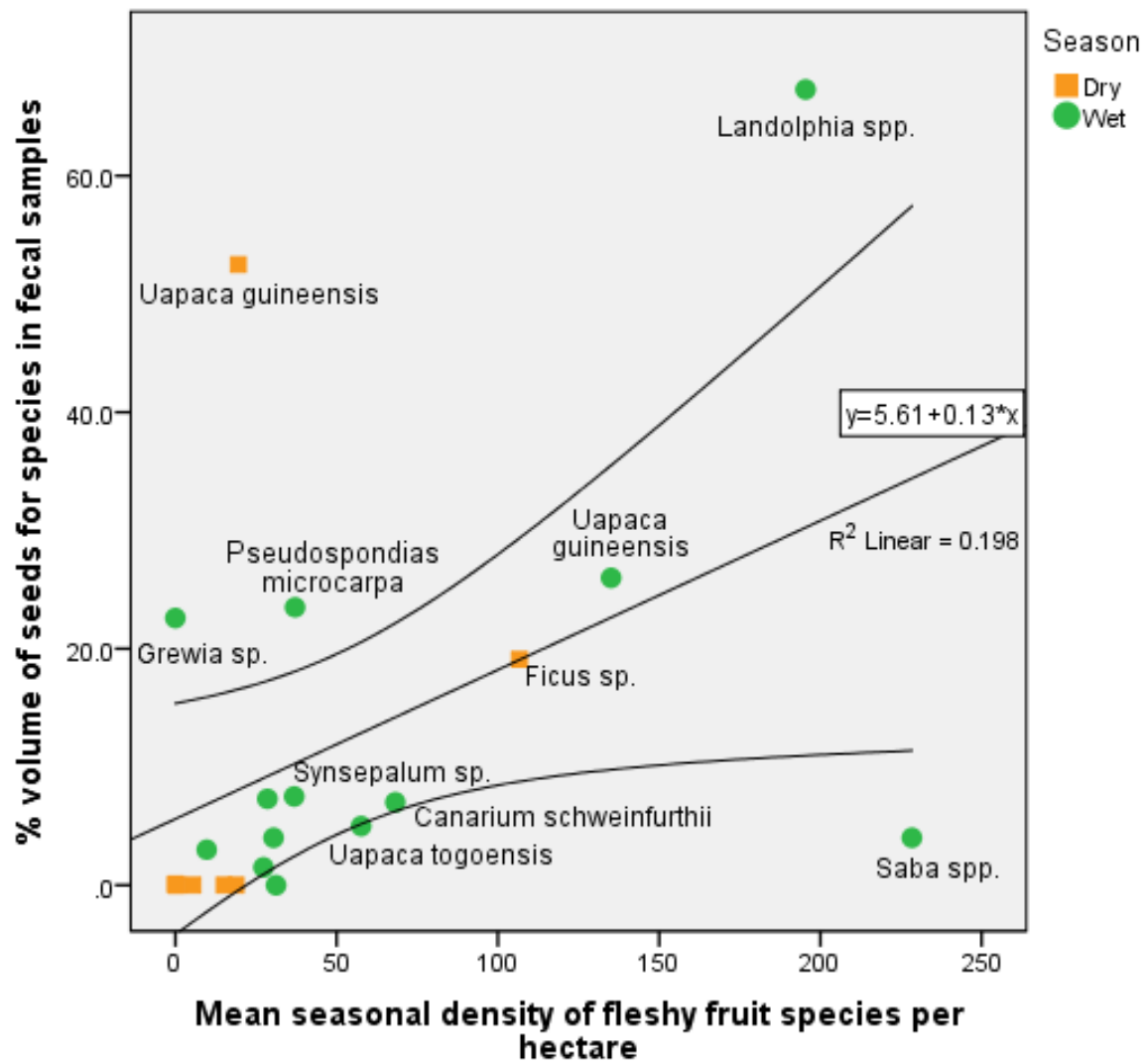
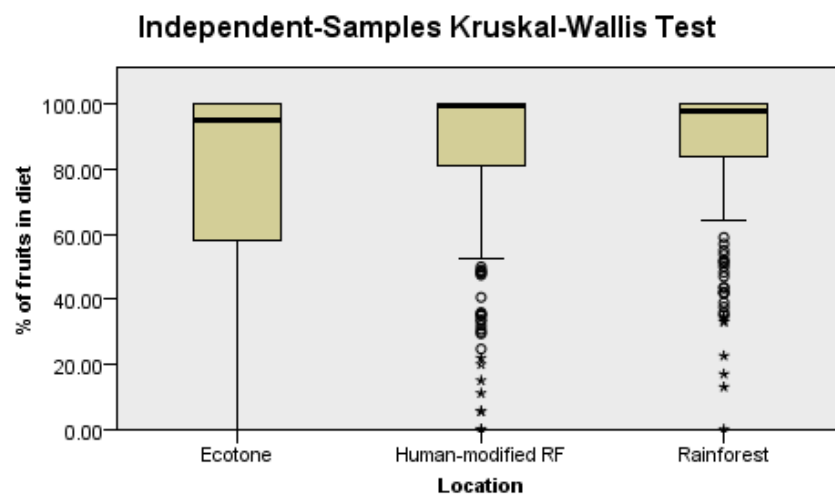


Figure 3.2: Correlation between fruit species density and volume of species in fecal samples in the dry (squares) and wet (circles) seasons at Ganga



Figure 3.3. Chimpanzee feeding signs on fruit and nuts of *Irvingia gabonensis* at Ganga, February 2017



Total N	867
Test Statistic	22.110
Degrees of Freedom	2
Asymptotic Sig. (2-sided test)	.000

1. The test statistic is adjusted for ties.

Figure 3.4. Annual variation in the proportion of fruit in the diet across the three sites



Figure 3.5. Chimpanzee feeding signs on *Aframomum* sp. at Ganga, November 2016



Figure 3.6. Chimpanzee feeding signs on *Marantaceae* sp. at Ganga, November 2017



Figure 3.7. Chimpanzee feeding signs on *Palisota ambigua* at Ganga, December 2017



Figure 3.8. Chimpanzee feces with whole leaves swallowed at Ganga, July 2016



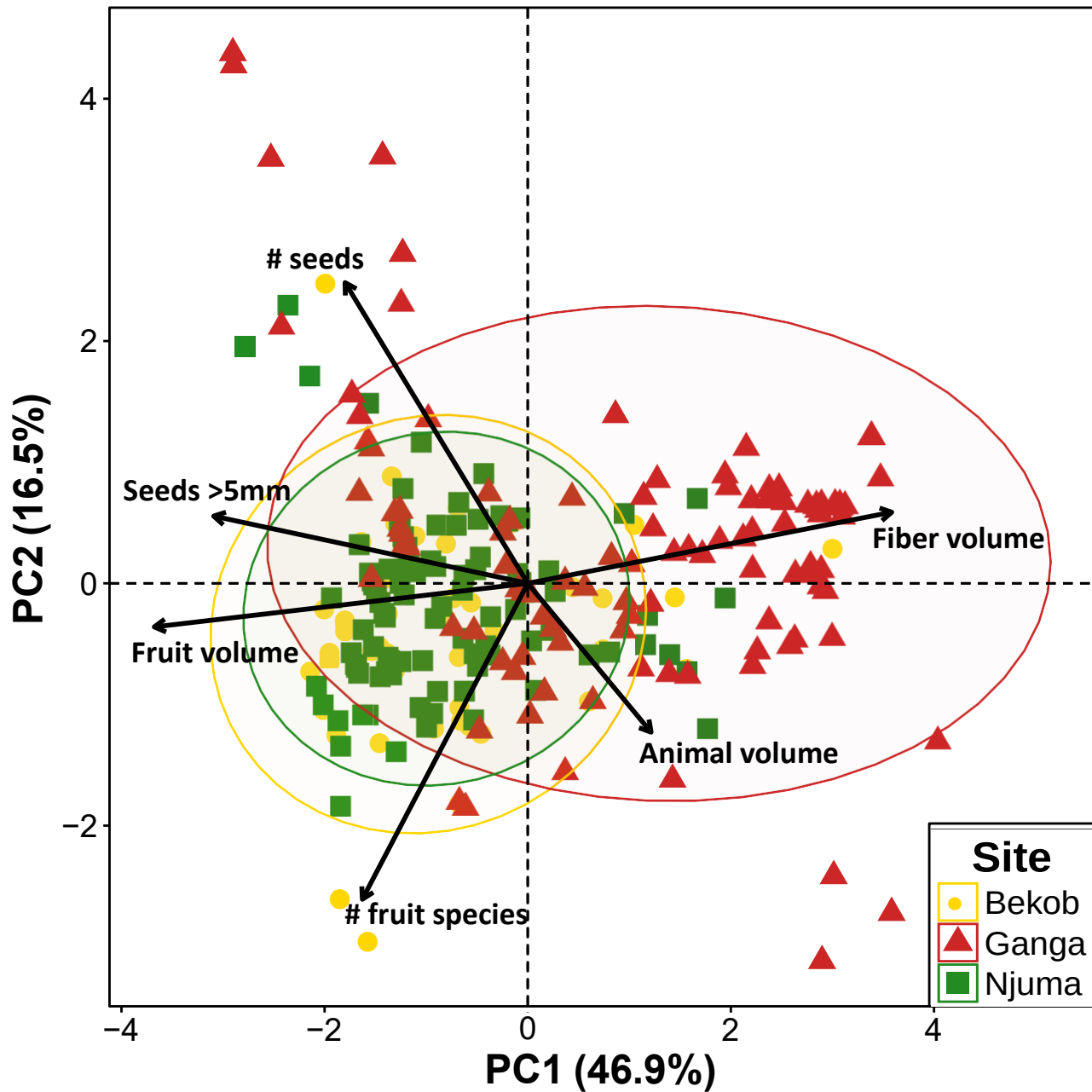
Figure 3.9. Stingless bee subterranean hive with digging tools of different sizes and honeycomb at Ganga, July 2016



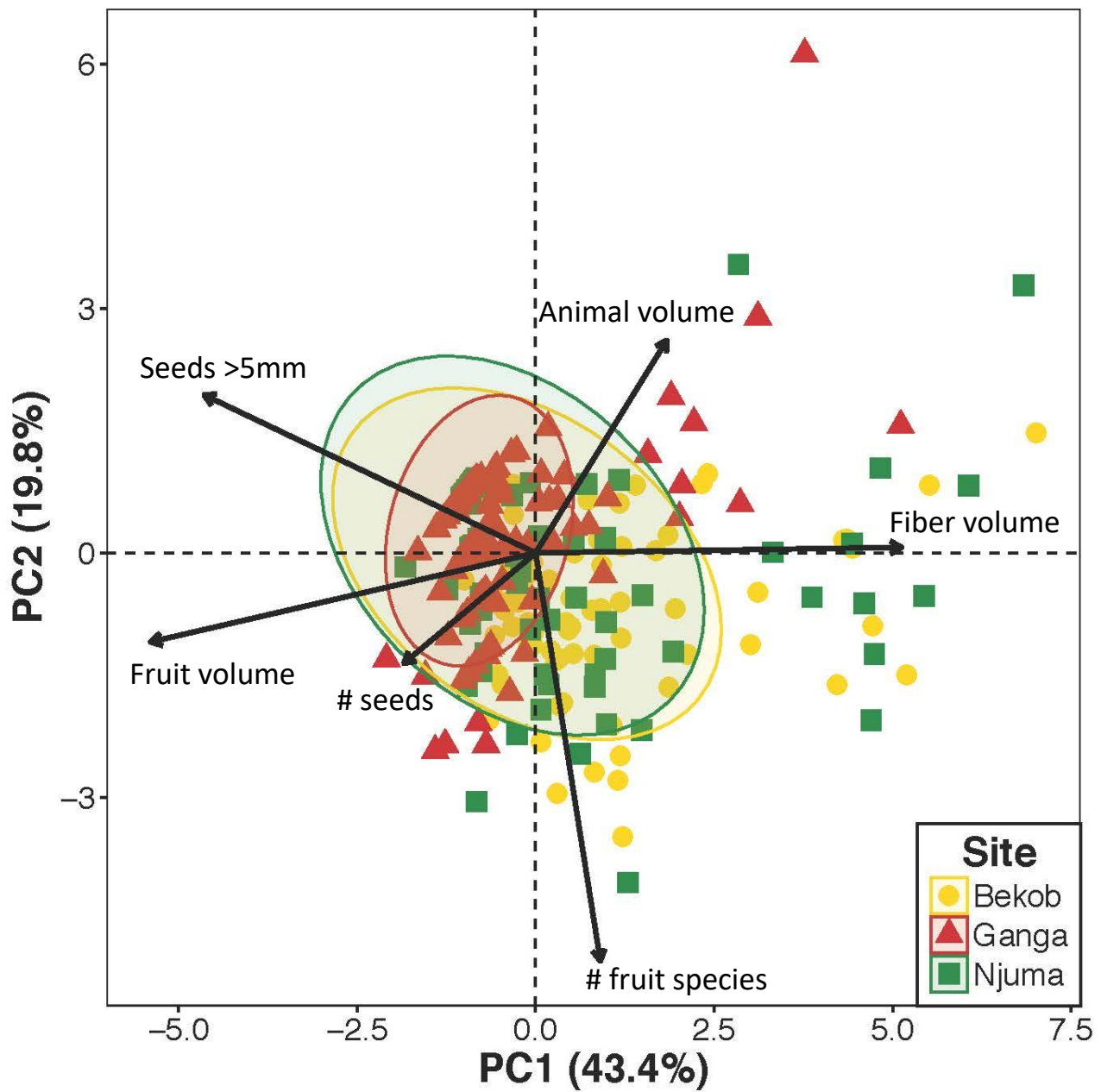
Figure 3.10. Tuft of mammal fur in chimpanzee feces, probably from a guereza colobus (A) at Ganga (October 2016) and crowned guenon (B) at Ganga (July 2018)



Figure 3.11. Primate hand bones in chimpanzee feces at Ganga, February 2016



3.12. Principal component analysis (PCA). PCA generated based on food components in individual chimpanzee fecal samples collected during the dry season (December – February). Samples are symbol coded by site: (1) circle – Bekob and (2) square – Njuma and (3) triangle – Ganga



3.13. Principal component analysis (PCA). PCA generated based on food components in individual chimpanzee fecal samples collected during the wet season (May – September). Samples are symbol coded by site: (1) circle – Bekob and (2) square – Njuma and (3) triangle – Ganga

CHAPTER FOUR

4. ECOLOGICAL CORRELATES OF NESTING BEHAVIOR IN NIGERIA-CAMEROON CHIMPANZEES (*Pan troglodytes ellioti*) IN CAMEROON

Abstract

The two major branches of the chimpanzee (*Pan troglodytes*) phylogenetic tree split from one another in Cameroon. Three distinct gene pools of the species are found in the country. The Sanaga River in central Cameroon separates the Central African chimpanzee (*P. t. troglodytes*) from the Nigeria-Cameroon chimpanzee (*P. t. ellioti*). In addition, the Nigeria-Cameroon chimpanzee is further subdivided into two distinctive gene pools that occupy two distinctive habitats, one deme that localized to the mountainous forests of western Cameroon and another deme that is found in a pronounced ecotone located in central Cameroon. This diversification of the species and the gene pools within subspecies have been attributed in part to allopatric speciation due to separation from one another across Cameroon's Sanaga River. In addition, local adaptation to the ecological distinctiveness of habitats is important for both differentiation of the lineages and to different gene pools within *P. t. ellioti* – the subspecies that occurs north and west of the Sanaga River.

In this study, I investigated nesting patterns using nesting site location and nest characteristics in relation to habitat variation at three locations that represent the range of standing genetic- and ecological- diversity found in the Nigeria-Cameroon chimpanzee. I used straight-line and reconnaissance transects across Ebo forest (rainforest) and Mbam & Djerem National Park (ecotone) to locate nesting sites and assess ecological variation including floristic composition, fruit phenology and threats linked to predation. Ecological and nesting data were

collected monthly and simultaneously across Bekob and Njuma (rainforest) and Ganga (ecotone) between January 2016 and December 2017.

Chimpanzee nesting site selection at Ganga was linked with the availability of fleshy fruits, while at Bekob and Njuma, closed-canopy habitats and steep slopes were preferentially selected. Nest group sizes were linked to fruit seasonality, with larger nest groups in the wet season that was characterized by higher fruit availability especially at Ganga. There were site specific preferences for nesting tree species, but *Strombosia grandifolia* was preferred across the three sites, while nesting in *Elaeis guineensis* was exclusive to chimpanzees at Bekob.

Nesting patterns in rainforest and ecotone populations can be important in our understanding of chimpanzee habitat use and ranging patterns. More pronounced seasonality in fleshy fruit availability affected nesting site location and habitat use at the ecotone, and smaller nest group sizes at the site may also reflect smaller foraging parties and relatively lower levels of cohesion geared at limiting intra-group feeding competition in the dry season. Nesting site location at the rainforest may be linked to predation avoidance and relatively larger group sizes may reflect large foraging parties and greater group cohesion. Local differentiation in chimpanzee socioecology linked to environmental variation can be important in chimpanzee local adaptation and gene patterning observed in *P. t. ellioti* populations across Cameroon.

4.1. Introduction

Daily nest building for sleep, especially at night, is a trademark of all wild great apes (Baldwin et al., 1981, Fruth and Hohmann, 1994, Fruth and Hohmann, 1996, Sugardjito, 1983, Tutin et al., 1995). Nesting site and nest structure characteristics have been studied across great ape populations for several decades and these have been posited to be influenced by ecological,

environmental, and anthropogenic factors (Baldwin et al., 1981, Basabose and Yamagiwa, 2002, De Vere et al., 2011, Furuichi and Hashimoto, 2004, Hernandez-Aguilar et al., 2013, Koops et al., 2012a, McCarthy et al., 2017, Stewart and Pruetz, 2013). Chimpanzees have the widest geographical range of all great apes with concomitant diversity in habitat types ranging from closed-canopy moist rainforest to open dry savanna (Caldecott and Miles, 2005, Mittermeier et al., 2013). Diversity in habitats leads to behavioral variation between populations due to local adaptation (Stumpf, 2011).

Chimpanzees mainly build nests in trees, although increasingly overnight terrestrial nests have been documented across their range (Abwe and Morgan, 2008, Koops et al., 2012b, Tagg et al., 2013). Nests have been hypothesized to provide comfort, thermoregulation, and safety from predators (Koops et al., 2012a, Ogawa et al., 2014, Pruetz et al., 2008, Samson and Hunt, 2012, Samson and Hunt, 2014). Given the spatial and temporal variation in ecological and environmental variables within and between habitats across their range, chimpanzee nest group size, nesting site location, nest characteristics including height, nest position within the tree crown and nesting tree selection are expected to be influenced by a range of prevailing local factors within each habitat.

From rainforest to savanna populations, chimpanzees have been observed to show preference for closed-canopy habitats including rainforest, gallery, and woodland as nesting site locations (Anderson et al., 1983, Basabose and Yamagiwa, 2002, Koops et al., 2012b, Pruetz et al., 2008, Sanz et al., 2007). Closed-canopy habitats provide concealment especially in areas where apes are sympatric with predators (Ogawa et al., 2007). Fruit availability also influence great ape nesting site location, with nesting sites selected at or near feeding sites (Basabose and Yamagiwa, 2002, Furuichi and Hashimoto, 2004, Mulavwa et al., 2010, Serckx et al., 2014).

Microclimatic conditions vary between terrestrial and arboreal locations (Samson and Hunt, 2012, Stewart, 2011), and between altitudinal gradients (Koops et al., 2012a). Prevailing climatic conditions influence nest site selection, nest construction effort as well as terrestrial or arboreal nesting decisions in great apes (Baldwin et al., 1981, De Vere et al., 2011, Koops et al., 2007, Koops et al., 2012a, Mehlman and Doran, 2002, Samson and Hunt, 2012, Sunderland-Groves et al., 2009). More nesting sites were located at higher altitudes during the wet season at Seringbara, Guinea (Koops et al., 2012a). Gorillas make more arboreal nests in the wet season (De Vere et al., 2011, Mehlman and Doran, 2002, Sunderland-Groves et al., 2009), while chimpanzees nest higher in the trees in the wet season (Baldwin et al., 1981), and pad nests more during cold nights (Stewart, 2011).

Nesting site selection and arboreal nests are geared at reducing the risk of predation. At Ugalla, Tanzania, chimpanzees select steep hills and forested areas preferentially for nesting site location (Ogawa et al., 2014). Chimpanzees preferentially select larger trees with higher first branches and build higher nests at sites where they are sympatric with predators (Hernandez-Aguilar et al., 2013, Pruetz et al., 2008, Stewart and Pruetz, 2013). Medium-sized trees are preferred in rainforest habitats where the risk of predation is lower (Furuichi and Hashimoto, 2004, Granier et al., 2014). The choice of tree species for nest building between populations varies, but is generally conditioned by comfort, safety and food availability (Basabose and Yamagiwa, 2002, Samson and Hunt, 2014, Stanford and O'Malley, 2008). Terrestrial nesting on the other hand is prevalent at sites where predation pressure is low (Abwe and Morgan, 2008, Koops et al., 2007, Koops et al., 2012b, Last and Muh, 2013, Pruetz et al., 2008). Many great ape populations and their habitats are under increasing anthropogenic pressure, and behaviors of

chimpanzees in human-modified landscapes are distinct (Abwe and Morgan, 2008, Hockings et al., 2009, Last and Muh, 2013, McCarthy et al., 2017, McLennan, 2013, Sousa et al., 2014, Tagg et al., 2013, Yamakoshi, 1998). Chimpanzee nesting groups are generally larger in rainforest compared to drier habitats (Hunt and McGrew, 2002), though the need for safety may cause small foraging parties to congregate at nesting sites in populations that are sympatric with predators (Ogawa et al., 2007).

The Gulf of Guinea is a biodiversity hotspot harboring many endemic species of plants and animals including primates (Oates et al., 2004). The remote causes for this diversity are attributed to neutral processes including forest history and biogeographical barriers (Cheek et al., 2001, Mitchell et al., 2015b), while proximate causes are linked to natural selection including ecological gradients (Cheek et al., 2001, Smith et al., 2011b, Smith et al., 1997) and anthropogenic changes (Freedman et al., 2010a). The Sanga River in central Cameroon is at the convergence of two chimpanzee groups and the area is an active site for chimpanzee speciation (Mitchell et al., 2015a). Local adaption in large vertebrates across ecological gradients in this area is unexplored. Such knowledge could be key in our understanding of the rich primate diversity in Cameroon and the Gulf of Guinea region in general. In addition, chimpanzees are our closest living relatives and understanding their adaptations to ecological gradients may help shed light on hominin evolution across Africa. This research is aimed at understanding the ranging behavior of Nigeria-Cameroon chimpanzees in Cameroon using nests.

The Nigeria-Cameroon chimpanzee was only recently distinguished as a subspecies (Gonder et al., 2006, Gonder et al., 1997, Oates et al., 2009) and to date, very little is understood about their socioecology compared to other chimpanzee subspecies (Morgan et al., 2011,

Stumpf, 2011). Few studies have focused on the nesting ecology of Nigeria-Cameroon chimpanzees. At both rainforest and ecotone habitats in Nigeria and Cameroon, *P. t. ellioti* nesting site location and nest characteristics are influenced by anthropogenic pressure (Abwe and Morgan, 2008, Dutton et al., 2016, Fowler, 2006, Last and Muh, 2013). Rainforest populations across Cameroon build terrestrial nests (Abwe and Morgan, 2008, Last and Muh, 2013), while in Nigeria, chimpanzees at the ecotone habitats of Ngel Nyaki and GGNP show preference for specific tree species for nesting (Dutton et al., 2016, Fowler, 2006).

Comparative chimpanzee nesting studies have generally focused on variation between rainforest and savanna populations (Baldwin et al., 1981, Hunt and McGrew, 2002), predator-sympatric and predator-free populations (Hernandez-Aguilar et al., 2013, Stewart and Pruetz, 2013), or species-wide population differences (Tagg et al., 2013). But no previous studies have spanned an active diversification zone within and between chimpanzee subspecies making it difficult to directly address the hypothesis regarding how nesting (grouping) patterns in relation to local ecological adaptations may govern chimpanzee socioecology and genetic diversification.

With two distinct chimpanzee subspecies (*P. t. troglodytes* and *P. t. ellioti*) and two distinct gene pools within *P. t. ellioti* (Gonder et al., 2006, Mitchell et al., 2015b), Cameroon is a ‘natural laboratory’ for chimpanzee evolutionary and socioecology investigations. Diversification between and within chimpanzee subspecies across the country have been attributed to environmental and ecological variation (Mitchell et al., 2015b). However, what is poorly understood is how environmental and ecological variation impacts populations, and how local adaptations to these conditions may influence diversification within and between subspecies occupying distinct environments. This study was aimed at assessing the influence of

environmental and ecological factors on the nesting behavior of Nigeria-Cameroon chimpanzees. I selected two genetically and ecologically distinct populations: Ebo forest (*P. t. ellioti*-rainforest) versus Mbam & Djerem National Park (*P. t. ellioti*-ecotone), and assessed ranging behavior in relation to: nest site selection and nest group size, and nest characteristics including nest height, terrestrial nesting and nest tree species preference.

Given the variation in habitats across genetically distinct *P. t. ellioti* populations, I asked the question “*Do niche differences have a measurable effect on the nesting ecology of Nigeria-Cameroon chimpanzee populations?*” With respect to nest site selection, I assessed a range of factors including relief, habitat types, fruit phenology, predation risk, as well as seasonality. I predicted (1) that there would be greater diversity in nesting site selection and reuse at the ecotone due to greater heterogeneity in habitat types and seasonality. Second, I assessed nest group size between rainforest and ecotone populations. I predicted (2) that nest group size will be smaller at the ecotone than rainforest due to more marked seasonality in fruit availability at the former. Third, I assessed nest height and predicted (3) that nest heights would be higher in the ecotone due to greater climatic seasonality. Finally, I assessed nesting tree species choice and predicted (4) that preferences will be site specific across the ecotone and rainforest sites, because differences in floristic composition between the sites.

4.2. Methods

4.2.1. Data collection

Nesting data were collected at two sites in the Ebo forest (rainforest), hereafter: Bekob (human-modified, rainforest) and Njuma (near pristine, rainforest) between January 2016 and March 2017, and at one site in the MDNP hereafter: Ganga (ecotone) between January 2016 and

December 2017. Since chimpanzees across these sites are not habituated to human observers, nesting sites were located opportunistically along straight line transects (10 transects of 2 km length per site) and recces. Each transect was surveyed monthly and recces were used to access the start and at the transects to increase nesting site encounters. Details of transect layout in Chapter Two (Methods Section: 2.2.1.2.).

4.2.1.1. Nesting site habitat characteristics and nest group size

At each nesting site encountered, I described the habitat: with particular focus whether the vegetation canopy was open or closed (Stewart and Pruetz, 2013); location characteristics including geographic coordinates, altitude, and relief: flat, gentle, steep or very steep slopes (Koops et al., 2007); plant phenology: fruiting, flowering or non-fruiting (Basabose and Yamagiwa, 2002) and human indices: machete cuts, wire snares, trails, and spent cartridge shells within a 30 m radius of the nesting site (Last and Muh, 2013, Tagg et al., 2013). When newer nests were found at a previously used site, the site was considered reused. Reused sites were also determined from overlays of monthly geographic coordinates of nesting sites in ArcGIS. The size of the nest group was determined by searching for nests of the same age within 30 m of each observed nest. The 30 m radius has been used by other studies in similar habitats (Mulavwa et al., 2010, Koops et al., 2012a).

4.2.1.2. Individual nest characteristics

A series of data were collected for each nest in the nesting group including details of the tree species on which it was built, its location within the tree, and its age. For each tree in which a nest was built, I identified the tree species, measured the tree size at ~1.3 m from the ground

with a DBH tape, height of the tree and height of the first branch. I also measured the height of the nest from the ground, the position of the nest in the tree and number of nests in the tree (Koops et al., 2012a). Tree, nest and branch heights were measured using a laser range finder. Where this did not work, for example when focus was difficult because of poor lighting, I employed estimations which became more consistent with increased use of the laser range finder.

The position of nests was either terrestrial or arboreal, and in the latter case was further assessed based on position within the tree canopy: trunk (when attached to main stem), horizontal (when built on a branch and away from the main stem), and crown (built either on last tree fork or crown of the tree) (Prasetyo et al., 2009). When the material (leaves and branches) used in building the nest was derived from a single tree, the nest was considered as a simple nest, while when material was derived from more than one plant, it was considered an integrated nest (Humble, 2003).

Nest ages were classified as fresh: couple of days old (fresh green leaves, often associated with fresh feces or strong urine odor); recent: between three days and one week (green but no odor); and old: more than one week (green and brown leaves) (Koops et al., 2007). All encountered nesting sites and individual nests were tagged with flagging tape to avoid duplication. Chimpanzees are sympatric with gorillas at Bekob and their nests were distinguished by their habitat types, presence of feces and/or the presence other signs from the species including knuckle and foot prints (Sanz et al., 2007).

4.2.1.3. Nesting tree species preference

The tree species in which the nest was built was identified to assess preferences in tree species selection across each site (Stanford and O'Malley, 2008). To determine nesting tree species availability and preferences, the densities for all trees ≥ 10 cm diameter were assessed from botanical surveys along ten 2 km transects, covering an area of 10 hectares per site. All trees on a 5 m band along each transect were enumerated, marked, measured and identified (for details, see Chapter Two, Section: 2.2.1.2.).

4.2.1.4. Rainfall seasonality

Rainfall was recorded daily from rain gauges across the three sites; the ≤ 100 mm monthly value was used as the dry season threshold (Willie et al., 2014). The wet season extended between March and November at Ebo forest, while at MDNP, it was between April and October (for details, see Chapter Two, Methods, Section: 2.2.1.1 and Results, Section: 2.3.1.1.).

4.2.2. Data analysis

All data analyses were performed in SPSS (IBM SPSS Statistics 24). Analyses were two-tailed, with 0.05 significance. Mann-Whitney U Tests were used to test intra-site seasonal differences in nesting variables including nest group size, nest height and tree size (DBH). One sample Chi square tests were used to test for variability in nesting location in relation to topography, fruit phenology as well as nest position within the tree crown. Kruskal-Wallis tests were performed for inter-site comparisons, and where significant, were adjusted for multiple comparisons with a Bonferroni correction. Pearson R tests were used to determine the

association between number of nests in tree and tree size, as well as nest structure (simple or integrated) and tree size.

For nesting tree species preference, the observed number of nests built in each tree species was compared to the expected number, determined from the availability of the species on a 5 m band across ten 2 km long transects at each site calculated as: $\text{expN} = Y * X_i / 100$, where Y is the total number of trees with nests and X_i is the relative density of species i (Mulavwa et al., 2010, Willie et al., 2014, Koops et al., 2012a). Preferred tree species (positive Preference Index value) were used disproportionately more in relation to their availability and less preferred species (negative Preference Index value) were used less proportionately. In addition, I calculated the Manly's α to further ascertain tree choice for nesting (Brownlow et al., 2001, Humle, 2003, Koops et al., 2012a, Krebs, 1989, Mulavwa et al., 2010). Manly's α was also calculated based on tree species prevalence using the equation:

$$\alpha_i = \frac{r_i}{n_i} * \frac{1}{\sum (r_j / n_j)}$$

Where

- α_i Manly's α for tree species i
- r_i, r_j Proportion of tree i or r_j used for nesting (i and $j = 1, 2, 3, \dots, m$)
- n_i, n_j Proportion of tree species i and j available in the habitat
- m Number of tree species available for nesting, based on densities along transects

The neutral Manly's α value of $1/m$ was 0.007256 (Bekob), 0.026119 (Njuma) and 0.008103 (Ganga). Species were considered preferred if their Manly's α was $>1/m$ and less preferred if values were $<1/m$ (Brownlow et al., 2001, Koops et al., 2012a, Krebs, 1989).

4.2.2.1. Factorial analysis of mixed data for nesting site location and individual nest characteristics

I conducted factorial analysis for mixed data (FAMD) in R (R version 3.4.3) using the FactoMiner function (Lê et al., 2008) to test for variation in a dataset including both quantitative and qualitative correlating nesting variables. These correlating variables for nesting site selection in Bekob, Njuma and Ganga included habitat type, topography, fruit phenology, nest group size and predation threats. Furthermore, I separated and analyzed nesting site data for the dry and wet seasons to account for seasonality in nesting site location variation. I also used FAMD for variation and patterns in individual nest characteristics including nest height, nest position in tree, nesting tree size, and nest type (terrestrial or arboreal) across the ecotone and rainforest sites.

4.3. Results

Across the two rainforest sites, 430 nests in 112 nest groups and 752 nests in 184 groups were recorded for Bekob and Njuma respectively, while at Ganga there were 2077 nests in 714 nest groups.

4.3.1. Nest site location

4.3.1.1. Slope and nesting site selection

Steep slopes were preferentially selected as nesting sites at Bekob (Mann Whitney U: $N = 112$, $X^2 = 86.643$, $df = 2$, $P < 0.001$) and Njuma ($N = 184$, $X^2 = 223.043$, $df = 3$, $P < 0.001$), while at Ganga, gentle slopes were preferred ($N = 714$, $X^2 = 653.339$, $df = 3$, $P < 0.001$) – see Figures 4.1, 4.2, and 4.3.

4.3.1.2. Habitat and nesting site selection

Closed-canopy habitats were preferred over open-canopy as nesting sites at Bekob ($N = 112$, $Z = -9.544$, $P < 0.001$) and Njuma ($N = 184$, $Z = 12.164$, $P < 0.001$), but there was no habitat preference at Ganga for nesting sites ($N = 710$, $Z = 358.000$, $P = 0.851$). Closed- and open-canopy habitats were selected both in high and low closed-canopy forest, and high and low open-canopy secondary forest (Figure 4.4).

4.3.1.3. Fruit and flowering phenology and nesting site selection

Non-fruiting sites were preferred nesting locations over fruiting and flowering locations at the rainforest sites: Bekob ($N = 112$, $X^2 = 42.875$, $df = 2$, $P < 0.001$) and Njuma ($N = 184$, $X^2 = 114.207$, $df = 2$, $P < 0.001$). Conversely at Ganga, sites with fruiting trees were preferred nesting site locations ($N = 714$, $X^2 = 576.521$, $df = 2$, $P < 0.001$) – see Figures 4.5, 4.6 and 4.7.

4.3.2. Mean nest group size

The mean nest group sizes including single nest groups were $3.81 \pm SD 3.616$ nests at Bekob ($N = 112$), $4.08 \pm SD 3.730$ nests at Njuma ($N = 184$), and $2.93 \pm SD 4.366$ nests at Ganga ($N = 714$). Mean nest group sizes across ecotone and rainforest were smaller ($N = 1010$, $X^2 = 50.038$, $df = 2$, $P < 0.001$). Mean group sizes at the rainforest sites were higher than at the ecotone: Bekob-Ganga ($Z = 4.681$, $P < 0.001$), Njuma-Ganga ($Z = -6.009$, $P < 0.001$) and there was no difference between the two rainforest sites.

The mean nest group sizes without single nest groups were $4.62 \pm SD 3.730$ nests at Bekob ($N = 87$), 5.14 ± 3.783 nests at Njuma ($N = 137$) and 4.42 ± 5.357 nests at Ganga ($N = 403$). The mean nest group size without single nest was larger at Njuma than Ganga ($Z = -4.146$, $P <$

0.001), but there was no significant difference between Njuma and Bekob, or between Bekob and Ganga.

There were no seasonal differences in nest group sizes at Bekob ($N = 112$, $Z = 0.929$, $P = 0.353$), Njuma ($N = 184$, $Z = -1.492$, $P = 0.136$) and Ganga ($N = 714$, $Z = 1.052$, $P = 0.293$). Without single nest groups, dry season nest mean nest group size was larger wet season mean nest group size ($N = 137$, $Z = -2.248$, $P = 0.025$) at Njuma. There was no significant difference in mean nest group size between the dry and wet season at Bekob ($N = 87$, $Z = 0.465$, $P = 0.642$) and Ganga ($N = 403$, $Z = 1.201$, $P = 0.230$) even when single nest groups were excluded.

Nest group sizes at the rainforest ranged from 1 – 24 and 1 – 25 at Bekob and Njuma respectively, while at Ganga, the range was 1 – 53 nests. The ecotone site had a larger proportion of single nest groups (43%) compared to about 25% for the rainforest sites. Nest group sizes of between two and four nests were however common across the three sites representing 50% at Bekob, 42.9% at Njuma and 43.5% at Ganga (Appendix 4.8).

4.3.3. Variation in nesting site locations and nest group sizes based on FAMD

4.3.3.1. General nest site selection variation between the three sites

Based on the FAMD of the nesting site variables, the rainforest chimpanzee populations (Bekob and Njuma) clustered together and separated from the chimpanzees at Ganga with Dim 1 and Dim 2 accounting for 21% and 17.9% of the variation – Figure 4.8. In Dim 1, slope with a contribution of >40% and canopy - >35% (Appendix 4.14) were the main distinguishing variables between the sites. In Dim 2, fruit phenology contributed to more than 40% of the variation between Ganga on the one hand, and Bekob and Njuma on the other hand (Appendix 4.15).

4.3.3.2. Dry season nest site selection and group size variation

In the dry season, nesting site selection and nest group sizes between Bekob, Njuma and Ganga varied based on the FAMD, with Dim 1 and Dim 2 accounting for 25.3% and 18.7% of the variation respectively – Figure 4.9. The main contributory factors were slope (>40%) and canopy (>30%) in Dim1 – Appendix 4.16, and fruit phenology (>60%) and group size (>25%) in Dim 2 – Appendix 4.17. Chimpanzees at Bekob and Njuma preferentially selected steep slopes for nesting while gentle and flat slopes were selected at Ganga. The chimpanzees at Bekob and Njuma preferred nesting in closed-canopy habitats while the Ganga chimpanzees showed no habitat preference. Larger nest group sizes were associated with fruit availability especially at Ganga.

4.3.3.3. Wet season nest site selection and group size variation

In the wet season, nesting site selection and group sizes between Bekob, Njuma and Ganga varied based on the FAMD, with Dim 1 and Dim 2 accounting for 25.1% and 18.2% of the variation – Figure 4.10. The main distinguishing variables were slope (>40%) and canopy (>40%) in Dim 1 (Appendix 4.18), and fruit phenology (>50%) and (nest group size >45%) in Dim 2 – Appendix 4.19. Just like in the dry season, steep slopes and closed-canopy habitats were preferred nesting site location at Bekob and Njuma, while the availability of fruits was more important at Ganga and was associated with larger nest group sizes.

4.3.4. Nest heights

The mean nest heights for the rainforest were $10.81 \pm \text{SD } 5.416 \text{ m}$ ($N = 397$) and $13.18 \pm \text{SD } 5.852 \text{ m}$ ($N = 639$) for Bekob and Njuma respectively, and $13.28 \pm \text{SD } 5.896 \text{ m}$ ($N = 2053$) for

Ganga. There were significant differences in mean nest heights between the sites ($X^2 = 69.099$, $df = 2$, $P < 0.001$). Mean nest height at Ganga was higher than at Bekob ($Z = -8.246$, $P < 0.001$), Njuma was higher than Bekob ($Z = -6.660$, $P < 0.001$) and there was no difference between Njuma and Ganga.

For height classes 76.7% of nests at Bekob were between 5-20 m high, 68% for Njuma and 79% for Ganga. The two rainforest sites had a higher proportion of nests <5 m height (>15%) compared to the ecotone site with 5.6% (see Figure 4.9).

There were differences between the three sites in relation to seasonality in nest heights. At Bekob, there were no seasonal differences in mean nest heights ($N = 397$, $Z = -0.260$, $P = 0.795$), while at Njuma dry season nests were higher than wet season nests ($N = 639$, $Z = -2.154$, $P = 0.031$). Conversely, at Ganga wet season mean nest heights were significantly higher than dry season mean nest heights ($N = 2053$, $Z = 6.430$, $P < 0.001$).

4.3.5. Nesting tree size

There was no significant difference in the mean size of trees selected for nesting across the three sites ($N = 2954$, $X^2 = 3.484$, $df = 2$, $P = 0.175$). The mean tree sizes used for nesting across the rainforest sites were $23.411 \pm SD 15.53$ cm ($N = 384$) and $22.744 \pm SD 17.88$ cm ($N = 622$) for Bekob and Njuma respectively, and $23.13 \pm SD 16.27$ cm ($N = 1948$) for Ganga.

Chimpanzees across the rainforest and ecotone built most of their nests in medium-sized trees, that is, between 10 and 25 cm (Bekob – 57.2%, Njuma – 60%, and Ganga – 57.6%) – Figure 4.10.

There were differences across the three sites in seasonal variation in the sizes of nesting trees. At Bekob, there was no seasonal difference in the mean diameter of nesting trees ($Z = -0.941$, $P = 0.347$), and Njuma larger trees were preferred in the dry season ($Z = -6.342$, $P <$

0.001). At Ganga, nesting tree sizes were significantly larger in the wet season ($N = 1948$, $Z = -3.972$, $P < 0.001$).

4.3.6. Number of nests in individual trees

There was no difference between the three sites in the mean number of nests made in a single tree ($N = 2590$, $X^2 = 3.511$, $df = 2$, $P = 0.173$). The average number of nests in a single tree across the rainforest was $1.14 \pm SD 0.428$ (range 1 – 4, $N = 334$) for Bekob and $1.14 \pm SD 0.345$ (range 1 – 4, $N = 563$) for Njuma. At Ganga, the mean number of nests in a single tree was $1.14 \pm SD 0.487$ (range 1 – 7, $N = 1693$). Multiple nests in a single tree were associated with larger trees across the three sites (Bekob: Pearson $R = 0.111$, $N = 334$, $P = 0.042$, Njuma: $R = 0.223$, $N = 563$, $P < 0.001$, and Ganga: $R = 0.258$, $N = 1693$, $P < 0.001$).

4.3.7. Integrated and simple nests

At Bekob, 50 (12.5%) of nests were integrated, 64 (9.9%) for Njuma and 243 (11.8%) for Ganga. There was a negative correlation between tree size and integrated nests across the three sites. Integrated nests were associated with smaller trees across the three sites (Bekob: Pearson $R = -0.172$, $N = 383$, $P = 0.001$, Njuma: $R = -0.104$, $N = 621$, $P = 0.010$, and Ganga: $R = -0.178$, $N = 1938$, $P < 0.001$).

4.3.8. Terrestrial nesting

Terrestrial nests were found across the three sites, including (Bekob: $n=30$ (6.9%), Njuma: $n=112$ (14.9%) and Ganga: $n=24$ (1.2%)). Only chimpanzees at Njuma used overnight terrestrial nests. Of the 112 terrestrial nests at Njuma, 42 (37.5%) were day nests and 67 (59.8%) were overnight nests and three nests could not be attributed to either day or night category.

Seasonality (dry: N = 59, wet: N = 63) did not influence terrestrial nesting behavior (N = 112, Z = -0.427, P = 0.637) at Njuma.

4.3.9. Nesting tree species preferences

Chimpanzees made arboreal nests in more than 60, 30 and 80 tree species at Bekob, Njuma and Ganga respectively, but across each site, some nesting tree species were selected more often. At Bekob ten tree species including *Zenkerella citrina*, *Diogoia zenkeri*, and *Strombosia grandifolia* accounted for 71.3% of the nests, while five species including *S. grandifolia*, *D. zenkeri*, *Diospyros* sp., *Garcinia* sp. and *Santiria trimera* accounted for 83.5% of nests at Njuma. At Ganga, ten species including *Xylopia aethiopica*, *Hymenocardia lyrata*, *Uapaca guineensis* and *Synsepalum* sp. accounted for 55.2% of the nests (Table 4.1).

Some tree species were selected for nesting disproportionately more than expected based on their availability across the sites and were thus considered preferred, while others were used disproportionately less and were considered less preferred. Preferred species had a positive Preference Index and Manly's α higher than the neutral value (1/ – see Table 4.1 and Figure 4.15. At Bekob *Z. citrina* (with 16.5% of nests), *D. zenkeri* (8.4%), and *S. grandifolia* (17.2%) were preferred species. At Njuma *S. grandifolia* (32.2%), *D. zenkeri* (31.5%) and *Diospyros bipindensis* (9%) were preferred. And lastly at Ganga *X. aethiopica* (19.9%), *U. guineensis* (9.7%) and *Synsepalum* sp. (8%) were preferred species (Table 4.1., Figure 4.15 and Appendices 4.11, 4.12, 4.13).

4.3.10. FAMD – individual nest characteristic variation between Bekob, Njuma and Ganga

The clustering of individual nesting characteristics between Bekob, Njuma and Ganga based on the FAMD was tight – Figure xxx, with Dim 1 and Dim 2 accounting for 33.6% and 16.9% of the

variation between the sites. The main distinguishing variables in Dim 1 that separated individual nests within each population included nest position in tree (30%), nest height (>25%) and nest type (20%) – Appendix 4.20. In Dim 2, nest position in the tree was the most important variable with ~60% of the variation – Appendix 4.21.

4.4. Discussion

Environmental and ecological conditions in habitats occupied by genetically distinct *P. t. ellioti* populations in Cameroon differ significantly from one another, (Sesink Clee et al., 2015) with the main differences being in rainfall seasonality, botanical composition and fruit phenology patterns (Chapter Two). Variation in relief between rainforest and ecotone habitats was one of the distinguishing variables across *P. t. ellioti* range in the EMNs (Sesink Clee et al., 2015). Though this variable was not directly quantified in this study, the altitudinal range at Njuma was ~100-900 m and at Bekob ~500-1200 m. At Ganga, there was less altitudinal variation (~700-900 m). Chimpanzee nesting behavior is linked to ecological, environmental and anthropogenic conditions (Koops et al., 2012a, Samson and Hunt, 2014, Sanz et al., 2007, Tagg et al., 2013). Nesting patterns can be important in our understanding of chimpanzee habitat use and population dynamics in relation to the temporal and spatial availability of fruits and other ecological influences. Thus, I investigated nesting patterns in *P. t. ellioti* in Ebo forest (rainforest) and Mbam & Djerem National Park (ecotone) to assess how local differentiation in socioecology may be linked to habitat variation, and how these differences correspond with the gene pools observed in Nigeria-Cameroon chimpanzees found across this region.

The first prediction I tested was that there would be more variability in habitats for nesting site location at the ecotone compared to the rainforest, which was supported by the nesting

data from the three study sites. Closed-canopy habitats were preferred nesting site locations at rainforest sites (Njuma and Bekob). Closed-canopy habitats are preferentially chosen by chimpanzees across their range with primary forest, gallery forest and woodlands favored over more open vegetation at Goualougo, Congo Republic, Kahuzi-Biega, DR Congo, Sapo, Liberia, Seringbara, Guinea, Ugalla, Tanzania and Fongoli, Senegal for nesting site location (Anderson et al., 1983, Basabose and Yamagiwa, 2002, Koops et al., 2012b, Ogawa et al., 2007, Pruetz et al., 2008, Sanz et al., 2007). At Ganga, there was no marked preference for any habitat type at the ecotone site for nesting site locations, but the distribution of nesting sites was associated with the availability of fruits in different habitats. More nesting sites were associated with closed-canopy forests (low closed-canopy secondary forest and high closed-canopy gallery) when plant species restricted to these classes including *Pseudospondias microcarpa*, *Synsepalum* sp. and *Myrianthus arboreus* were fruiting. When plant species with wider distribution across different habitats were in fruit, especially species of *Landolphia* spp., *Saba* spp., *Uapaca guineensis*, *U. togoensis* and *Vitex doniana*, nesting sites occurred in both closed- and open-canopy habitats. There were differences, however, between the two rainforest sites. At Njuma, chimpanzees consistently chose mature closed-canopy habitats for nesting site location. At Bekob, fruit availability was not significant in nesting site selection, but most nesting sites in the dry season (between November and March) were associated with secondary vegetation where *Elaeis guineensis*, *U. guineensis*, *P. microcarpa* and other species in this habitat type were in fruit. These secondary and introduced species were important in the dietary ecology of chimpanzees at this site, and thus their ranging patterns. Although the Bekob chimpanzees might be an exception, chimpanzees generally avoid secondary forest, which are preferred nesting sites for

gorillas (Sanz et al., 2007). In light of the high importance of fruit availability in secondary vegetation, especially during periods of fruit scarcity, I hypothesize that this is a primary factor in determining chimpanzee nest site preferences in human-modified landscapes. Evidence from other sites suggest that fruit abundance in secondary vegetation is an important factor that contributes to nesting site selection in chimpanzees (Basabose, 2005, Basabose and Yamagiwa, 2002, Furuichi and Hashimoto, 2004, Stanford and O'Malley, 2008). The bonobos at Wamba, DR Congo nested in swamp and dry forests based on fruit availability in each habitat category (Mulavwa et al., 2010) and gorilla nesting site locations at Lope, Gabon and Bai Hokou, Central Africa Republic were also correlated to food availability in that habitat (Remis, 1993, Tutin et al., 1995).

Nesting site locations at Bekob and Njuma were associated with steep slopes. The selection of nesting sites in relation to topography or other geographic factors can be linked to safety or comfort (Ogawa et al., 2014, Koops et al., 2012a). There are no known non-human predators of chimpanzees across the Ebo forest, but the prevalence of poaching especially at night with shotguns could explain the choice of hard-to-access sites to humans for nest building. The prevalence of terrestrial nests at swamps in the Dja, Cameroon is attributed to safety since poachers cannot easily access swamps especially at night (Tagg et al., 2013). Chimpanzees at Ugalla, Tanzania select mountainous areas for nesting to reduce the risk of predation (Ogawa et al., 2007) while at Seringbara, Guinea higher altitudes were preferred nesting sites in the wet season for thermoregulation (Koops et al., 2012a).

The second prediction that nest group sizes would be larger at the rainforest than at the ecotone was supported. But the nest group size for GGNP, Nigeria - an ecotone site for *P. t.*

elliotti (Fowler, 2006) is higher than values recorded for the two rainforest sites in this study (Table 4.2). This difference could be a function of higher predation risk since GGNP chimpanzees are sympatric with leopards (Sommer et al., 2004). Nest group size categories had similar patterns across the rainforest and ecotone sites with a dominance of nest groups with single nests while categories with between two and four nests were common. Similar nest group size category patterns were observed in the GGNP (Fowler, 2006) and the Nimba Mts., Cote d'Ivoire (Granier et al., 2014). Nest group sizes from other rainforest and dry habitats across the chimpanzee range are different (Table 4.2). Habitat differences were also associated with variation in nest group sizes for bonobos, with larger mean group size in dry than swamp forests (Mulavwa et al., 2010).

Across savanna and other dry chimpanzee habitats, mean nest group sizes are higher than any sites in this study (Hunt and McGrew, 2002, Ogawa et al., 2007, Stewart and Pruetz, 2013) – Table 4.2. Chimpanzees preferentially select closed-canopy habitats for nesting (Ogawa et al., 2007, Ogawa et al., 2014, Pruetz et al., 2008, Sanz et al., 2007), and where these are restricted as in the case of many dry and open habitats nesting parties tend to be clustered and larger (Hunt and McGrew, 2002, Ogawa et al., 2007, Pruetz et al., 2008). Sleeping parties at Ugalla, Tanzania were larger than foraging parties, and this was hypothesized as an antipredation strategy, as well as restricted suitable nesting sites (Ogawa et al., 2007). Conversely, foraging and nesting party sizes were similar for bonobos at Wamba, Democratic Republic of Congo (Mulavwa et al., 2010). Larger nest group size may reflect more fruit availability and sociality between community members (Newton-Fisher et al., 2000). However, large party sizes may also correlate with males aggregating to gain access to females in estrous (Hashimoto et al., 2001).

Mean nest heights were higher at Ganga and Njuma than at the Bekob. Variation in chimpanzee nest heights have been attributed to a range of factors including ecological and environmental variables (Baldwin et al., 1981, Koops et al., 2012a). Higher mean nest heights for Ganga could be attributed to a high proportion of nests in *X. aethiopica*, which is a tall and slim tree species with very high first branches. Most nests in this species exceeded >15 m in height. Njuma on the other hand is characterized by the highest canopies across the three sites, and the opportunities of finding of adequate nesting spots in mid- and high-canopies may be higher. Bekob is characterized by secondary forest and mature submontane forest that may offer nesting opportunities at lower heights. Most of the nests in Ganga and Njuma, and to a lesser extend Bekob were in the middle layer of the canopy, that is, between 10 and <20 m in height. Similar nest height patterns were observed at Bwindi, Uganda (Stanford and O'Malley, 2008), Seringbara and Bossou, Guinea (Koops et al., 2012b, Humle, 2003), Hoima and Masindi, Uganda (McCarthy et al., 2017), Lagoas de Cufada Natural Park, Guinea Bissau (Carvalho et al., 2015b), Goualougo, Congo (Sanz et al., 2007) as well as for bonobos at Lomako and Wamba, DRC (Fruth and Hohmann, 1993, Mulavwa et al., 2010). A significant proportion of nests at Bekob were below 10 m, which is similar to nest heights in the montane secondary and primary forest habitats at Kahuzi-Biega, DRC (Basabose and Yamagiwa, 2002).

There was greater seasonality in nest heights Ganga and Njuma, while at Bekob there were no seasonal differences in nest heights. Thermoregulation has been suggested as the main hypothesis for seasonal variation in nest heights with higher heights in the wet than the dry season (Baldwin et al., 1981, Koops et al., 2012a, Samson and Hunt, 2012, Stewart, 2011). Higher nests during the wet season could be aimed at reducing wetness and discomfort which might be

prolonged by water dripping from leaves at lower canopies or heights after downpours (Baldwin et al., 1981). Seasonal variation in nest heights was also observed at Fongoli and Assirik, Senegal (Baldwin et al., 1981, Pruetz et al., 2008), Seringbara, Guinea (Koops et al., 2012a) and Ngel Nyaki, Nigeria (Dutton et al., 2016). Seasonal variation in nest heights including arboreal and terrestrial nesting choice, as well as construction effort have also been noted in gorillas. During the wet season, gorillas construct more arboreal nests and avoid sleeping on bare ground (De Vere et al., 2011, Mehlman and Doran, 2002, Sunderland-Groves et al., 2009).

Arboreal nesting and higher nests are also associated with predation avoidance (Hernandez-Aguilar et al., 2013), but there was no evidence of non-human predators across the ecotone or rainforest habitats. These sites might have harbored leopards in the past. At GGNP, Nigeria with similar habitat as MDNP (ecotone), leopards are sympatric with chimpanzees (Fowler, 2006, Sommer et al., 2004). Nest heights at GGNP are however lower compared to ecotone and rainforest populations in this study (Table 4.2). The difference in nest heights could be the result of forest structure and nesting tree species choice, rather than safety from predators. The mean nest heights at the dry habitats of Ugalla, Tanzania and Assirik, Senegal where chimpanzees cohabit with predators are characteristic of mid canopies (Pruetz et al., 2008, Hernandez-Aguilar et al., 2013). But at Fongoli, Senegal which is associated with lower predation pressure, mean nest heights are lower and terrestrial nests are common (Pruetz et al., 2008, Baldwin et al., 1981). The chimpanzees across the rainforest and ecotone sites preferentially selected medium-sized trees, that is, between 10-30 cm diameter. This category of tree size was also preferred by chimpanzees at Kalinzu, Uganda (Furuichi and Hashimoto, 2004) and at Nimba Mts., Cote d'Ivoire (Granier et al., 2014). Larger trees tend to be selected for

nesting at sites where chimpanzees are sympatric with predators (Baldwin et al., 1981, Pruetz et al., 2008). The mean nesting tree sizes for Issa and Ugalla, Tanzania where chimpanzees are sympatric with predators were larger as compared to many other study sites, and this is linked to sympatry with predators at the sites (Hernandez-Aguilar et al., 2013, Ogawa et al., 2007) – Table 4.2.

Terrestrial night nesting behavior in great apes is linked to sites with low predation pressure (Koops et al., 2007) (but see Tagg et al., 2013) and the seasonality of the behavior at some sites has been attributed to thermoregulation (De Vere et al., 2011, Pruetz et al., 2008, Tagg et al., 2013, Tutin et al., 1995). The difference in terrestrial nesting behavior between the three sites could be linked to differences in sympatry with large terrestrial mammals. At Bekob and Ganga, elephant signs (dung, feeding, prints) were common, but these were rare at Njuma. Avoidance of nocturnal disturbance by large mammals influenced terrestrial or arboreal nesting decisions in gorillas (Remis, 1993, Tutin et al., 1995). Terrestrial nests including overnight nests have been reported at several chimpanzee study sites: Nimba Mts., Seringbara, Fongoli, Hoima and Masindi, Lebialem-Mone, Dja, and Ebo (Abwe and Morgan, 2008, Granier et al., 2014, Koops et al., 2007, Last and Muh, 2013, McCarthy et al., 2017, Pruetz et al., 2008, Tagg et al., 2013) and reflect low predatory pressure (Granier et al., 2014, Pruetz et al., 2008).

Differences in tree species preferences may be based on ecological variation or cultural differences (Humble, 2003). Though nests were made in many tree species, there were site specific preferences in tree species choice. In relation to their densities across the sites, some tree species were used more than expected (preferred) while the use of others was less proportionate (less preferred). There was more overlap in preferred tree species between the

rainforest sites including *Z. citrina*, *S. D. zenkeri*, and *Drypetes* sp. On the other hand, *Strombosia grandifolia* was a common preferred species between the rainforest and ecotone populations. There were also differences in nesting tree species preferences across the sites, for example, though *U. guineensis* occurred commonly across the ecotone and rainforest sites it was only preferred and regularly used as a nesting tree species at the ecotone. Nesting in *Elaeis guineensis* was exclusive to the chimpanzee population at Bekob. The species occurs at the other rainforest and ecotone sites albeit in lower densities but was not selected for nesting at these sites. At other sites where their natural habitats have been modified by humans, chimpanzees nest in *E. guineensis* (Carvalho et al., 2015b, Humle, 2003, Sousa et al., 2014, Sousa et al., 2011) and other exotic species like *Eucalyptus grandis*, *Psidium guajava*, and *Theobroma cacao* (McCarthy et al., 2017).

Some nesting tree species across the rainforest and ecotone sites including *U. guineensis*, *P. longifolia*, *Synsepalum* sp., *Coula edulis*, *E. guineensis*, *Pycnanthus angolensis*, *Irvingia gabonensis*, *Santiria trimera*, *V. doniana*, and *Olex subscorpioidea* were also important fruit sources for the different populations, but nesting time did not synchronize with fruit availability. Chimpanzee populations at many study sites also nest in trees that produce fruits they feed on, but avoid nesting in them when they are in fruit (Dutton et al., 2016, Furuichi and Hashimoto, 2004, Koops et al., 2012a, Stanford and O'Malley, 2008). Conversely, chimpanzees at Tshibati, DR Congo preferentially nested in trees with ripe fruits they consumed in secondary forest, a behavior attributed to interspecific competition with sympatric gorillas (Basabose and Yamagiwa, 2002). Various tree species selected for nesting vary in crown form, biomechanical properties of

branches, leaf size, tree size, and food source; but evidence suggests that choice is dictated by comfort and safety (Samson and Hunt, 2014).

Differences in nesting patterns between populations inhabiting distinct habitats can be used to infer ranging behavior and sociality, and this can particularly useful in understanding the socioecology of populations that are not habituated to humans. For example, smaller nest group sizes and the influence of fruit phenology in nesting site choice could mean that chimpanzees at the ecotone site are subjected to greater foraging costs, albeit seasonally. This could mirror low levels of gregariousness, especially during periods of low fruit availability. Nesting behavior has been used to infer ranging behavior and sociality in relation to food availability in chimpanzees and bonobos (Basabose, 2005, Furuichi and Hashimoto, 2004, Hohmann et al., 2012, Mulavwa et al., 2010, Serckx et al., 2014). Affiliations common between males at sites with low seasonality in resource availability may be difficult to maintain at sites with marked spatial and temporal variation in food availability (Boesch, 1996, Stanford, 1998, Wrangham and Smuts, 1980). Low levels of gregariousness associated with large ranges is one of the distinguishing factors between rainforest and savanna chimpanzee populations (Arandjelovic et al., 2011, Inoue et al., 2008, Langergraber et al., 2007, McGrew et al., 1981, Pruett and Bertolani, 2009, Stumpf, 2011). Grouping patterns in central and Nigeria-Cameroon chimpanzees are unexplored (Stumpf, 2011). But a recent study found that *P. t. ellioti*-rainforest males are more closely related than *P. t. ellioti*-ecotone males, and this has been attributed to their socioecological responses to different ecological and environmental conditions (Mitchell et al., in prep).

Understanding local adaptations in chimpanzees, our closest ancestral relatives especially across an active speciation zone may shed light on hominin evolution in different paleo-

environments that could have been akin to the broad range of habitats occupied by chimpanzees today. Nesting patterns across populations of *P. t. ellioti* inhabiting significantly different habitats reveal adaptation patterns which can be useful in understanding divergence across the subspecies and chimpanzee speciation across Cameroon in general.

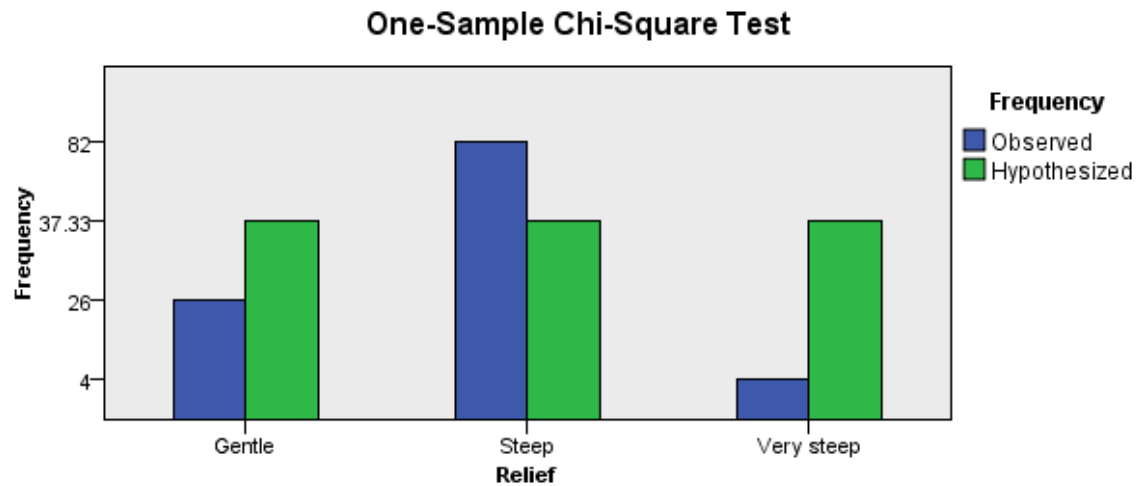
Table 4.1. Nesting tree preferences for Bekob, Njuma and Ganga: tree species, stem density for the species at each site based on botanical enumeration across 10 hectares (including % of total tree stems), number of nests in species (including % of total nests at site made in the species), Preference Index (from expected and observed used based on number of stems), and the Manly's α .

Human-modified rainforest Bekob					Pristine-Rainforest Njuma					Ecotone Ganga				
Species	Stems along transects (%)	Number of nest (%)	Pref. Index	Manly's α Neutral 0.00725	Species	Stems along transects (%)	Number of nests (%)	Pref. Index	Manly's α Neutral 0.02621	Species	Stems along transects (%)	Number of nests (%)	Pref. Index	Manly's α Neutral 0.0081
<i>Zenkerella citrina</i>	84 (2.53)	43 (16.5)	36.4	0.0472	<i>S. grandifolia</i>	235 (10.7)	94 (35.2)	65.63	0.0865	<i>S. grandifolia</i>	8(0.2)	68(4.1)	65.0	0.1863
<i>Diogoia zenkeri</i>	80 (2.41)	22 (8.4)	15.7	0.0253	<i>D. zenkeri</i>	298 (13.5)	84 (31.5)	48.02	0.0610	<i>Synsepalum</i> sp.	72(1.6)	132(8.0)	105.4	0.0402
<i>Hymenostegia</i> sp.	101 (3.04)	22 (8.4)	14.1	0.0201	<i>S. trimera</i>	43 (1.9)	9 (3.4)	3.81	0.0453	<i>Tricalysia</i> sp.	31(0.7)	51(3.1)	39.5	0.0360
<i>Strombosia grandifolia</i>	334 (10.07)	45 (17.2)	18.7	0.0124	<i>Diopyros bipidensis</i>	168 (7.6)	24 (9.0)	3.71	0.0309	Sapindaceae sp.	91(2.0)	118(7.2)	84.4	0.0284
<i>Elaeis guineensis</i>	33 (1)	4 (1.5)	1.4	0.0112	<i>Z. citrina</i>	32 (1.4)	4 (1.5)	0.14	0.0270	<i>Klainedoxa gabonensis</i>	26(0.6)	33(2.0)	23.4	0.0278
<i>Pseudospondias</i> sp.	28 (0.8)	3 (1.1)	0.8	0.0099	<i>Coula edulis</i>	59 (2.7)	7 (2.6)	-0.12	0.0257	<i>Olex subscorpioidea</i>	76(1.7)	70(4.3)	41.9	0.0202
<i>Rinorea oblongifolia</i>	32 (1)	3 (1.1)	0.48	0.0086	<i>Hymenostegia</i> sp.	20 (0.9)	2 (0.7)	-0.41	0.0216	<i>Xylopia aethiopica</i>	374(8.4)	328(19.9)	189.7	0.0192
<i>Pycnanthus angolensis</i>	112 (3.4)	9 (3.4)	0.18	0.0074	<i>Hylo dendron gabunense</i>	23 (1.0)	2 (0.7)	-0.78	0.0188	<i>U. guineensis</i>	194(4.4)	159(9.7)	87.3	0.0180
<i>Garcinia</i> sp.	276 (8.3)	21 (8.0)	-0.73	0.0070	<i>Garcinia</i> sp.	198 (9.0)	15 (5.6)	-8.91	0.0164	<i>Detarium microcarpum</i>	54(1.2)	44(2.8)	24.0	0.0179
<i>Drypetes</i> sp.	326 (9.8)	19 (7.3)	-6.67	0.0054	<i>Dacryodes</i> sp.	39 (1.8)	2 (0.7)	-2.71	0.0111	<i>Sorindeia</i> sp.	134(3.0)	67(4.1)	17.4	0.0110
<i>Santiria trimera</i>	84 (2.5)	3 (1.1)	-3.61	0.0033	<i>P. angolensis</i>	87 (3.9)	4 (1.5)	-6.50	0.0099	<i>Hymenocardia lyrata</i>	573(12.9)	114(6.9)	-97.9	0.0044
<i>Cola</i> sp.	299 (9.0)	7 (2.7)	-16.5	0.0022	<i>Strychnos</i> sp.	22 (1.0)	1 (0.4)	-1.66	0.0098	<i>Spondianthus preussii</i>	288(6.5)	42(2.6)	-64.5	0.0032
<i>Uapaca guineensis</i>	155 (4.7)	3 (1.1)	-9.20	0.0018	<i>Berlinia</i> sp.	29 (1.3)	1 (0.4)	-2.50	0.0075	<i>Lannea acida</i>	153(3.4)	20(1.2)	-36.6	0.0029

Positive Preference Index indicates preferred species and negative Preference Index indicates less preferred. Manly's $\alpha > 1/m$ indicates preferred (bold) while Manly's $\alpha < 1/m$ indicates less preferred.

Table 4.2. Chimpanzee nesting characteristics across Africa

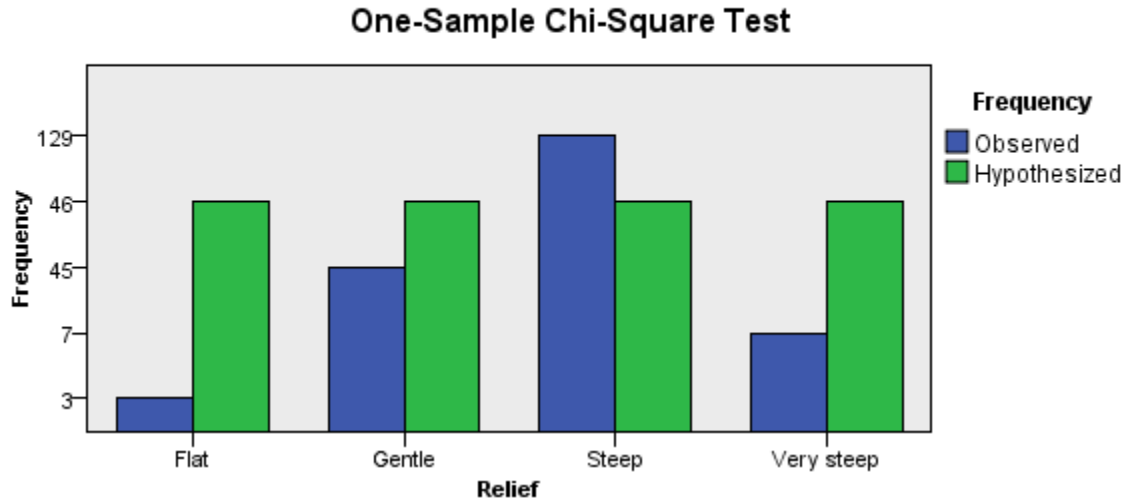
Study site	Subspecies & species	Nest group size			Nesting tree diameter (cm)			Nest height			Terrestrial nesting		References
		Mean	SD	N	Mean	SD	N	Mean	SD	N	Presence	%	
Bekob, Cameroon	<i>P. t. ellioti</i>	3.81	3.61	112	23.46	15.52	383	10.81	5.41	397	-		This study
Ganga, Cameroon	<i>P. t. ellioti</i>	2.95	4.4	697	23.11	16.4	1910	13.27	5.9	2014	-		This study
Njuma, Cameroon	<i>P. t. ellioti</i>	4.08	3.7	184	22.71	17.89	623	13.18	5.85	639	+	8.9	This study
Gashaka Gumti NP, Nigeria	<i>P. t. ellioti</i>	4.8	4.7	147				8			-		(Fowler, 2006)
Ngel Nyaki, Nigeria	<i>P. t. ellioti</i>				37.6	23	311	20.5	7.18	311	-		(Dutton et al., 2016)
Takamanda-Mone, Cameroon	<i>P. t. ellioti</i>	4.3	1.9	8				17.4	5.6		+	32.4	(Last and Muh, 2013)
Dja Reserve, Cameroon	<i>P. t. troglodytes</i>									1008	+	3.47	(Tagg et al., 2013)
Goualougo, Congo Republic	<i>P. t. troglodytes</i>							17.3	7.4	247	-		(Sanz et al., 2007)
Seringbara, Guineas	<i>P. t. verus</i>	3.7	3.96	280				11.3	6.3	1376	+	4.8	(Koops et al., 2012a)
Lagoas de Cufada NP, Guinea Bissau	<i>P. t. verus</i>							16.08	5.21	164	-		(Sousa et al., 2014)
Yeale, Cote d'Ivoire	<i>P. t. verus</i>				42.4	34.8	192	18.7	10.7	222	+	2.9	(Humle, 2003)
Nimba Mts., Cote d'Ivoire	<i>P. t. verus</i>	2.23	1.57	338	27.9	24.01	764	8.02	4.57	764	+	8.2	(Granier et al., 2014)
Bossou, Guinea	<i>P. t. verus</i>				32.1	20.5	218	13	5	245	+		(Humle, 2003)
Fongoli, Senegal	<i>P. t. verus</i>							8.33	4.13	1665	+	2.7	(Pruetz et al., 2008)
Assirik, Senegal	<i>P. t. verus</i>							13.55	4.24	694	-		(Pruetz et al., 2008)
Kahuzi-Biega, DR Congo	<i>P. t. schweinfurthii</i>	4.3	2.5		24.9	13.3	104	9.4	4.8	104	-		(Basabose and Yamagiwa, 2002)
Hoima & Masindi, Uganda	<i>P. t. schweinfurthii</i>							10.9	5.5	881	+	1	(McCarthy et al., 2017)
Budongo, Uganda	<i>P. t. schweinfurthii</i>	4.5		147	26.4		411	12.1		601	-		(Brownlow et al., 2001)
Bwindi, Uganda	<i>P. t. schweinfurthii</i>							16.06	6.2	3414	-		(Stanford and O'Malley, 2008)
Gishwati, Rwanda	<i>P. t. schweinfurthii</i>	3.8	3	314									(Chancellor et al., 2012)
Rubondo, Tanzania	<i>P. t. schweinfurthii</i>	3.42	0.29	138							-		(Moscovice et al., 2007)
Ugalla, Tanzania	<i>P. t. schweinfurthii</i>				35.2	15.8	1451	12.15	4.19	2164	-		(Hernandez-Aguilar et al., 2013)
Ugalla, Tanzania	<i>P. t. schweinfurthii</i>	5.4		104	36.9	19.3	549	13.4	5.1	549	-		(Ogawa et al., 2007)
Semliki, Uganda	<i>P. t. schweinfurthii</i>	5	3.23	348	45			11	5.81	324	-		(Hunt and McGrew, 2002)
Wamba, DR Congo	<i>P. paniscus</i>	9.3	4.9	215				15.3	5.3	1534	-		(Mulavwa et al., 2010)



Total N	112
Test Statistic	86.643
Degrees of Freedom	2
Asymptotic Sig. (2-sided test)	.000

1. There are 0 cells (0%) with expected values less than 5. The minimum expected value is 37.333.

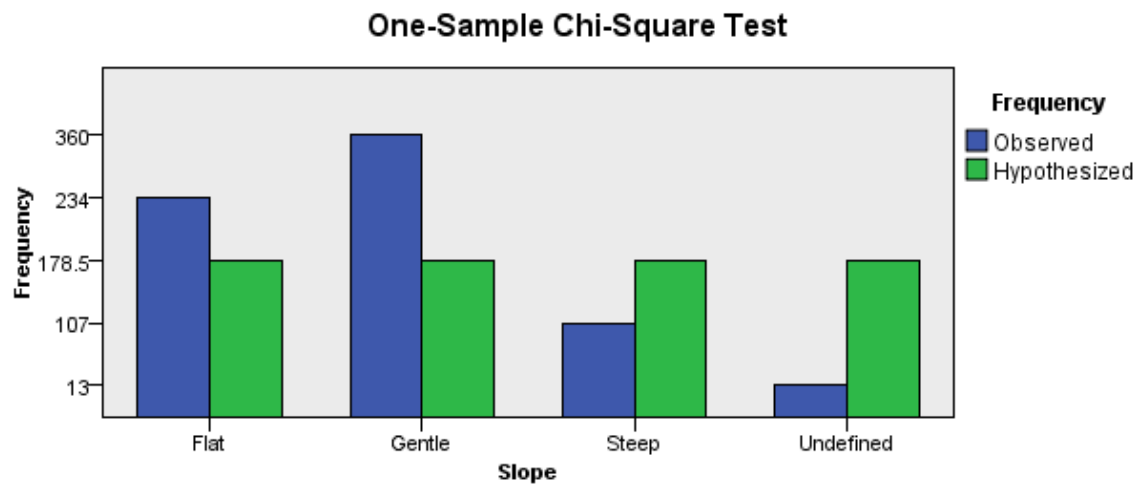
Figure 4.1. Nesting site location in relation to relief at Bekob



Total N	184
Test Statistic	223.043
Degrees of Freedom	3
Asymptotic Sig. (2-sided test)	.000

1. There are 0 cells (0%) with expected values less than 5. The minimum expected value is 46.

Figure 4.2. Nesting site location in relation to relief at Njuma



Total N	714
Test Statistic	383.894
Degrees of Freedom	3
Asymptotic Sig. (2-sided test)	.000

1. There are 0 cells (0%) with expected values less than 5. The minimum expected value is 178.500.

Figure 4.3. Nesting site location in relation to relief at Ganga

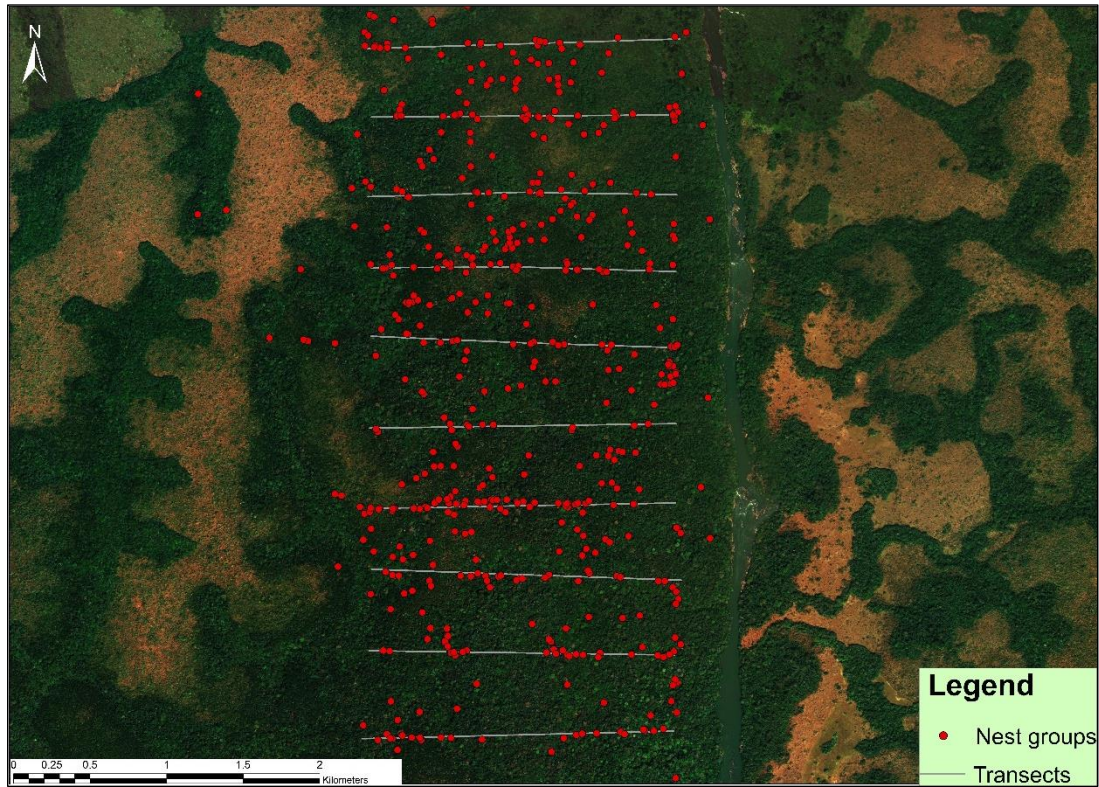
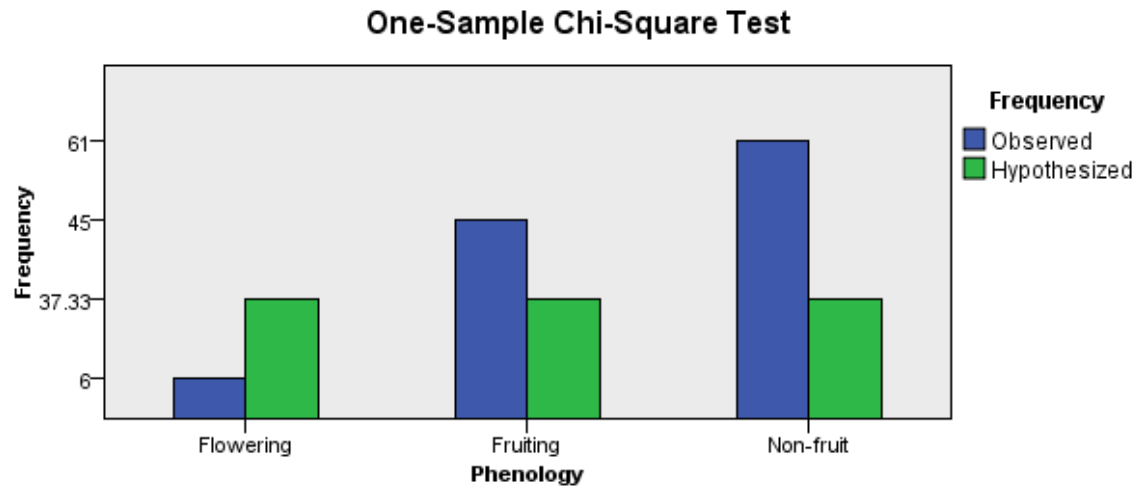


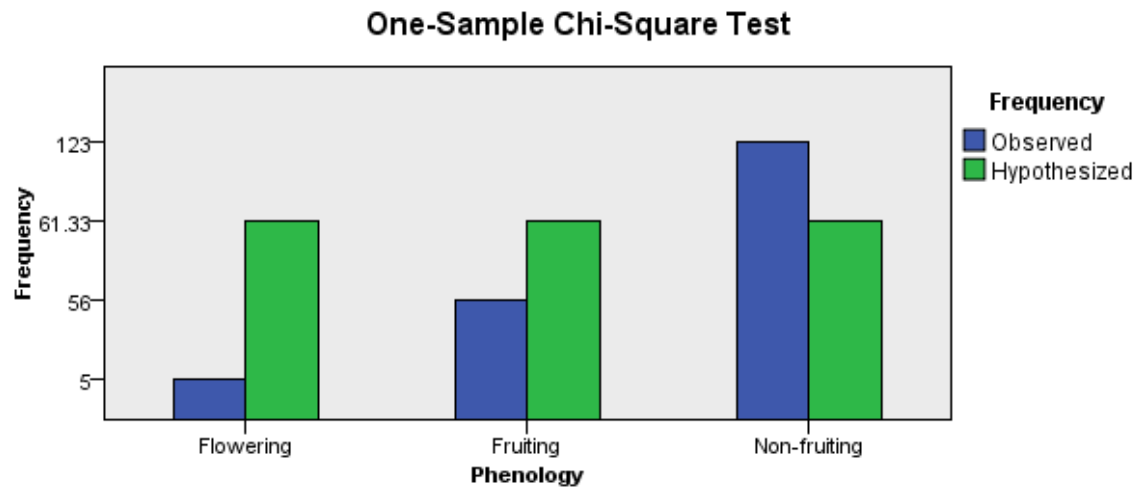
Figure 4.4. Nesting site locations at Ganga between January 2016 and December 2017



Total N	112
Test Statistic	42.875
Degrees of Freedom	2
Asymptotic Sig. (2-sided test)	.000

1. There are 0 cells (0%) with expected values less than 5. The minimum expected value is 37.333.

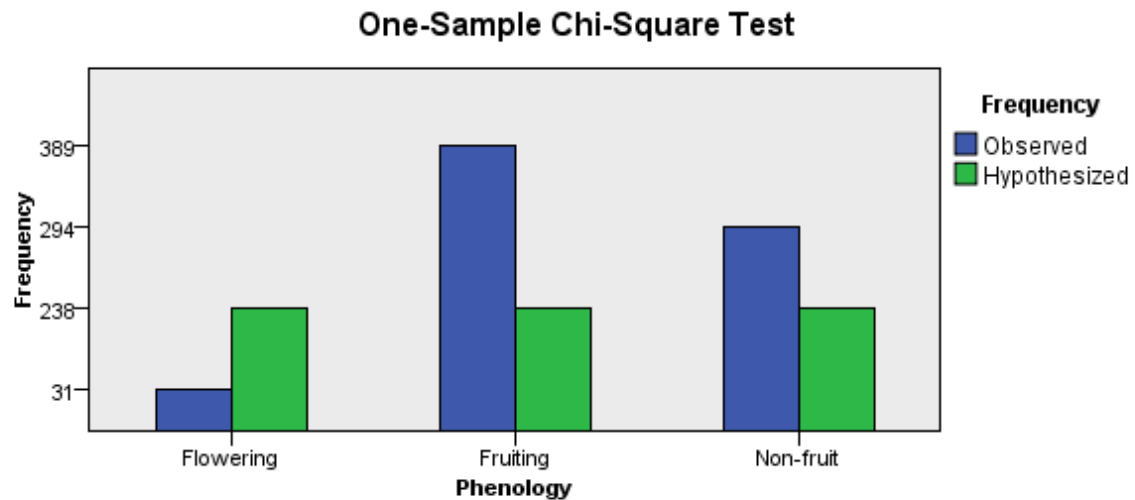
Figure 4.5. Nesting site location in relation to fruit phenology at Bekob



Total N	184
Test Statistic	114.207
Degrees of Freedom	2
Asymptotic Sig. (2-sided test)	.000

1. There are 0 cells (0%) with expected values less than 5. The minimum expected value is 61.333.

Figure 4.6. Nesting site location in relation to fruit phenology at Njuma



Total N	714
Test Statistic	289.017
Degrees of Freedom	2
Asymptotic Sig. (2-sided test)	.000

1. There are 0 cells (0%) with expected values less than 5. The minimum expected value is 238.

Figure 4.7. Nesting site location in relation to fruit phenology at Ganga

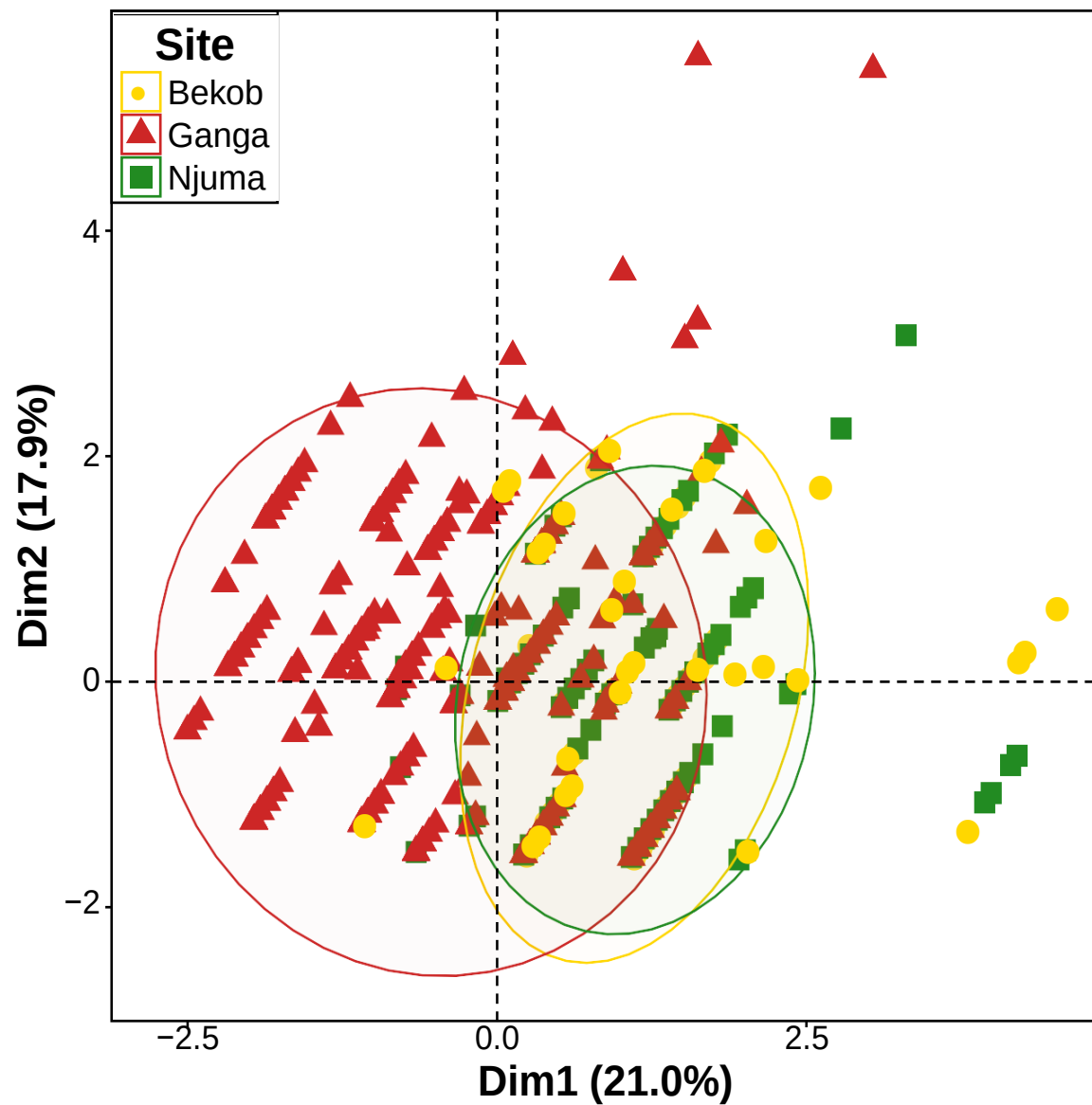


Figure 4.8: Variation in nesting site selection for chimpanzees at Bekob (circles), Njuma (squares) and Ganga (triangles). Site selection and group size differences are linked to slope, canopy and fruiting phenology

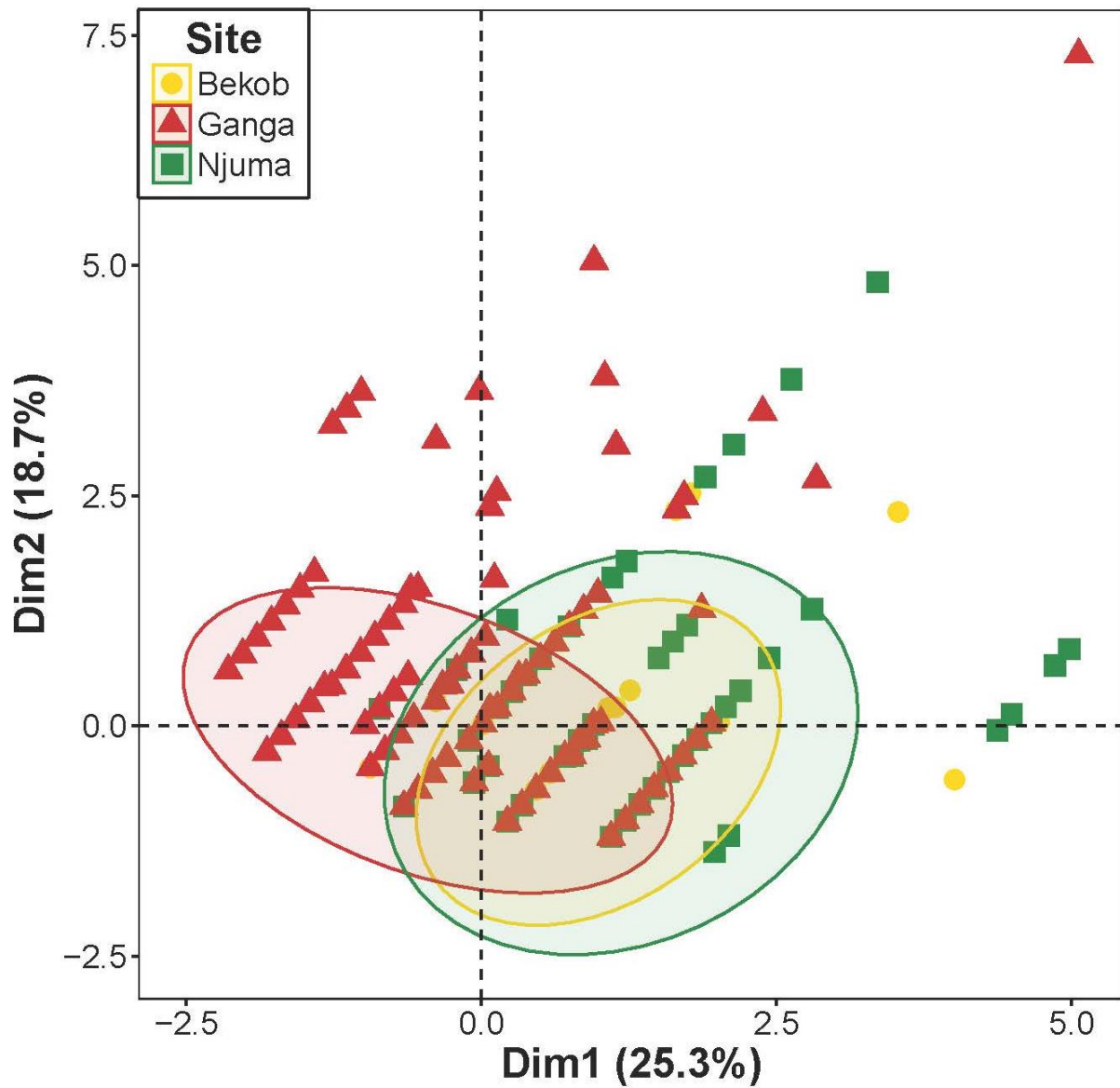


Figure 4.9: Variation in nesting site selection for chimpanzees at Bekob (circles), Njuma (squares) and Ganga (triangles) in the dry season. Site selection and group size differences are linked to slope, canopy and fruiting phenology

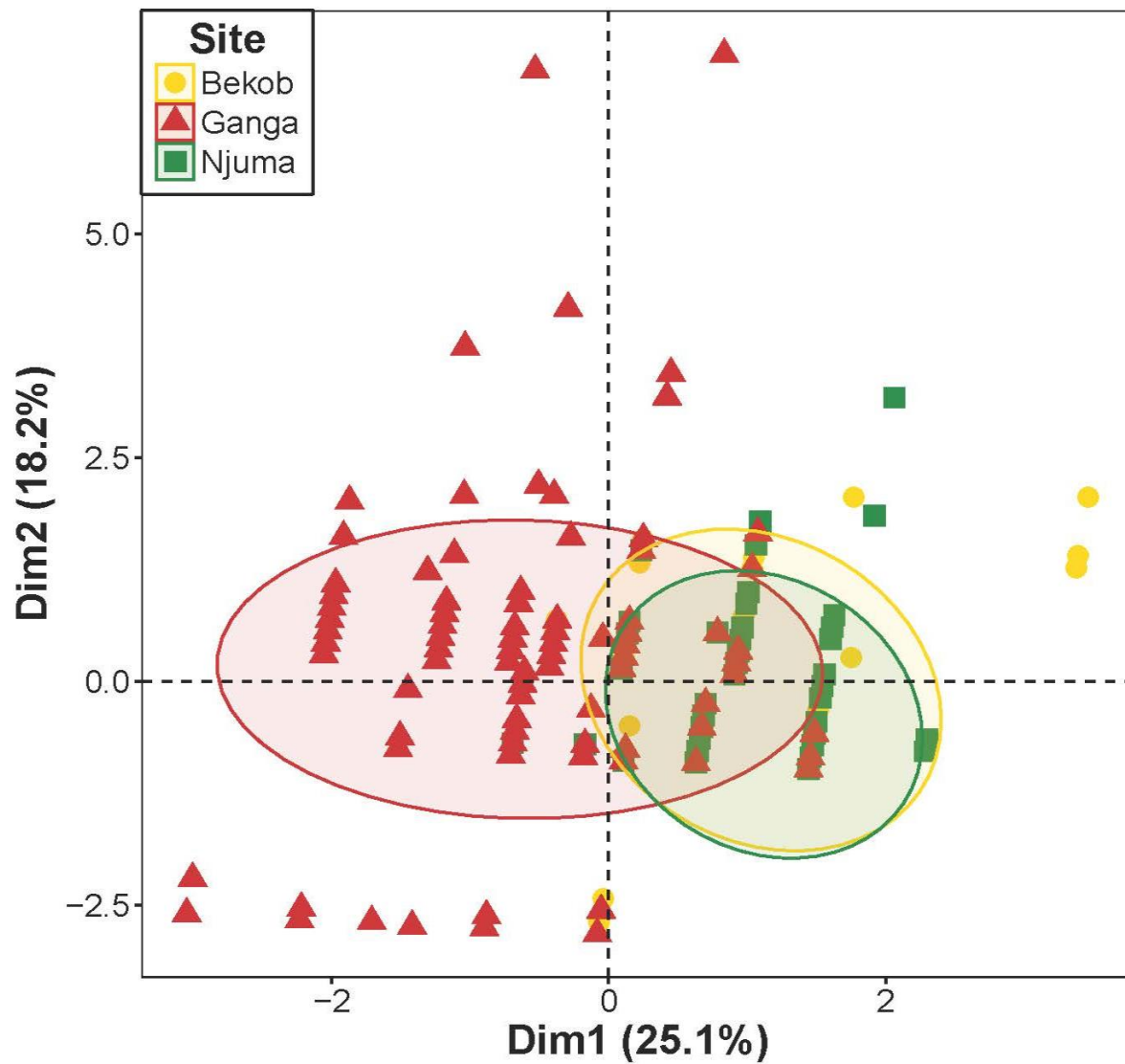


Figure 4.10: Variation in nesting site selection for chimpanzees at Bekob (circles), Njuma (squares) and Ganga (triangles) in the wet season. Site selection and group size differences are linked to slope, canopy and fruiting phenology

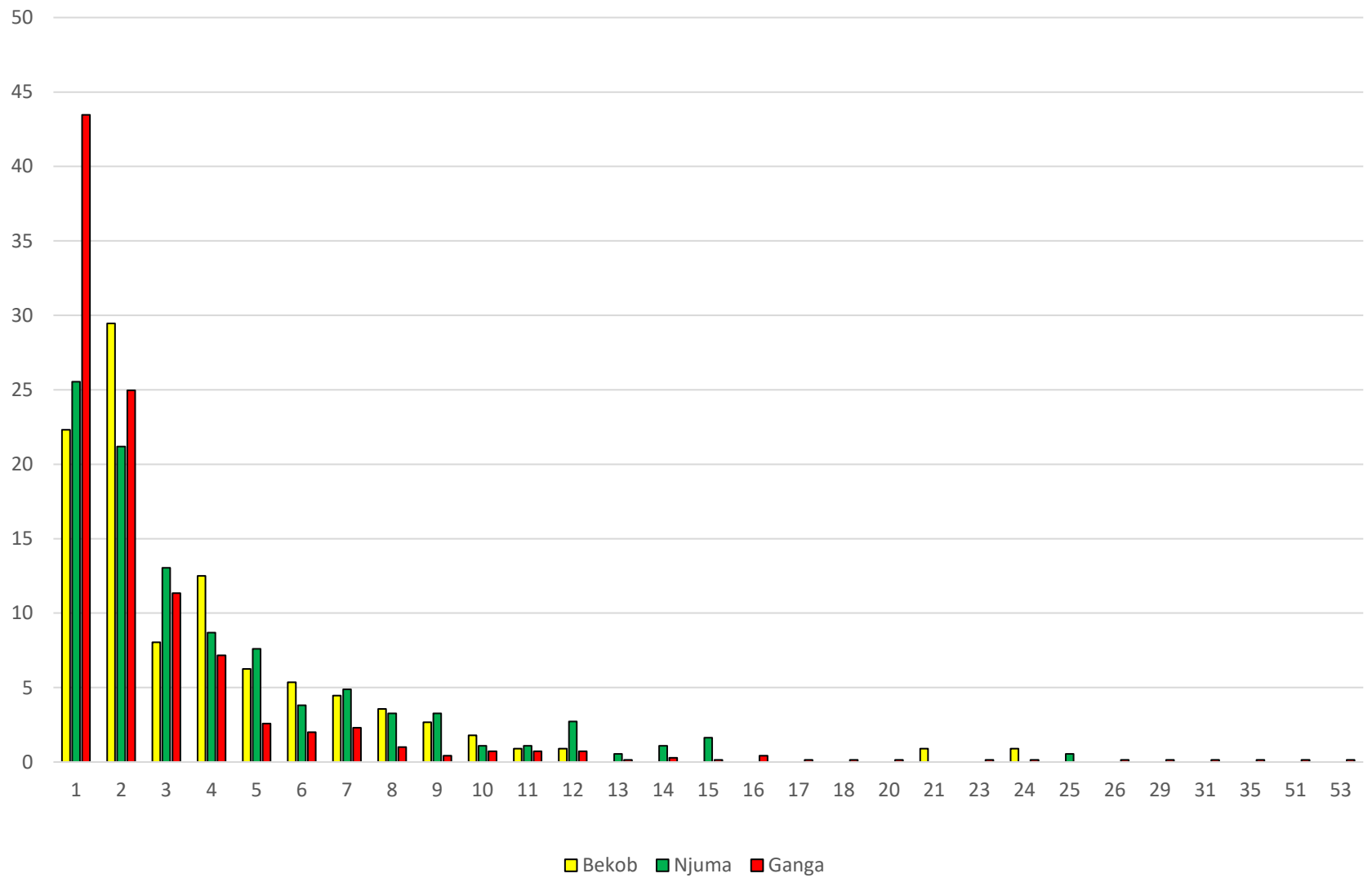


Figure 4.11. Percentage of nests in different size categories across the three sites

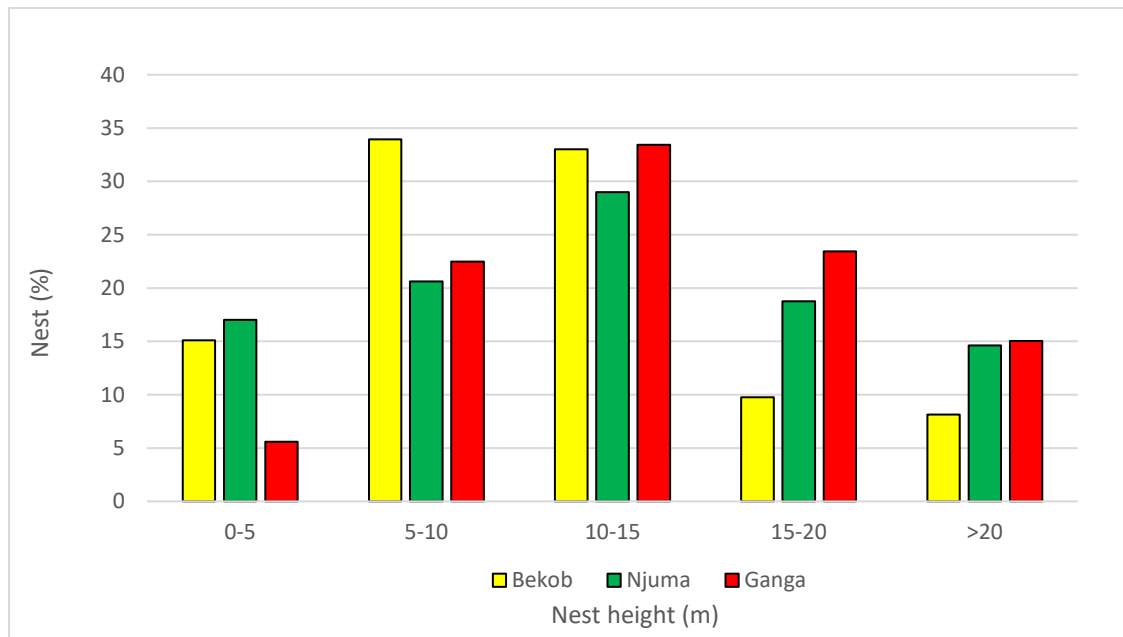


Figure 4.12. Percentage of nests in different height categories at each site

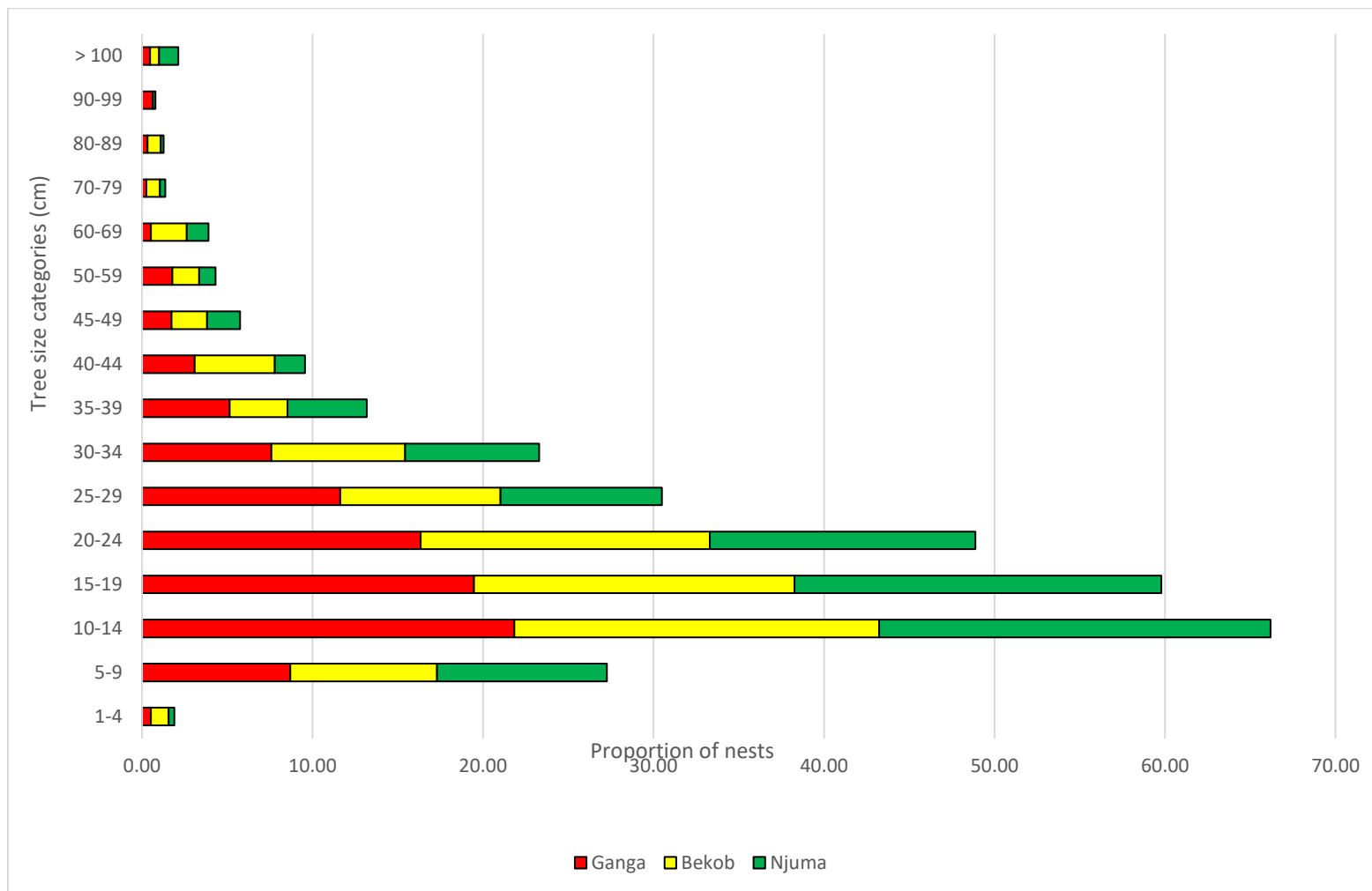


Figure 4.13. Percentage of nests in different tree size categories across the three sites

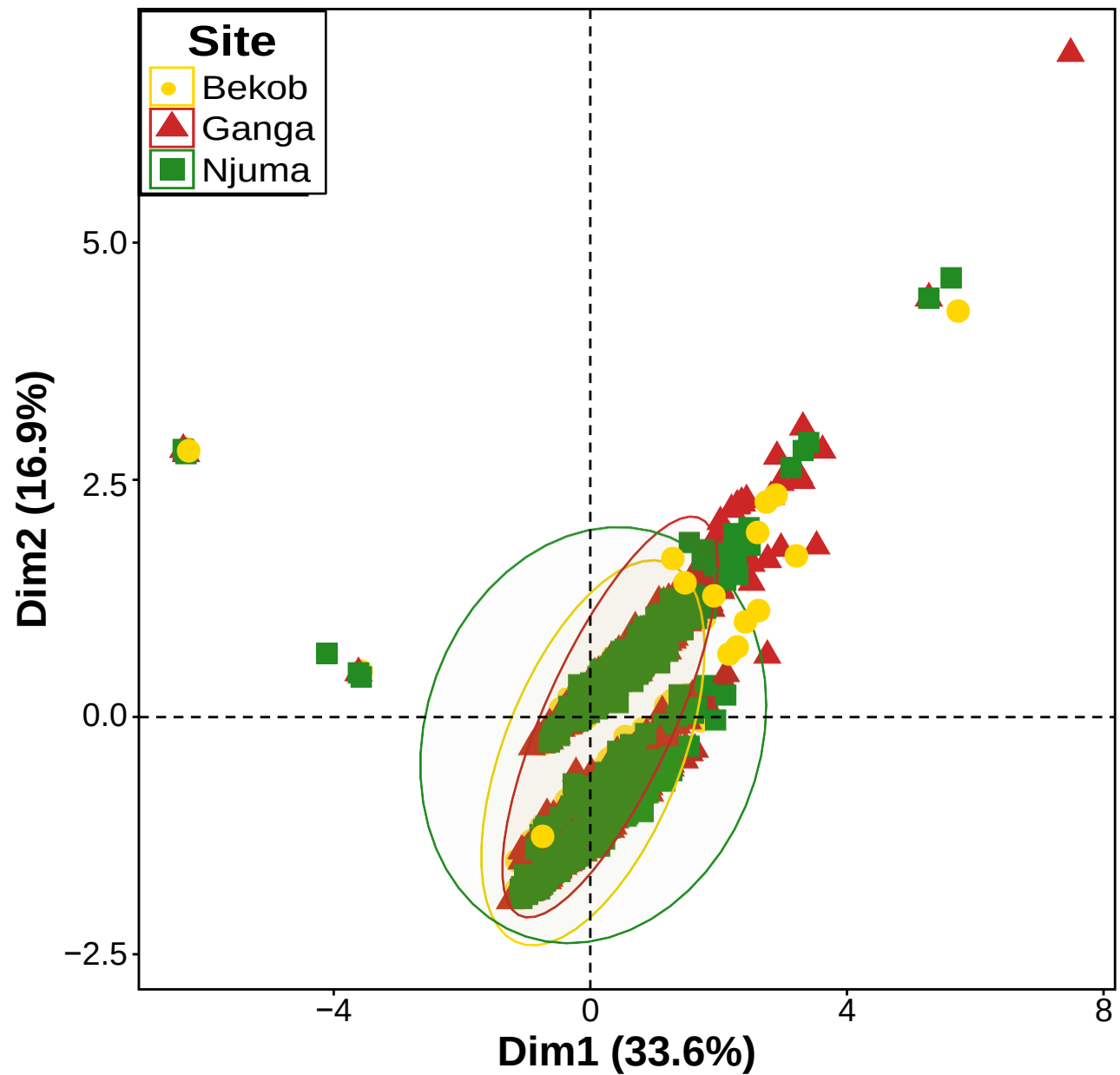


Figure 4.14: Variation in individual nest characteristics for chimpanzees at Bekob, Njuma and Ganga based on FAMD. Differences are linked to nest position in the tree, nest heights and type (arboreal or terrestrial)

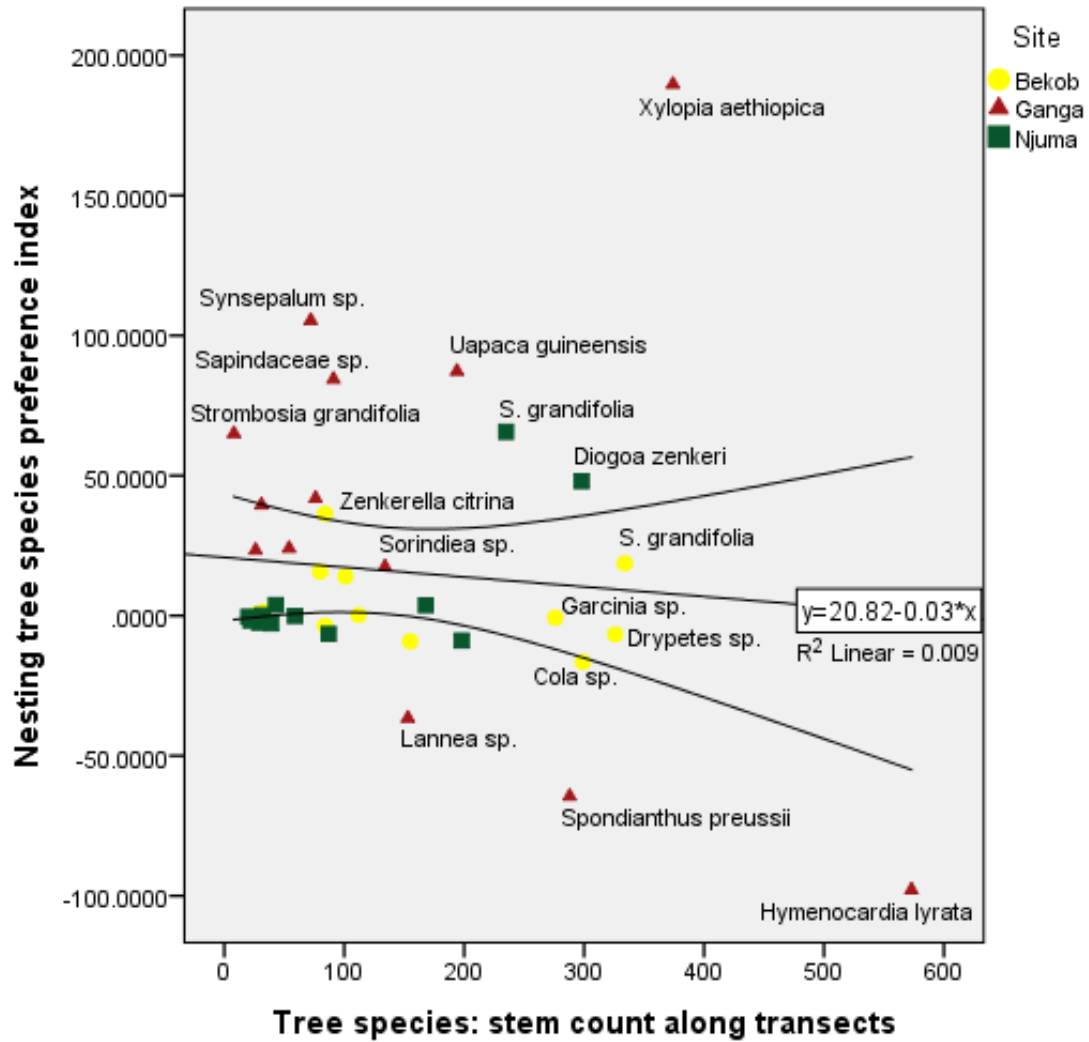


Figure 4.15: Nesting tree species preferences for Bekob (circles), Njuma (squares) and Ganga (triangles). Correlation between tree species density and preference index.

CHAPTER FIVE

5. SYNTHESIS OF RESULTS

Cameroon harbors two chimpanzee subspecies and three distinct chimpanzee gene pools associated with environmentally and ecologically defined habitats (Mitchell et al., 2015b, Sesink Clee et al., 2015), including two populations of the Nigeria-Cameroon chimpanzee (*P. t. ellioti*) one of which is found in the Ebo Forest and the other found at Mbam & Djerem National Park (MDNP). The overall goal of my dissertation was to quantify the differences in feeding and nesting ecology between these populations in three different environments (rainforest, a human-modified rainforest and an ecotone) in order to understand if these two genetically-distinct populations might also have distinctive ‘cultures’ in a rainforest versus a more open ecotone environment, as well as the degree plasticity in these behaviors found among chimpanzees living in a human-modified rainforest environment. The core question in this dissertation is: *‘Are genetic and ecological variation linked with differences in the behavioral ecology of chimpanzees?’*

To answer this broad question, I tested two specific hypotheses including:

1. *‘The niches occupied by the two distinct gene pools of the Nigeria-Cameroon chimpanzee in Cameroon are significantly different at a fine geographic scale’.*
2. *‘Niche differences have a measurable effect on the socioecology of Nigeria-Cameroon chimpanzee populations’.*

To assess niche variation, I collected data on a suit of abiotic and biotic variables including rainfall, botanical indices (tree species richness, tree sizes, tree stem density, and terrestrial herb species richness) and monthly fruit phenology through fruitfall across Ebo forest (Bekob and Njuma) and Mbam & Djerem National Park (Ganga). Rainfall data were collected daily from a traditional rain gauge

at each site, while botanical and monthly fruit phenology data were collected along ten 2 km long transects at each site.

To examine influence of habitat variation on chimpanzee socioecology, I assessed the diets of chimpanzee populations at Bekob, Njuma and Ganga using fresh fecal samples collected from nesting and feeding sites, in relation to fruit availability measured through monthly fruitfall along transects. I also examined nesting patterns through nesting site locations, nest group sizes, nest heights and tree species in which nests were built across the three populations. These data were analyzed for patterns of variation between the habitats, as well as variation in socioecological patterns within and between chimpanzee populations across these habitats.

Njuma – near pristine rainforest

Annual rainfall at Njuma was >3000 mm with a short dry season between late November and early February. These stable climatic conditions supported a diverse lowland and submontane rainforest vegetation. The tree canopy was largely closed, high and relatively homogenous, and dominated by Leguminosae and Myristicaceae. Plant species diversity was high, the result of stable climatic conditions and relatively wide altitudinal range: 100-900 m above sea level. During the wet season, there was a greater availability of fruit species that are important in the diet of chimpanzees. Many species including *Landolphia* spp., *Grewia coriacea*, and *Coula edulis* produced fruits synchronously in the wet season while *Uapaca guineensis*, *Pycnanthus angolensis*, *Antrocaryon klaineum* and *Uapaca* sp. had asynchronous fruiting patterns, producing fruits over several months in the dry and wet seasons. The encounter rate of mammals including other primates across this site was low, the result of high poaching pressure (Whytock and Morgan, 2010). Army ant and termite mound frequencies were also low.

The diversity of fleshy fruits in the diet of chimpanzees at Njuma was high, with more than 60 fruit species consumed, and fruit consumption was higher in the dry season, but seasonal dietary shifts were not very conspicuous. The cracking of nuts of *C. edulis* using stone and wooden hammers, and anvils was prevalent at Njuma (Morgan and Abwe, 2006). *Ficus* spp. were widely consumed in the dry season and could function as a fallback food resource. In addition, the consumption of fibrous foods including Marantaceae and Zingiberaceae species was more marked in the wet season. Chimpanzees at Njuma also consumed ants and termites, as well as vertebrates. But overall, the frequency of invertebrate and vertebrate consumption was relatively low.

Nesting site locations were associated with closed-canopy habitats and steep slopes. Nocturnal poaching by humans with shotguns was common across the site and locating nesting sites at hard-to-access areas for humans could be an anti-predation strategy. Nest group sizes were relatively large and could be an indication of high levels of gregariousness. Some tree species including *Strombosia grandifolia*, *Diogoia zenkeri* and *Diospyros bipidensis* were preferred nesting tree species, and the chimpanzees at Njuma made terrestrial night nests relatively frequently.

Bekob (human-modified, rainforest)

Bekob is <20 km east of Njuma (near-pristine rainforest), and altitudinally ranges between 500-1200 m. Annual rainfall at Bekob was ~2500 mm with three months of dry season between November and February. The vegetation at Bekob is heterogeneous, including abandoned villages and farmland at various stages of ecological succession following the dislocation of local human populations in the late 1950s. Higher altitude areas still harbor mature submontane vegetation dominated by *Garcinia* spp. The diversity of plant species of ≥ 10 cm DBH is high at Bekob, the result of climate, altitudinal range and anthropogenic influence. Pioneer species like *Musanga cecropioides* (umbrella tree) as well as introduced species like *Elaeis guineensis* (oil palm), *Dacryodes edulis*, and *Psidium guajava* (guava) are

common in secondary forest and abandoned farmland. Fruit availability from introduced and secondary forest species was important both in the dry and wet seasons. As a result, there was low seasonality in the availability of fleshy fruits that are important in the diets of chimpanzees at Bekob. In addition to fruit availability from introduced and secondary forest species at Bekob, the result of anthropogenic modification, fruit phenology at the site could also be linked to shifts along the elevational gradient (500 – 1200 m) and stable climatic conditions. The encounter frequency of diurnal primates was low and could be attributed to high poaching pressure (Whytock and Morgan, 2010).

Fruits were the most important component in the diet of chimpanzees at Bekob, and 59 different species were observed in 270 feces collected across the site. Seasonal variation in fleshy fruit consumption at Bekob was low. The dry season was characterized by relatively high consumption of *Ficus* spp., as well as secondary and introduced species including *M. cecropioides* (umbrella tree) and *E. guineensis* (oil palm). Seasonal shifts in fruit diets were less conspicuous at Bekob because of the consumption of these secondary and introduced species. Terrestrial herbs were also important for the feeding ecology of chimpanzees at Bekob especially in the wet season. Termites, army ants and honey were consumed by chimpanzees and were harvested with the use of tools. There were signs of mammal remains in feces, but overall the consumption of vertebrates and invertebrates was relatively low.

Fruit availability did not significantly influence nesting site location at Bekob, even though nesting in secondary forest was associated with the dry season when tree species in this habitat were fruiting. Nesting site location was associated with steep topography, and this could be attributed to the prevalence of poaching especially at night with shotguns. The mean nest group size at Bekob was 3.81 nests (4.62 nests without singletons), while mean nest height was 10.81 m. Though nests were built in

many tree species, some species were preferred including *Zenkerella citrina*, *Diogoia zenkeri*, *Strombosia grandifolia* and *Elaeis guineensis*.

Ganga (ecotone)

The MDNP is located ~300 km north east of Ebo forest at the interface of the Congo Basin and Gulf of Guinea rainforests, and the Sahel. Annual rainfall at MDNP was ~2000 mm with a marked dry season between November and March. The habitat at Ganga was heterogenous comprising high and low closed-canopy gallery forest, high and low open-canopy secondary forest and savanna. Species diversity of trees and lianas of ≥ 10 cm DBH was relatively low, the result of climatic variation and anthropogenic influence (bushfires). But the frequency and stem density of tree species producing fruits on which chimpanzees feed including *Landolphia* spp., *Saba* spp., *Pseudospondias microcarpa*, *Uapaca guineensis* and *Myrianthus arboreus* was relatively high at Ganga. The site also had a high frequency and diversity of terrestrial herb species in the Marantaceae and Zingiberaceae families. Fruit availability was high at Ganga with many species producing fruits synchronously between April and October which coincided with the wet season. Fruit availability was low in the dry season and restricted to *U. guineensis* and *Ficus* spp. The occurrence of diurnal primates, army ant nests and termite mounds across Ganga was relatively high.

More than 50 fruit species were consumed by the chimpanzees at Ganga. The proportion of fruit in chimpanzee diets at Ganga during the wet season was high, and was dominated by a few species including *Landolphia* spp., *Pseudospondias microcarpa* and *Myrianthus arboreus*. The proportion of fibrous foods in the diet as well as feeding signs on Marantaceae and Zingiberaceae species were high in the dry season. The consumption of vertebrates and invertebrates at Ganga was regular and consistent and was inversely proportional to fruit consumption. Either meat consumption was a fallback food resource, or it was a supplement to the largely fibrous food diet in the dry season.

Nesting behavior at Ganga was closely linked to fruit availability. Nesting site locations were correlated to the presence of fruits in various habitats. Larger nest groups were associated with the wet season, while single nest groups accounted for more than 40% of the nests, mainly in the dry season. Wet season nests were constructed at higher locations in the trees, and this may be associated with thermoregulation – limiting the discomfort of water dripping from overhead leaves and branches after downpours. Many tree species were used for nesting but there were preferences for some species including *Xylopia aethiopica*, *Uapaca guineensis*, and *Stombosia grandifolia*.

Ecotone and rainforest habitat variation

The hypothesis that ecotone and rainforest habitats were significantly different at a fine geographic scale was supported. The main abiotic and biotic variables that separated the ecotone and rainforest habitats were: rainfall, tree species diversity, tree and liana density, and the density and diversity of THV. The rainforest habitats were characterized by more rainfall and less seasonality compared to Ganga. The density and diversity of tree species were higher at Bekob and Njuma than Ganga. But the density of lianas, and the frequency and diversity of THV in the Marantaceae and Zingiberaceae families were higher at Ganga than either Bekob or Njuma. Finally, the availability of fleshy fruits was higher at Ganga, but with more pronounced seasonality. The wet season had a higher density and diversity of fleshy fruits than the dry season. The wet season at Njuma was also characterized by higher fruit availability compared to the dry season. There was no seasonal difference in fruit availability at Bekob, which was linked to the asynchronous fruiting patterns of introduced and secondary forest species, and fruit phenology shifts along the elevational gradient.

Ecotone and rainforest dietary variation

Fruits were the most important component of chimpanzee diet at Bekob, Njuma and Ganga, which lends support to the widespread finding that frugivorous diet is a species-typical feature of the species. But there were significant differences in the dietary patterns between the different populations, which taken together support the hypothesis that ecological variation is linked with variation in socioecology of chimpanzees. Some of the key findings that lend support to this hypothesis, include differences in the numbers and kinds of fruits eaten at each site throughout the year and the amount of protein and fibrous foods eaten at each site during periods of fruit scarcity. The diversity of fleshy fruit species as well as the proportion of fruits in chimpanzee diets at Bekob and Njuma were higher than at Ganga. In addition, there were seasonal differences in fleshy fruit consumption across the three sites. The consumption of fleshy fruits was higher in the dry season at Bekob and Njuma but was less significant in the wet season. The diversity of fleshy fruit species consumed in the wet and dry seasons was higher at Bekob and Njuma than Ganga. At Bekob, introduced and secondary forest species including *Elaeis guineensis* (oil palm) and *Musanga cecropioides* (umbrella tree) fruits were present in 14.8% and 33.3% of fecal samples respectively. Conversely, fleshy fruit consumption was higher for the chimpanzees at Ganga during the wet season and less significant in the dry season. Contrary to my expectations, the dietary diversity in fleshy fruit was not positively associated with the fruit species diversity based on monthly fruitfall along transects. Rather, some fruit species were preferred especially at Ganga.

There was no significant difference in the proportion of fibrous food remains in the diets of chimpanzees at Bekob, Njuma and Ganga. However, there were seasonal differences in the significance of fibrous foods for the ecotone and rainforest chimpanzee populations. The consumption of fibrous foods was marked at Bekob and Njuma during the wet season, but at Ganga, the

consumption of fibrous foods peaked during the wet season. The significance of fibrous foods in the diet as well as feeding signs on THV was associated with the dry season at Ganga during which the availability of fleshy fruits was low.

Animals comprised a significantly higher fraction of chimpanzee diet at Ganga compared to Bekob and Njuma occurring in 36.9%, 9.6% and 10.9% respectively in fecal samples collected across the sites. Across the three sites, animal consumption was inversely proportional to fleshy fruit consumption, with a pronounced peak of predation occurring in the dry season especially at Ganga. Signs of vertebrate preys in fecal samples at Ganga included crowned guenon (*Cercopithecus pogonias*), black and white colobus (*Guereza colobus*) and duikers. Termites (*Macrotermes* spp.) and army ants (*Dorylus* spp.) were targeted across the three sites. In addition, at Ganga, chimpanzees also targeted carpenter ants (*Camponotus brutus*) and black ants (*Pachycondyla* spp.)

Ecotone and rainforest nesting variation

Nesting patterns varied between rainforest and ecotone habitats, consistent with the hypothesis linking ecological variation with socioecological variation. At Bekob and Njuma, closed-canopy habitats were preferred chimpanzee nesting site locations, while the chimpanzees at Ganga did not show preference for any habitat type for nesting. Open- and closed-canopy habitats were selected at Ganga, and this was linked to the availability of fruits within these habitat classes. Nesting site locations at Bekob and Njuma were also associated with steep relief, which was attributed to safety from poachers who hunt at night with shotguns across these sites. Nest group sizes were also linked to fruit availability with larger groups associated with periods of higher fruit availability especially at Ganga where groups of more than 50 nests were encountered during the wet season. Chimpanzee parties encountered between June and September across Ganga were also generally large, often more >30 individuals. The largest nest group size for Bekob was 24 nests and 25 nests for Njuma. The

chimpanzees at Ganga and Njuma nested higher in the trees than chimpanzees at Bekob, and at all sites, some tree species were preferred for nesting.

Habitat and ecological correlates to chimpanzee socioecology

There were key links between ecological variation and socioecological behaviors across the three sites. Fruiting phenology underpins many aspects of chimpanzee socioecology, Bekob and Njuma (rainforest) and Ganga (ecotone) chimpanzee populations altered their dietary and nesting behavior seasonally based on fruit availability. In general, the diversity of fleshy fruits in chimpanzee diets at Bekob and Njuma which are associated with higher plant species diversity were similar and higher than for chimpanzees at Ganga. However, seasonal dietary shifts between fruits and fibrous foods were less marked for Bekob compared to Njuma. This could be attributed to lower seasonality in fruit availability at Bekob where introduced and secondary forest species were important dietary components especially during periods of low fleshy fruit availability. Fruit consumption was marked at Ganga in the wet season, and the shift to fibrous food diet in the dry season was pronounced. The availability of diverse THV species at Ganga provided the ecotone chimpanzees with a fallback food resource when fruits were scarce. Terrestrial herbs were important in diets of the rainforest chimpanzees in the wet season though dietary shifts were not as pronounced as with the ecotone chimpanzees in the dry- and wet- seasons.

Nesting patterns were also linked to ecological and environmental conditions across the sites. Chimpanzees at Ganga preferentially selected nesting sites that were near or adjacent to locations with trees that were fruiting. This site selection may be aimed at reducing travel costs in a heterogenous habitat, consisting of shifts between forest, woodland and savanna across mostly flat landscape. At the mountainous rainforests sties of Bekob and Njuma, nesting site selection was linked to slopes (especially well-hidden slopes near well-hidden gorges). I speculate that this nest site

selection may be geared towards safety since steep, well-hidden gorges likely allows these chimpanzees to hide from poachers who hunt at night across the sites. The chimpanzees at Njuma made terrestrial night nests, but this behavior was not observed at Bekob and Ganga. This may be linked to the presence of elephants at Bekob and Ganga and their absence at Njuma, because elephants can disturb chimpanzees sleeping on the ground while foraging at night.

Seasonality in fruit availability was also associated with nest group sizes, especially at Ganga. During the wet season which was associated with higher fruit availability, nest group sizes were larger compared to the dry season that had a high prevalence of single nest groups. Nest heights were higher at Njuma and Ganga than Bekob. This could be linked to forest structure at Njuma which was characterized by largest mean tree sizes, and the fact that at Ganga, chimpanzees preferentially nested in *Xylopia aethiopica* – a tall tree species with high first branches.

Chimpanzees at ecotone and rainforest habitats across Africa

Socioecology of ecotone and savanna communities

Ecotone and savanna habitats across Africa are characterized by relatively low annual rainfall and pronounced seasonality (Table 1), which leads to marked seasonal variation in the availability of fruits on which chimpanzees depend for survival (Hohmann et al., 2012, Pruetz and Bertolani, 2009). Fruit dietary diversity of chimpanzees in such habitats is low throughout the year. In response to seasonal fruit scarcity, dietary shifts including the consumption of non-fruit plant parts are marked, and chimpanzees in the ecotones and savannas tend to incorporate more protein into their diets across the year. The consumption of invertebrates and vertebrates is significantly high in some dry habitat populations compared to rainforest habitats (Bogart and Pruetz, 2011, Fowler and Sommer, 2007, Sommer et al., 2017) – Table 3.7. This could be a fallback food strategy or a supplement to lower non-fruit diets consumed during periods of fruit scarcity (Bogart and Pruetz, 2011). Other socioecological

adaptations in dry savanna habitats include ranging wider and low levels of affiliation between members (Dutton and Chapman, 2015, Hohmann et al., 2012, Hunt and McGrew, 2002, McGrew et al., 1981, McGrew et al., 1988, Pruetz, 2006, Pruetz and Bertolani, 2009). Savanna chimpanzees develop strategies to cope with water scarcity including digging wells on dry river beds and feeding on water-rich tubers (Hunt and McGrew, 2012, Lanjouw, 2012). But dry habitat chimpanzees are also documented to have physiological adaptations to water scarcity (Wessling et al., in press). But nest group sizes at some dry habitats are larger than foraging parties and this is linked to predation risk and restricted closed-canopy habitats, that are preferred nesting sites (Ogawa et al., 2007, Hunt and McGrew, 2002). Dietary patterns at Ganga with pronounced seasonal differences in the importance of fleshy fruit, fibrous food, and animal components reflect the patterns of chimpanzees in these drier habitats. Mean nest group size at Ganga is smaller than for some savanna habitats, where safety from predators or dearth of adequate nesting site influence foraging parties to congregate at nesting sites (Ogawa et al., 2007) – Table 4.2.

Socioecology of rainforest chimpanzee communities

Chimpanzees inhabit many rainforest habitats across Africa which are all characterized by high annual rainfall and short dry seasons (Basabose, 2002, Head et al., 2011, Herbinger et al., 2001, Newton-Fisher, 1999, Sugiyama, 1989) – Table 1. Plant diversity in rainforests are high, and as result, rainforest chimpanzee populations have a high dietary diversity (Deblauwe, 2009, Head et al., 2011, Morgan and Sanz, 2006, Newton-Fisher, 1999, Watts et al., 2012a) – Table 3.7. Chimpanzee ranging patterns under these conditions are characterized by larger foraging parties which are also reflected in larger nest group sizes (Brownlow et al., 2001, Basabose and Yamagiwa, 2002, Lehmann and Boesch, 2004, Mitani et al., 2002a) – Table 4.2, and high levels of bonding between group members (Boesch, 1996, Herbinger et al., 2001). Chimpanzees at both Bekob and Njuma have a diverse fleshy fruit diet,

and though THV is important in their diet, seasonal shifts in dietary components are less pronounced at Njuma and Bekob. Nest group sizes were relatively large and stable in size throughout the year, which mirrors those of other rainforest chimpanzee populations (Brownlow et al., 2001, Basabose and Yamagiwa, 2002, Lehmann and Boesch, 2004, Mitani et al., 2002a).

There are important distinctions between Bekob and Njuma, however, since Bekob had a long period of human habitation. Habitat heterogeneity is characteristic of many human-modified landscapes, with temporal and spatial availability of fruits from exotic, secondary and primary species influencing the socioecology of chimpanzees (Humle and Matsuzawa, 2001, Sugiyama and Koman, 1992, Yamakoshi, 1998). At such landscapes, primary and secondary forest fruit species and cultivars are important components of chimpanzee diets (McLennan, 2010, Sugiyama and Koman, 1992). Chimpanzee use of cultivars especially during periods of wild fruit scarcity has often resulted to conflicts with humans across many sites (McLennan, 2010, Hockings et al., 2009). Due to the alteration of natural species composition of habitats, chimpanzee in such habitats build nests in introduced species (Carvalho et al., 2014, Humle, 2003, McCarthy et al., 2017). The chimpanzees at Bekob exhibited characteristics of adapting to human-modified habitats in their including dietary dependence on introduced and secondary forest species especially during periods of fleshy fruit scarcity, as well as nesting in oil palm trees.

Limitations and future directions

There were some limitations associated with this project. First, conducting comparative studies simultaneously across geographically remote sites can be challenging, and working with different field assistants at each site may have resulted in some inconsistencies in data recording between the sites. Second, the use of fecal sample to assess chimpanzee diets is widespread but is biased toward food items that leave discernible traces in feces. The full range of the dietary repertoire at each site and

variation between these sites can only be understood with long term direct observation of feeding behaviors. In addition, fecal samples used in the analysis for Bekob and Njuma spanned several years (2005-2017), as the sample sizes from the two sites during the study period were small. This made it impossible to correlate fruit availability from fruit monthly fruitfall along transects and fruit consumption at these sites. Finally, locating chimpanzee signs including nests, feces, tool use and feeding remains at Bekob and Njuma was arduous due to the rugged topography and the fact that chimpanzees were even more wary of humans at these two sites because of high hunting pressure.

Chimpanzee habituation can increase the scope of socioecological research and conservation for the species in Cameroon. There is currently no habituated group of wild chimpanzees for either *P. t. ellioti* or *P. t. troglodytes* in Cameroon. Investing on habituation especially in populations with low human threats like Ganga in the MDNP could foster conservation and research efforts, and even impact positively on government policy for other chimpanzee populations across the country. There is however the need for careful planning with a range of stakeholders including concerned government departments, NGOs, habituation experts, research and educational institutions, local administrative and municipal authorities, local communities as well as other civil society groups.

This study was limited to ecological and socioecological variation in the two gene pools of *P. t. ellioti*, and it will be important to do a more comprehensive assessment that will include *P. t. troglodytes* populations, which also live in a distinctive Congo Basin rainforest habitat (Sesink Clee et al. 2015) in order to have a better understanding of the socioecological factors that contribute to, or results from, chimpanzee diversification in Cameroon. It will also be important to investigate other aspects of chimpanzee socioecology across these sites including subsistence tool use behavior and predation on other mammals. Variation in tool use behavior between chimpanzee populations is linked to ecological and cultural differences (McGrew et al., 1997, Whiten et al., 1999). Mammal species

targeted, and hunting techniques vary between chimpanzees inhabiting closed- and open-canopy habitats (Stanford et al., 1994, Boesch and Boesch, 1989), but cultural differences could also be important in the apparent absence of mammal hunting in some populations (Morgan and Sanz, 2006, Fowler, 2006). A broader understanding of the socioecological differentiation based on ecological and cultural variation could be important in assessing patterns of location adaptation and intraspecific divergence in chimpanzee populations across this region.

Previous studies ascertained the genetic history of chimpanzees across Cameroon, and have considered broadly how ecological variation may have contributed to the development of the unique genetic history of this species in this region where two rainforest biomes, the Sahel and the desert all converge with one another. This study, which was carried out at a finer geographic scale, ascertained how environmental variation contributes to socioecological variation within the Nigeria-Cameroon chimpanzee habitats in the rainforest of Bekob, Njuma and at a forest-savanna ecotone at Ganga. Specifically, this study ascertained differentiation in chimpanzee socioecology linked with distinct habitat types: human-modified rainforest, pristine rainforest and ecotone. However, there is a need to jointly analyze how local variation in the socioecology of rainforest and ecotone chimpanzee populations correspond with adaptive genetic variation found across this region. Moving forward, it will be important to combine these environmental and ecological data with SNP genotype panel of wild chimpanzees sampled across this area to examine gene-by-environment interactions. Jointly these data will allow for detailed examination of how local chimpanzees cultures shape patterns of local adaptation in this species.

Conservation status of P. t. ellioti in Cameroon

The results of this study highlight the diversity and uniqueness of habitats harboring important chimpanzee populations including rainforest, ecotone and human-modified habitats in Cameroon, and

the chimpanzee range across Africa in general. With persistent human population increase and the quest for economic development, more natural habitats will be converted into various human land-use forms, increasing human-wildlife conflicts especially for great apes in the coming decades. Many chimpanzee populations have adapted and persisted in human-modified or dominated landscapes (McLennan, 2010, Hockings et al., 2009, Sugiyama and Koman, 1992). Such habitats should be considered in conservation planning.

Differential socioecological behavior across chimpanzee populations is linked to environmental and ecological variation. Chimpanzee populations in different habitat types across Africa respond to seasonal variability in fruit availability, predation pressure from humans and carnivores, and other ecological and environmental variation in different ways (Basabose & Yamagiwa, 2002, Hashimoto et al., 2001, Ogawa et al., 2007, Pruetz & Bertolani, 2009, Tagg et al., 2013, Tutin et al., 1997, Wrangham et al., 1998). All chimpanzee populations are frugivorous, but dietary diversity and seasonality in fruit consumption differs between populations (Stumpf, 2011). Secondary forest species as well as cultivars are important dietary components of chimpanzees at human-dominated or modified landscapes especially during periods of fruit scarcity (McLennan, 2010, Hockings et al., 2009).

Many chimpanzee populations use tools for subsistence to acquire termites, ants as well as honey (Bogart & Pruetz, 2011, Deblauwe, 2009, Fowler & Sommer, 2007, Sanz & Morgan 2006). The use of stone and wooden hammers to crack nuts is restricted to some *P. t. verus* populations and *P. t. ellioti* in the Ebo forest (Abwe & Morgan, 2008, Boesch & Boesch, 1983, Morgan & Abwe, 2006, Wrangham, 2006). Chimpanzee nesting behavior is linked to the fruiting phenology, habitat types, safety and comfort (Basabose & Yamagiwa, 2002, Furuichi & Hashimoto, 2004, Koops et al., 2012, Ogawa et al., 2007, Samson & Hunt, 2014, Stanford & O'Malley, 2008). Patterns of nesting in human-modified landscapes including tree species choice, arboreal and terrestrial nesting decisions vary from

more natural habitats (Humble, 2003, McCarthy et al., 2017, Tagg et al., 2013). Comprehensive chimpanzee conservation planning should consider habitat, socioecology and genetic diversity in the species.

Chimpanzees are protected in Cameroon by national (Law N° 94/01) and international wildlife laws <www.iucnredlist.org>. In addition, several protected areas span the chimpanzee range, but law enforcement is lacking in most of these protected area, and as a result, many populations of chimpanzees in and outside protected areas are targeted for meat and pet trade (Fa et al., 2006, Morgan et al., 2011, Oates et al., 2004, Tutin et al., 2005). The Ebo forest and MDNP harbor the largest remaining *P. t. ellioti* populations in Cameroon (Morgan et al., 2011). Unfortunately, the Ebo forest is unprotected and subjected to high hunting pressure, habitat loss through subsistence and agro-industrial agriculture. Since 2005, the San Diego Zoo Global - Ebo Forest Research Project, has been carrying out biological research and conservation outreach in and around the Ebo forest to protect chimpanzees, gorillas, drills, Preuss's red colobus monkeys and other endangered primates; mammals and other species. This program works with local communities and a range of stakeholders to conserve the rich biodiversity of the forest for posterity (Abwe and Morgan, 2012, Abwe et al. 2014). The MDNP is officially protected by the government of Cameroon (MINFOF) through a network of rangers who are stationed around the park (<https://cameroon.wcs.org>). Conservation outreach by the Wildlife Conservation Society (WCS) and MINFOF in human communities adjacent to the MDNP are also ongoing (WCS, 2015). While this paints a positive portrait of conservation and protection at this park, the effort and resources are not nearly at the scale they need to be to ensure the continued survival of chimpanzees and other vulnerable wildlife at MDNP. To put the conservation effort into perspective, MDNP is the size of the Grand Canyon, but is only patrolled by a team of 34 MINFOF park rangers (WCS, 2011). The situation for Nigeria-Cameroon chimpanzees outside these two areas is even

less-certain. *P. t. ellioti* populations also occur in Mount Cameroon National Park, Korup National Park, and the Banyang-Mbo Wildlife Sanctuary, but most of these parks lack the technical and logistical capacity for effective conservation. The status of the chimpanzee populations remains largely unknown. There is an urgent to assess the status of these remaining populations, as well as to bolster protection efforts at Ebo Forest and Mbam & Djerem National Park to help ensure the survival of these populations.

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Appendix Chapter 2

Appendix 2.1. Shared species and similarity statistics – between 10 transects at human-modified rainforest-Bekob

First Sample	Second Sample	^{Sobs} First Sample	^{Sobs} Second Sample	Shared Species Observed	ACE First Sample	ACE Second Sample	Chao Shared Estimated	Chao-Jaccard-Raw Abundance-based	Chao-Jaccard-Est Abundance-based	Chao-Sorensen-Raw Abundance-based	Chao-Sorensen-Est Abundance-based	Morisita-Horn	Bray-Curtis
1	2	120	93	52	195.903	142.667	92.067	0.49	0.597	0.658	0.748	0.586	0.416
1	3	120	114	68	195.903	164.792	123.31	0.656	0.882	0.792	0.937	0.707	0.498
1	4	120	100	54	195.903	129.732	75.407	0.609	0.741	0.757	0.851	0.428	0.392
1	5	120	116	73	195.903	154.548	119.051	0.748	0.906	0.856	0.951	0.821	0.62
1	6	120	98	55	195.903	140.944	91.252	0.583	0.759	0.737	0.863	0.694	0.505
1	7	120	106	61	195.903	154.292	92.532	0.593	0.737	0.745	0.849	0.699	0.479
1	8	120	126	65	195.903	178.804	104.847	0.56	0.715	0.718	0.834	0.685	0.478
1	9	120	106	59	195.903	150.746	77.201	0.595	0.759	0.746	0.863	0.701	0.5
1	4	120	104	58	195.903	136.556	87.941	0.594	0.716	0.745	0.834	0.789	0.548
2	3	93	114	54	142.667	164.792	84.183	0.594	0.746	0.745	0.855	0.763	0.534
2	4	93	100	59	142.667	129.732	82.809	0.767	0.875	0.868	0.933	0.793	0.58
2	5	93	116	58	142.667	154.548	84.269	0.582	0.671	0.736	0.803	0.677	0.511
2	6	93	98	51	142.667	140.944	73.116	0.639	0.735	0.78	0.847	0.634	0.476
2	7	93	106	52	142.667	154.292	73.721	0.651	0.739	0.788	0.85	0.861	0.592
2	8	93	126	54	142.667	178.804	87.396	0.599	0.756	0.749	0.861	0.781	0.536
2	9	93	106	54	142.667	150.746	70.506	0.713	0.906	0.832	0.951	0.787	0.555
2	10	93	104	47	142.667	136.556	65.054	0.59	0.639	0.743	0.78	0.704	0.552
3	4	114	100	60	164.792	129.732	93.358	0.674	0.783	0.805	0.878	0.609	0.491
3	5	114	116	62	164.792	154.548	83.445	0.637	0.744	0.778	0.853	0.797	0.559
3	6	114	98	57	164.792	140.944	90.765	0.645	0.742	0.785	0.852	0.633	0.47
3	7	114	106	70	164.792	154.292	145.832	0.73	0.9	0.844	0.947	0.773	0.555
3	8	114	126	72	164.792	178.804	155.282	0.69	0.837	0.817	0.911	0.809	0.583
3	9	114	106	55	164.792	150.746	84.836	0.646	0.736	0.785	0.848	0.77	0.523
3	10	114	104	56	164.792	136.556	75.632	0.628	0.667	0.772	0.8	0.783	0.556

4	5	100	116	63	129.732	154.548	90.194	0.688	0.78	0.816	0.876	0.575	0.499
4	6	100	98	52	129.732	140.944	69.237	0.671	0.801	0.803	0.889	0.363	0.376
4	7	100	106	58	129.732	154.292	107.732	0.692	0.805	0.818	0.892	0.745	0.505
4	8	100	126	64	129.732	178.804	105.626	0.685	0.827	0.813	0.906	0.584	0.459
4	9	100	106	55	129.732	150.746	78.899	0.7	0.827	0.823	0.905	0.552	0.454
4	10	100	104	57	129.732	136.556	68.39	0.71	0.774	0.83	0.872	0.461	0.492
5	6	116	98	52	154.548	140.944	71.033	0.55	0.653	0.71	0.79	0.568	0.412
5	7	116	106	52	154.548	154.292	67.909	0.546	0.611	0.706	0.759	0.673	0.447
5	8	116	126	64	154.548	178.804	90.497	0.615	0.718	0.762	0.836	0.697	0.507
5	9	116	106	54	154.548	150.746	67.226	0.559	0.652	0.717	0.789	0.651	0.467
5	10	116	104	55	154.548	136.556	62.744	0.595	0.608	0.746	0.756	0.781	0.567
6	7	98	106	58	140.944	154.292	72.969	0.731	0.784	0.845	0.879	0.749	0.601
6	8	98	126	60	140.944	178.804	80.31	0.657	0.75	0.793	0.857	0.7	0.52
6	9	98	106	63	140.944	150.746	84.59	0.819	0.919	0.901	0.958	0.855	0.668
6	10	98	104	53	140.944	136.556	65.912	0.673	0.716	0.805	0.835	0.808	0.579
7	8	106	126	66	154.292	178.804	93.982	0.679	0.762	0.809	0.865	0.812	0.569
7	9	106	106	64	154.292	150.746	88.256	0.74	0.809	0.85	0.894	0.858	0.639
7	10	106	104	52	154.292	136.556	75.754	0.595	0.652	0.746	0.79	0.724	0.514
8	9	126	106	67	178.804	150.746	107.117	0.675	0.809	0.806	0.895	0.789	0.591
8	10	126	104	56	178.804	136.556	75.547	0.615	0.729	0.762	0.843	0.772	0.552
9	10	106	104	61	150.746	136.556	83.926	0.717	0.782	0.835	0.878	0.79	0.607

Appendix 2.2. Shared species and similarity statistics – between 10 transects at rainforest-Njuma

First Sample	Second Sample	^{Sobs} First Sample	^{Sobs} Second Sample	Shared Species Observed	ACE First Sample	ACE Second Sample	Chao Shared Estimated	Chao-Jaccard-Raw Abundance-based	Chao-Jaccard-Est Abundance-based	Chao-Sorensen-Raw Abundance-based	Chao-Sorensen-Est Abundance-based	Morisita-Horn	Bray-Curtis
1	2	93	127	67	124.971	205.198	121.362	0.741	0.872	0.851	0.932	0.836	0.605
1	3	93	113	62	124.971	189.287	80.528	0.778	0.856	0.875	0.923	0.901	0.691
1	4	93	114	58	124.971	170.44	72.622	0.72	0.771	0.837	0.871	0.836	0.63
1	5	93	109	62	124.971	161.741	84.891	0.745	0.801	0.854	0.889	0.805	0.599
1	6	93	125	60	124.971	206.304	83.251	0.697	0.744	0.822	0.853	0.872	0.658
1	7	93	106	57	124.971	153.521	77.251	0.677	0.757	0.807	0.862	0.773	0.589
1	8	93	116	59	124.971	216.117	85.502	0.697	0.772	0.821	0.871	0.87	0.616
1	9	93	116	54	124.971	160.989	68.123	0.601	0.64	0.751	0.781	0.772	0.529
1	10	93	116	60	124.971	159.921	83.381	0.664	0.764	0.798	0.866	0.767	0.559
2	3	127	113	76	205.198	189.287	132.211	0.773	0.988	0.872	0.994	0.812	0.608
2	4	127	114	78	205.198	170.44	123.915	0.785	0.912	0.88	0.954	0.926	0.699
2	5	127	109	77	205.198	161.741	150.193	0.731	0.866	0.844	0.928	0.865	0.618
2	6	127	125	71	205.198	206.304	111.049	0.724	0.811	0.84	0.896	0.798	0.582
2	7	127	106	64	205.198	153.521	103.147	0.675	0.772	0.806	0.871	0.835	0.555
2	8	127	116	71	205.198	216.117	132.568	0.718	0.905	0.836	0.95	0.76	0.551
2	9	127	116	70	205.198	160.989	110.016	0.654	0.806	0.791	0.893	0.755	0.536
2	10	127	116	74	205.198	159.921	130.047	0.694	0.835	0.819	0.91	0.799	0.54
3	4	113	114	68	189.287	170.44	101.007	0.741	0.906	0.851	0.951	0.84	0.641
3	5	113	109	71	189.287	161.741	124.75	0.751	0.876	0.858	0.934	0.845	0.644
3	6	113	125	71	189.287	206.304	127.177	0.721	0.909	0.838	0.953	0.853	0.638
3	7	113	106	60	189.287	153.521	85.659	0.676	0.753	0.807	0.859	0.795	0.582
3	8	113	116	65	189.287	216.117	97.329	0.709	0.839	0.83	0.913	0.821	0.596
3	9	113	116	63	189.287	160.989	87.879	0.646	0.819	0.785	0.901	0.787	0.534
3	10	113	116	69	189.287	159.921	98.899	0.705	0.852	0.827	0.92	0.79	0.56
4	5	114	109	68	170.44	161.741	98.2	0.726	0.78	0.842	0.876	0.857	0.644
4	6	114	125	63	170.44	206.304	77.218	0.707	0.745	0.829	0.854	0.85	0.629

4	7	114	106	64	170.44	153.521	84.914	0.716	0.825	0.834	0.904	0.871	0.616
4	8	114	116	65	170.44	216.117	103.593	0.718	0.813	0.836	0.897	0.802	0.59
4	9	114	116	62	170.44	160.989	75.129	0.652	0.729	0.789	0.843	0.749	0.525
4	10	114	116	66	170.44	159.921	83.74	0.663	0.723	0.797	0.839	0.833	0.557
5	6	109	125	67	161.741	206.304	90.838	0.723	0.817	0.839	0.899	0.781	0.546
5	7	109	106	64	161.741	153.521	88.1	0.698	0.818	0.822	0.9	0.797	0.538
5	8	109	116	64	161.741	216.117	96.108	0.691	0.808	0.818	0.894	0.737	0.498
5	9	109	116	62	161.741	160.989	91.083	0.662	0.731	0.797	0.844	0.763	0.521
5	10	109	116	64	161.741	159.921	91.12	0.66	0.789	0.795	0.882	0.781	0.513
6	7	125	106	65	206.304	153.521	93.477	0.679	0.757	0.809	0.862	0.819	0.615
6	8	125	116	73	206.304	216.117	150.587	0.725	0.849	0.841	0.919	0.886	0.658
6	9	125	116	67	206.304	160.989	88.422	0.612	0.68	0.759	0.809	0.783	0.552
6	10	125	116	69	206.304	159.921	85.438	0.676	0.723	0.807	0.839	0.807	0.582
7	8	106	116	63	153.521	216.117	94.907	0.659	0.749	0.795	0.857	0.801	0.61
7	9	106	116	64	153.521	160.989	86.791	0.657	0.724	0.793	0.84	0.765	0.559
7	10	106	116	63	153.521	159.921	85.788	0.656	0.719	0.792	0.837	0.834	0.606
8	9	116	116	57	216.117	160.989	72.385	0.595	0.65	0.746	0.788	0.784	0.548
8	10	116	116	66	216.117	159.921	99.357	0.673	0.8	0.804	0.889	0.8	0.584
9	10	116	116	62	160.989	159.921	73.168	0.567	0.606	0.724	0.754	0.682	0.491

Appendix 2.3. Shared species and similarity statistics – between 10 transects at ecotone-Ganga

First Sample	Second Sample	^{Sobs} First Sample	^{Sobs} Second Sample	Shared Species Observed	ACE First Sample	ACE Second Sample	Chao Shared Estimated	Chao-Jaccard-Raw Abundance-based	Chao-Jaccard-Est Abundance-based	Chao-Sorensen-Raw Abundance-based	Chao-Sorensen-Est Abundance-based	Morisita-Horn	Bray-Curtis
1	2	71	65	44	89.024	105.588	69.172	0.837	0.914	0.911	0.955	0.936	0.765
1	3	71	57	42	89.024	76.281	54.477	0.851	0.884	0.919	0.938	0.826	0.61
1	4	71	68	42	89.024	121.098	76.39	0.839	0.952	0.912	0.975	0.902	0.708
1	5	71	73	40	89.024	97.238	45.783	0.795	0.828	0.886	0.906	0.822	0.569
1	6	71	78	36	89.024	106.248	41.345	0.639	0.8	0.779	0.889	0.411	0.367
1	7	71	64	40	89.024	89.754	60.448	0.736	0.818	0.848	0.9	0.764	0.581
1	8	71	66	41	89.024	81.043	48.162	0.683	0.73	0.811	0.844	0.631	0.508
1	9	71	86	42	89.024	117.628	57.051	0.59	0.646	0.742	0.785	0.476	0.432
1	10	71	80	44	89.024	110.984	64.319	0.678	0.935	0.808	0.966	0.528	0.447
2	3	65	57	40	105.588	76.281	89.093	0.824	0.91	0.904	0.953	0.784	0.603
2	4	65	68	42	105.588	121.098	74.683	0.86	0.943	0.925	0.971	0.949	0.756
2	5	65	73	35	105.588	97.238	53.467	0.706	0.855	0.828	0.922	0.719	0.483
2	6	65	78	40	105.588	106.248	84.916	0.608	0.977	0.756	0.988	0.266	0.284
2	7	65	64	35	105.588	89.754	54.816	0.737	0.849	0.849	0.919	0.809	0.614
2	8	65	66	40	105.588	81.043	62.856	0.622	0.74	0.767	0.851	0.512	0.426
2	9	65	86	42	105.588	117.628	81.133	0.554	0.709	0.713	0.83	0.326	0.355
2	10	65	80	42	105.588	110.984	64.271	0.645	0.836	0.784	0.911	0.416	0.377
3	4	57	68	42	76.281	121.098	61.342	0.865	0.962	0.928	0.981	0.77	0.602
3	5	57	73	38	76.281	97.238	43.432	0.783	0.813	0.878	0.897	0.789	0.61
3	6	57	78	34	76.281	106.248	38.692	0.682	0.795	0.811	0.886	0.43	0.4
3	7	57	64	38	76.281	89.754	53.074	0.709	0.792	0.83	0.884	0.696	0.543
3	8	57	66	38	76.281	81.043	42.281	0.747	0.815	0.855	0.898	0.686	0.531
3	9	57	86	38	76.281	117.628	46.559	0.652	0.747	0.79	0.855	0.453	0.398
3	10	57	80	38	76.281	110.984	49.069	0.678	0.822	0.808	0.903	0.534	0.439
4	5	68	73	45	121.098	97.238	70.959	0.82	0.917	0.901	0.956	0.758	0.547
4	6	68	78	44	121.098	106.248	64.513	0.74	0.921	0.851	0.959	0.292	0.332

4	7	68	64	43	121.098	89.754	82.956	0.799	0.958	0.888	0.979	0.86	0.667
4	8	68	66	46	121.098	81.043	66.546	0.77	0.848	0.87	0.918	0.557	0.501
4	9	68	86	46	121.098	117.628	74.526	0.675	0.803	0.806	0.891	0.376	0.411
4	10	68	80	46	121.098	110.984	71.877	0.715	0.929	0.834	0.963	0.458	0.428
5	6	73	78	44	97.238	106.248	54.047	0.736	0.797	0.848	0.887	0.667	0.532
5	7	73	64	41	97.238	89.754	50.238	0.731	0.815	0.845	0.898	0.718	0.534
5	8	73	66	47	97.238	81.043	62.444	0.763	0.808	0.866	0.894	0.832	0.673
5	9	73	86	54	97.238	117.628	87.319	0.727	0.835	0.842	0.91	0.729	0.566
5	10	73	80	49	97.238	110.984	66.457	0.739	0.868	0.85	0.929	0.74	0.556
6	7	78	64	37	106.248	89.754	46.994	0.722	0.962	0.839	0.981	0.33	0.331
6	8	78	66	44	106.248	81.043	53.346	0.798	0.873	0.888	0.932	0.807	0.607
6	9	78	86	49	106.248	117.628	65.69	0.735	0.811	0.847	0.896	0.851	0.62
6	10	78	80	46	106.248	110.984	57.03	0.726	0.804	0.841	0.891	0.798	0.603
7	8	64	66	41	89.754	81.043	50.208	0.816	0.88	0.898	0.936	0.662	0.531
7	9	64	86	46	89.754	117.628	67.097	0.702	0.777	0.825	0.875	0.426	0.422
7	10	64	80	45	89.754	110.984	61.53	0.79	0.943	0.883	0.971	0.54	0.468
8	9	66	86	54	81.043	117.628	77.396	0.814	0.909	0.898	0.952	0.877	0.712
8	10	66	80	56	81.043	110.984	79.726	0.844	0.939	0.915	0.969	0.891	0.73
9	10	86	80	59	117.628	110.984	93.95	0.827	0.998	0.905	0.999	0.891	0.688

Appendix 2.4. Species diversity output – trees ≥10 cm DBH, across 10 transects at human-modified rainforest – Bekob

Transects	Individuals (computed)	S(est)	S(est) 95% CI Lower Bound	S(est) 95% CI Upper Bound	S Mean (runs)	Singletons Mean	Uniques Mean	Uniques SD (runs)	Cole Rarefaction	Alpha Mean	Alpha SD (analytical)	Shannon Mean	Simpson Inv Mean
1	548.2	108.3	97.1	119.5	109.67	43.02	109.67	10.1	136.07	41.6	2.89	3.94	30.07
2	1096.4	158.11	145.13	171.09	159.69	54.89	100.79	10.3	183.44	51.56	2.65	4.16	33.49
3	1644.6	191.79	178.09	205.49	192.25	59.91	101.07	8.14	213.04	56.54	2.48	4.24	34.21
4	2192.8	217.04	203	231.08	217.13	63.16	101.14	8.28	234.29	59.9	2.36	4.29	34.57
5	2741	237.17	222.93	251.41	237.24	66.27	101.81	7.34	250.7	62.32	2.27	4.32	35.28
6	3289.2	253.86	239.45	268.26	253.92	67.81	100.91	6.28	264	64.19	2.2	4.35	36.1
7	3837.4	268.08	253.48	282.67	267.88	68.83	99.74	5.69	275.18	65.58	2.13	4.37	36.5
8	4385.6	280.42	265.59	295.26	280.29	70.12	99.12	5.55	284.82	66.72	2.08	4.38	36.78
9	4933.8	291.3	276.15	306.45	290.98	71.31	98.02	4.61	293.34	67.62	2.03	4.39	36.98
10	5482	301	285.43	316.57	301	73	97	0	301	68.49	2	4.41	37.31

Appendix 2.5. Species diversity output – trees ≥10 cm DBH, across 10 transects at rainforest – Njuma

Transects	Individuals (computed)	S(est)	S(est) 95% CI Lower Bound	S(est) 95% CI Upper Bound	S Mean (runs)	Singletons Mean	Uniques Mean	Uniques SD (runs)	Cole Rarefaction	Alpha Mean	Alpha SD (analytical)	Shannon Mean	Simpson Inv Mean
1	501.6	113.5	101.63	125.37	112.79	47.75	112.79	8.63	130.64	45.6	3.28	4.06	35.07
2	1003.2	161.56	148.27	174.84	159.79	60.98	94.89	8.5	177.25	53.75	2.85	4.23	38.18
3	1504.8	194.18	180.44	207.92	192.75	69.65	97.88	9.08	208.24	58.66	2.63	4.3	39.14
4	2006.4	219.36	205.4	233.32	218.73	75.5	101.28	9.64	231.42	62.35	2.51	4.35	39.69
5	2508	239.87	225.75	253.98	239.82	77.75	102.92	8.94	249.76	65.15	2.41	4.38	40.24
6	3009.6	257.1	242.83	271.36	257.08	78.97	103.3	7.72	264.82	67.25	2.34	4.41	40.69
7	3511.2	271.87	257.42	286.31	271.58	79.47	103.51	7.08	277.5	68.62	2.27	4.42	40.72
8	4012.8	284.71	270.03	299.4	284.86	79.1	103.06	6.24	288.36	70.03	2.22	4.43	40.96
9	4514.4	296	281	311	295.86	78.24	101.96	4.69	297.77	70.92	2.16	4.44	41.03
10	5016	306	290.58	321.42	306	77	100	0	306	71.83	2.12	4.45	41.22

Appendix 2.6. Species diversity output – trees ≥ 10 cm DBH, across 10 transects at ecotone – Ganga

Transects	Individuals (computed)	Species (est)	S(est) 95% CI Lower Bound	S(est) 95% CI Upper Bound	S Mean (runs)	Singletons Mean	Uniques Mean	Uniques SD (runs)	Cole Rarefaction	Alpha Mean	Alpha SD (analytical)	Shannon Mean	Simpson Inv Mean
1	490.8	70.8	60.79	80.81	70.16	24.64	70.16	7.95	85.23	22.93	1.79	3.44	19.72
2	981.6	98.6	87.34	109.86	97.75	30.75	54.86	9.14	111.69	27.17	1.6	3.62	22.25
3	1472.4	117.43	105.62	129.23	116.62	34.65	55.97	9.91	128.97	29.75	1.51	3.68	22.83
4	1963.2	131.89	119.75	144.02	130.93	37.19	56.87	8.68	141.87	31.6	1.45	3.72	23.3
5	2454	143.71	131.32	156.1	143.98	39.58	59.75	7.81	152.11	33.41	1.43	3.76	24.02
6	2944.8	153.77	141.14	166.39	153.43	40.04	60.09	7.16	160.58	34.41	1.39	3.79	24.66
7	3435.6	162.56	149.67	175.44	162.42	41.39	61.69	6.96	167.75	35.44	1.36	3.8	24.67
8	3926.4	170.4	157.21	183.59	170.77	42.35	63.01	5.68	173.92	36.42	1.34	3.82	24.94
9	4417.2	177.5	163.95	191.05	177.71	43.61	64.46	3.89	179.3	37.12	1.32	3.82	24.98
10	4908	184	170.01	197.99	184	44	65	0	184	37.74	1.31	3.84	25.28

Appendix 2.7. Plant species list (≥10 cm DBH), number of stems per species and family for human-modified rainforest-Bekob

Species	Count	Family		Species	Count	Family
<i>Afraegle paniculata</i>	1	Rutaceae		<i>Antidesma</i> sp.	18	Phyllanthaceae
<i>Afrostryax lepidophyllus</i>	16	Huaceae		<i>Antrocaryon klaineianum</i>	3	Anacardiaceae
<i>Afrostryax</i> sp.	10	Huaceae		<i>Aptandra</i> sp.	1	Olacaceae
<i>Afzelia bipindensis</i>	1	Leguminosae		<i>Aulacocalyx</i> sp.	5	Rubiaceae
<i>Afzelia</i> sp.	1	Leguminosae		<i>Balanites</i> sp.	1	Zygophyllaceae
<i>Albizia adianthifolia</i>	9	Leguminosae		<i>Baphia</i> sp.	9	Leguminosae
<i>Albizia</i> sp.	1	Leguminosae		<i>Barteria fistulosa</i>	1	Passifloraceae
<i>Albizia zygia</i>	5	Leguminosae		<i>Beilschmiedia mannii</i>	1	Lauraceae
<i>Allanblackia floribunda</i>	2	Clusiaceae		<i>Beilschmiedia</i> sp.	47	Lauraceae
<i>Allanblackia gabonensis</i>	10	Clusiaceae		<i>Bersama</i> sp.	1	Melanthaceae
<i>Allanblackia</i> sp.	6	Clusiaceae		<i>Blighia</i> sp.	9	Sapindaceae
<i>Allophylus africanus</i>	4	Sapindaceae		<i>Bridelia micrantha</i>	5	Phyllanthaceae
<i>Allophylus</i> sp.	4	Sapindaceae		<i>Bridelia</i> sp.	1	Phyllanthaceae
<i>Alstonia boonei</i>	7	Apocynaceae		<i>Campylospermum calanthum</i>	2	Ochnaceae
<i>Amphimas ferrugineus</i>	1	Leguminosae		<i>Canarium schweinfurthii</i>	3	Burseraceae
<i>Amphimas pterocarpoides</i>	2	Leguminosae		<i>Carapa dinklagei</i>	5	Meliaceae
<i>Amphimas</i> sp.	3	Leguminosae		<i>Carapa</i> sp.	40	Meliaceae
<i>Anisophyllea</i> sp.	55	Anisophylleaceae		<i>Cassipourea</i> sp.	2	Rhizophoraceae
<i>Annickia chlorantha</i>	8	Annonaceae		<i>Ceiba pentandra</i>	1	Malvaceae
<i>Anonidium mannii</i>	1	Annonaceae		<i>Chytranthus</i> sp.	3	Sapindaceae
<i>Anthocleista nobilis</i>	1	Gentianaceae		<i>Clausena anisata</i>	4	Rutaceae
<i>Anthocleista schweinfurthii</i>	1	Gentianaceae		<i>Cleistopholis glauca</i>	5	Annonaceae
<i>Anthonothea ferruginea</i>	20	Leguminosae		<i>Cleistopholis</i> sp.	1	Annonaceae
<i>Anthonothea</i> sp.	9	Leguminosae		<i>Coelocaryon preussi</i>	30	Myristicaceae
<i>Anthostema aubryanum</i>	1	Euphorbiaceae		<i>Coffea</i> sp.	1	Rubiaceae
<i>Antiaris africana</i>	1	Moraceae		<i>Cola acuminata</i>	12	Malvaceae
<i>Antiaris</i> sp.	1	Moraceae		<i>Cola cauliflora</i>	6	Malvaceae
<i>Antidesma laciniatum</i>	2	Phyllanthaceae		<i>Cola lateritia</i>	9	Malvaceae
<i>Antidesma membranaceum</i>	51	Phyllanthaceae		<i>Cola lepidota</i>	5	Malvaceae

Species	Count	Family		Species	Count	Family
<i>Cola nitida</i>	5	Malvaceae		<i>Dovyalis zenkeri</i>	4	Salicaceae
<i>Cola pachycarpa</i>	1	Malvaceae		<i>Dracaena cerasifera</i>	6	Asparagaceae
<i>Cola rostrata</i>	5	Malvaceae		<i>Dracaena</i> sp.	1	Asparagaceae
<i>Cola</i> sp.	230	Malvaceae		<i>Drypetes aframensis</i>	5	Putranjivaceae
<i>Cola verticillata</i>	26	Malvaceae		<i>Drypetes aylmeri</i>	5	Putranjivaceae
<i>Cordia platythyrsa</i>	8	Boraginaceae		<i>Drypetes principum</i>	19	Putranjivaceae
<i>Cordia</i> sp.	1	Boraginaceae		<i>Drypetes</i> sp.	297	Putranjivaceae
<i>Coula edulis</i>	5	Olacaceae		<i>Duboscia macrocarpa</i>	1	Malvaceae
<i>Crateranthus cameroonensis</i>	38	Lecythidaceae		<i>Elaeis guineensis</i>	33	Arecaceae
<i>Croton oligandrus</i>	7	Euphorbiaceae		<i>Elaeophorbia drupifera</i>	1	Euphorbiaceae
<i>Cuviera longiflora</i>	14	Rubiaceae		<i>Englerophytum stelechanta</i>	2	Sapotaceae
<i>Cyathea camerooniana</i>	1	Cyatheaceae		<i>Entandrophragma</i> sp.	1	Meliaceae
<i>Cynometra hankei</i>	1	Leguminosae		<i>Eriocoelum macrocarpum</i>	8	Sapindaceae
<i>Cyrtogonone argentea</i>	5	Euphorbiaceae		<i>Eriocoelum</i> sp.	3	Sapindaceae
<i>Dacryodes</i> sp.	39	Burseraceae		<i>Euadenia trifoliolata</i>	2	Capparaceae
<i>Dasylepis racemosa</i>	1	Achariaceae		<i>Eugenia</i> sp.	3	Myrtaceae
<i>Deinbollia</i> sp.	2	Sapindaceae		<i>Ficus</i> sp.	12	Moraceae
<i>Desbordesia glaucescens</i>	4	Irvingiaceae		<i>Funtumia elastica</i>	11	Apocynaceae
<i>Desplatsia dewevrei</i>	4	Malvaceae		<i>Gambeya</i> sp.	3	Sapotaceae
<i>Desplatsia</i> sp.	10	Malvaceae		<i>Garcinia conrauana</i>	185	Clusiaceae
<i>Dialium pachyphyllum</i>	2	Leguminosae		<i>Garcinia lucida</i>	5	Clusiaceae
<i>Dialium</i> sp.	13	Leguminosae		<i>Garcinia mannii</i>	16	Clusiaceae
<i>Dichostemma glaucescens</i>	4	Euphorbiaceae		<i>Garcinia ovalifolia</i>	8	Clusiaceae
<i>Dicranolepis</i> sp.	4	Thymelaeaceae		<i>Garcinia smeathmannii</i>	32	Clusiaceae
<i>Dictyandra</i> sp.	1	Rubiaceae		<i>Garcinia</i> sp.	30	Clusiaceae
<i>Diogoa zenkeri</i>	80	Olacaceae		<i>Greenwayodendron suaveolens</i>	9	Annonaceae
<i>Diospyros hoyleana</i>	3	Ebenaceae		<i>Grewia coriacea</i>	40	Malvaceae
<i>Diospyros</i> sp.	68	Ebenaceae		<i>Grewia</i> sp.	7	Malvaceae
<i>Discoglyprena caloneura</i>	9	Euphorbiaceae		<i>Guarea mayombensis</i>	7	Meliaceae

Species	Count	Family		Species	Count	Family
<i>Guarea</i> sp.	16	Meliaceae		<i>Leosenera talbotii</i>	1	Leguminosae
<i>Guarea thompsonii</i>	3	Meliaceae		<i>Lepidobotrys staudtii</i>	5	Lepidobotryaceae
<i>Harungana madagascariensis</i>	5	Hypericaceae		<i>Leptonychia</i> sp.	4	Malvaceae
<i>Heinsia crinita</i>	3	Rubiaceae		Liana	70	Undefined
<i>Heisteria parviflora</i>	3	Olacaceae		<i>Lophira alata</i>	14	Ochnaceae
<i>Heisteria</i> sp.	8	Olacaceae		<i>Lovoa trichilioides</i>	5	Meliaceae
<i>Homalium le-testui</i>	11	Salicaceae		<i>Lychnodiscus</i> sp.	2	Sapindaceae
<i>Homalium</i> sp.	1	Salicaceae		<i>Macaranga barteri</i>	4	Euphorbiaceae
<i>Hoplostigma cf. pierreanum</i>	1	Boraginaceae		<i>Macaranga lunifolia</i>	41	Euphorbiaceae
<i>Hoplostigma</i> sp.	1	Boraginaceae		<i>Macaranga</i> sp.	9	Euphorbiaceae
<i>Hylodendron gabunense</i>	15	Leguminosae		<i>Maesobotrya barteri</i>	22	Phyllanthaceae
<i>Hylodendron</i> sp.	2	Leguminosae		<i>Maesobotrya</i> sp.	33	Phyllanthaceae
<i>Hymenocardia</i> sp.	6	Phyllanthaceae		<i>Maesopsis eminii</i>	7	Rhamnaceae
<i>Hymenocardia ulmoides</i>	2	Phyllanthaceae		<i>Magnistipula</i> sp.	3	Chrysobalanaceae
<i>Hymenostegia afzelii</i>	96	Leguminosae		<i>Mallotus oppositifolius</i>	3	Euphorbiaceae
<i>Hymenostegia cf. brachyura</i>	1	Leguminosae		<i>Mammea africana</i>	25	Calophyllaceae
<i>Hymenostegia</i> sp.	4	Leguminosae		<i>Maranthes</i> sp.	3	Chrysobalanaceae
<i>Hypodaphnis zenkeri</i>	13	Lauraceae		<i>Mareyopsis longifolia</i>	16	Euphorbiaceae
<i>Irvingia gabonensis</i>	2	Irvingiaceae		<i>Mareyopsis</i> sp.	1	Euphorbiaceae
<i>Ixora</i> sp.	2	Rubiaceae		<i>Margaritaria discoidea</i>	94	Phyllanthaceae
<i>Kigelia africana</i>	1	Bignoniaceae		<i>Markhamia tomentosa</i>	2	Bignoniaceae
<i>Klainedoxa gabonensis</i>	14	Irvingiaceae		<i>Massularia acuminata</i>	3	Rubiaceae
<i>Klainedoxa</i> sp.	2	Irvingiaceae		<i>Medusandra mpomiana</i>	22	Peridiscaceae
<i>Klainedoxa trillesii</i>	4	Irvingiaceae		<i>Milicia excelsa</i>	17	Moraceae
<i>Lannea welwitschii</i>	17	Anacardiaceae		<i>Millettia</i> sp.	1	Leguminosae
<i>Lasiodiscus mannii</i>	2	Rhamnaceae		<i>Monodora myristica</i>	1	Annonaceae
<i>Lasiodiscus</i> sp.	1	Rhamnaceae		<i>Monodora</i> sp.	30	Annonaceae
<i>Leonardoxa (false)</i>	1	Leguminosae		<i>Morinda lucida</i>	3	Rubiaceae
<i>Leonardoxa africana</i>	53	Leguminosae		<i>Musanga cecropioides</i>	9	Urticaceae

Species	Count	Family		Species	Count	Family
<i>Myrianthus arboreus</i>	1	Urticaceae		<i>Petersianthus macrocarpus</i>	4	Lecythidaceae
<i>Myrianthus serratus</i>	5	Urticaceae		<i>Picralima nitida</i>	39	Apocynaceae
<i>Myrianthus</i> sp.	1	Urticaceae		<i>Piptadeniatrum africanum</i>	1	Leguminosae
<i>Nauclea diderrichii</i>	4	Rubiaceae		<i>Piptostigma fuscum</i>	6	Annonaceae
<i>Nauclea pobeguinii</i>	5	Rubiaceae		<i>Piptostigma</i> sp.	21	Annonaceae
<i>Neoboutonia laevis</i>	1	Euphorbiaceae		<i>Pittosporum</i> or <i>Peddea</i>	2	Pittospaceae
<i>Neoboutonia mannii</i>	11	Euphorbiaceae		<i>Placodiscus</i> sp.	2	Sapindaceae
<i>Ochna calodendron</i>	10	Ochnaceae		<i>Plagiosiphon emarginatus</i>	3	Leguminosae
<i>Ochna</i> sp.	1	Ochnaceae		<i>Plagiosiphon longitubus</i>	3	Leguminosae
<i>Octoknema affinis</i>	26	Olacaceae		<i>Plagiosiphon multijugus</i>	1	Leguminosae
<i>Octoknema</i> sp.	16	Olacaceae		<i>Plagiosiphon</i> sp.	22	Leguminosae
<i>Oddoniodendron</i> sp.	1	Leguminosae		<i>Plagiostyles africana</i>	1	Euphorbiaceae
<i>Oldfieldia</i> sp.	1	Picrodendraceae		<i>Porterandia cladantha</i>	2	Rubiaceae
<i>Omphalocarpum</i> sp.	1	Sapotaceae		<i>Pouteria</i> sp.	5	Sapotaceae
<i>Oncoba blackii</i>	39	Salicaceae		<i>Prioria joveri</i>	3	Leguminosae
<i>Oncoba calodendron</i>	2	Salicaceae		<i>Prioria/Oxystigma?</i>	1	Leguminosae
<i>Oncoba dentata</i>	7	Salicaceae		<i>Pseudagrostistachys africana</i>	1	Euphorbiaceae
<i>Oncoba glauca</i>	45	Salicaceae		<i>Pseudospondias microcarpa</i>	28	Anacardiaceae
<i>Oncoba</i> sp.	5	Salicaceae		<i>Psidium guajava</i>	2	Myrtaceae
<i>Oncoba welwitschii</i>	164	Salicaceae		<i>Psychotria camptopus</i>	1	Rubiaceae
<i>Ongokea gore</i>	2	Olacaceae		<i>Psychotria</i> sp.	1	Rubiaceae
<i>Oxystigma/Gossuselerodendron</i>	1	Leguminosae		<i>Psychotria venosa</i>	13	Rubiaceae
<i>Parinari excelsa</i>	2	Chrysobalanaceae		<i>Psydrax arnoldiana</i>	1	Rubiaceae
<i>Pauridiantha efferata</i>	14	Rubiaceae		<i>Psydrax</i> sp.	4	Rubiaceae
<i>Pauridiantha efulensis</i>	2	Rubiaceae		<i>Pterocarpus soyauxii</i>	2	Leguminosae
<i>Pauridiantha</i> sp.	2	Rubiaceae		<i>Pycnanthus angolensis</i>	112	Myristicaceae
<i>Pausinystalia macroceras</i>	5	Rubiaceae		<i>Quassia sanguinea</i>	5	Simaroubaceae
<i>Pausinystalia</i> sp.	1	Rubiaceae		<i>Raphia regalis</i>	3	Arecaceae
<i>Pentaclethra macrophylla</i>	1	Leguminosae		<i>Raphia</i> sp.	6	Arecaceae

Species	Count	Family		Species	Count	Family
<i>Rauvolfia macrophylla</i>	21	Apocynaceae		<i>Strychnos staudtii</i>	1	Loganiaceae
<i>Rauvolfia</i> sp.	1	Apocynaceae		<i>Symphonia globulifera</i>	13	Clusiaceae
<i>Rauvolfia vomitoria</i>	27	Apocynaceae		<i>Synsepalum msolo</i>	4	Sapotaceae
<i>Rhabdophyllum</i> sp.	8	Ochnaceae		<i>Synsepalum</i> sp.	3	Sapotaceae
<i>Rhaptopetalum sessilifolium</i>	1	Lecythidaceae		<i>Syzygium guineensis</i>	3	Myrtaceae
<i>Rhaptopetalum</i> sp.	2	Lecythidaceae		<i>Syzygium</i> sp.	9	Myrtaceae
<i>Ricinodendron heudelotii</i>	3	Euphorbiaceae		<i>Tabernaemontana crassa</i>	476	Apocynaceae
<i>Rinorea oblongifolia</i>	20	Violaceae		<i>Tapura africana</i>	13	Dichapetalaceae
<i>Rinorea</i> sp.	12	Violaceae		<i>Tapura</i> sp.	4	Dichapetalaceae
<i>Ritchiea erecta</i>	3	Capparaceae		<i>Terminalia superba</i>	9	Combretaceae
<i>Rothmannia</i> sp.	8	Rubiaceae		<i>Tetrapleura tetraptera</i>	2	Leguminosae
<i>Santiria trimera</i>	84	Burseraceae		<i>Thomandersia</i> sp.	8	Acanthaceae
<i>Sapium cuneatum</i>	1	Euphorbiaceae		<i>Treculia obovoidea</i>	9	Moraceae
<i>Schumanniphyton magnificum</i>	19	Rubiaceae		<i>Tricalysia</i> sp.	35	Rubiaceae
<i>Scottellia coriacea</i>	3	Achariaceae		<i>Trichilia prieuriana</i>	10	Meliaceae
<i>Scyphocephalum mannii</i>	12	Myristicaceae		<i>Trichilia rubescens</i>	54	Meliaceae
<i>Shirakiopsis elliptica</i>	6	Euphorbiaceae		<i>Trichilia</i> sp.	40	Meliaceae
<i>Sorindeia</i> sp.	1	Anacardiaceae		<i>Trichoscypha acuminata</i>	4	Anacardiaceae
<i>Spathodea campanulata</i>	1	Bignoniaceae		<i>Trichoscypha</i> sp.	88	Anacardiaceae
<i>Staudtia kamerunensis</i>	1	Myristicaceae		<i>Trilepisium madagascariense</i>	3	Moraceae
<i>Stemonocoleus micranthus</i>	1	Leguminosae		<i>Uapaca guineensis</i>	155	Phyllanthaceae
<i>Sterculia oblonga</i>	1	Malvaceae		<i>Uapaca</i> sp.	10	Phyllanthaceae
<i>Sterculia tragacantha</i>	8	Malvaceae		Unknown	405	Undefined
<i>Strombosia grandifolia</i>	166	Olacaceae		<i>Uvariadendron connivens</i>	3	Annonaceae
<i>Strombosia pustulata</i>	4	Olacaceae		<i>Uvariopsis</i> sp.	1	Annonaceae
<i>Strombosia scheffleri</i>	22	Olacaceae		<i>Vepris</i> sp.	2	Rutaceae
<i>Strombosia</i> sp.	142	Olacaceae		<i>Vepris trifoliolata</i>	6	Rutaceae
<i>Strombosiopsis tetrandra</i>	15	Olacaceae		<i>Vismia guineensis</i>	1	Clusiaceae
<i>Strychnos</i> sp.	6	Loganiaceae		<i>Vismia</i> sp.	1	Clusiaceae

Species	Count	Family
<i>Vitex grandifolia</i>	138	Lamiaceae
<i>Vitex</i> sp.	2	Lamiaceae
<i>Warneckea</i> sp.	2	Melastomataceae
<i>Xylopia aethiopica</i>	10	Annonaceae
<i>Xylopia africana</i>	5	Annonaceae
<i>Xylopia phliocodora</i>	1	Annonaceae
<i>Xylopia</i> sp.	16	Annonaceae
<i>Zanthoxylum</i> sp.	28	Rutaceae
<i>Zanthoxylum tessmannii</i>	1	Rutaceae
<i>Zenkerella citrina</i>	84	Leguminosae

Appendix 2.8. Plant species list (≥10 cm DBH), number of stems per species and family for rainforest-Njuma

Species	Count	Family	Species	Count	Family
<i>Afzelia bipindensis</i>	2	Leguminosae	<i>Berlinia grandifolia</i>	2	Leguminosae
<i>Afzelia</i> sp.	2	Leguminosae	<i>Berlinia</i> sp.	14	Leguminosae
<i>Aidia micrantha</i>	4	Rubiaceae	<i>Bikinia letestui</i>	3	Leguminosae
<i>Albizia adianthifolia</i>	1	Leguminosae	<i>Bikinia</i> sp.	1	Leguminosae
<i>Allanblackia</i> sp.	3	Clusiaceae	<i>Blighia</i> sp.	2	Sapindaceae
<i>Alstonia boonei</i>	24	Apocynaceae	<i>Brachystegia cynometroides</i>	33	Leguminosae
<i>Anisophyllea polyneura</i>	2	Anisophylleaceae	<i>Brachystegia mildbraedii</i>	1	Leguminosae
<i>Anisophyllea</i> sp.	139	Anisophylleaceae	<i>Brazzea</i> sp.	8	Scytopetalaceae
<i>Annickia chlorantha</i>	23	Annonaceae	<i>Brenania brieyi</i>	1	Rubiaceae
<i>Anthocleista nobilis</i>	4	Gentianaceae	<i>Bridelia micrantha</i>	7	Phyllanthaceae
<i>Anthocleista vogelli</i>	1	Gentianaceae	<i>Calpocalux</i> sp.	1	Leguminosae
<i>Anthonotha lamprophylla</i>	5	Leguminosae	<i>Calpocalyx dinklagei</i>	2	Leguminosae
<i>Anthonotha macrophylla</i>	2	Leguminosae	<i>Calycobolus africana</i>	2	Convolvulaceae
<i>Anthonotha schweinfurthii</i>	1	Leguminosae	<i>Campylospermum</i> sp.	1	Ochnaceae
<i>Anthonotha</i> sp.	9	Leguminosae	<i>Canarium schweinfurthii</i>	1	Burseraceae
<i>Antiaris africana</i>	2	Moraceae	<i>Carapa dinklagei</i>	24	Meliaceae
<i>Antidesma laciniatum</i>	2	Phyllanthaceae	<i>Carapa</i> sp.	29	Meliaceae
<i>Antidesma membranaceum</i>	13	Phyllanthaceae	<i>Cavacoa quintassi</i>	1	Euphorbiaceae
<i>Antidesma</i> sp.	27	Phyllanthaceae	<i>Chrysophyllum</i> sp.	2	Sapotaceae
<i>Antidesma vogelii</i>	2	Phyllanthaceae	<i>Chytranthus</i> sp.	17	Sapindaceae
<i>Aulacocalyx</i> sp.	2	Rubiaceae	<i>Cleistopholis glauca</i>	13	Annonaceae
<i>Baphia</i> sp.	5	Leguminosae	<i>Cleistopholis patens</i>	6	Annonaceae
<i>Barteria fistulosa</i>	3	Passifloraceae	<i>Coelocaryon preussi</i>	41	Myristicaceae
<i>Barteria</i> sp.	1	Passifloraceae	<i>Coelocaryon</i> sp.	1	Myristicaceae
<i>Beilschmiedia mannii</i>	1	Lauraceae	<i>Cola argentea</i>	1	Malvaceae
<i>Beilschmiedia obscura</i>	1	Lauraceae	<i>Cola chlamydantha</i>	4	Malvaceae
<i>Beilschmiedia</i> sp.	21	Lauraceae	<i>Cola lateritia</i>	8	Malvaceae
<i>Berlinia bracteosa</i>	13	Leguminosae	<i>Cola lepidota</i>	3	Malvaceae
<i>Berlinia grandifolia</i>	2	Leguminosae	<i>Cola nitida</i>	7	Malvaceae

Species	Count	Family	Species	Count	Family
<i>Cola rostrata</i>	11	Malvaceae	<i>Diospyros suaveolens</i>	10	Ebenaceae
<i>Cola</i> sp.	131	Malvaceae	<i>Discoglypremna caloneura</i>	2	Euphorbiaceae
<i>Cola verticillata</i>	7	Malvaceae	<i>Distemonanthus benthamianus</i>	5	Leguminosae
<i>Coula edulis</i>	59	Olacaceae	<i>Drypetes aframensis</i>	42	Putranjivaceae
<i>Crateranthus</i> sp.	1	Lecythidaceae	<i>Drypetes aylmeri</i>	15	Putranjivaceae
<i>Craterispermum</i> sp.	3	Rubiaceae	<i>Drypetes leonensis</i>	9	Putranjivaceae
<i>Croton oligandrus</i>	7	Euphorbiaceae	<i>Drypetes molunduana</i>	7	Putranjivaceae
<i>Cryptosepalum</i> sp.	7	Leguminosae	<i>Drypetes principum</i>	45	Putranjivaceae
<i>Cylicodiscus gabunensis</i>	3	Leguminosae	<i>Drypetes</i> sp.	306	Putranjivaceae
<i>Cynometra hankei</i>	15	Leguminosae	<i>Duboscia macrocarpa</i>	3	Malvaceae
<i>Cyrtogonone argentea</i>	7	Euphorbiaceae	<i>Duguetia staudtii</i>	5	Annonaceae
<i>Dacryodes macrophylla</i>	2	Burseraceae	<i>Elaeis guineensis</i>	2	Arecaceae
<i>Dacryodes</i> sp.	37	Burseraceae	<i>Englerophytum hallei</i>	1	Sapotaceae
<i>Dasylepis racemosa</i>	16	Achariaceae	<i>Englerophytum</i> sp.	4	Sapotaceae
<i>Desbordesia glaucescens</i>	92	Irvingiaceae	<i>Entandophragma utile</i>	1	Meliaceae
<i>Dialium dinklagei</i>	1	Leguminosae	<i>Erythrina mildbraedii</i>	1	Leguminosae
<i>Dialium pachyphyllum</i>	4	Leguminosae	<i>Eugenia</i> sp.	2	Myrtaceae
<i>Dialium</i> sp.	23	Leguminosae	<i>False Coula</i>	1	Olacaceae
<i>Dichostemma glaucescens</i>	55	Euphorbiaceae	<i>False Mareyopsis</i>	1	Euphorbiaceae
<i>Dicranolepis</i> sp.	2	Thymelaeaceae	<i>False Ochna calodendron</i>	1	Ochnaceae
<i>Dictyandra</i> sp.	2	Rubiaceae	<i>False Rhabdophyllum</i>	1	Ochnaceae
<i>Diogoia zenkeri</i>	298	Olacaceae	<i>Ficus</i> sp.	6	Moraceae
<i>Diospyros bipidensis</i>	168	Ebenaceae	<i>Ficus sur</i>	2	Moraceae
<i>Diospyros cinnabarina</i>	4	Ebenaceae	<i>Funtumia elastica</i>	2	Apocynaceae
<i>Diospyros exprudensis</i>	1	Ebenaceae	<i>Garcinia conrauana</i>	32	Clusiaceae
<i>Diospyros hoyleana</i>	3	Ebenaceae	<i>Garcinia kola</i>	1	Clusiaceae
<i>Diospyros longifolia</i>	1	Ebenaceae	<i>Garcinia lucida</i>	25	Clusiaceae
<i>Diospyros preussi</i>	1	Ebenaceae	<i>Garcinia mannii</i>	28	Clusiaceae
<i>Diospyros</i> sp.	338	Ebenaceae	<i>Garcinia ovalifolia</i>	7	Clusiaceae

Species	Count	Family		Species	Count	Family
<i>Garcinia smeathmannii</i>	26	Clusiaceae		<i>Irvingia grandifolia</i>	4	Irvingiaceae
<i>Garcinia</i> sp.	78	Clusiaceae		<i>Irvingia</i> sp.	3	Irvingiaceae
<i>Garcinia thompsonii</i>	1	Clusiaceae		<i>Isolona</i> sp.	2	Annonaceae
<i>Gilbertiodendron brachystegioides</i>	1	Leguminosae		<i>Julbernardia pellegriniana</i>	4	Leguminosae
<i>Gilbertiodendron ebo</i>	7	Leguminosae		<i>Julbernardia seretii</i>	1	Leguminosae
<i>Gilbertiodendron</i> sp.	2	Leguminosae		<i>Keayodendron bridelioides</i>	4	Phyllanthaceae
<i>Greenwayodendron</i> sp.	1	Annonaceae		<i>Klainedoxa gabonensis</i>	16	Irvingiaceae
<i>Greenwayodendron suaveolens</i>	25	Annonaceae		<i>Klainedoxa trillesii</i>	7	Irvingiaceae
<i>Grewia coriacea</i>	30	Malvaceae		<i>Lannea welwitschii</i>	4	Anacardiaceae
<i>Grewia</i> sp.	4	Malvaceae		<i>Lasiodiscus mannii</i>	1	Rhamnaceae
<i>Grossera</i> sp.	4	Euphorbiaceae		<i>Lasiodiscus</i> sp.	1	Rhamnaceae
<i>Grossera vignei</i>	4	Euphorbiaceae		<i>Lecaniodiscus cupanioides</i>	3	Sapindaceae
<i>Guarea mayombensis</i>	2	Meliaceae		<i>Leonardoxa africana</i>	9	Leguminosae
<i>Guarea</i> sp.	8	Meliaceae		<i>Lepidobotrys staudtii</i>	6	Lepidobotryaceae
<i>Guarea thompsonii</i>	3	Meliaceae		<i>Leptaulus</i> sp.	5	Cardiopteridaceae
<i>Heinsia crinita</i>	1	Rubiaceae		Liana	63	Undefined
<i>Heisteria parviflora</i>	1	Olacaceae		<i>Loesenera talbotii</i>	3	Leguminosae
<i>Heisteria</i> sp.	39	Olacaceae		<i>Lophira alata</i>	27	Ochnaceae
<i>Heisteria trillesiana</i>	6	Olacaceae		<i>Macaranga lunifolia</i>	9	Euphorbiaceae
<i>Hexalobus crispiflorus</i>	1	Annonaceae		<i>Maesobotrya barteri</i>	3	Euphorbiaceae
<i>Hexalobus</i> sp.	1	Annonaceae		<i>Maesobotrya dugetii</i>	1	Euphorbiaceae
<i>Homalium le-testui</i>	6	Salicaceae		<i>Maesobotrya</i> sp.	1	Euphorbiaceae
<i>Hylodendron gabunense</i>	23	Leguminosae		<i>Maesopsis eminii</i>	4	Rhamnaceae
<i>Hymenocardia</i> sp.	2	Phyllanthaceae		<i>Magnistipula</i> sp.	2	Chrysobalanaceae
<i>Hymenocardia ulmoides</i>	2	Phyllanthaceae		<i>Maprounea africana</i>	1	Euphorbiaceae
<i>Hymenostegia afzelii</i>	19	Leguminosae		<i>Maranthes</i> sp.	2	Chrysobalanaceae
<i>Hymenostegia</i> sp.	1	Leguminosae		<i>Mareyopsis longifolia</i>	63	Euphorbiaceae
<i>Hypodaphnis zenkeri</i>	23	Lauraceae		<i>Mareyopsis</i> sp.	7	Euphorbiaceae
<i>Irvingia gabonensis</i>	36	Irvingiaceae		<i>Margaritaria discoidea</i>	11	Phyllanthaceae

Species	Count	Family	Species	Count	Family
<i>Massularia acuminata</i>	2	Rubiaceae	<i>Panda oleosa</i>	10	Pandaceae
<i>Medusandra mpomiana</i>	1	Peridiscaceae	<i>Parinari excelsa</i>	2	Chrysobalanaceae
<i>Microberlinia bisulcata</i>	17	Leguminosae	<i>Parkia bicolor</i>	1	Leguminosae
<i>Milicia excelsa</i>	1	Moraceae	<i>Pauridiantha efferata</i>	2	Rubiaceae
<i>Milletia</i> sp.	3	Leguminosae	<i>Pausinystalia macroceras</i>	32	Rubiaceae
<i>Mitragyna</i> sp.	1	Rubiaceae	<i>Pausinystalia</i> sp.	2	Rubiaceae
<i>Monodora myristica</i>	3	Annonaceae	<i>Pausinystalia talbotii</i>	1	Rubiaceae
<i>Monodora</i> sp.	8	Annonaceae	<i>Pausinystalia yohimbe</i>	2	Rubiaceae
<i>Morinda lucida</i>	1	Rubiaceae	<i>Pentaclethra macrophylla</i>	7	Leguminosae
<i>Musanga cecropioides</i>	8	Urticaceae	<i>Pentadesma</i> sp.	4	Clusiaceae
<i>Napolaeona egertonii</i>	2	Lecythidaceae	<i>Pentandesma grandifolia</i>	1	Clusiaceae
<i>Napolaeona</i> sp.	7	Lecythidaceae	<i>Petersianthus macrocarpus</i>	3	Lecythidaceae
<i>Nauclea diderrichii</i>	6	Rubiaceae	<i>Picralima nitida</i>	15	Apocynaceae
<i>Nauclea pobeguinii</i>	1	Rubiaceae	<i>Piptadeniastrum africanum</i>	10	Leguminosae
<i>Neoboutonia mannii</i>	3	Euphorbiaceae	<i>Piptostigma</i> sp.	5	Annonaceae
<i>Neuropeltis</i> sp.	3	Convolvulaceae	<i>Placodiscus</i> sp.	6	Sapindaceae
<i>Newbouldia laevis</i>	1	Bignoniaceae	<i>Plagiosiphon (faux)</i>	1	Leguminosae
<i>Newtonia</i> sp.	1	Leguminosae	<i>Plagiosiphon emarginatus</i>	10	Leguminosae
<i>Ochna</i> sp.	2	Ochnaceae	<i>Plagiosiphon longitubus</i>	5	Leguminosae
<i>Octoknema affinis</i>	18	Olacaceae	<i>Plagiosiphon</i> sp.	14	Leguminosae
<i>Octoknema</i> sp.	2	Olacaceae	<i>Plagiostyles africana</i>	2	Euphorbiaceae
<i>Oldfieldia</i> sp.	1	Picrodendraceae	<i>Podocarpus latifolius</i>	3	Podocarpaceae
<i>Oncoba blackii</i>	44	Salicaceae	<i>Poga oleosa</i>	1	Anisophylleaceae
<i>Oncoba glauca</i>	6	Salicaceae	<i>Poga</i> sp.	2	Anisophylleaceae
<i>Oncoba</i> sp.	2	Salicaceae	<i>Porterandia cladantha</i>	1	Rubiaceae
<i>Oncoba welwitschii</i>	6	Salicaceae	<i>Pouteria robusta</i>	1	Sapotaceae
<i>Ongokea gore</i>	7	Olacaceae	<i>Prioria balsamifirum</i>	1	Leguminosae
<i>Oubanguia</i> sp.	3	Lecythidaceae	<i>Pseudospondias microcarpa</i>	2	Anacardiaceae
<i>Oxyanthus</i> sp.	1	Rubiaceae	<i>Psychotria venosa</i>	4	Rubiaceae

Species	Count	Family	Species	Count	Family
<i>Psyrdrax</i> sp.	1	Rubiaceae	<i>Sterculia tragacantha</i>	4	Malvaceae
<i>Pterocarpus mildbraedii</i>	7	Leguminosae	<i>Strombosia grandifolia</i>	115	Olacaceae
<i>Pterocarpus soyauxii</i>	2	Leguminosae	<i>Strombosia pustulata</i>	64	Olacaceae
<i>Pycnanthus angolensis</i>	87	Myristicaceae	<i>Strombosia scheffleri</i>	35	Olacaceae
<i>Quassia sanguinea</i>	2	Simaroubaceae	<i>Strombosia</i> sp.	200	Olacaceae
<i>Quassia</i> sp.	1	Simaroubaceae	<i>Strombosiosis tetrandra</i>	39	Olacaceae
<i>Raphia</i> sp.	3	Arecaceae	<i>Strychnos</i> sp.	22	Loganiaceae
<i>Rauvolfia macrophylla</i>	10	Apocynaceae	<i>Strychnos staudtii</i>	5	Loganiaceae
<i>Rauvolfia</i> sp.	1	Apocynaceae	<i>Symphonia globulifera</i>	9	Clusiaceae
<i>Rauvolfia vomitoria</i>	4	Apocynaceae	<i>Synsepalum msolo</i>	3	Sapotaceae
<i>Rhabdophyllum</i> sp.	53	Ochnaceae	<i>Syzygium guineensis</i>	1	Myrtaceae
<i>Ricinodendron heudelotii</i>	5	Euphorbiaceae	<i>Syzygium</i> sp.	10	Myrtaceae
<i>Rinorea dentata</i>	1	Violaceae	<i>Syzygium guineensis</i>	1	Myrtaceae
<i>Rinorea oblongifolia</i>	71	Violaceae	<i>Tabernaemontana</i> sp.	1	Apocynaceae
<i>Rinorea</i> sp.	4	Violaceae	<i>Tabernaemontana contorta</i>	3	Apocynaceae
<i>Ritchiea erecta</i>	2	Capparaceae	<i>Tabernaemontana crassa</i>	110	Apocynaceae
<i>Rothmannia</i> sp.	8	Rubiaceae	<i>Terminalia superba</i>	16	Combretaceae
<i>Santaloidella giletii</i>	1	Connaraceae	<i>Tetracera alnifolia</i>	3	Dilleniaceae
<i>Santiria trimera</i>	43	Burseraceae	<i>Thomandersia</i> sp.	4	Acanthaceae
<i>Schumanniphyton magnificum</i>	1	Rubiaceae	<i>Treculia africana</i>	2	Moraceae
<i>Scottellia coriacea</i>	3	Achariaceae	<i>Treculia obovoidea</i>	7	Moraceae
<i>Scyphocephalum mannii</i>	71	Myristicaceae	<i>Treculia</i> sp.	22	Moraceae
<i>Sorindeia grandifolia</i>	1	Anacardiaceae	<i>Tricalysia</i> sp.	22	Rubiaceae
<i>Sorindeia</i> sp.	2	Anacardiaceae	<i>Trichilia prieuriana</i>	1	Meliaceae
<i>Spathodea campanulata</i>	1	Bignoniaceae	<i>Trichilia rubescens</i>	18	Meliaceae
<i>Spondianthus preussi</i>	1	Phyllanthaceae	<i>Trichilia</i> sp.	20	Meliaceae
<i>Staudtia kamerunensis</i>	57	Myristicaceae	<i>Trichilia welwitschi</i>	1	Meliaceae
<i>Sterculia</i> sp.	1	Malvaceae	<i>Trichoscypha acuminata</i>	2	Anacardiaceae

Species	Count	Family
<i>Trichoscypha</i> sp.	26	Anacardiaceae
<i>Tridesmostemon omphalocarpoides</i>	4	Sapotaceae
<i>Uapaca guineensis</i>	55	Phyllanthaceae
<i>Uapaca</i> sp.	4	Phyllanthaceae
Unknown	288	Undefined
<i>Uvariodendron connivens</i>	1	Annonaceae
<i>Uvariodendron giganteum</i>	1	Annonaceae
<i>Uvariodendron</i> sp.	6	Annonaceae
<i>Uvariopsis congolana</i>	1	Annonaceae
<i>Uvariopsis</i> sp.	4	Annonaceae
<i>Vitex grandifolia</i>	36	Lamiaceae
<i>Xylopia aethiopica</i>	2	Annonaceae
<i>Xylopia rubescens</i>	2	Annonaceae
<i>Xylopia</i> sp.	7	Annonaceae
<i>Xylopia staudtii</i>	5	Annonaceae
<i>Zanthoxylum gilletii</i>	3	Rutaceae
<i>Zanthoxylum</i> sp.	5	Rutaceae
<i>Zenkerella citrina</i>	32	Leguminosae

Appendix 2.9. Plant species list (≥ 10 cm DBH), number of stems per species and family for ecotone-Ganga

Species	Count	Family	Species	Count	Family
<i>Afzelia africana</i>	33	Leguminosae	<i>Carapa</i> sp.	29	Meliaceae
<i>Aidia</i> sp.	2	Rubiaceae	<i>Ceiba pentandra</i>	10	Malvaceae
<i>Albizia adianthifolia</i>	4	Leguminosae	<i>Celtis milbraedii</i>	1	Cannabaceae
<i>Albizia africana</i>	1	Leguminosae	<i>Celtis</i> sp.	4	Cannabaceae
<i>Albizia glaberrima</i>	3	Leguminosae	<i>Chytranthus</i> sp.	2	Sapindaceae
<i>Albizia</i> sp.	8	Leguminosae	<i>Coelocaryon preussii</i>	1	Myristicaceae
<i>Allophylus africanus</i>	9	Sapindaceae	<i>Cola chlamydantha</i>	7	Malvaceae
<i>Amphimas pterocarpoides</i>	3	Leguminosae	<i>Cola cordifolia</i>	12	Malvaceae
<i>Amphimas</i> sp.	3	Leguminosae	<i>Cola lateritia</i>	6	Malvaceae
<i>Anisophyllea</i> sp.	10	Anisophylleaceae	<i>Cola</i> sp.	117	Malvaceae
<i>Anthonothea ferruginea</i>	7	Leguminosae	<i>Combretum</i> sp.	5	Combretaceae
<i>Anthonothea macrophylla</i>	2	Leguminosae	<i>Dacryodes</i> sp.	16	Burseraceae
<i>Anthonothea</i> sp.	8	Leguminosae	<i>Dasylepis racemosa</i>	4	Achariaceae
<i>Antiaris africana</i>	1	Moraceae	<i>Deinbollia</i> sp.	1	Sapindaceae
<i>Antiaris</i> sp.	1	Moraceae	<i>Desbordesia glaucescens</i>	4	Irvingiaceae
<i>Antidesma membranacea</i>	11	Phyllanthaceae	<i>Desplatsia</i> sp.	1	Malvaceae
<i>Antidesma</i> sp.	125	Phyllanthaceae	<i>Detarium macrocarpa</i>	54	Leguminosae
<i>Aubrevillea</i> sp.	2	Leguminosae	<i>Dialium dinklagei</i>	2	Leguminosae
<i>Baikiaea</i> sp.	1	Leguminosae	<i>Dialium</i> sp.	4	Leguminosae
<i>Bartiera fistulosa</i>	1	Passifloraceae	<i>Dichostemma glaucescens</i>	1	Euphorbiaceae
<i>Beilschmiedia</i> sp.	5	Lauraceae	<i>Dichrostachys cinerea</i>	2	Leguminosae
<i>Berlinia bracteosa</i>	5	Leguminosae	<i>Dictyandra involucrata</i>	1	Rubiaceae
<i>Berlinia</i> sp.	128	Leguminosae	<i>Diospyros</i> sp.	32	Ebenaceae
<i>Bersama engerana</i>	1	Melanthaceae	<i>Discoglyprena caloneura</i>	2	Euphorbiaceae
<i>Blighia</i> sp.	1	Sapindaceae	<i>Donella</i> sp.	1	Sapotaceae
<i>Bombax</i> sp.	1	Malvaceae	<i>Dovyalis zenkeri</i>	1	Salicaceae
<i>Borassus aethiopum</i>	1	Arecaceae	<i>Drypetes aframensis</i>	2	Phyllanthaceae
<i>Bridelia micrantha</i>	1	Euphorbiaceae	<i>Drypetes</i> sp.	55	Phyllanthaceae
<i>Canarium schweinfurthii</i>	28	Burseraceae	<i>Duboscia macrocarpa</i>	1	Malvaceae

Species	Count	Family		Species	Count	Family
<i>Duguetia</i> sp.	1	Annonaceae		<i>Hymenocardia acida</i>	27	Phyllanthaceae
<i>Duguetia staudtii</i>	13	Annonaceae		<i>Hymenocardia lyrata</i>	573	Phyllanthaceae
<i>Englerophytum</i> sp.	30	Sapotaceae		<i>Irvingia gabonensis</i>	1	Irvingiaceae
<i>Eribroma oblonga</i>	3	Malvaceae		<i>Irvingia grandifolia</i>	1	Irvingiaceae
<i>Eriocoelum macrocarpum</i>	2	Sapindaceae		<i>Irvingia</i> sp.	3	Irvingiaceae
<i>Eriocoelum</i> sp.	3	Sapindaceae		<i>Khaya grandifolia</i>	3	Meliaceae
<i>Erythrophleum suaveolens</i>	9	Leguminosae		<i>Khaya</i> sp.	3	Meliaceae
<i>Fernandoa ferdinandi</i>	11	Bignoniaceae		<i>Klainedoxa gabonensis</i>	26	Irvingiaceae
<i>Fernandoa</i> sp.	15	Bignoniaceae		<i>Lannea acida</i>	153	Anacardiaceae
<i>Ficus mucoso</i>	1	Moraceae		Liana	170	Undefined
<i>Ficus</i> sp.	9	Moraceae		<i>Lovoa trichilioides</i>	35	Meliaceae
<i>Ficus sur</i>	2	Moraceae		<i>Macaranga barteri</i>	5	Euphorbiaceae
<i>Funtumia elastica</i>	16	Apocynaceae		<i>Macaranga hurifolia</i>	4	Euphorbiaceae
<i>Gaertnera longevaginalis</i>	4	Rubiaceae		<i>Macaranga</i> sp.	2	Euphorbiaceae
<i>Gaertnera</i> sp.	1	Rubiaceae		<i>Maesobotrya barteri</i>	1	Euphorbiaceae
<i>Gambeya boukokoensis</i>	9	Sapotaceae		<i>Maesobotrya klaineana</i>	2	Euphorbiaceae
<i>Gambeya</i> sp.	74	Sapotaceae		<i>Maesobotrya</i> sp.	3	Euphorbiaceae
<i>Garcinia mannii</i>	1	Clusiaceae		<i>Maesopsis eminii</i>	2	Rhamnaceae
<i>Garcinia</i> sp.	7	Clusiaceae		<i>Malacantha alnifolia</i>	7	Sapotaceae
<i>Greenwayodendron suaveolens</i>	6	Annonaceae		<i>Mallotus oppositifolius</i>	13	Euphorbiaceae
<i>Guarea</i> sp.	1	Meliaceae		<i>Mallotus</i> sp.	2	Euphorbiaceae
<i>Guarea thompsonii</i>	1	Meliaceae		<i>Mammea africana</i>	2	Calophyllaceae
<i>Harungana madagascariensis</i>	1	Hypericaceae		<i>Maprounea membranacea</i>	2	Euphorbiaceae
<i>Heisteria parviflora</i>	2	Olacaceae		<i>Maranthes</i> sp.	2	Chrysobalanaceae
<i>Heisteria</i> sp.	1	Olacaceae		<i>Margaritaria discoidea</i>	7	Euphorbiaceae
<i>Holarrhena floribunda</i>	154	Apocynaceae		<i>Markhamia lutea</i>	1	Bignoniaceae
<i>Homalium le-testui</i>	2	Salicaceae		<i>Markhamia</i> sp.	5	Bignoniaceae
<i>Homalium</i> sp.	2	Salicaceae		<i>Milicia excelsa</i>	38	Moraceae
<i>Hylodendron gabunense</i>	8	Leguminosae		<i>Mitragyna ciliata</i>	8	Rubiaceae

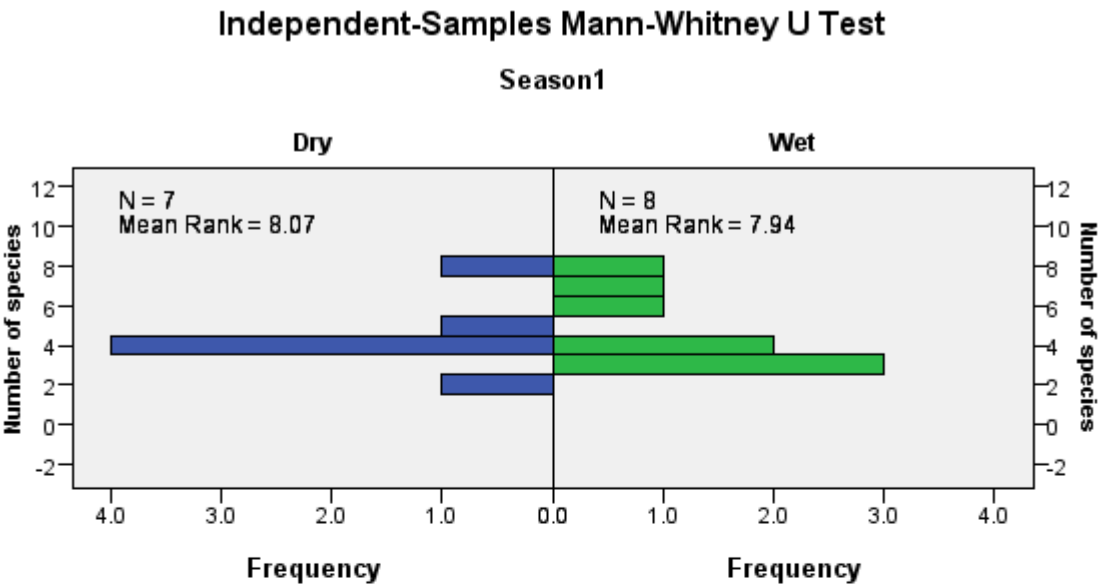
Species	Count	Family	Species	Count	Family
<i>Monodora myristica</i>	1	Annonaceae	<i>Rothmannia</i> sp.	1	Rubiaceae
<i>Monodora</i> sp.	2	Annonaceae	<i>Shirakiopsis elliptica</i>	19	Euphorbiaceae
<i>Myrianthus arboreus</i>	44	Urticaceae	<i>Sorindeia</i> sp.	134	Anacardiaceae
<i>Nauclea pobeguinii</i>	1	Rubiaceae	<i>Spathodea campanulata</i>	1	Bignoniaceae
<i>Nauclea</i> sp.	1	Rubiaceae	<i>Spondianthus preussii</i>	288	Phyllanthaceae
<i>Ochna afzelii</i>	242	Ochnaceae	<i>Staudtia kamerunensis</i>	4	Myristicaceae
<i>Ochna membranacea</i>	2	Ochnaceae	<i>Sterculia</i> sp.	2	Malvaceae
<i>Ochna</i> sp.	58	Ochnaceae	<i>Sterculia tragacantha</i>	1	Malvaceae
<i>Ochthocosmus</i> sp.	21	Ixonanthaceae	<i>Strombosia grandifolia</i>	4	Olacaceae
<i>Olax subscorpioidea</i>	76	Olacaceae	<i>Strombosia</i> sp.	4	Olacaceae
<i>Oncoba dentata</i>	3	Salicaceae	<i>Swartzia fistuloides</i>	1	Leguminosae
<i>Oncoba</i> sp.	12	Salicaceae	<i>Swartzia</i> sp.	1	Leguminosae
<i>Oncoba spinosus</i>	2	Salicaceae	<i>Symphonia globulifera</i>	1	Clusiaceae
<i>Oncoba welwitschii</i>	24	Salicaceae	<i>Synsepalum</i> sp.	72	Sapotaceae
<i>Parinari excelsa</i>	23	Chrysobalanaceae	<i>Syzygium</i> sp.	37	Myrtaceae
<i>Parkia bicolor</i>	23	Leguminosae	<i>Tabernaemontana crassa</i>	15	Apocynaceae
<i>Parkia biglobosa</i>	23	Leguminosae	<i>Terminalia</i> sp.	10	Combretaceae
<i>Parkia</i> sp.	116	Leguminosae	<i>Terminalia superba</i>	6	Combretaceae
<i>Piptadeniastrum africanum</i>	5	Leguminosae	<i>Tetrapleura tetraptera</i>	29	Leguminosae
<i>Plagiostyles africana</i>	1	Euphorbiaceae	<i>Tetrorchidium didymostemon</i>	2	Euphorbiaceae
<i>Pouteria</i> sp.	24	Sapotaceae	<i>Treculia africana</i>	8	Moraceae
<i>Pseudospondias microcarpa</i>	31	Anacardiaceae	<i>Treculia</i> sp.	2	Moraceae
<i>Pseudospondias</i> sp.	3	Anacardiaceae	<i>Tricalysia</i> sp.	31	Rubiaceae
<i>Pterocarpus milbraedii</i>	1	Leguminosae	<i>Trichilia prieureana</i>	1	Meliaceae
<i>Pycnanthus angolensis</i>	25	Myristicaceae	<i>Trichilia rubescens</i>	21	Meliaceae
<i>Quassia sanguinea</i>	6	Simaroubaceae	<i>Trichilia</i> sp.	6	Meliaceae
<i>Quassia</i> sp.	7	Simaroubaceae	<i>Trilepisium madagascariensis</i>	15	Moraceae
<i>Rauvolfia vomitoria</i>	6	Apocynaceae	<i>Uapaca guineensis</i>	194	Phyllanthaceae
<i>Rinorea oblongifolia</i>	7	Violaceae	<i>Uapaca</i> sp.	153	Phyllanthaceae

Species	Count	Family
Unknown	235	Undefined
<i>Vepris</i> sp.	1	Rutaceae
<i>Vismia</i> sp.	1	Hypericaceae
<i>Vitex doniana</i>	156	Lamiaceae
<i>Vitex grandifolia</i>	2	Lamiaceae
<i>Voacanga poecilocalyx</i>	2	Apocynaceae
<i>Voacanga</i> sp.	2	Apocynaceae
<i>Xylopia aethiopica</i>	374	Annonaceae
<i>Xylopia rubescens</i>	3	Annonaceae
<i>Xylopia</i> sp.	1	Annonaceae
<i>Zanthoxylum</i> sp.	4	Rutaceae

Appendix 2.10: Eigenvector values for environmental and ecological variables that accounted for variation in habitat characteristics between the ecotone (Ganga) and rainforest (Bekob and Njuma) Nigeria-Cameroon chimpanzee habitats

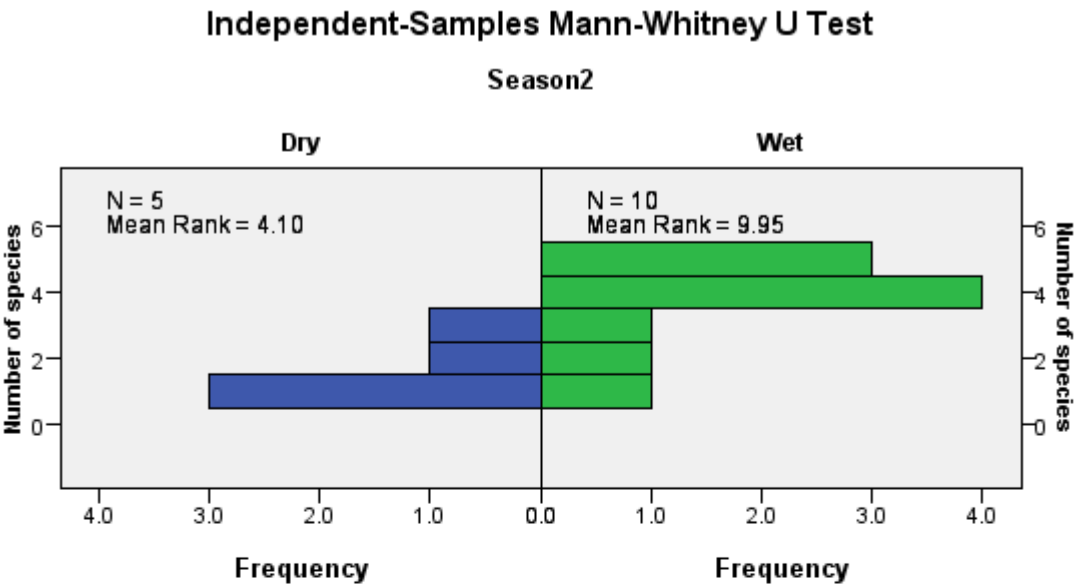
Variables	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Stem density of trees	0.038972	-0.609057	0.626597	0.343415	-0.329000	-0.093183	0.007043
Stem density lianas	-0.335918	0.373472	0.168332	0.724507	0.397070	-0.185225	-0.049584
Number of tree species	0.431720	-0.254061	-0.219080	0.382883	0.322469	0.652410	0.157639
Mean tree size	0.363567	0.414909	-0.206720	0.385566	-0.709737	-0.023286	-0.002545
Quadrats with THV	-0.430708	0.278726	0.342327	-0.113353	-0.242364	0.727688	-0.136002
Rainfall	0.486297	0.169133	0.305446	-0.101412	0.207031	-0.010842	-0.767039
Seasonality	0.380899	0.382855	0.527092	-0.196880	0.157413	-0.034361	0.604806
<i>Importance of components</i>							
	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Standard deviation	1.9179	1.3326	0.7967	0.733	0.44783	0.40403	0.10092
Proportion of Variance	0.5255	0.2537	0.09067	0.07676	0.02865	0.02332	0.00145
Cumulative Proportion	0.5255	0.7792	0.86982	0.94658	0.97523	0.99855	1

Appendix 2.11. Seasonality in fruit availability for the 12 most consumed fruit species at the human-modified rainforest-Bekob



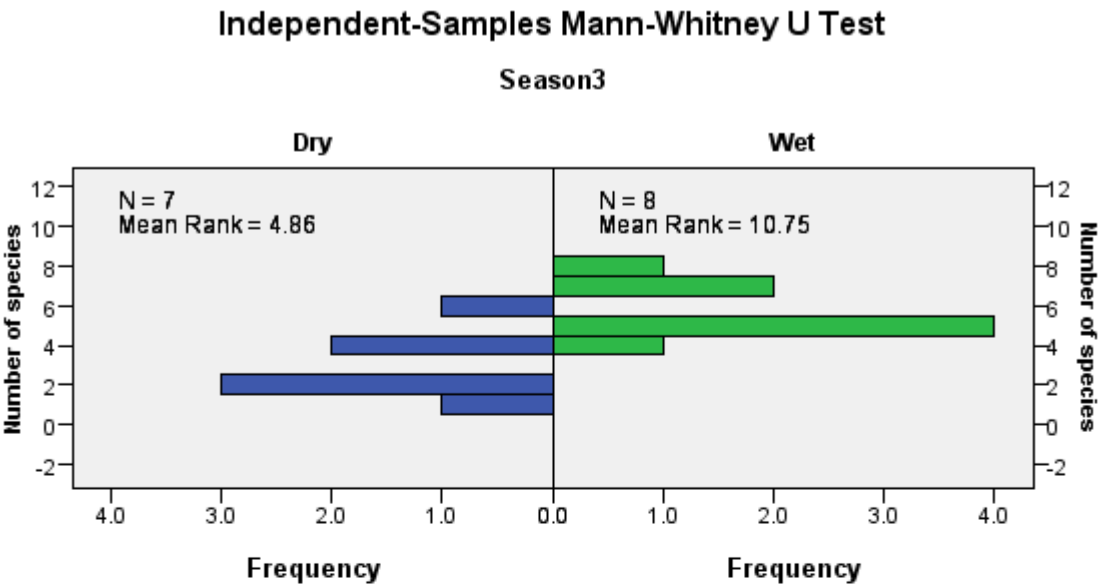
Total N	15
Mann-Whitney U	27.500
Wilcoxon W	63.500
Test Statistic	27.500
Standard Error	8.327
Standardized Test Statistic	-.060
Asymptotic Sig. (2-sided test)	.952
Exact Sig. (2-sided test)	.955

Appendix 2.12. Seasonality in fruit availability for the 12 most consumed fruit species at the rainforest-Njuma



Total N	15
Mann-Whitney U	44.500
Wilcoxon W	99.500
Test Statistic	44.500
Standard Error	7.973
Standardized Test Statistic	2.446
Asymptotic Sig. (2-sided test)	.014
Exact Sig. (2-sided test)	.013

Appendix 2.13. Seasonality in fruit availability for the 12 most consumed fruit species at the ecotone-Ganga

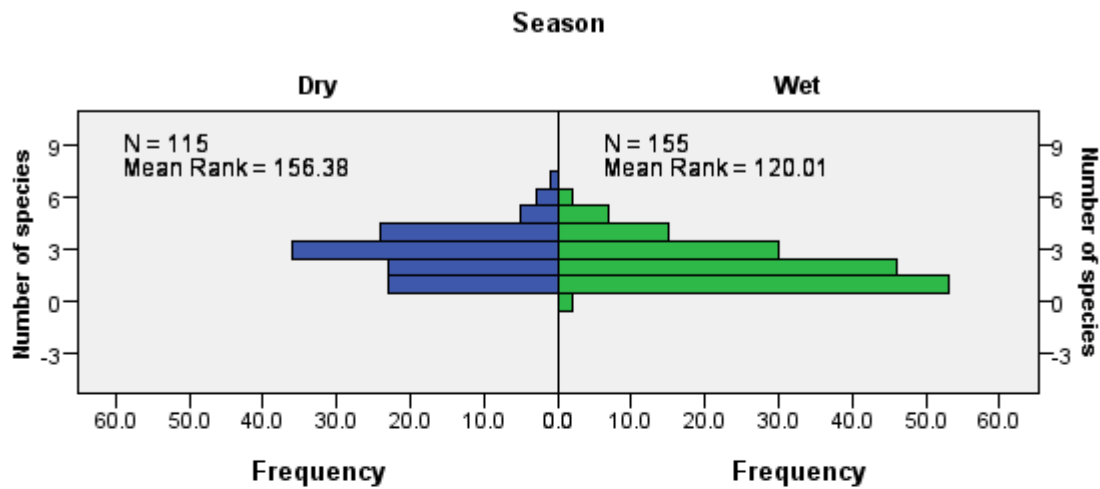


Total N	15
Mann-Whitney U	50.000
Wilcoxon W	86.000
Test Statistic	50.000
Standard Error	8.493
Standardized Test Statistic	2.590
Asymptotic Sig. (2-sided test)	.010
Exact Sig. (2-sided test)	.009

Appendix Chapter 3

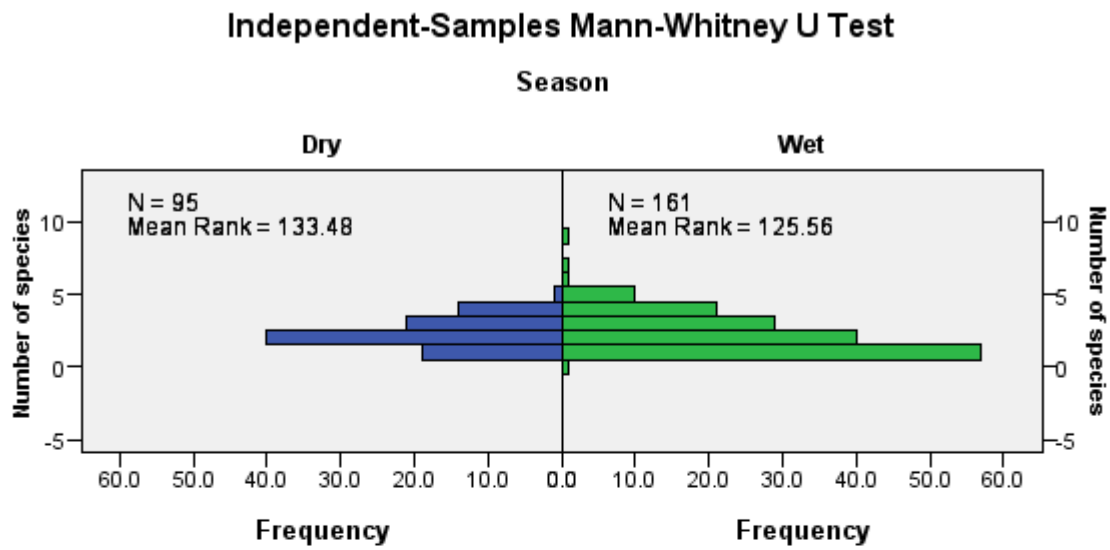
Appendix 3.1. Seasonality in the number of fruit species in chimpanzee fecal samples at Bekob

Independent-Samples Mann-Whitney U Test



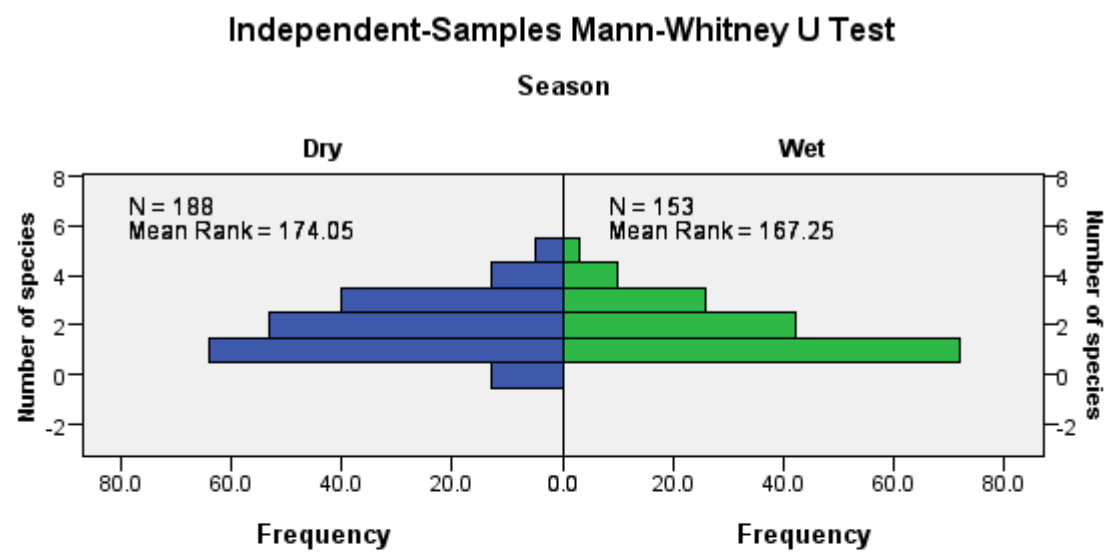
Total N	270
Mann-Whitney U	6,511.000
Wilcoxon W	18,601.000
Test Statistic	6,511.000
Standard Error	616.219
Standardized Test Statistic	-3.897
Asymptotic Sig. (2-sided test)	.000

Appendix 3.2. Seasonality in the number of fruit species in chimpanzee fecal samples Njuma



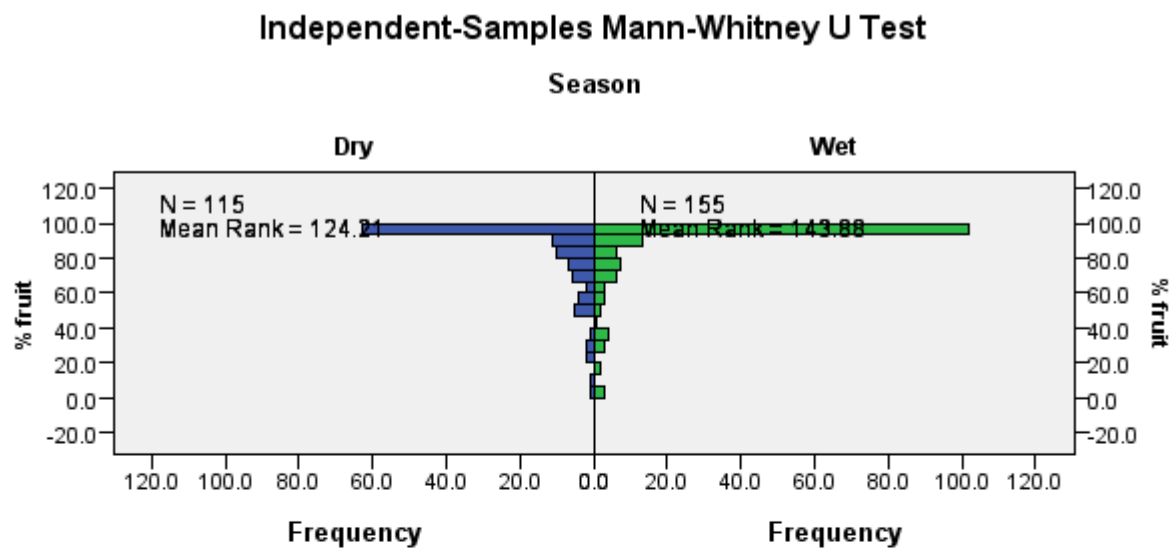
Total N	256
Mann-Whitney U	7,174.000
Wilcoxon W	20,215.000
Test Statistic	7,174.000
Standard Error	552.903
Standardized Test Statistic	-.856
Asymptotic Sig. (2-sided test)	.392

Appendix 3.3. Seasonality in the number of fruit species in chimpanzee fecal samples Ganga



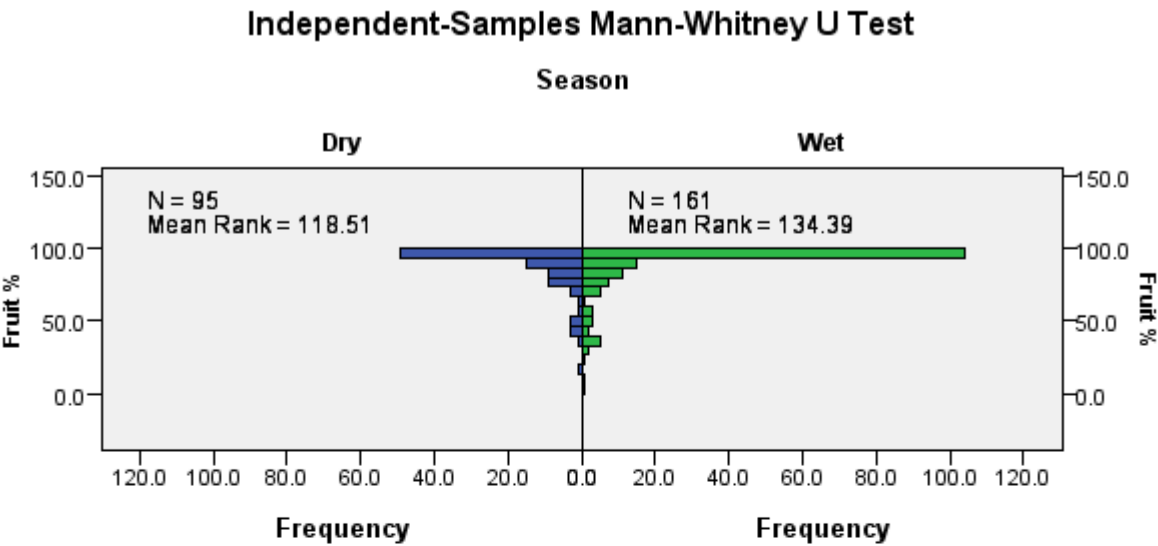
Total N	341
Mann-Whitney U	13,808.500
Wilcoxon W	25,589.500
Test Statistic	13,808.500
Standard Error	862.437
Standardized Test Statistic	-.665
Asymptotic Sig. (2-sided test)	.506

Appendix 3.4. Seasonality in fleshy fruit consumption – seasonal variation in proportion of fruits in chimpanzee diets at human-modified rainforest-Bekob



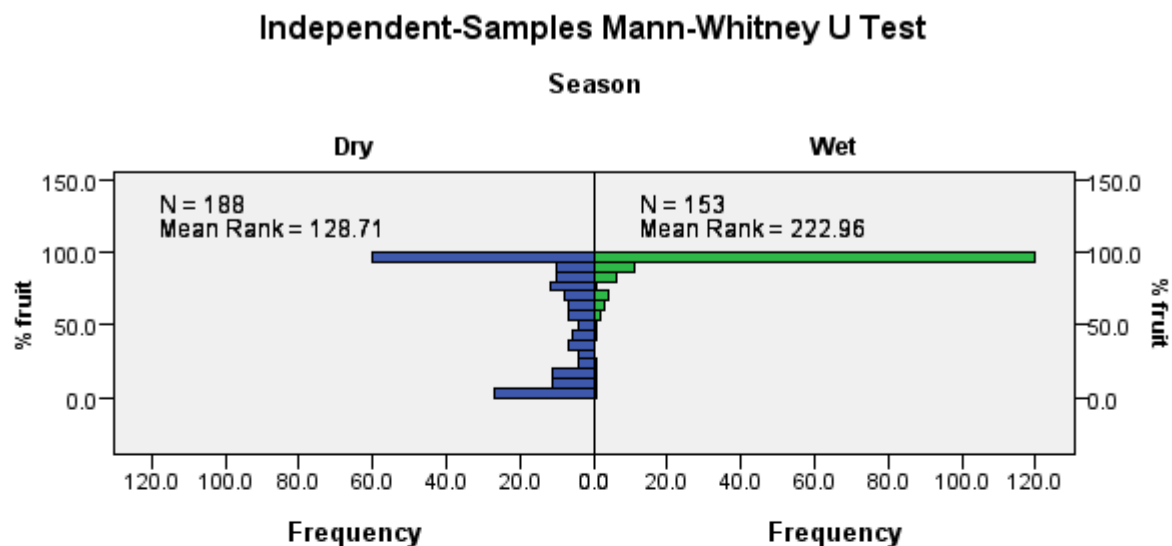
Total N	270
Mann-Whitney U	10,211.000
Wilcoxon W	22,301.000
Test Statistic	10,211.000
Standard Error	597.134
Standardized Test Statistic	2.175
Asymptotic Sig. (2-sided test)	.030

Appendix 3.5. Seasonality in fleshy fruit consumption – seasonal variation in proportion of fruits in chimpanzee diets rainforest-Njuma



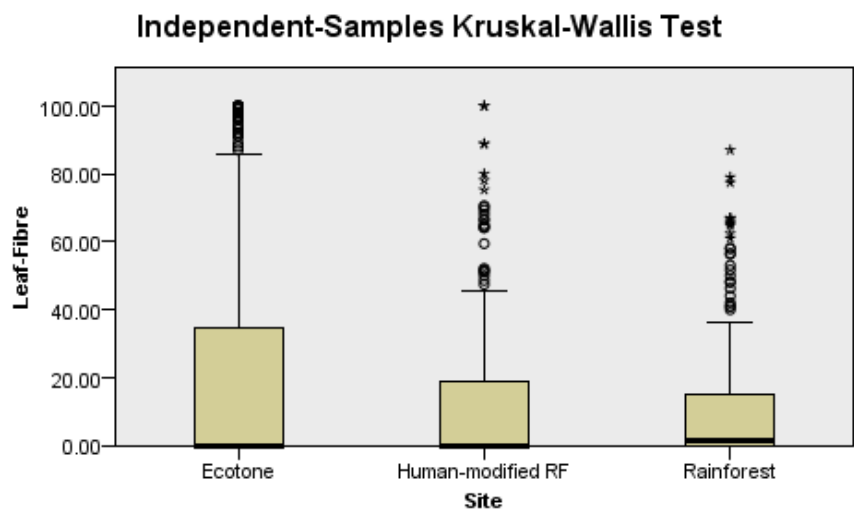
Total N	256
Mann-Whitney U	8,596.500
Wilcoxon W	21,637.500
Test Statistic	8,596.500
Standard Error	539.658
Standardized Test Statistic	1.759
Asymptotic Sig. (2-sided test)	.079

Appendix 3.6. Seasonality in fleshy fruit consumption – seasonal variation in proportion of fruits in chimpanzee diets ecotone-Ganga



Total N	341
Mann-Whitney U	22,332.500
Wilcoxon W	34,113.500
Test Statistic	22,332.500
Standard Error	884.282
Standardized Test Statistic	8.991
Asymptotic Sig. (2-sided test)	.000

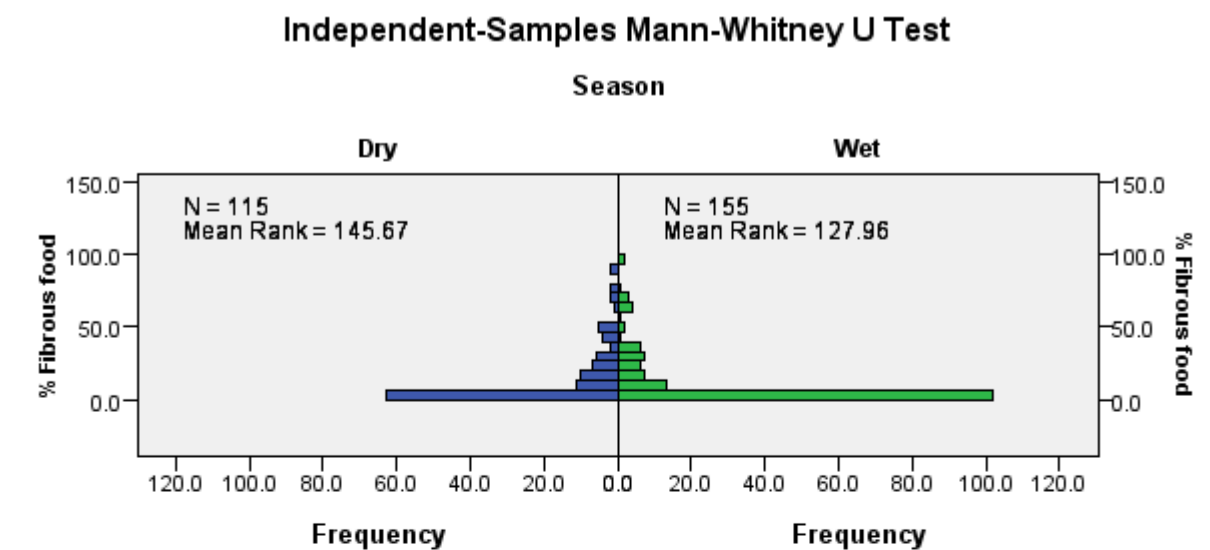
Appendix 3.7. Annual variation in fibrous food consumption at Ganga (ecotone), Bekob (human-modified RF) and Njuma (rainforest)



Total N	867
Test Statistic	4.719
Degrees of Freedom	2
Asymptotic Sig. (2-sided test)	.094

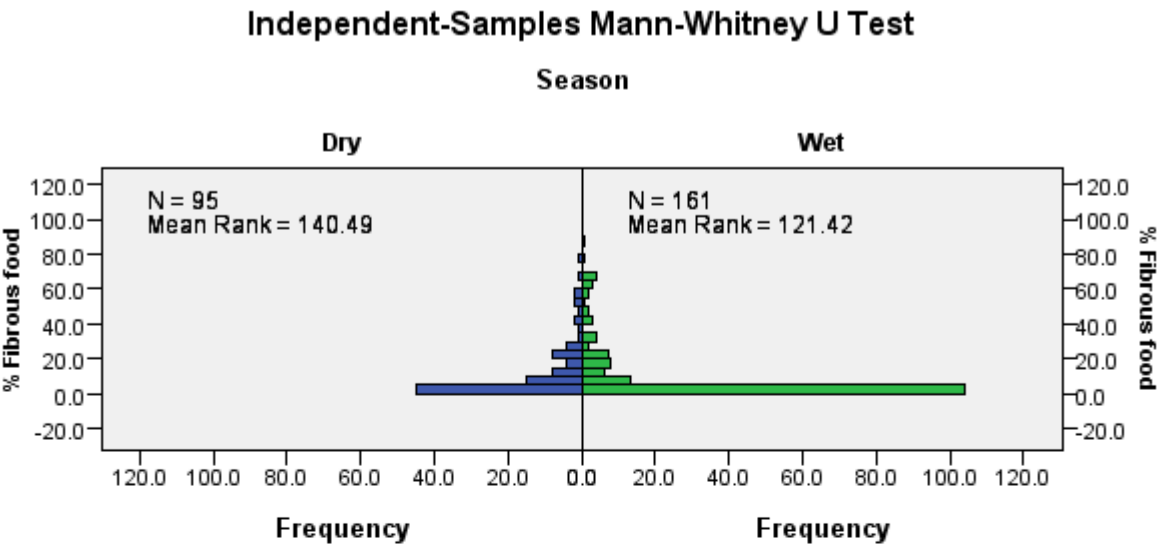
1. The test statistic is adjusted for ties.
2. Multiple comparisons are not performed because the overall test does not show significant differences across samples.

Appendix 3.8. Seasonality in fibrous food consumption at human-modified rainforest, Bekob



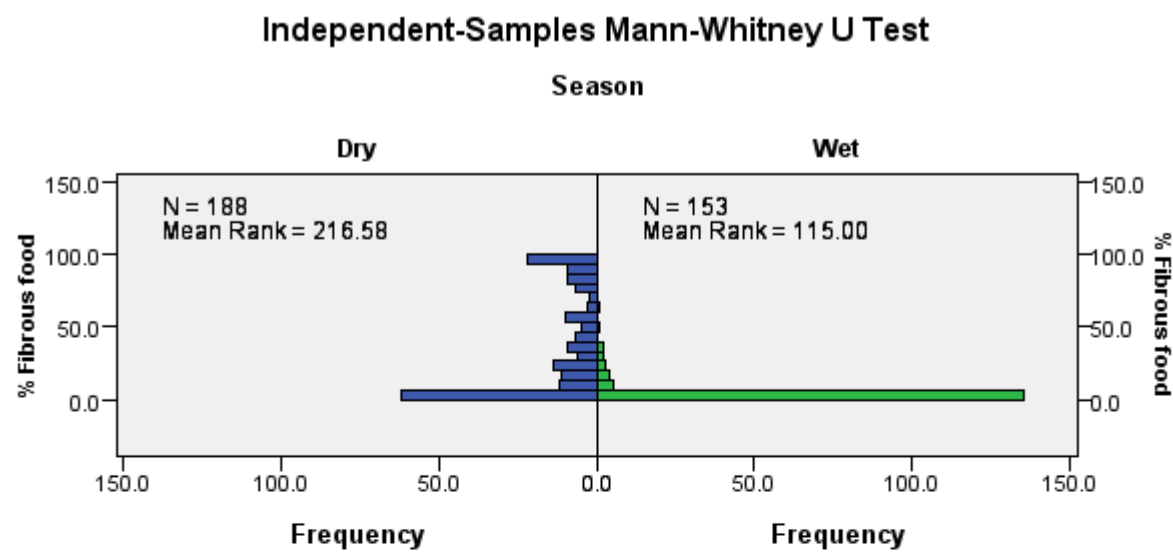
Total N	270
Mann-Whitney U	7,743.500
Wilcoxon W	19,833.500
Test Statistic	7,743.500
Standard Error	587.552
Standardized Test Statistic	-1.990
Asymptotic Sig. (2-sided test)	.047

Appendix 3.9. Seasonality in fibrous food consumption at rainforest-Njuma



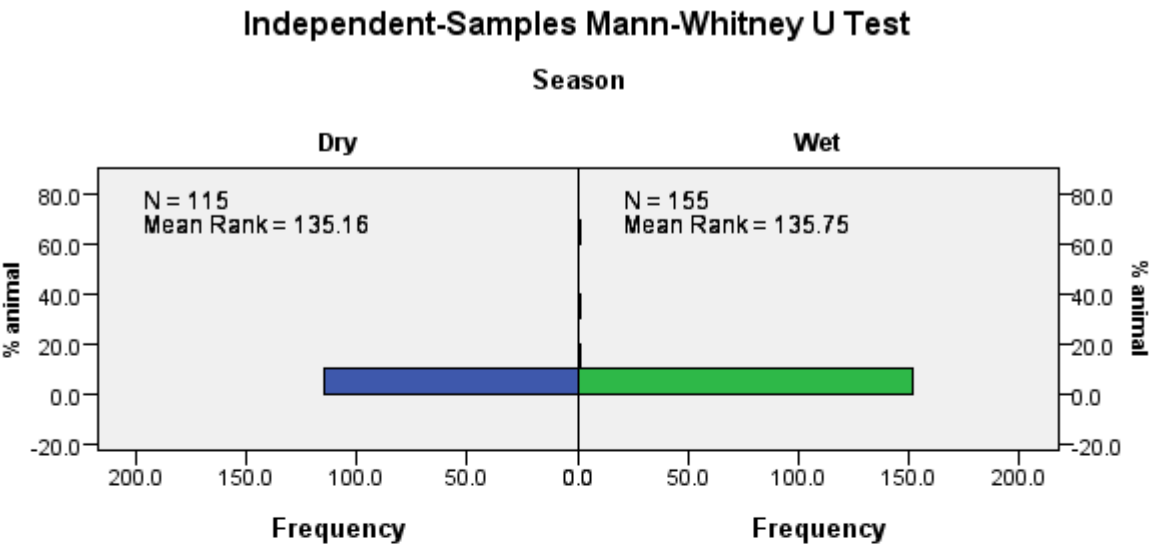
Total N	256
Mann-Whitney U	6,508.000
Wilcoxon W	19,549.000
Test Statistic	6,508.000
Standard Error	536.257
Standardized Test Statistic	-2.125
Asymptotic Sig. (2-sided test)	.034

Appendix 3.10. Seasonality in fibrous food consumption at ecotone-Ganga



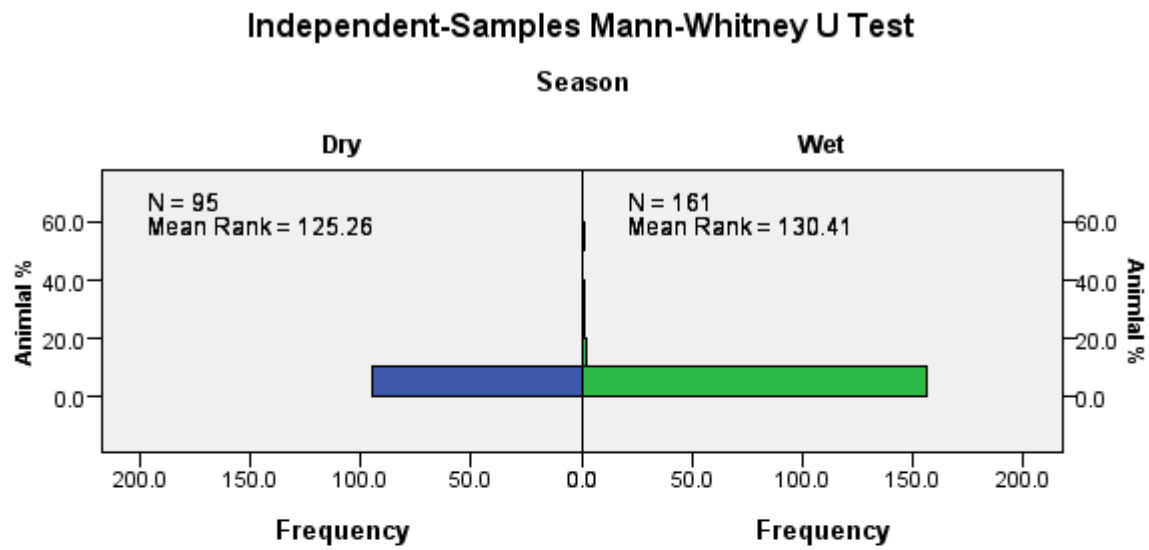
Total N	341
Mann-Whitney U	5,813.500
Wilcoxon W	17,594.500
Test Statistic	5,813.500
Standard Error	846.385
Standardized Test Statistic	-10.124
Asymptotic Sig. (2-sided test)	.000

Appendix 3.11. Seasonality in animal prey consumption at human-modified rainforest-Bekob



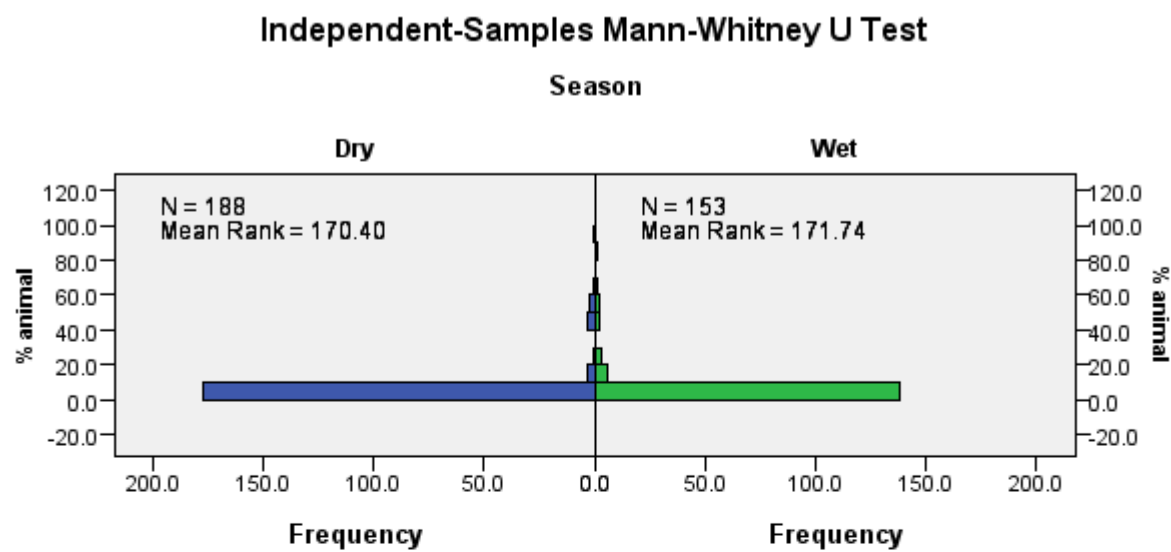
Total N	270
Mann-Whitney U	8,951.500
Wilcoxon W	21,041.500
Test Statistic	8,951.500
Standard Error	324.732
Standardized Test Statistic	.120
Asymptotic Sig. (2-sided test)	.904

Appendix 3.12. Seasonality in animal prey consumption at rainforest-Njuma



Total N	256
Mann-Whitney U	7,955.500
Wilcoxon W	20,996.500
Test Statistic	7,955.500
Standard Error	310.089
Standardized Test Statistic	.993
Asymptotic Sig. (2-sided test)	.321

Appendix 3.13. Seasonality in animal prey consumption at ecotone-Ganga



Total N	341
Mann-Whitney U	14,495.000
Wilcoxon W	26,276.000
Test Statistic	14,495.000
Standard Error	783.002
Standardized Test Statistic	.144
Asymptotic Sig. (2-sided test)	.885

Appendix 3.14. Eigenvector values for variation in diet composition between Nigeria-Cameroon chimpanzee populations at Ganga, Bekob, Njuma during the dry season (December to February)

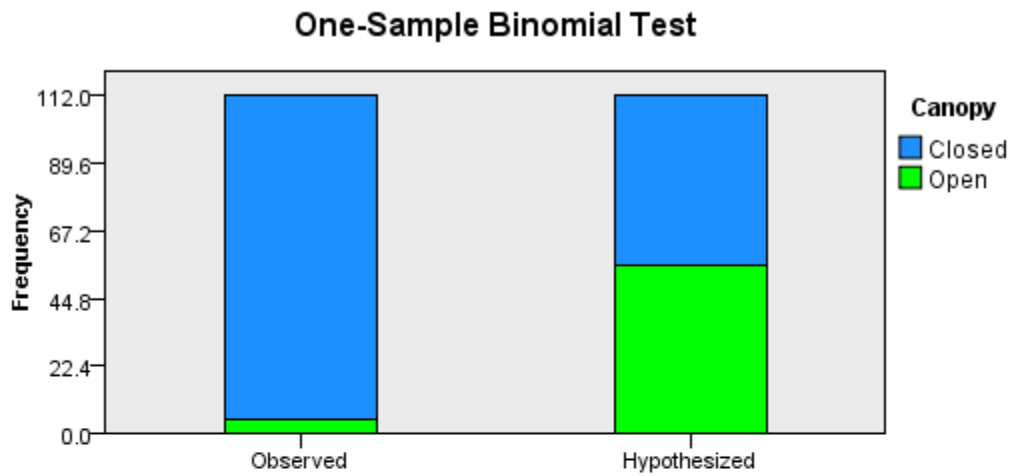
<i>Variables</i>	PC1	PC2	PC3	PC4	PC5	PC6
Number of fruit species	-0.247488	-0.667649	0.133811	-0.685485	-0.072113	0.000031
Fruit volume	-0.558866	-0.092102	0.014580	0.321609	-0.259045	0.713047
Fiber volume	0.544755	0.150327	0.147077	-0.341328	0.256416	0.690477
Animal volume	0.184638	-0.314663	-0.919344	0.053691	0.063366	0.121673
Volume of seeds >5 mm	-0.469949	0.142072	-0.087977	-0.076701	0.863331	0.000054
Number of seeds >5 mm	-0.273345	0.635584	-0.327592	-0.549007	-0.335545	0.000275
<i>Importance of components</i>						
	PC1	PC2	PC3	PC4	PC5	PC6
Standard deviation	1.6783	0.9963	0.9739	0.8821	0.68135	0.009577
Proportion of Variance	0.4694	0.1654	0.1581	0.1297	0.07737	0.00002
Cumulative Proportion	0.4694	0.6349	0.7929	0.9226	0.99998	1

Appendix 3.15. Eigenvector values for variation in diet composition between Nigeria-Cameroon chimpanzee populations at Ganga, Bekob, Njuma during the wet season (May to September)

<i>Variables</i>	PC1	PC2	PC3	PC4	PC5	PC6
Number of fruit species	0.098643	0.805171	0.218340	0.334195	0.427324	0.002044
Fruit volume	-0.586677	0.175649	0.132747	0.179015	0.264308	0.710936
Fiber volume	0.557359	0.011114	0.153271	0.406329	0.291452	0.644738
Animal volume	0.199886	0.419717	0.685426	0.484705	0.016754	0.280811
Volume of seeds >5 mm	-0.505129	0.311681	0.035193	0.136204	0.792395	0.004375
Number of seeds >5 mm	-0.200799	0.217750	0.663450	0.661570	0.185525	0.001989
<i>Importance of components</i>						
	PC1	PC2	PC3	PC4	PC5	PC6
Standard deviation	1.6115	1.0905	1.0183	0.921	0.5711	0.04823
Proportion of variance	0.4329	0.1982	0.1728	0.1414	0.05436	0.00039
Cumulative proportion	0.4329	0.6311	0.8039	0.9453	0.99961	1

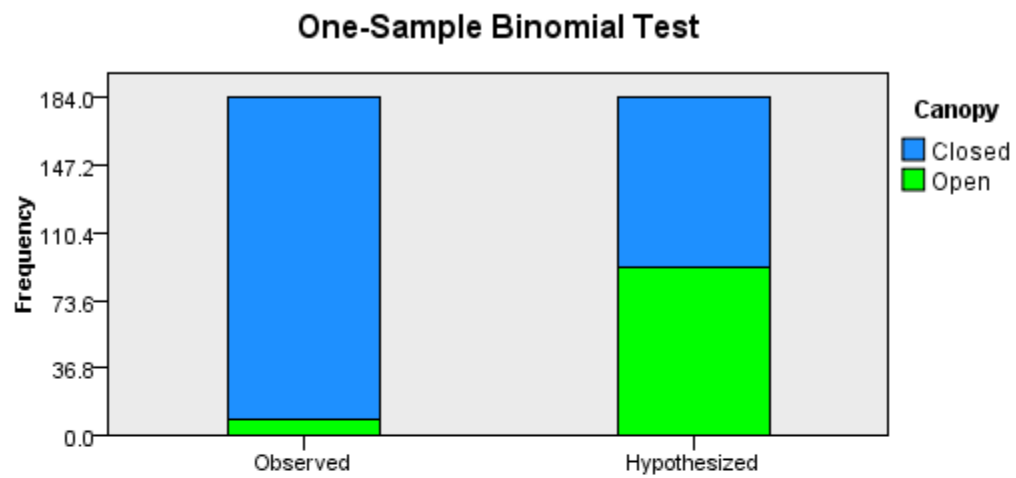
Appendix Chapter 4

Appendix 4.1. Nesting site location in relation to habitat type at human-modified rainforest-Bekob



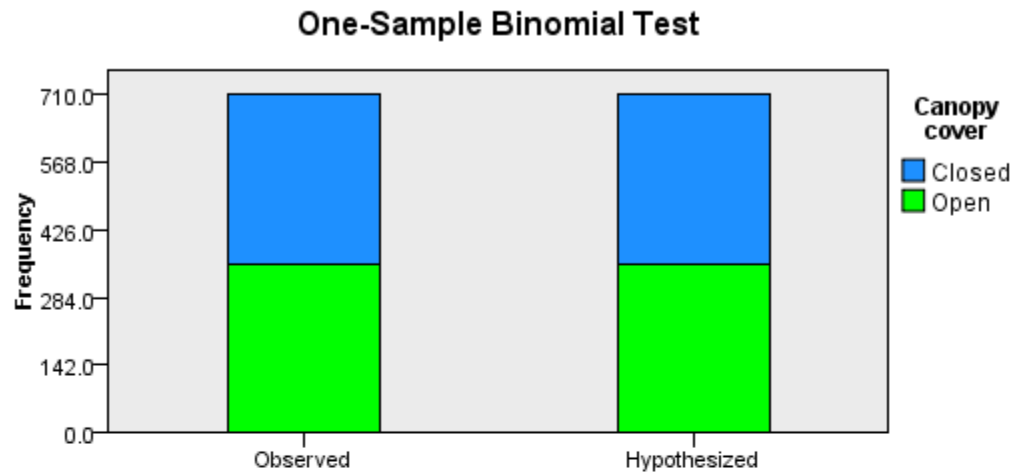
Total N	112
Test Statistic	107.000
Standard Error	5.292
Standardized Test Statistic	9.544
Asymptotic Sig. (2-sided test)	.000

Appendix 4.2. Nesting site location in relation to habitat type at rainforest-Njuma



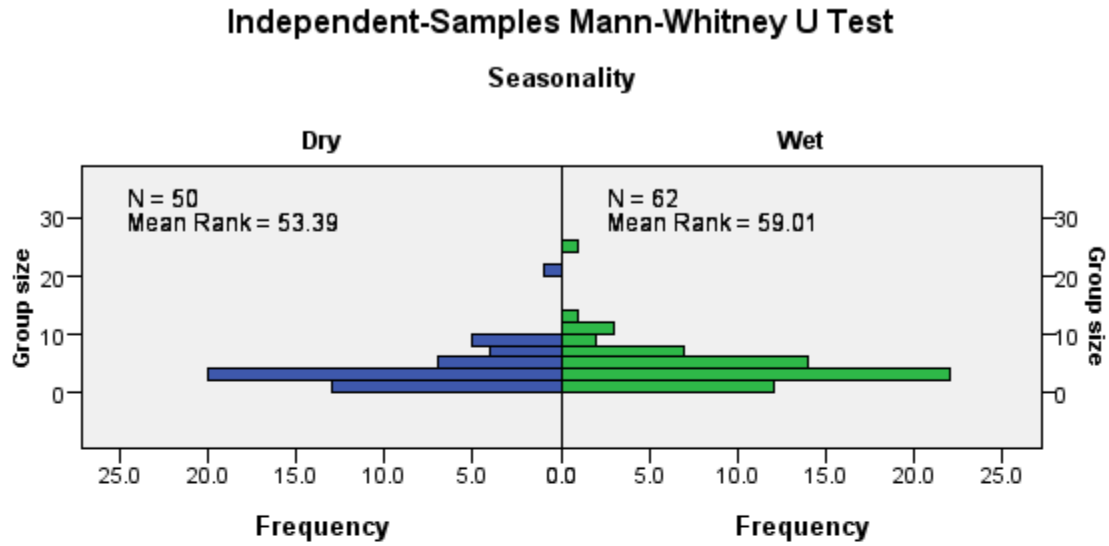
Total N	184
Test Statistic	175.000
Standard Error	6.782
Standardized Test Statistic	12.164
Asymptotic Sig. (2-sided test)	.000

Appendix 4.3. Nesting site location in relation to habitat type at Ganga



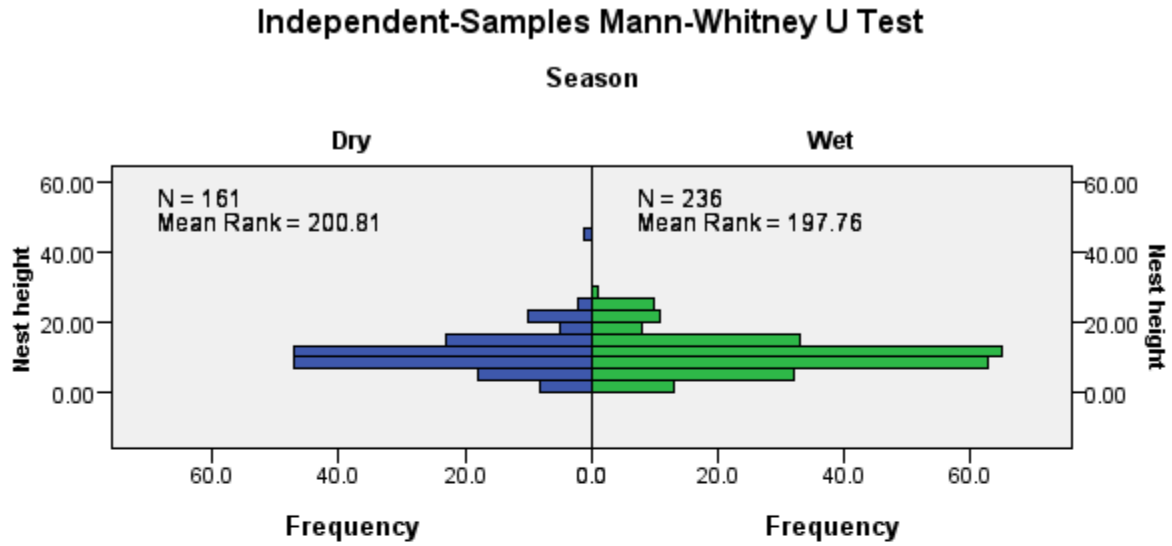
Total N	710
Test Statistic	358.000
Standard Error	13.323
Standardized Test Statistic	.188
Asymptotic Sig. (2-sided test)	.851

Appendix 4.4. Seasonality in mean nest group size at Bekob



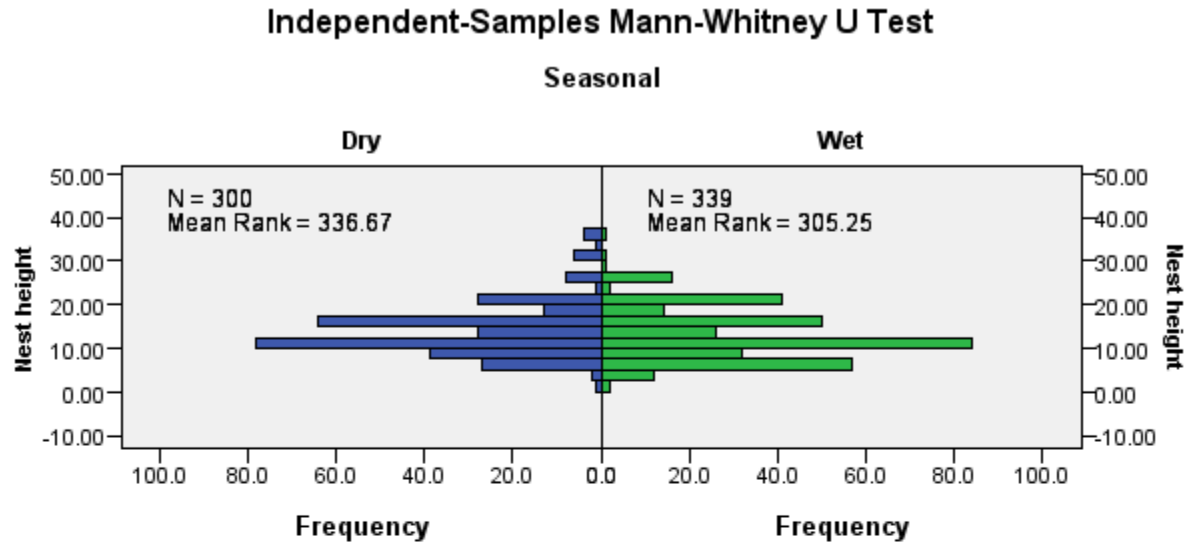
Total N	112
Mann-Whitney U	1,705.500
Wilcoxon W	3,658.500
Test Statistic	1,705.500
Standard Error	167.434
Standardized Test Statistic	.929
Asymptotic Sig. (2-sided test)	.353

Appendix 4.5. Seasonal variation in chimpanzee mean nest heights at Bekob



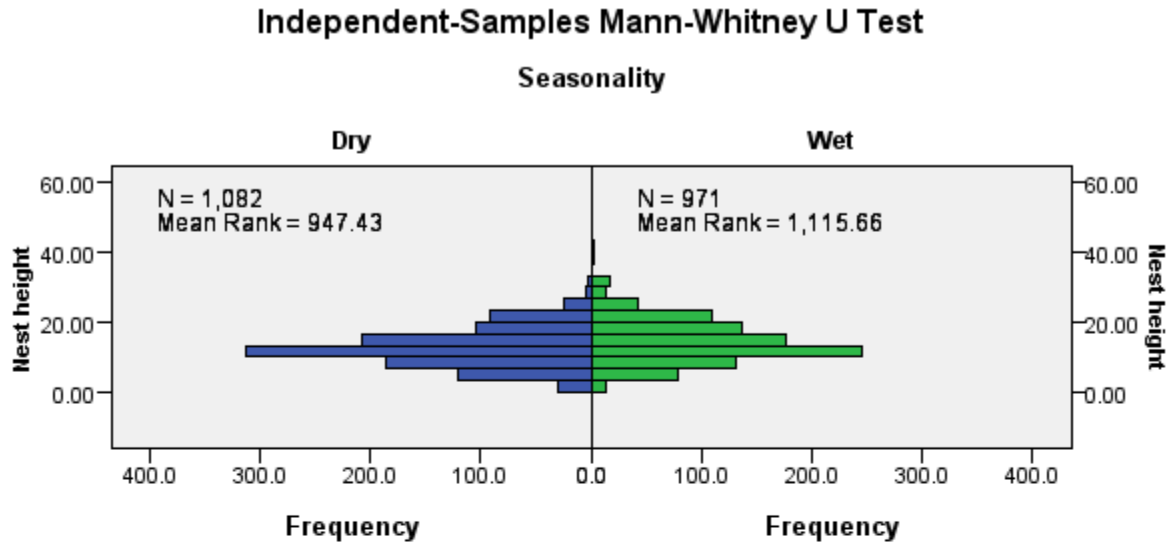
Total N	397
Mann-Whitney U	18,706.500
Wilcoxon W	46,672.500
Test Statistic	18,706.500
Standard Error	1,119.654
Standardized Test Statistic	-.260
Asymptotic Sig. (2-sided test)	.795

Appendix 4.6. Seasonal variation chimpanzee mean nest heights at Njuma



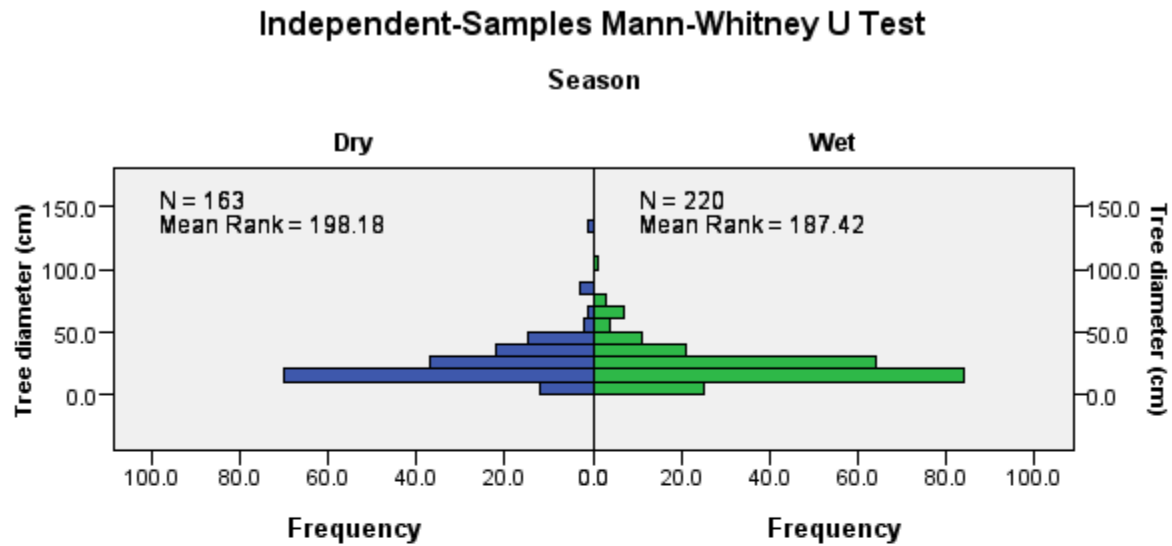
Total N	639
Mann-Whitney U	45,849.500
Wilcoxon W	103,479.500
Test Statistic	45,849.500
Standard Error	2,321.380
Standardized Test Statistic	-2.154
Asymptotic Sig. (2-sided test)	.031

Appendix 4.7. Seasonal variation in chimpanzee mean nest heights at Ganga



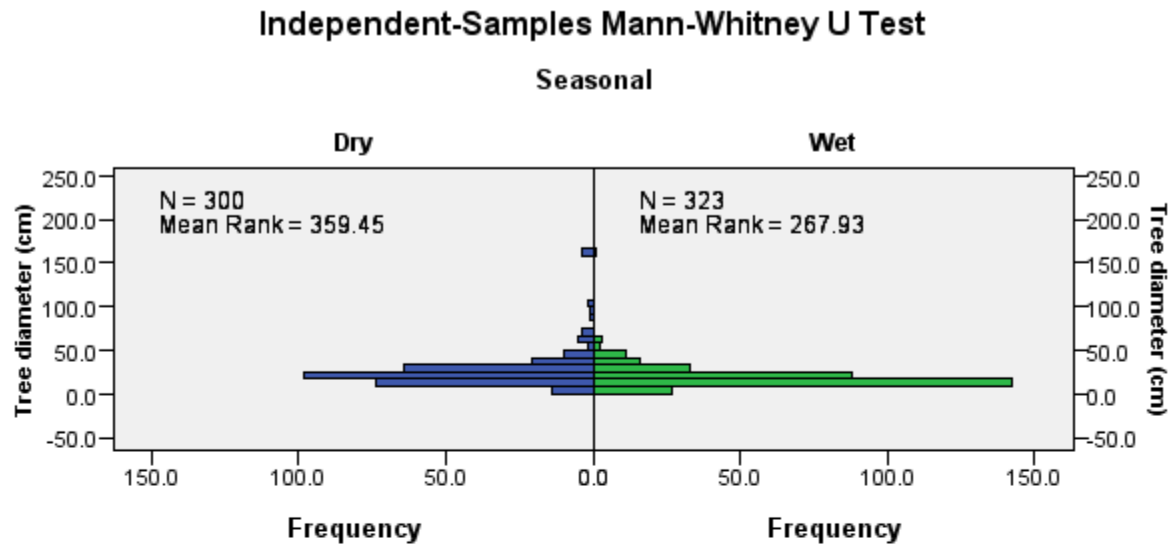
Total N	2,053
Mann-Whitney U	611,403.000
Wilcoxon W	1,083,309.000
Test Statistic	611,403.000
Standard Error	13,388.839
Standardized Test Statistic	6.430
Asymptotic Sig. (2-sided test)	.000

Appendix 4.8. Seasonal variation in mean tree sizes selected by chimpanzees for nesting at Bekob



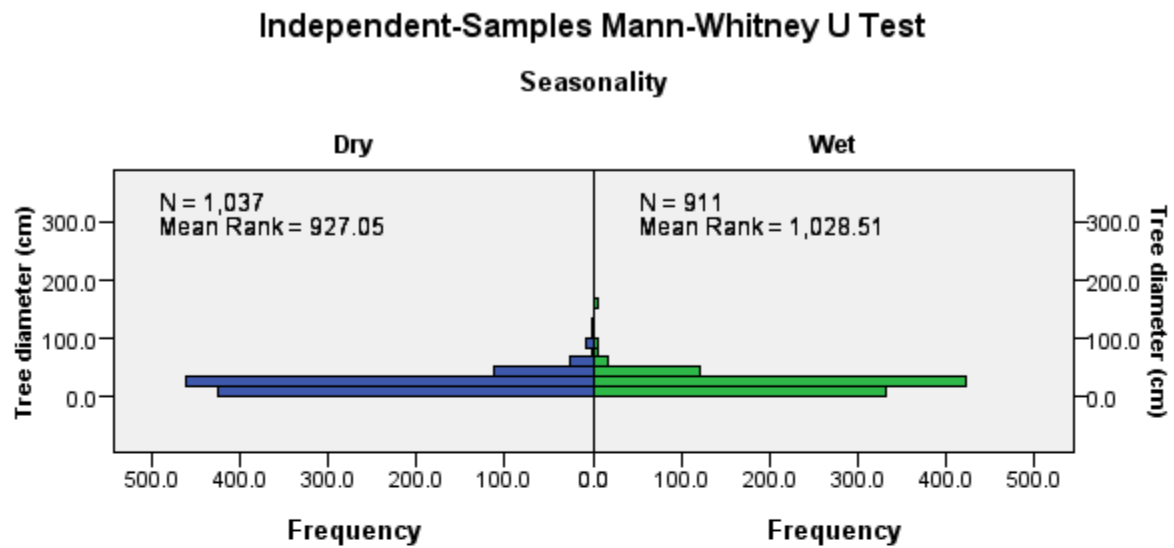
Total N	383
Mann-Whitney U	16,922.500
Wilcoxon W	41,232.500
Test Statistic	16,922.500
Standard Error	1,071.182
Standardized Test Statistic	-.941
Asymptotic Sig. (2-sided test)	.347

Appendix 4.9. Seasonal variation in mean tree sizes selected by chimpanzees for nesting at Njuma



Total N	623
Mann-Whitney U	34,215.000
Wilcoxon W	86,541.000
Test Statistic	34,215.000
Standard Error	2,244.612
Standardized Test Statistic	-6.342
Asymptotic Sig. (2-sided test)	.000

Appendix 4.10. Seasonal variation in mean tree sizes selected by chimpanzees for nesting at Ganga



Total N	1,948
Mann-Whitney U	521,559.000
Wilcoxon W	936,975.000
Test Statistic	521,559.000
Standard Error	12,386.689
Standardized Test Statistic	3.972
Asymptotic Sig. (2-sided test)	.000

Appendix 4.11. Nesting tree species preferences at Bekob showing percentage frequency of species, number of times and % species is used in nest building, expected use based on frequency of occurrence and preference

Species	Number (%) on transects	Number used (%)	Expected use (#)	Preference Index	Manly's α neutral 0.007256
<i>Coffea</i> sp.	1 (0.03)	3 (1.14)	0.1	2.92	0.276471
<i>Uvariadendron</i> sp.	3 (0.09)	2 (0.76)	0.2	1.76	0.061438
<i>Zenkerella citrina</i>	84 (2.53)	43 (16.47)	6.6	36.39	0.047176
<i>Diogoa zenkeri</i>	80 (2.41)	22 (8.42)	6.3	15.70	0.025343
<i>Thomandersia</i> sp.	8 (0.24)	2 (0.76)	0.6	1.37	0.023039
<i>Hymenostegia</i> sp.	101 (3.04)	22 (8.42)	8.0	14.05	0.020074
<i>Tapura africana</i>	13 (0.39)	2 (0.76)	1.0	0.98	0.014178
<i>Strombosia grandifolia</i>	334 (10.07)	45 (17.24)	26.3	18.70	0.012416
<i>Dialium</i> sp.	15 (0.45)	2 (0.76)	1.2	0.82	0.012288
<i>Elaeis guineensis</i>	33 (0.99)	4 (1.53)	2.6	1.40	0.011171
<i>Pseudospondias</i> sp.	28 (0.84)	3 (1.14)	2.2	0.80	0.009874
<i>Rinorea oblongifolia</i>	32 (0.96)	3 (1.14)	2.5	0.48	0.008640
<i>Pycnanthus angolensis</i>	112 (3.37)	9 (3.44)	8.8	0.18	0.007405
<i>Garcinia</i> sp.	276 (8.32)	21 (8.04)	21.7	-0.73	0.007012
<i>Drypetes</i> sp.	326 (9.83)	19 (7.27)	25.7	-6.67	0.005371
<i>Crateranthus kamerunensis</i>	38 (1.14)	2 (0.76)	3.0	-0.99	0.004850
<i>Santiria trimera</i>	84 (2.5)	3 (1.14)	6.6	-3.61	0.003291
<i>Cola</i> sp.	299 9.02)	7 (2.68)	23.5	-16.54	0.002158
<i>Uapaca guineensis</i>	155 (4.67)	3 (1.14)	12.2	-9.20	0.001784
<i>Tabernaemontana crassa</i>	476 (14.36)	4 (1.53)	37.5	-33.48	0.000774

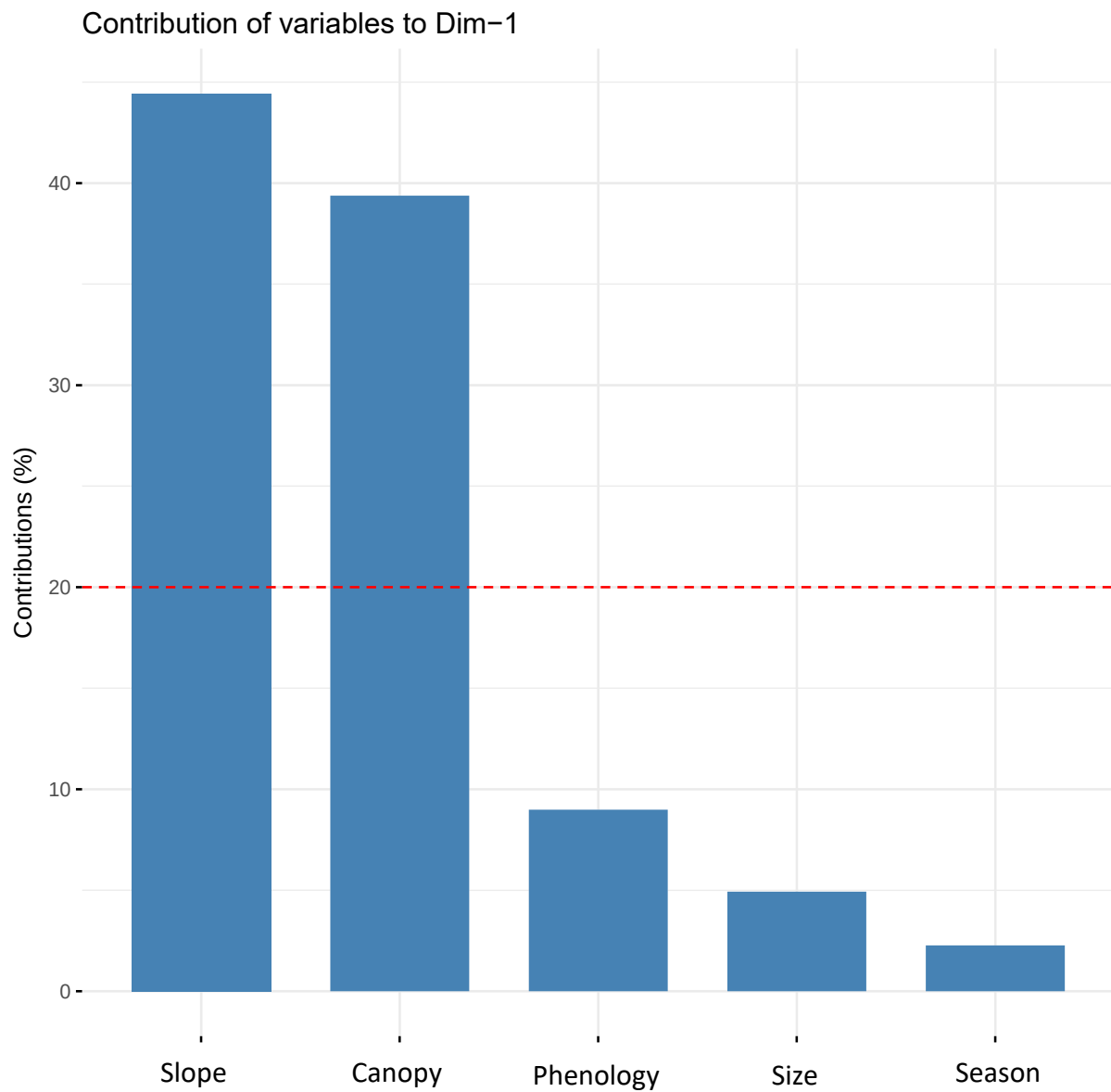
Appendix 4.12. Nesting tree species preferences at Njuma showing percentage frequency of species, number of times and % species is used in nest building, expected use based on frequency of occurrence and preference

Species	Number (%) on transects	Number used (%)	Expected use (#)	Preference Index	Manly's α neutral 0.02612
<i>Pseudospondias</i> sp.	2 (0.09)	4 (1.50)	0.241489	3.758511	0.43265
<i>Parinari excelsa</i>	2 (0.09)	1 (0.37)	0.241489	0.758511	0.10816
<i>Strombosia grandifolia</i>	235 (10.66)	94 (35.20)	28.37494	65.62506	0.08653
<i>Diogoa zenkeri</i>	298 (13.53)	84 (31.46)	35.98184	48.01816	0.06098
<i>Santiria trimera</i>	43 (1.95)	9 (3.37)	5.192011	3.807989	0.04528
<i>Lepidobotrys staudtii</i>	6 (0.27)	1 (0.37)	0.724467	0.275533	0.03605
<i>Diopyros bapidensis</i>	168 (7.62)	24 (8.98)	20.28507	3.714934	0.03090
<i>Zenkerella citrina</i>	32 (1.45)	4 (1.49)	3.863822	0.136178	0.02704
<i>Coula edulis</i>	59 (2.67)	7 (2.62)	7.123922	-0.12392	0.02567
<i>Hymenostegia</i> sp.	20 (0.91)	2 (0.75)	2.414889	-0.41489	0.02163
<i>Hylodendron gabunense</i>	23 (1.04)	2 (0.75)	2.777122	-0.77712	0.01881
<i>Garcinia</i> sp.	198 (8.98)	15 (5.61)	23.9074	-8.9074	0.01639
<i>Cynometra hankei</i>	15 (0.68)	1 (0.37)	1.811167	-0.81117	0.01442
<i>Dacryodes</i> sp.	39 (1.77)	2 (0.75)	4.709033	-2.70903	0.01109
<i>Pycnanthus angolensis</i>	87 (3.95)	4 (1.50)	10.50477	-6.50477	0.00995
<i>Strychnos</i> sp.	22 (0.99)	1 (0.37)	2.656378	-1.65638	0.00983
<i>Berlinia</i> sp.	29 (1.32)	1 (0.37)	3.501589	-2.50159	0.00746
<i>Plagiosiphon</i> sp.	30 (1.36)	1 (0.37)	3.622333	-2.62233	0.00721
<i>Irvingia gabonensis</i>	36 (1.63)	1 (0.37)	4.3468	-3.3468	0.00601
<i>Strombosiosis tetandra</i>	39 (1.77)	1 (0.37)	4.709033	-3.70903	0.00555

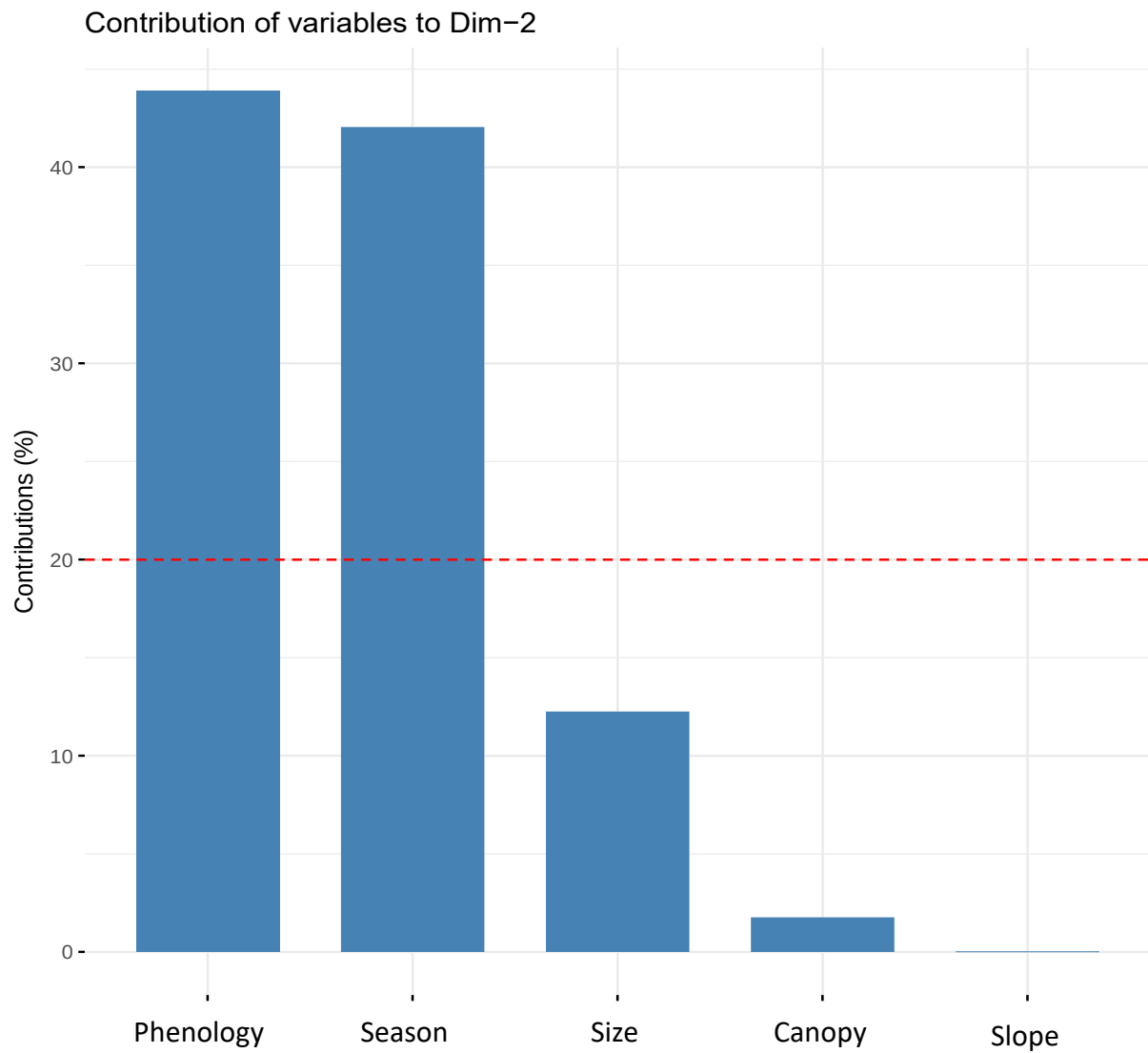
Appendix 4.13. Nesting tree species preferences at Ganga: showing percentage frequency of species, number of times and % species is used in nest building, expected use based on frequency of occurrence and preference

Species	Number (%) on transects	Number used (%)	Expected use (#)	Preference Index	Manly's α neutral 0.008103
<i>Strombosia grandifolia</i>	8(0.2)	68(4.1)	3.0	65.0	0.186254
<i>Trichilia</i> sp.	6(0.1)	19(1.2)	2.2	16.8	0.069389
<i>Anthonotha</i> sp.	8(0.2)	24(1.5)	3.0	21.0	0.065737
<i>Synsepalum</i> sp.	72(1.6)	132(8.0)	26.6	105.4	0.040172
<i>Tricalysia</i> sp.	31(0.7)	51(3.1)	11.5	39.5	0.036049
Sapindaceae sp.	91(2.0)	118(7.2)	33.6	84.4	0.028414
<i>Klainedoxa gabonensis</i>	26(0.6)	33(2.0)	9.6	23.4	0.027812
<i>Olax subscorpioidea</i>	76(1.7)	70(4.3)	28.1	41.9	0.020182
<i>Xylopia aethiopica</i>	374(8.4)	328(19.9)	138.3	189.7	0.019217
<i>Uapaca guineensis</i>	194(4.4)	159(9.7)	71.7	87.3	0.017959
<i>Detarium microcarpum</i>	54(1.2)	44(2.8)	20.0	24.0	0.017854
<i>Syzygium</i> sp.	37(0.8)	30(1.8)	13.7	16.3	0.017767
<i>Sorindeia</i> sp.	134(3.0)	67(4.1)	49.6	17.4	0.010956
<i>Drypetes</i> sp.	58(1.3)	26(1.6)	21.4	4.6	0.009823
<i>Hymenocardia lyrata</i>	573(12.9)	114(6.9)	211.9	-97.9	0.004359
<i>Antidesma</i> sp.	136(3.1)	20(1.2)	50.3	-30.3	0.003222
<i>Spondianthus preussii</i>	288(6.5)	42(2.6)	106.5	-64.5	0.003196
<i>Lannea acida</i>	153(3.4)	20(1.2)	56.6	-36.6	0.002864
<i>Ochna afzeli</i>	242(5.4)	18(1.1)	89.5	-71.5	0.00163

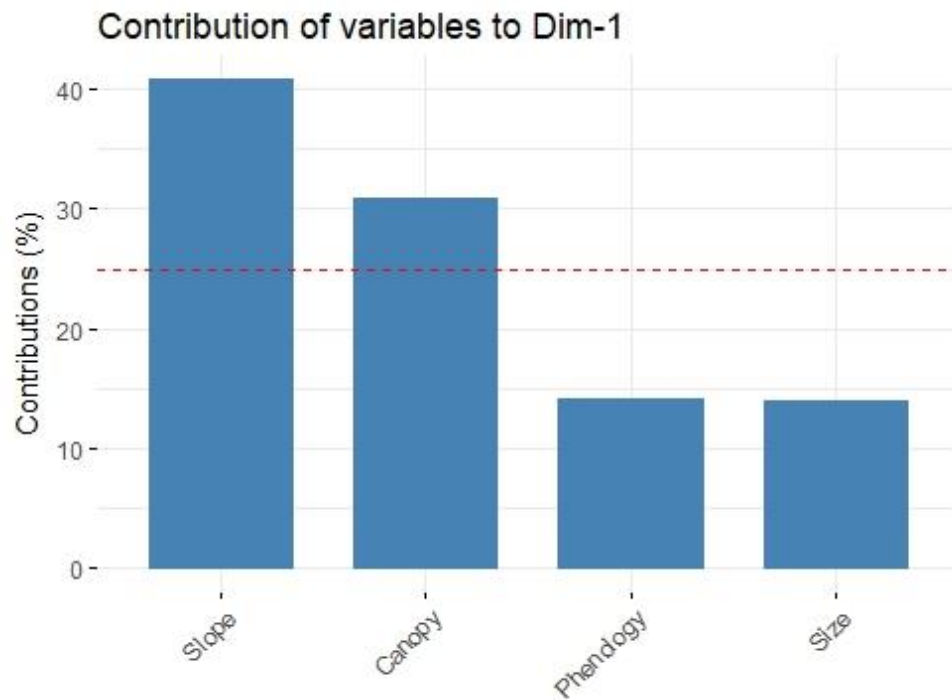
Appendix 4.14: Factorial analysis of mixed data – variables accounting for variation in nesting site location and nest group size across Bekob, Njuma and Bekob – Dim 1



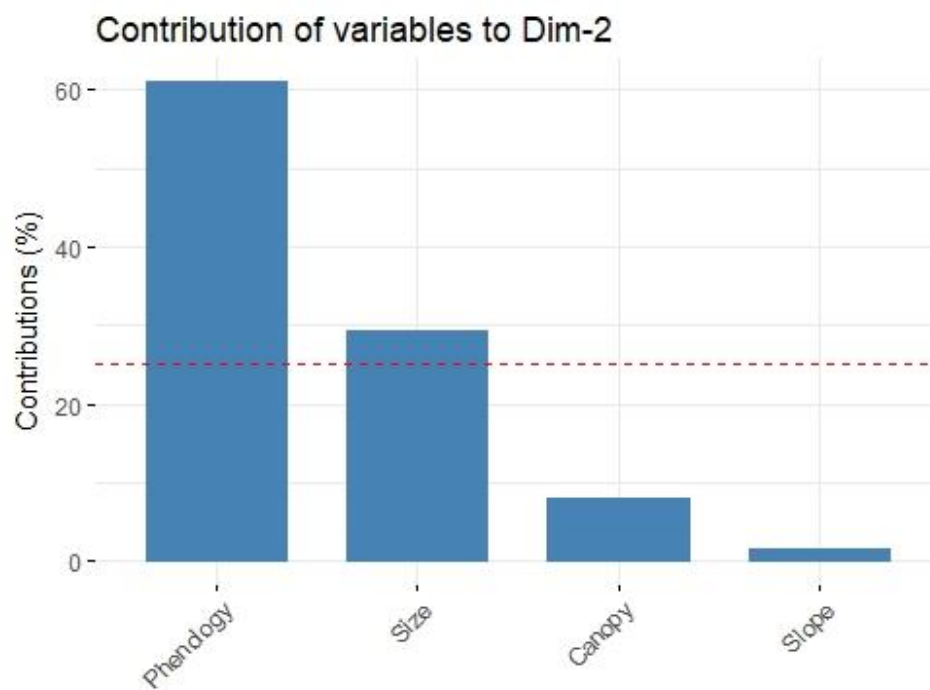
Appendix 4.15: Factorial analysis of mixed data – variables accounting for variation in nesting site location and nest group size across Bekob, Njuma and Bekob – Dim 2



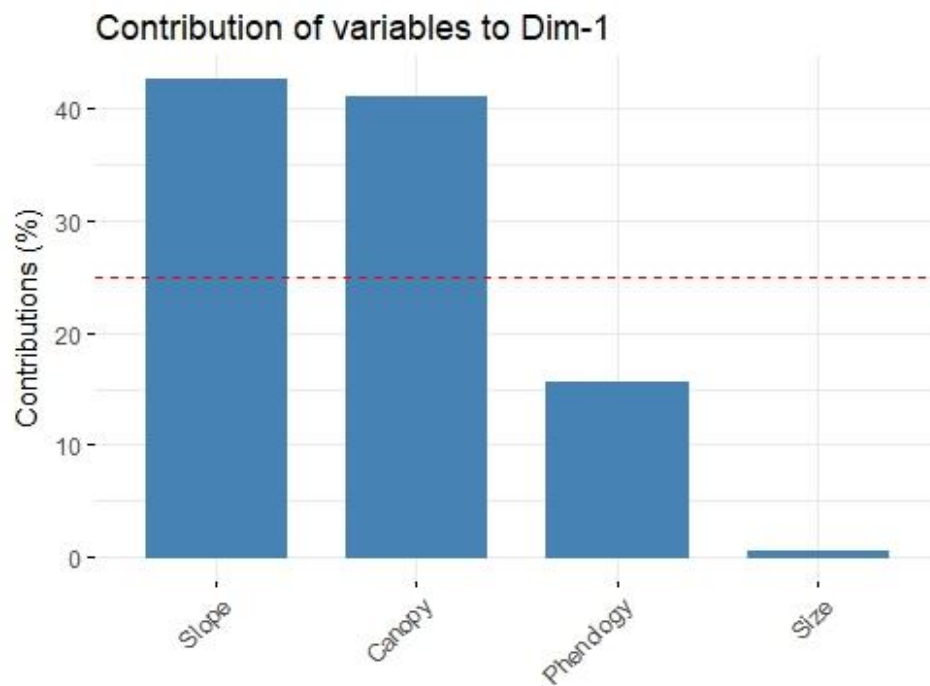
Appendix 4.16: Factorial analysis of mixed data – variables accounting for variation in nesting site location and nest group size across Bekob, Njuma and Bekob in the dry season – Dim 1



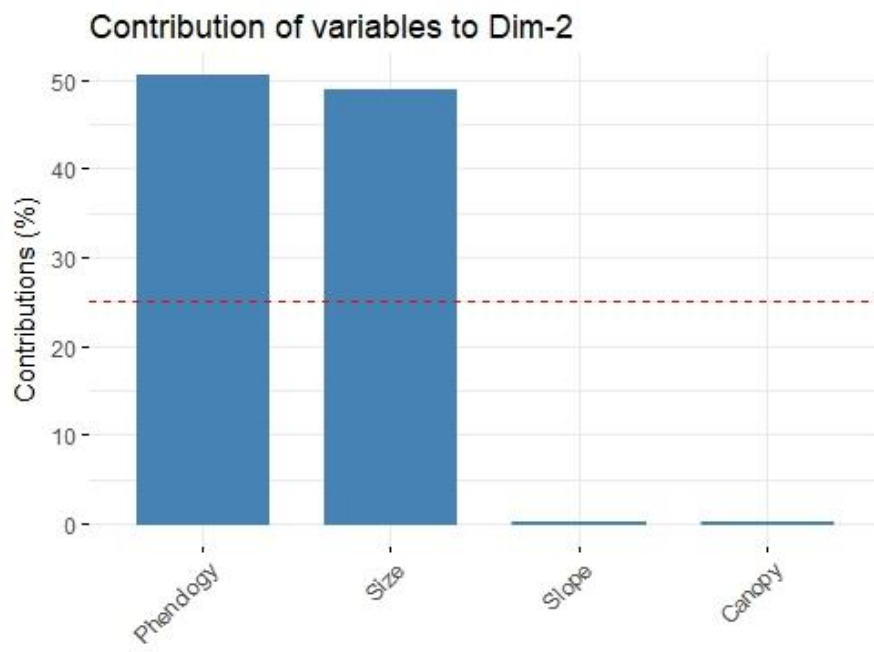
Appendix 4.17: Factorial analysis of mixed data – variables accounting for variation in nesting site location and nest group size across Bekob, Njuma and Bekob in the dry season – Dim 2



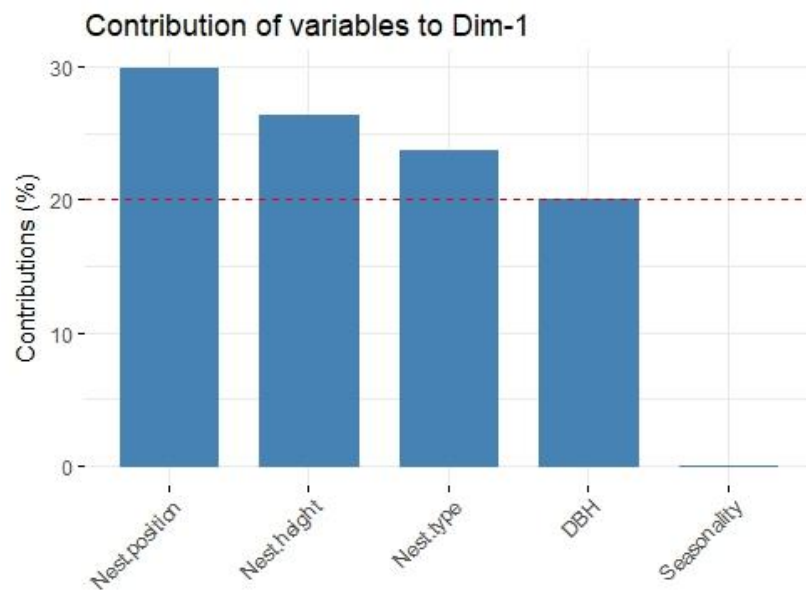
Appendix 4.18: Factorial analysis of mixed data – variables accounting for variation in nesting site location and nest group size across Bekob, Njuma and Bekob in the wet season – Dim 1



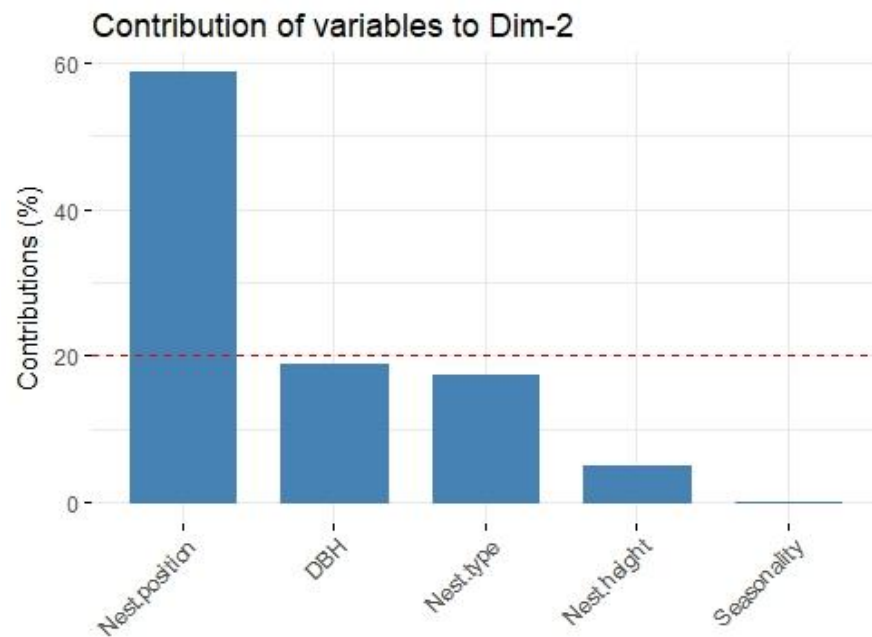
Appendix 4.19: Factorial analysis of mixed data – variables accounting for variation in nesting site location and nest group size across Bekob, Njuma and Bekob in the wet season – Dim 2



Appendix 4.20: Factorial analysis of mixed data – variables accounting for variation in individual nest characteristics between Bekob, Njuma and Ganga – Dim 1



Appendix 4.21: Factorial analysis of mixed data – variables accounting for variation in individual nest characteristics between Bekob, Njuma and Ganga – Dim 2



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GIS Technician, WWF and Northern Savanna Program, Cameroon	1998-2003
High School Teacher, Government High School, Nyasoso, Cameroon	1995-1997

AWARDS AND GRANTS

Leakey Foundation	2016
Primate Conservation Inc.	2016
Whitley Fund for Nature Award	2013
Primate Habitat Country Scholarship	2009

SELECTED PUBLICATIONS

Clee, P. R. S., **Abwe, E. E.**, Ambahe, R. D., Anthony, N. M., Fotso, R., Locatelli, S., . . . Pokempner, A. A. (2015). Chimpanzee population structure in Cameroon and Nigeria is associated with habitat variation that may be lost under climate change. *BMC Evolutionary Biology*, 15(1), 2.

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