NM-AIST Repository

https://dspace.mm-aist.ac.tz

Life sciences and Bio-engineering

Masters Theses and Dissertations [LISBE]

2021-12

Anthropogenic disturbance and chimpanzee (pan troglodytes) habitat use in the Masito-Ugalla ecosystem, Tanzania

Maijo, Simula

NM-AIST

https://doi.org/10.58694/20.500.12479/1303

Provided with love from The Nelson Mandela African Institution of Science and Technology

ANTHROPOGENIC DISTURBANCE AND CHIMPANZEE (Pan troglodytes) HABITAT USE IN THE MASITO-UGALLA ECOSYSTEM, TANZANIA

a• 1			TA /	• •
Simul	la F	'eres	VI	3110

A Dissertation Submitted in Partial Fulfillment of the Requirements for the Degree of Master's in Life Sciences of the Nelson Mandela African Institution of Science and Technology

Arusha, Tanzania

ABSTRACT

The habitat quality of chimpanzee (Pan troglodytes), including the availability of food and nesting resources, is important to ensure the long-term survival of chimpanzees. Botanical composition of vegetation is spatially variable and depends on numerous biotic and abiotic factors. There are few data regarding the availability of chimpanzee plant food and nesting species in the Masito-Ugalla ecosystem (MUE), and how these resources vary with human disturbance. It was hypothesized that chimpanzee plant food species richness, diversity, and abundance, decline with increasing disturbance. Further, it was predicted that chimpanzee abundance and habitat use is influenced negatively by disturbance. Published literature from Issa Valley, Gombe, and Mahale Mountains National Parks, was used to document plant species consumed by chimpanzees, and quantify their richness, diversity, and abundance, along 32 transects totaling 63.8 km in length across four sites of varying human disturbance in MUE. A total of 102 plant food species was documented and found significant differences in their species richness (H = 55.09, P < 0.001) and diversity (H = 36.81, P < 0.001) across disturbance levels. Chimpanzees built nests in 17 tree species. The abundance of nesting tree species did not vary across survey sites (H = 0.279, P > 0.964). The least disturbed site exhibited the highest encounter rate of chimpanzee nests km⁻¹, with rates declining towards the highly disturbed sites. Thus, severe anthropogenic disturbance in MUE is associated with the loss of chimpanzee plant food species and negatively influences chimpanzee habitat use, a relationship that threatens the future of all chimpanzee populations outside national parks.

DECLARATION

I, Simula Peres Maijo, hereby declare to the senate of Nelson Mandela African Institution of Science and Technology (NM-AIST) that, this is my own original work, and that it has neither been submitted nor concurrently submitted for any degree award at any other Institution.

Candidate's name: Simula Peres Maijo

Signature: Date: 29/12/2020

SUPERVISORS

1st Supervisor: Prof. Anna C. Treydte

Signature: Date: 29/12/2020

2nd Supervisor: Dr. Alex K. Piel

Signature: Date: 29/12/2020

COPYRIGHT

This dissertation is copyright material protected under the Berne Convention, the Copyright Act of 1999 and other international and national enactments, in that behalf, on intellectual property. It must not be reproduced by any means, in full or in part, except for short extracts in fair dealing; for researcher private study, critical scholarly review or discourse with an acknowledgement, without the written permission of the office of Deputy Vice Chancellor for Academic, Research and Innovation on behalf of both the author and Nelson Mandela African Institution of Science and Technology (NM-AIST).

CERTIFICATION

This is to certify that, the undersigned have read the dissertation titled "Anthropogenic disturbance and chimpanzee (*Pan troglodytes*) habitat use in the Masito-Ugalla ecosystem, Tanzania" submitted in Partial Fulfillment of the Requirements for the Degree of Master's in Life Sciences of the Nelson Mandela African Institution of Science and Technology, Arusha, Tanzania.

Name and signature of supervisors:

1st Supervisor: Prof. Anna C. Treydte

Signature: Date: 29/12/2020

2nd Supervisor: Dr. Alex K. Piel

Signature: Date: 29/12/2020

ACKNOWLEDGEMENTS

I would like to express my heartfelt thanks to the Almighty God for keeping me healthy and giving me strength in the whole course of accomplishing this dissertation. I thank the Greater Mahale Ecosystem Research and Conservation (GMERC) Project for sponsoring my studies at the Nelson Mandela African Institution of Science and Technology (NM-AIST) and for funding this research. My gratitude is also extended to the Rufford Foundation for the additional financial support (Grant no. 27075-1) to conduct this research.

This dissertation would not be possible if it is not for the tireless efforts of my supervisors. I am greatly thankful to Prof. Anna C. Treydte and Dr. Alex K. Piel for their patience, efforts, encouragement and guidance ever since the commencement of this study. I am greatly indebted to them for their constructive suggestions, all sorts of help and encouragement throughout this study.

I am pleased to extend my thanks to all people who directly participated in this study. I am thankful to the field assistants (Shabani Kabangula and Mwami Rashidi), field guides (Arcado Hassan, Patrick Hassan, Mariana Marco, Judie Phaustas, Jonas Bukende, and Shadrack Lucas) and to the botanist (Yahya Abeid) who helped with identification of plant species. Their help was remarkable during field data collection. My sincere thanks also go to all friends and colleagues who in one way or another devoted their energy, time and skills in accomplishing this study but their names are not mentioned here.

Lastly, I express my gratitude to Tanzania Wildlife Research Institute (TAWIRI), the Commission for Science and Technology (COSTECH), and Mpanda District Council for granting permits to conduct this study.

DEDICATION

This dissertation is dedicated to my parents for their great love, determined support, and guidance. The work is exclusively dedicated to them for giving me a greater dimension in education and for their unwavering material and moral support since childhood.

TABLE OF CONTENTS

ABSTR	RACT	i
DECLA	ARATION	ii
COPYF	RIGHT	iii
CERTII	IFICATION	iv
ACKNO	IOWLEDGEMENTS	v
DEDIC	CATION	vi
TABLE	E OF CONTENTS	vii
LIST O	OF TABLES	ix
LIST O	OF FIGURES	x
LIST O	OF APPENDICES	xi
LIST O	OF ABBREVIATIONS AND SYMBOLS	xii
СНАРТ	TER ONE	1
INTRO	DDUCTION	1
1.1	Background of the Problem	1
1.2	Statement of the Problem	2
1.3	Rationale of the Study	3
1.4	Objectives of the Study	4
	1.4.1 General Objective	4
	1.4.2 Specific Objectives	4
1.5	Hypotheses	4
1.6	Significance of the Study	5
1.7	Delineation of the Study	5
СНАРТ	TER TWO	6
LITERA	ATURE REVIEW	6
СНАРТ	TER THREE	9
MATEI	ERIALS AND METHODS	9

3.1	Study A	rea	9
3.2	Data Co	ollection	11
	3.2.1	Survey for Chimpanzee Plant Food Species	11
	3.2.2	Survey for Chimpanzee Abundance and Habitat Use	12
	3.2.3	Quantification of Anthropogenic Disturbance Across Survey Sites	12
3.3	Data Ar	nalyses	13
	3.2.4	Categorizing Survey Sites into Different Disturbance Levels	13
	3.2.5	Calculating Species Richness, Diversity and Abundance	14
	3.2.6	Chimpanzee Abundance and Habitat Use	14
СНАРТ	TER FOU	R	15
RESUL	TS AND	DISCUSSION	15
4.1	Results		15
	4.1.1	Human Disturbance Across Survey Sites	15
	4.1.2	Availability of Chimpanzee Plant Food Species in MUE	17
	4.1.3	Chimpanzee Abundance and Habitat Use	23
4.2	Discuss	ion	23
СНАРТ	ER FIVE	3	28
CONCI	LUSION .	AND RECOMMENDATIONS	28
5.1	Conclus	sion	28
5.2	Recomm	mendations	28
REFER	ENCES		30
APPEN	DICES		43
RESEA	RCH OU	TTPI ITS	47

LIST OF TABLES

Table 1:	Chimpanzee diet data summarized from Western Tanzania7
Table 2:	Human activities recorded across MUE with respective weight of destructive impacts (impact score) on chimpanzee habitat
Table 3:	Encounter rates of human activities per km walked in each survey site and the
Table 3.	severity of disturbance calculated by multiplying the weighted impact scores and
	the frequency of encounters of each human activity and then summed as an overall
	measure of severity of human disturbance
Table 4:	Average (± SE) density (i.e., number of individuals of each species km ⁻²) of the
	ten most abundant chimpanzee feeding plant species with $DBH > 10 \text{ cm}$ identified
	in MUE across sites of different disturbance levels
Table 5:	Average, minimum, maximum and the sum as well as relative proportions of
	number of nests observed per plant species that chimpanzees selected for nesting
	across all survey sites within Masito-Ugalla ecosystem

LIST OF FIGURES

Figure 1:	Map of the four sampling sites located in the Masito-Ugalla ecosystem, Tanzania10
Figure 2:	A view of chimpanzees in the Issa Valley in Tongwe East Forest Reserve, Tanzania
Figure 3:	Pterocarpus angolensis logged (A) for timber (B) at Mlofwesi in Tongwe West Forest Reserve, March 2019
Figure 4:	Brachystegia speciformis, a chimpanzee plant food and a nesting tree species, debarked (A) to make local beehives (B) at Mlofwesi in Tongwe West Forest Reserve, March 2019
Figure 5:	Variation in average chimpanzee plant food species richness across the four sites of different disturbance levels in the MUE
Figure 6:	Variation in average chimpanzee plant food diversity across the four sites of different disturbance levels in the MUE
Figure 7:	Variation in average chimpanzee plant food species richness across vegetation types

LIST OF APPENDICES

Appendix 1: A list of chimpanzee plant feeding species documented in the M	Aasito-Ugalla
ecosystem based on direct observations and the compiled diet list	sts from Issa
Valley, Gombe, and Mahale Mountains National Park (Goodall 196	8; Nakamura
et al., 2015; Nishida & Uehara 1983; Piel et al., 2017)	43

LIST OF ABBREVIATIONS AND SYMBOLS

COSTECH The Commission for Science and Technology

DBH Diameter at Breast Height

GME The Greater Mahale Ecosystem

GMERC Greater Mahale Ecosystem Research and Conservation

km kilometer

km⁻¹ per kilometer

km² square kilometer

km⁻² per square kilometer

m meter

masl meters above sea level

m² square meter

MUE Masito-Ugalla ecosystem

NM-AIST The Nelson Mandela African Institution of Science and Technology

TAWIRI Tanzania Wildlife Research Institute

TRFs Tongwe Forest Reserves

CHAPTER ONE

INTRODUCTION

1.1 Background of the Problem

Habitat loss and over-exploitation of natural resources are major challenges for biodiversity conservation (Rands *et al.*, 2010; Sarkar *et al.*, 2006). These processes are driven mainly by human poverty and increasing human population size, which, when combined, result in over-dependence on nature, thus threatening wildlife (Hackel, 1999). Increasing human population sizes and encroachment on wildlife habitat are the core incitement of human-wildlife conflicts, habitat fragmentation and loss, and associated biodiversity loss in most areas (Brooks *et al.*, 2002; Fahrig, 2003; Hanski, 2011). A number of primate species including chimpanzees (*Pan troglodytes*) inhabit human-impacted landscapes (Bryson-Morrison *et al.*, 2016, 2017; Hockings *et al.*, 2012, 2015), following continuous contraction of their natural ranges as a result of human encroachment. To understand how chimpanzees will persist in human encroached landscapes, there is a need to assess the relationship between chimpanzee habitat degradation and the availability of resources used by this species.

The availability and quantity of food resources in chimpanzee habitat is a primary factor that drives chimpanzee abundance and distribution (Chapman *et al.*, 2004; Foerster *et al.*, 2018; Stevenson, 2001). Hence, as the density of food resources declines, chimpanzee range tends to increase to compensate for reduced food availability (Baldwin *et al.*, 1982; Nakamura, 2015; Wrangham *et al.*, 1996). Alternatively, chimpanzees might instead consume more nutrient poor foods (Basabose, 2005; Doran, 1997), which may reduce their fitness and survival. Chimpanzees are omnivorous and feed on fruits, leaves and other plant parts, vertebrates and invertebrates as well as on inorganic substances (i.e., termite mound soil and rocks) (Goodall, 1968; Itoh & Nakamura, 2015; Newton-Fisher, 1999; Nishida, 2012; Nishida & Uehara, 1983; Piel *et al.*, 2017; Watts *et al.*, 2012a, 2012b). Notwithstanding, chimpanzees predominantly depend on plant matter, especially ripe fruits, which constitute the majority of their diet (Goodall, 1968; Nakamura *et al.*, 2013, 2015; Nishida, 1968; Nishida & Uehara, 1983).

In addition to food resources, the availability of nesting sites is another key factor influencing chimpanzee presence, abundance, and distribution (Carvalho *et al.*, 2015). Nesting is a daily behaviour in all great ape species (Fruth *et al.*, 2018; Goodall, 1968). All weaned great apes,

including chimpanzees, build night nests for sleeping, occasionally build daytime nests for resting and rarely re-use nests (Goodall, 1962; Plumptre & Reynolds, 1996, 1997; Rothman *et al.*, 2006). Though any woody species is a potential nesting site, chimpanzees nest non-randomly wherever the behaviour has been studied (Basabose & Yamagiwa, 2002; Hernandez-Aguilar, 2009; Last & Muh, 2013; Stewart *et al.*, 2011). Chimpanzee nests, therefore, are a good proxy for chimpanzee presence (Hernandez-Aguilar *et al.*, 2013), and reveal chimpanzee habitat use as well as population density and trends (Kühl *et al.*, 2017). Indeed, most approaches for estimating wild chimpanzee populations rely on nest counts (Bonnin *et al.*, 2018; Plumptre & Reynolds, 1996, 1997; Sanz *et al.*, 2007). In some areas, chimpanzees occur at low densities and thus nest counts are impracticable over a large area. Nevertheless, recent work using drones (Bonnin *et al.*, 2018), demonstrates the effectiveness of nest counts for population size estimates in wild chimpanzees.

Chimpanzee populations are declining rapidly (Junker *et al.*, 2012), threatened by habitat loss, poaching, disease, and the pet trade (Hockings *et al.*, 2015; Kühl *et al.*, 2017; Leendertz *et al.*, 2006). In Tanzania, Eastern chimpanzees (*P. t. schweinfurthii*) are distributed across the Western region (TAWIRI, 2018), with an estimated total population of less than 2500 individuals (Moyer *et al.*, 2006; Piel & Stewart, 2014). More than 75% of the current population lives outside national park boundaries (Piel *et al.*, 2015a). Chimpanzee numbers outside national parks have significantly declined in the 2000s (Ogawa *et al.*, 2013; Yoshikawa *et al.*, 2008) and a significant sub-population is found in the Masito-Ugalla ecosystem (MUE) (Moore & Vigilant, 2013; Piel *et al.*, 2015a), an ecosystem partly protected as Tongwe Forest Reserves (TFRs). Surveys across MUE in 2012 revealed a density of 0.1 individuals km⁻² (Piel *et al.*, 2015a), and a total population of about 288 individuals, or >10% of Tanzania's chimpanzees. Despite high ecological relevance of MUE and the presence of a significant chimpanzee sub-population, some parts of this ecosystem are threatened by recurrent anthropogenic disturbances due to their proximity to human settlements.

1.2 Statement of the Problem

Human-wildlife interaction is a historic and growing challenge for conservation biologists (Bryson-Morrison *et al.*, 2017; Hockings *et al.*, 2012). In Tanzania, chimpanzee ecosystems outside national park boundaries are vulnerable to disruption and increasing habitat utilization by people (TAWIRI, 2018) as a result of human poverty and increasing human population size. Anthropogenic activities carried out by people in these ecosystems have caused

disturbance to habitats and chimpanzees. For example, land use activities have been reported to greatly reduce the size of chimpanzee ranges (TAWIRI, 2018). The increasing human population is anticipated to greatly escalate encroachment deeper even into protected chimpanzee habitats.

Across Africa, different livelihood activities by humans e.g., expansion of settlements and farms, increasing number of livestock keeping etc., has resulted in human encroachment on wildlife habitats. Western Tanzania is no exception. The MUE, a vast area outside national park boundaries in Western Tanzania, is under increasing pressure from anthropogenic activities. Increased threats from agricultural expansion, settlements, cattle herding, fires, logging and poaching have been reported in the region (Pintea, 2012; Plumptre *et al.*, 2010; Wilfred & MacColl, 2014) and threaten chimpanzee resources, habitats, and the survival of chimpanzees. Whilst there are some data on chimpanzee diet (Piel *et al.*, 2017), population size and density (Moore & Vigilant, 2013; Piel *et al.*, 2015a; Yoshikawa *et al.*, 2008) in the MUE, and given the rate of anthropogenic disturbance in the ecosystem, information on how anthropogenic disturbance is related to chimpanzee resource availability, habitat use, and abundance remain uncertain.

1.3 Rationale of the Study

Studies on the relationship between disturbance and primate populations have been conducted on a number of species. Chapman and Chapman (2000) found that anthropogenic disturbance affected the abundance and group size of red colobus and red-tailed guenons in Kibale National Park, Uganda. Cavada *et al.* (2019) described the relationship between anthropogenic disturbance and the density of arboreal primate species in the Udzungwa Mountains of Tanzania and showed that disturbance negatively affected primate density. Herrera *et al.* (2011), examining the effects of disturbance on lemurs at Ranomafana National Park, Madagascar, found that, anthropogenic disturbance does not always have deleterious effects on primates. The variation in lemur abundance was related to diet (i.e., feeding guilds) rather than disturbance, with frugivorous species more prone to population declines than folivores or insectivores. Moreover, anthropogenic disturbance not only affects primate densities but also affects their behaviors (Kühl *et al.*, 2019). In most environments where nonhuman primates coexist with people, primates exhibit behavioral flexibility, including dietary adjustments, to survive (McCarthy *et al.*, 2017; McLennan *et al.*, 2017).

Whilst Balcomb *et al.* (2000) found a positive relationship between the density of fleshy fruit trees and chimpanzee density, measured across six sites in Kibale Forest, Uganda, a similar study on plant food availability and habitat disturbance has yet to be conducted at MUE, where anthropogenic disturbance is high (Plumptre *et al.*, 2010; Wilfred & MacColl, 2014). Increasing threats from agricultural expansion, settlements, cattle herding, annual fires, logging, and poaching, have been reported in the region and threaten chimpanzee habitat. Given the rate of disturbance across MUE and the direct result disturbance has on chimpanzees (Kühl *et al.*, 2019), a clearer understanding of the relationship between habitat disturbance, resource availability, chimpanzee habitat use, and abundance, is required. Therefore, conducting a comparative study between sites with different levels of human disturbance is critical to assess the influence of anthropogenic disturbance on chimpanzee adaptability across MUE and to understand how chimpanzees respond to disturbance for effective conservation of this endangered great ape species and their habitat.

1.4 Objectives of the Study

1.4.1 General Objective

To document the availability of chimpanzee plant food species and nesting tree species in MUE, and find out the relationship between anthropogenic disturbance and chimpanzee resources availability, habitat use, and chimpanzee abundance.

1.4.2 Specific Objectives

- (i) To document chimpanzee plant food species available in MUE based on chimpanzee diet data summarized from Western Tanzania.
- (ii) To assess the relationship between anthropogenic disturbance and chimpanzee plant food species richness, diversity, and abundance.
- (iii) To assess how anthropogenic disturbance influence chimpanzee abundance and habitat use.

1.5 Hypotheses

(i) Chimpanzee plant food species richness, diversity, and abundance, decline with increasing anthropogenic disturbance.

(ii) Chimpanzee abundance (as inferred from nest counts) and habitat use is negatively influenced by anthropogenic disturbance.

1.6 Significance of the Study

This study provides an updated list of chimpanzee plant food and nesting tree species available in MUE. By comparing richness, diversity, and abundance of food and nesting tree species in plots with different levels of anthropogenic disturbance, the influence of anthropogenic disturbance on the availability of chimpanzee resources, is related. The study also offers an understanding of the relationship between anthropogenic disturbance and chimpanzee habitat use and abundance. A better understanding of the above relationships is important for conservation planners to expand knowledge, think for feasible conservation strategies for conservation of chimpanzees, and re-define conservation initiatives for chimpanzees living outside national park boundaries in Tanzania.

1.7 Delineation of the Study

This study focused on documenting the availability of chimpanzee (*P. t. schweinfurthii*) plant food species and nesting tree species available in the MUE, and to realize the relationship between anthropogenic disturbance and chimpanzee resources availability, habitat use, and chimpanzee abundance. A comparative study between sites with different levels of human disturbance was conducted to assess the influence of anthropogenic disturbance on chimpanzee habitat use, abundance, availability of plant food species and nesting tree species. While this study has yielded good and solid results, all the factors which might have influenced the results were not measured and hence potential sources of bias. As it was not possible to measure all the factors, particularly in the time allowed for a master's project, recommendations are put forward for the improvement of this study.

CHAPTER TWO

LITERATURE REVIEW

Chimpanzee (*Pan troglodytes*), is a species of great ape which its geographic distribution spanning East to Central to West Africa (Teleki, 1989). Chimpanzees are the most abundant and widespread species of all great ape. There are four subspecies of chimpanzees (Humle *et al.*, 2016); the Eastern chimpanzee (*P. t. schweinfurthii*), the Central chimpanzee (*P. t. troglodytes*), the Nigeria-Cameroon chimpanzee (*P. t. ellioti*), and the Western chimpanzee (*P. t. verus*). All of the four subspecies are classified as endangered following decades of population declines (Junker *et al.*, 2012; Plumptre *et al.*, 2010).

Chimpanzee populations across Africa are primarily threatened by habitat loss, poaching, disease, and the pet trade (Hockings *et al.*, 2015; Kühl *et al.*, 2019, 2017; Leendertz *et al.*, 2006). The IUCN indicate that chimpanzees are mainly threatened by habitat loss due to agriculture, logging and wood harvesting, livestock farming and ranching, hunting and trapping, deforestation and illegal wildlife trade (Chapman & Peres, 2001; Estrada *et al.*, 2017; Plumptre *et al.*, 2010). Anthropogenic activities in chimpanzee ranges destroy chimpanzee feeding and nesting environments (Ogawa *et al.*, 2007) leading to change in the plant species available for nesting and feeding (Carvalho *et al.*, 2015).

The habitat quality of chimpanzee, including the availability of chimpanzee plant food and nesting tree species, is critical to ensure the long-term survival of this endangered great ape. There are a number of studies that described chimpanzee diet from Western Tanzania (Table 1). The long-term observational studies from Gombe and Mahale provide detailed information on chimpanzee feeding behavior, food culture, the key food species that sustain chimpanzee populations, the most preferred parts of plant food species (i.e., fruits, leaves etc.), dietary repertoire in relation to plant phenology, dietary breadth, and other non-plant diet components of chimpanzee in Western Tanzania (Nakamura *et al.*, 2015). Nevertheless, the only two studies that described chimpanzee diet in MUE used indirect methods (fecal analyses and food remains) as MUE chimpanzees were not habituated to human presence to allow for focal follows. The two studies were conducted in the Issa Valley and at Nguye and Bhukalai sites. Referring to the methods used to study chimpanzee diet in MUE, little is known about the availability of chimpanzee diet outside national parks boundaries and how they are associated with disturbance, chimpanzee abundance and habitat use.

Table 1: Chimpanzee diet data summarized from Western Tanzania

Site	Vegetation	Method	# Fecal samples	# Species consumed	Reference
	Open				
Issa Valley	habitat	Indirect	810	69	Piel et al. (2017)
Nguye and	Open				Yoshikawa and Ogawa
Bhukalai	habitat	Indirect	465	100	(2015)
					Nishida and Uehara
Mahale	Forested	Direct	NA	198	(1983)
Gombe	Forested	Direct	NA	147	Wrangham (1975)

Based on chimpanzee diet studies across Western Tanzania, Yoshikawa and Ogawa (2015), found a proportion (range: 20% - 39%) of the identified chimpanzee plant food species to overlap between Ugalla (Nguye and Bhukalai), Gombe, and Mahale Mountains National Parks. For example, of 100 plant food species identified in Nguye and Bhukalai, 39% of the plant food species were also consumed by the Mahale chimpanzees, and 33% by the Gombe chimpanzees. Out of 198 plant food species identified in Mahale Mountains National Park, Nguye and Bhukalai chimpanzees consumed 20%, and of 147 plant food species identified in Gombe National Park, Nguye and Bhukalai chimpanzees consumed 22%.

Other studies on chimpanzee feeding ecology, have revealed that chimpanzee foods may change year by year (Nishida & Uehara, 1983). Nishida (2012) indicates that food availability within a particular chimpanzee habitat customarily varies with seasons. There are some foods that are only available or are abundant in a certain season of the year. Conversely, there are other food sources that are available throughout the year. Foods that are available throughout the year are essential for chimpanzees in any habitat and most of these foods are fig plants (Clark *et al.*, 1993; Nishida, 2012). Figs are important food sources that chimpanzees depend on when there is scarcity of preferred foods, particularly fruits (Dominy *et al.*, 2016).

It is well acknowledged that nesting is a daily behaviour in all great ape species including chimpanzees. Although any woody tree is a potential nesting tree species, Chimpanzees have known to show great selectivity for the trees in which they nest (Goodall, 1968; Hernandez-Aguilar *et al.*, 2013). Selection of nesting tree species by chimpanzees is presumed to be influenced by some physical characteristics of the trees. However, no a distinctive feature that has been found adequate to explain preferences in terms of nest tree species (Hernandez-Aguilar *et al.*, 2013). The combination of more than one physical characteristics of the trees and the habitat types are the key factors determining where chimpanzees nest and in which trees (Basabose & Yamagiwa, 2002; Hernandez-Aguilar, 2009; Ogawa *et al.*, 2007). For

example, Goodall (1968) noted that trees with lowest branches less than 3 m from the ground were not usually used for nest construction in Gombe. Hernandez-Aguilar *et al.* (2013) examining chimpanzee nesting patterns in Issa Valley, revealed that Issa chimpanzees preferred tall trees with high first branches for nesting. Thus, with other factors in place e.g., tree height, the height of a tree from the ground to the first branch is a key factor presumed to influence nest tree selection by chimpanzees. That is, chimpanzee select a tree in which to nest when the tree height is high and that the tree has a high lowest branch.

CHAPTER THREE

MATERIALS AND METHODS

3.1 Study Area

This study was carried out in the MUE at four sites (Issa Valley, Mfubasi, Mlofwesi and Mapalamane; Fig. 1) during the wet season from February to May, 2019. The MUE is a region located in Western Tanzania and forms a part of the Greater Mahale Ecosystem (GME), covering an area of 5756 km² (Piel *et al.*, 2015a). The region is a biodiversity-rich habitat (Moyer *et al.*, 2006) and is partly protected as Tongwe Forest Reserves (TFRs). Major threats to the region include agriculture, which represents the main economic income-source for people (Mwageni *et al.*, 2015), logging, livestock grazing, bush fires and poaching (Plumptre *et al.*, 2010; Pintea 2012; Wilfred & MacColl, 2014). Wilfred and MacColl (2014) reported on the pattern of illegal natural resource exploitation in Ugalla, Western Tanzania, and found poaching, logging and bushmeat hunting to be the dominant illegal activities.

Elevation across MUE ranges from 900 to 1800 m.a.s.l, with average annual temperatures from 11 to 35°C (Piel et al., 2015a) and average annual rainfall between 900 and 1400 mm, mainly falling between November and April (Piel et al., 2015b). The ecosystem is characterized by five different vegetation types: (a) miombo woodland, dominated by Brachystegia spp. and Julbernardia spp., interspersed with (b) seasonally inundated grasslands, (c) rocky outcrops, as well as (d) evergreen riparian and (e) thicket riverine forests (Piel et al., 2017). Open woodland (i.e., more open miombo woodland) is reported as wooded grassland in this study. Issa Valley, Mfubasi, Mlofwesi and Mapalamane, vary in protection status. Issa Valley and Mfubasi are located in Tongwe East Forest Reserve, Mlofwesi is located in Tongwe West Forest Reserve and Mapalamane is located in Mishamo Village Forest, a lower-level protection status from the TFRs, which are District forest reserves. Despite the difference in protection status, all the sites experience anthropogenic activities. Issa Valley (Fig. 2) has an established long-term research presence, which has been shown to deter some human activities (Piel et al., 2015b). In contrast, Mfubasi, Mlofwesi and Mapalamane have all experienced extensive disturbance over the last ten years (Piel & Stewart, 2014).

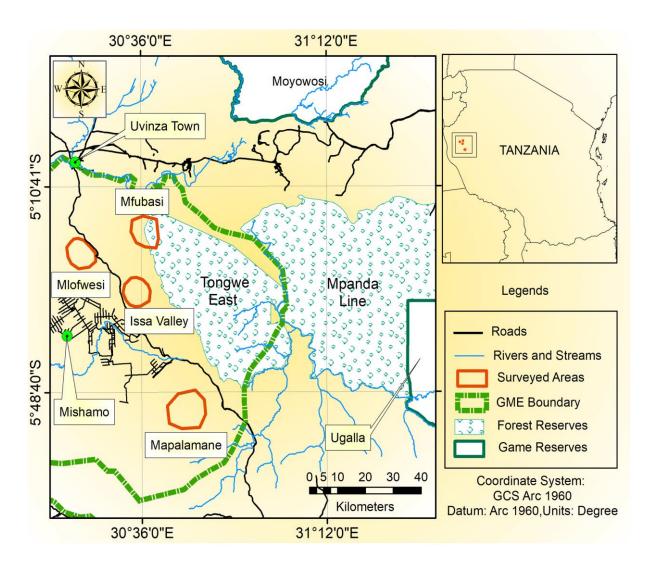


Figure 1: Map of the four sampling sites located in the Masito-Ugalla ecosystem, Tanzania

The MUE is endowed with a variety of primate species including Eastern chimpanzees (Moyer et al., 2006), red colobus monkeys (*Procolobus rufomitratus*), yellow baboons (*Papio cynocephalus*), blue monkey (*Cercopithecus mitis*), red-tailed monkeys (*Cercopithecus ascanius*), vervet monkeys (*Chlorocebus pygerythrus*), and greater galagos (*Otolemur crassicaudatus*). The region also has various ungulate species, carnivore species such as lion (*Panthera leo*), leopards (*Panthera pardus*) and serval cats (*Leptailurus serval*) (Moyer et al., 2006).



Figure 2: A view of chimpanzees in the Issa Valley in Tongwe East Forest Reserve, Tanzania

3.2 Data Collection

3.2.1 Survey for Chimpanzee Plant Food Species

To survey chimpanzee plant food species, eight 2 km long transects were laid radially around the centre point established in each study site. Approximately 1 km was walked from the centre point before starting transects, covering different vegetation types. In some cases, more than 1 km was walked until a particular vegetation type was reached. That is, the start point of transects depended on the availability of a particular vegetation type and the direction followed the extension of such vegetation type. Since riparian forests are rarely in cardinal directions, these forests were followed irrespective of the cardinal direction. Along each transect, ten vegetation plots of $25 \text{ m} \times 25 \text{ m}$ each were conducted, with 200 m between plots, summing up to $199375 \text{ m}^2 (0.199 \text{ km}^2)$ of the total sampled vegetation plot area across survey sites. Vegetation plots were not conducted in cultivated areas. Since most of MUE area is miombo woodland with few strips of riparian forest and very few patches of wooded grassland, stratified sampling was deliberately conducted to have sufficient representation of chimpanzee plant food species. The conducted vegetation plots covered riparian forest, miombo woodland, and wooded grassland. In total, 319 vegetation plots were sampled across all vegetation types. Six (2%) vegetation plots were sampled in wooded grassland, 137 (43%)

vegetation plots in riparian forest, and 176 (55%) in miombo woodland. Published literature (Goodall, 1968; Nakamura *et al.*, 2015; Nishida & Uehara, 1983; Piel *et al.*, 2017) was used to document chimpanzee plant food species (Appendix 1). In each plot, all known chimpanzee plant food species were documented, counted, and determined their growth form and Diameter at Breast Height (DBH).

3.2.2 Survey for Chimpanzee Abundance and Habitat Use

Chimpanzee abundance was inferred from chimpanzee nest presence (Bonnin *et al.*, 2018; Kouakou *et al.*, 2009; Plumptre & Reynolds, 1997) and identified nesting tree species. Chimpanzee nests visible along and from transects were counted and recorded. A 10 m radius around any nest was established to document nearby nests. Chimpanzee nest number served as a proxy for chimpanzee abundance as this study sample size did not warrant further analyses using distance to calculate population density (Buckland *et al.*, 2001). Using nest counts as a proxy measure for population density has known limitations. For instance, nest age and nest production rate (both of which influence density calculations) can vary by region and season. However, previous work in Tai Forest, Cote d'Ivoire, that tested the reliability of nest counts with known population sizes demonstrated nest counts as an effective method to document wild chimpanzee population sizes and confirmed that the method produced reasonable density estimates (Kouakou *et al.*, 2009). Furthermore, chimpanzee nests as a proxy for chimpanzee presence and distribution in a particular habitat (Hernandez-Aguilar *et al.*, 2013), was used to reveal chimpanzee habitat use (Kühl *et al.*, 2017).

3.2.3 Quantification of Anthropogenic Disturbance Across Survey Sites

To quantify anthropogenic disturbance, human activities that interrupted the natural state of chimpanzee habitat were documented. Different human activities were recorded based on the visible signs along transects and in vegetation plots (Table 2). All signs e.g., cattle boma, houses, farms, etc., within 50 m of transects and plots were documented. The presence of houses and people used to count households. Agricultural intensity was determined based on the cultivated fields and areas cleared for cultivation, and obtained the number of different farms based on farm demarcations. Livestock grazing was determined based on the visible cattle herds and cattle bomas. When more than one sign of different human activities was observed in a single location, e.g., logging on farms, or beekeeping on farms, etc., only the major activities presumed to cause greater impact on chimpanzee habitat were recorded, irrespective of the others. In general; the type, frequency, and locations of each event of

human activity was recorded and presumed that each activity had a different impact on chimpanzee habitat. Based on the presumed impact, impact scores between 1 (lowest impact) and 5 (highest impact) were assigned to all types of human activities observed across MUE (Table 2) following Morgan *et al.* (2018).

Table 2: Human activities recorded across MUE with respective weight of destructive

impacts (impact score) on chimpanzee habitat

Human activities	Signs for identification	Impact score		
Agriculture	Cultivated fields	5		
	Cleared areas for farming	5		
Beekeeping	Commercial beehives	1		
	Illegal beehives	2		
	Debarking tree for beehives	2		
Harvesting medicinal plants	Peeling of tree barks	1		
	Digging for tree roots	1		
Livestock grazing	Cattle herds	3		
	Cattle bomas	4		
Logging	Logging sites	4		
	Cut logs	2		
	Logging stumps	2		
Poaching	Snares	1		
	Encountered poachers	2		
Settlement	Households	4		
Small fires	Burnt vegetation	3		

3.3 Data Analyses

3.2.4 Categorizing Survey Sites into Different Disturbance Levels

The frequency of anthropogenic evidence was computed by using encounter rates of the signs per kilometer walked. Following Morgan *et al.* (2018), the weighted impact scores were multiplied by the frequency of encounters of each sign and then summed an overall measure of severity of disturbance per site. Based on the disturbance measure, survey sites were placed into four categories, i.e., least disturbed, mildly disturbed, moderately disturbed and highly disturbed sites (Table 3).

3.2.5 Calculating Species Richness, Diversity and Abundance

Species richness is total number of different species present in a particular ecological community. Species richness does not account for the abundances of each species. Nonetheless, species abundance is the relative representation of a species in a particular ecological community and is measured as the total number of individuals. Species diversity is the number of different species present in an ecological community and their relative abundance. Species diversity account for both species richness and relative abundance.

Chimpanzee plant food species richness was calculated by counting the total number of plant food species in each vegetation plot and then Shannon-Wiener diversity indices was determined. Chimpanzee plant food abundance was defined as the total number of individual plant species with DBH > 10 cm per site. Based on the hypothesis that chimpanzee plant food species richness, diversity, and abundance decline with increasing human disturbance, the values were averaged and the inter-site values were compared across disturbance categories.

To determine if the data were normally or non-normally distributed, a Shapiro-Wilk test was performed and, subsequently, a Levene's test for homogeneity of variances (Shapiro & Wilk, 1965). Kruskal-Wallis test with Dunn's post hoc test was used to compare the variation of chimpanzee plant food species richness, diversity, and abundance between and within sites as the data sets were non-parametric. Also, chimpanzee plant food species richness, diversity, and abundance were compared across vegetation types. All statistical analyses were carried out in Paleontological Statistics Software (PAST Version 3.20) and for all statistical tests, statistical significance was set at P = 0.05.

3.2.6 Chimpanzee Abundance and Habitat Use

Chimpanzee nest number was converted into nests km⁻¹ walked in each survey site and related these proportions to disturbance categories. Inference on habitat use was drawn from the number of nests observed in an area. Nest data are vital for understanding habitat use by chimpanzees (Kühl *et al.*, 2017) because there is a strong association between the number of chimpanzee nests in a particular area and the extent the habitat is used by chimpanzees. Therefore, the higher the number of chimpanzee nests encountered in a particular area, the robust indication that the area is more used by chimpanzees.

CHAPTER FOUR

RESULTS AND DISCUSSION

4.1 Results

4.1.1 Human Disturbance Across Survey Sites

The types and frequency of anthropogenic activities differed across survey sites and disturbance categories (Table 3). At Issa Valley (the least disturbed site), anthropogenic signs were old and no active sign was observed during the survey. In Mfubasi (the mildly disturbed site), recent signs of livestock activities, traditional beekeeping practices, poaching and logging were documented. At Mlofwesi (the moderately disturbed site), evidence of active logging, poaching signs, livestock grazing, traditional beekeeping practices and commercial beekeeping were found. In Mapalamane (the highly disturbed site), predominantly active agricultural activities, numerous settlements, and livestock activities were observed. Mapalamane was inhabited with people in established settlements and contained cleared land for cultivation of maize (*Zea mays*), cassava (*Manihot esculenta*), tobacco (*Nicotiana tabacum*), cotton (*Gossypium sp*), sunflower (*Helianthus sp*), beans (*Phaseolus vulgaris*) and other crops.



Figure 3: *Pterocarpus angolensis* logged (A) for timber (B) at Mlofwesi in Tongwe West Forest Reserve, March 2019

Table 3: Encounter rates of human activities per km walked in each survey site and the severity of disturbance calculated by multiplying the weighted impact scores and the frequency of encounters of each human activity and then summed as an overall measure of severity of human disturbance

Human activity signs Issa Valley Mfubasi Mlofwesi Mapalamane						
Cultivated fields	0.00	0.00	0.00	2.00		
Cleared areas for farming	0.00	0.00	0.00	0.31		
Commercial beehives	0.00	0.00	2.06	0.00		
Illegal beehives	0.06	0.81	3.56	0.44		
Debarking tree for beehives	0.00	0.06	0.75	0.00		
Peeling of tree barks	0.06	0.00	0.06	0.00		
Digging for tree roots	0.00	0.00	0.00	0.13		
Cattle herds	0.00	0.31	0.13	0.63		
Cattle bomas	0.00	0.13	0.06	0.50		
Logging sites	0.13	0.31	0.81	0.19		
Cut logs	0.00	0.44	0.69	0.00		
Logging stumps	0.00	0.25	1.13	0.19		
Snares	0.19	0.00	0.38	0.00		
Encountered poachers	0.00	0.13	0.00	0.00		
Households	0.00	0.00	0.00	2.88		
Burnt vegetation	0.31	0.00	0.13	0.00		
Severity of disturbance	29	77	294	465		
Disturbance category	Least disturbed	Mildly disturbed	Moderately disturbed	Highly disturbed		

Logging and beekeeping practices were present across all four survey sites in MUE. Logging threatened *Pterocarpus angolensis* and *P. tinctorius* tree species (Fig. 3). The latter species is an important food source for MUE Chimpanzees (Piel *et al.*, 2017). Cut logs of both species in Mfubasi and Mlofwesi sites were observed. Seven locations of already cut logs (range: 1-4 logs) in Mfubasi and eleven locations (range: 1-6 logs) in Mlofwesi were recorded. Mlofwesi had a slightly but not significantly higher mean of cut logs 3.1 (3.1, SE = 0.5) than Mfubasi 2.1 (2.1, SE = 0.4; t = 1.049, P = 2.119). Traditional beekeeping threatened *J. globiflora* and *B. speciformis* as local people de-bark these tree species to make local beehives (Fig. 4). These two tree species provide chimpanzees with food (Piel *et al.*, 2017) and are important nesting tree species.



Figure 4: *Brachystegia speciformis*, a chimpanzee plant food and a nesting tree species, debarked (A) to make local beehives (B) at Mlofwesi in Tongwe West Forest Reserve, March 2019

4.1.2 Availability of Chimpanzee Plant Food Species in MUE

A total of 102 potential chimpanzee plant food species that occurred within MUE (Appendix 1), were identified. Of these plant species, most were trees (62%) followed by herbs (12%), shrubs (9%), lianas (8%), climbers (7%), and grasses or palms (1% each). Chimpanzee plant food species richness differed significantly between sites with different disturbance levels (H = 55.09, P < 0.001, Fig. 5), with Mlofwesi and Mapalamane exhibiting the highest richness values. These two sites also exhibited higher chimpanzee plant food diversity compared to the other two (H = 36.81, P < 0.001, Fig. 6). Chimpanzee plant food abundance (i.e., trees, shrubs and liana species with DBH > 10 cm) did not differ significantly across sites (H = 2.477, P = 0.478). Riparian forest exhibited chimpanzee plant food species richness that was nearly twice that of wooded grassland (H = 33.58, P < 0.001, Fig. 7). Chimpanzee plant food diversity did not differ significantly across vegetation types (H = 1.334, P = 0.513), however, chimpanzee plant food abundance (i.e., trees, shrubs and liana species with DBH > 10 cm) was higher in miombo woodland compared to riparian forest and wooded grassland (H = 9.163, P < 0.01).

The ten most abundant chimpanzee plant food species with DBH > 10 cm, were also identified across MUE (Table 4). The average density of the ten most abundant chimpanzee plant food species with DBH > 10 cm varied dramatically across sites with different disturbance levels (Table 4). The list of the ten most abundant plant foods contained species from five families: Fabaceae, Apocynaceae, Hypericaceae, Phyllanthaceae, and Chrysobalanaceae.

Further, eleven fig plant species were recorded across MUE, i.e., *Ficus artocarpoides*, *F. asperifolia*, *F. cyathistipula*, *F. glumosa*, *F. lutea*, *F. ottoniifolia*, *F. sonderi*, *Ficus sp*, *F. sur*, *F. sycomorus*, and *F. thonningii* (Appendix 1). The average abundance of fig tree species, one of the most important chimpanzee food sources (Marshall & Wrangham, 2007), did not differ significantly across sites (H = 2.059, P = 0.55).

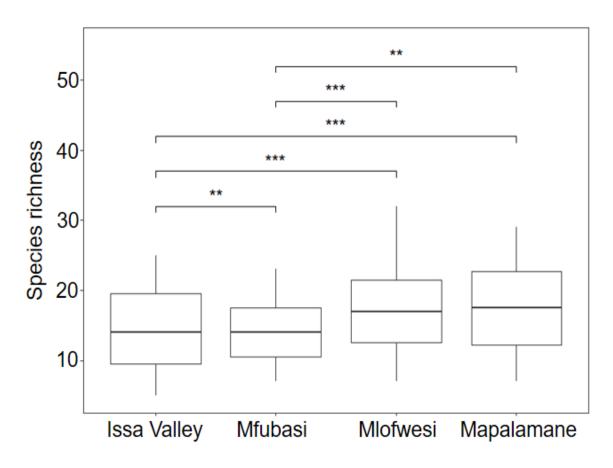


Figure 5: Variation in average chimpanzee plant food species richness across the four sites of different disturbance levels in the MUE

(The averages were calculated from vegetation plots (n = 80 in Issa Valley, 80 in Mfubasi, 79 in Mlofwesi, and 80 in Mapalamane). Issa Valley = least disturbed site, Mfubasi = mildly disturbed site, Mlofwesi = moderately disturbed site, and Mapalamane = highly disturbed site. The line in the box represents the median and the box the upper and lower quartile, each representing 25% of data scores. Whiskers are variability of data scores outside the upper and lower quartiles, and points represent outliers. **indicates P < 0.01, and *** P < 0.001 according to Kruskal-Wallis test)

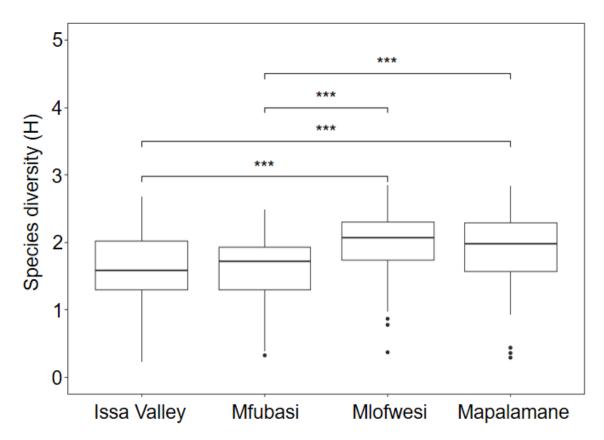


Figure 6: Variation in average chimpanzee plant food diversity across the four sites of different disturbance levels in the MUE

(The averages were calculated from vegetation plots (n = 80 in Issa Valley, 80 in Mfubasi, 79 in Mlofwesi and 80 in Mapalamane). Issa Valley = least disturbed site, Mfubasi = mildly disturbed site, Mlofwesi = moderately disturbed site, and Mapalamane = highly disturbed site. The line in the box represents the median and the box the upper and lower quartile, each representing 25% of data scores. Whiskers are variability of data scores outside the upper and lower quartiles, and points represent outliers. *** indicates P < 0.001 according to Kruskal-Wallis test)

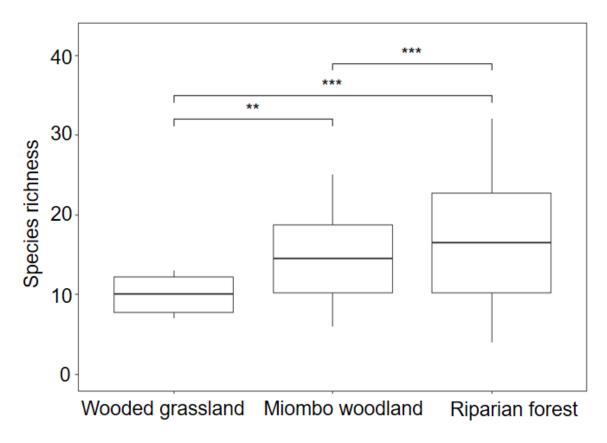


Figure 7: Variation in average Chimpanzee plant food species richness across vegetation types

(The averages were calculated from vegetation plots (n = 6 in wooded grassland, 176 in miombo woodland and 137 in riparian forest. The line in the box represents the median and the box the upper and lower quartile, each representing 25% of data scores. Whiskers are variability of data scores outside the upper and lower quartiles, and points represent outliers. **indicates P < 0.01, and *** P < 0.001 according to Kruskal-Wallis test)

Table 4: Average (± SE) density (i.e., number of individuals of each species km⁻²) of the ten most abundant chimpanzee feeding plant species with DBH > 10 cm identified in MUE across sites of different disturbance levels

Feeding species	Family	Issa Valley	Mfubasi	Mlofwesi	Mapalamane	Test	P-Value
Julbernadia globiflora	Fabaceae	$70^{a} \pm 27$	$628^{b} \pm 156$	$374^{ab} \pm 115$	$398^{ab} \pm 160$	F=6.529, DF=12.47	< 0.01
Brachystegia speciformis	Fabaceae	138 ± 84	148 ± 70	194 ± 49	568 ± 256	H = 6.745	0.07856
Julbernadia unijugata	Fabaceae	392 ± 236	256 ± 164	282 ± 166	68 ± 41	H = 0.2507	0.954
Brachystegia boehmii	Fabaceae	$178^a \pm 78$	$238^{ab}\pm44$	$258^a \pm 50$	$52^{ab}\pm31$	$F_{(3,28)} = 2.989$	< 0.05
Diplorhynchus condylocarpon	Apocynaceae	$26^a \pm 14$	$618^b \pm 124$	$32^{ac}\pm19$	$38^{ac} \pm 11$	H = 17.6	< 0.001
Harungana madagascariensis	Hypericaceae	100 ± 74	0	0	608 ± 384	t = 1.2974	2.1448
Uapaca kirkiana	Phyllanthaceae	$104^a \pm 55$	$4^b \pm 4$	$114^{ac} \pm 44$	$392^{ac}\pm137$	H = 11.41	0.01
Pterocarpus angolensis	Fabaceae	$52^a \pm 26$	$244^b \pm 72$	$114^{ab}\pm32$	$128^{ab}\pm40$	$F_{(3,28)} = 3.043$	< 0.05
Parinari curatellifolia	Chrysobalanaceae	154 ± 40	22 ± 9	190 ± 73	104 ± 40	H = 5.958	0.1004
Brachystegia sp	Fabaceae	32 ± 32	114 ± 87	46 ± 44	228 ± 148	H = 4.442	0.1311

One-way ANOVA or Welch's ANOVA with Tukey post hoc test was used to compare variation between and within groups for normally distributed data sets, Kruskal Wallis test with Dunn's post hoc test was used to compare the variation between and within groups for non-parametric data. Different letters indicate significant differences at p = 0.05

4.1.3 Chimpanzee Abundance and Habitat Use

A total of 203 chimpanzee nests was recorded in four sites during the study period. The encounter rates of the number of chimpanzee nests (i.e., nests km⁻¹) differed significantly between sites with different disturbance levels. The least disturbed site had the highest encounter rate of chimpanzee nests (8.5 nests km⁻¹); encounter rates declined considerably towards the highly disturbed site (1.5 nests km⁻¹). Seventeen different plant species comprised the trees in which all nests were built (Table 5). The abundance of the identified nesting plant species did not vary significantly across sites (H = 0.279, P > 0.964). *Brachystegia boehmii* and *J. unijugata* were the most frequently used nesting species.

Table 5: Average, minimum, maximum and the sum as well as relative proportions of number of nests observed per plant species that chimpanzees selected for nesting across all survey sites within Masito-Ugalla ecosystem

Nesting plant species	Min	Mean	Max	Sum	%
Albizia adianthifolia	3	3.0	3	3	1.5
Albizia glaberrima	1	1.0	1	1	0.5
Brachystegia boehmii	1	7.4	16	67	33.0
Brachystegia bussei	1	2.3	3	7	3.4
Brachystegia microphylla	1	2.0	3	6	3.0
Brachystegia sp	2	2.0	2	4	2.0
Brachystegia speciformis	1	3.7	8	11	5.4
Combretum molle	2	2.7	4	8	3.9
Julbernadia globiflora	1	1.7	2	5	2.5
Julbernadia unijugata	1	2.6	7	49	24.0
Markhamia obtusifolia	2	2.5	3	5	2.5
Parinari curatellifolia	1	1.0	1	1	0.5
Pericopsis angolensis	2	2.0	2	2	1.0
Psydrax parviflora	2	2.0	2	2	1.0
Pterocarpus tinctorius	2	3.0	4	6	3.0
Syzygium guineense	1	2.3	3	14	6.9
Uapaca guineensis	1	2.0	4	12	5.9

4.2 Discussion

In this study, four sites in the MUE area of Western Tanzania were compared to investigate the relationship between anthropogenic disturbance and chimpanzee abundance as well as the

availability of chimpanzee plant food species (i.e., species richness, diversity, and abundance) and nesting tree species. In contrast to the hypothesis that chimpanzee plant food species richness, diversity, and abundance decline with increasing human disturbance, results indicate that chimpanzee plant food species richness and diversity increased with increasing human disturbance, while abundance did not. However, at the site with the highest level of human disturbance both species richness and diversity declined slightly.

The results are consistent with the intermediate disturbance hypothesis, which suggests that species richness and diversity may increase with disturbance in a particular habitat (Catford et al., 2012; Connell, 1978; Wilkinson, 1999), provided that the extent of disturbance is neither too low nor too severe. Moderate disturbance in a particular habitat creates unstable environments of low competitive exclusion between co-occurring species and, therefore, supports high species richness and diversity (Willig & Presley, 2018). In contrast, high disturbance interrupts and eliminates many species in plant communities, resulting in plant communities dominated by few tolerant species, a situation that may result in taxonomic homogenization (Lôbo et al., 2011). The intermediate disturbance hypothesis might explain why Mlofwesi, with moderate disturbance, exhibited higher values of chimpanzee plant food species richness and diversity compared to sites of relatively low disturbance such as Issa Valley and Mfubasi. Mfubasi, Mlofwesi and Mapalamane have all experienced extensive disturbance over the last ten years (Piel & Stewart, 2014) and the latter had the highest occurrence of human activities of severe negative influence (e.g., agriculture and settlement) on chimpanzee habitat, which might have influenced the decline of plant food species richness and diversity. Results suggest that more individual plant species are lost in areas of severe human disturbance than in areas of low human disturbance. This is in agreement with Köster et al. (2013), who reported that environmental conditions in disturbed habitats do not support a variety of tree species because only few tree species have the capacity to establish in these habitats.

Moreover, results show that human disturbance has not yet had an influence on the abundance of chimpanzee plant food and nesting tree species. This is in contrast to Fuller *et al.* (1998), who found that human disturbance resulted in changes to forest composition and plant species abundance in New England, USA, which granted was carried out in New England-Acadian

forest habitat, rather than Tropical forest. In this study, vegetation plots were not conducted in the cultivated fields and in areas already cleared for farming, as these activities were only observed in one of the four survey sites. However, signs of selective logging, livestock grazing, and traditional beekeeping practices were observed in all survey sites. Since livestock grazing has no immediate effect on the abundance of woody plant species (with the exception of cattle bomas, which were also not sampled for vegetation plots), selective logging and debarking of trees for making beehives, resulting in the death of the affected woody plant species, has potentially the largest influence on chimpanzee plant food and nesting tree abundance. Selective logging threatened *P. angolensis* and *P. tinctorius*. Traditional beekeeping practices threatened *J. globiflora* and *B. speciformis* because local people around MUE debark these tree species to make local beehives using barks. However, all these activities are often selective towards certain preferred woody species, and initially do not impact abundance of plant species (Brown & Gurevitch, 2004). The selective nature of these activities may explain why the abundance of chimpanzee plant food and nesting tree species did not differ across survey sites with different human disturbance levels.

Furthermore, it was found that riparian forests had significantly higher chimpanzee plant food species richness compared to miombo woodlands and wooded grasslands. Sabo et al. (2005) revealed that riparian habitats do not harbor higher number of species, but rather supports significantly different species from neighboring upland habitats (i.e., habitats along the sides of a river that are slightly higher in elevation and do not contain surface water). In the case of this study, upland habitats were denoted by miombo woodlands and wooded grasslands. High plant species richness in riparian forests has been considered an indication of high levels of biodiversity (Naiman et al., 1993). An array of plants comprising herbs, grasses, lianas, vines, shrubs and trees, grow in riparian forests, as was observed in this study. Therefore, riparian forests are of major conservation concern due to the support these habitats provide for a number of species (Sabo et al., 2005). In addition, these habitats can act as corridors between isolated habitats and play important roles in facilitating movement and migration of animals, providing shelter and maintaining biodiversity (Naiman et al., 1993). Despite the importance and ecological relevance of riparian forests, human encroachment through agricultural activities is a major threat to these habitats in MUE. During this study, people were observed establishing farms along the riverbanks in the highly disturbed survey site (i.e., Mapalamane), thereby encroaching and diminishing the quality of these habitats. This study was not able to quantify the extent these habitats have been reduced or even disappeared, however future studies that integrate remote sensing easily could calculate reliable estimates (Hansen *et al.*, 2013). While riparian forests are more threatened by farming activities, miombo woodlands and wooded grasslands are threatened by logging, debarking of trees for making local beehives, and livestock activities.

It was also hypothesized that chimpanzee abundance is influenced negatively by human disturbance and predicted that nest counts would be high in areas of low or no human disturbance. The results indicate that as human disturbance levels increase, there is a decrease in chimpanzee abundance despite resources being plentiful and more diverse in moderately disturbed sites. Based on the results, it is argued that resource availability is not the only factor driving chimpanzee population size in moderately disturbed sites. The results can be explored in the context of the deterring effect from human presence and activities. This argument is supported by Garriga et al. (2019), who revealed that in the Moyamba district in south-Western Sierra Leone, the presence and the proximity of humans through roads available in chimpanzee habitats negatively influenced chimpanzee relative abundance and their distribution due to the risks associated with the likelihood of encountering people. This study's results also are consistent with Bryson-Morrison et al. (2017), who showed that chimpanzees in a humandominated landscape of Bossou, Guinea, preferred habitat types both with low human presence and abundant food availability. As reported by Bryson-Morrison et al. (2017), Bossou chimpanzees preferred to travel, rest, and socialize in areas with low human-induced pressure. This study's results suggest that human disturbance in chimpanzee habitat may affect chimpanzee spatial and temporal distribution, regardless of resource availability, i.e., feeding tree species in our case. However, not all human activities increase chimpanzee vulnerability to anthropogenic disturbance. Some studies suggest that chimpanzees can tolerate human disturbance such as agriculture, settlements, and low levels of hunting (Brncic, Amarasekaran, McKenna, Mundry & Kühl, 2015; Rist, Milner-Gulland, Cowlishaw & Rowcliffe, 2009). This argument is similar to that of Garriga et al. (2019), who found that at larger spatial scales, settlements and human presence did not influence chimpanzee relative abundance. Yet, at a temporal level, they found that chimpanzees tended to reduce their activity at midday when human activity was more prevalent, indicating a certain degree of temporal divergence.

Although this study did not assess chimpanzee behaviour in relation to human disturbance, it is acknowledged that chimpanzees may adjust behaviorally to disturbance. Kühl *et al.* (2019) argued that human disturbance in chimpanzee habitat not only influences critical resources for chimpanzee survival, but also erodes behavioral diversity. Some anthropogenic features are likely to influence chimpanzee behavioral activities (e.g., feeding, nesting, grouping, etc.) in response to human encounters and pressures exerted in their habitats (Brncic *et al.*, 2015; Bryson-Morrison *et al.*, 2016; McLennan *et al.*, 2017). In support of this argument, Yuh *et al.* (2019) found that chimpanzees avoided nesting in frequently disturbed areas, similar to what may be occurring in MUE. Although chimpanzees are behaviorally flexible and are able to exploit human-influenced habitats (Bryson-Morrison *et al.*, 2016, 2017; Hockings *et al.*, 2012, 2015), anthropogenic activities, especially those that affect habitat integrity, threaten their survival.

CHAPTER FIVE

CONCLUSION AND RECOMMENDATIONS

5.1 Conclusion

This study showed that as human disturbance levels increase, there is a decrease in chimpanzee abundance despite resources being plentiful and more diverse in the disturbed sites. Therefore, this study recognize that resource availability is not the only factor driving chimpanzee population size in the disturbed sites but also the deterring effect from human presence and activities. Thus, anthropogenic disturbance in MUE negatively influences chimpanzee abundance/habitat use and is positively associated with the loss of chimpanzee resources, a relationship that that threatens the future of all chimpanzee populations outside of national parks.

5.2 Recommendations

Based on the findings of this study, conservation planners and researchers are encouraged to conduct extensive regular surveys to examine changes in chimpanzee critical resources over time in relation to levels of anthropogenic disturbance. Researchers should set up gradient studies of proximity to large settlements to examine thresholds for change in wildlife densities. Further, more effort should be employed to survey large areas and collect sufficient data that will allow for distance sampling rather than just nest counts. This will enable conservation planners to understand the causative relationships (i.e., effects of anthropogenic activities on chimpanzee resources and abundance), and opt for appropriate conservation actions to conserve MUE, the important habitat for chimpanzees living outside national parks in Western Tanzania. This study identified chimpanzee plant food species in MUE based entirely on the already summarized diet lists from Issa Valley, Gombe and Mahale Mountains National Parks (Goodall, 1968; Nakamura et al., 2015; Nishida and Uehara, 1983; Piel et al., 2017). This study provided a good proxy of plant food species in an important chimpanzee habitat outside national park boundaries in Western Tanzania. The findings of chimpanzee plant food species in MUE may be incomplete since there might be additional species that have not been documented in literature but are used in MUE. Therefore, an observational study with the habituated chimpanzees in the Issa Valley is recommended to exactly understand chimpanzee feeding ecology, plant food species, and the food items that are actually eaten by the Masito-Ugalla chimpanzees.

REFERENCES

- Balcomb, S. R., Chapman, C. A., & Wrangham, R. W. (2000). Relationship between chimpanzee (*Pan troglodytes*) density and large, fleshy-fruit tree density: conservation implications. *American Journal of Primatology*, 51(3), 197–203. https://doi.org/10.1002/1098-2345(200007)51:3<197::AID-AJP4>3.0.CO;2-C
- Baldwin, P. J., Mcgrew, W. C, & Tutin, E. G. (1982). Wide-ranging chimpanzees at Mt. Assirik, Senegal. *International Journal of Primatology*, 3(4), 367-385. https://doi.org/10.1007/BF02693739
- Basabose, A. K. (2005). Ranging patterns of chimpanzees in a montane forest of Kahuzi, Democratic Republic of Congo. *International Journal of Primatology*, 26(1), 33. https://doi.org/10.1007/s10764-005-0722-1
- Basabose, A. K., & Yamagiwa, J. (2002). Factors affecting nesting site choice in chimpanzees at Tshibati, Kahuzi-Biega National Park: influence of sympatric gorillas. *International Journal of Primatology*, 23(2), 263–282. https://doi.org/10.1023/A:1013879427335
- Bonnin, N., Van Andel, C. A., Kerby, T. J., Piel, K. A., Pintea, L., & Wich, A. S. (2018). Assessment of chimpanzee nest detectability in drone-acquired images. *Drones*. https://doi.org/10.3390/drones2020017
- Brncic, T., Amarasekaran, B., McKenna, A., Mundry, R., & Kühl, H. S. (2015). Large mammal diversity and their conservation in the human-dominated land-use mosaic of Sierra Leone. *Biodiversity and Conservation*, 24(10), 2417–2438. https://doi.org/10.1007/s10531-015-0931-7
- Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. B., Rylands, A. B., Konstant, W. R., ... Hilton-Taylor, C. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*, *16*(4), 909–923. https://doi.org/10.1046/j.1523-1739.2002.00530.x

- Brown, K. A., & Gurevitch, J. (2004). Long-term impacts of logging on forest diversity in Madagascar. *Proceedings of the National Academy of Sciences of the United States of America*, 101(16), 6045–6049. https://doi.org/10.1073/pnas.0401456101
- Bryson-Morrison, N., Matsuzawa, T., & Humle, T. (2016). Chimpanzees in an anthropogenic landscape: examining food resources across habitat types at Bossou, Guinea, West Africa. *American Journal of Primatology*, 78(12), 1237–1249. https://doi.org/10.1002/ajp.22578
- Bryson-Morrison, N., Tzanopoulos, J., Matsuzawa, T., & Humle, T. (2017). Activity and habitat use of chimpanzees (*Pan troglodytes verus*) in the anthropogenic landscape of Bossou, Guinea, West Africa. *International Journal of Primatology*, 38(2), 282–302. https://doi.org/10.1007/s10764-016-9947-4
- Buckland, S., Anderson, D., Burnham, K., Laake, J., Borchers, D., & Thomas, L. (2001). Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press, United Kingdom. SN - 0-19-850927-8
- Carvalho, J. S., Meyer, C. F. J., Vicente, L., & Marques, T. A. (2015). Where to nest? Ecological determinants of chimpanzee nest abundance and distribution at the habitat and tree species scale. *American Journal of Primatology*, 77(2), 186–199. https://doi.org/10.1002/ajp.22321
- Catford, J. A., Daehler, C. C., Murphy, H. T., Sheppard, A. W., Hardesty, B. D., Westcott, D. A., ... Hulme, P. E. (2012). The intermediate disturbance hypothesis and plant invasions: implications for species richness and management. *Perspectives in Plant Ecology, Evolution and Systematics*, *14*(3), 231–241. https://doi.org/ https://doi.org/ 10. 1016/ j. ppees. 2011.12.002
- Cavada, N., Tenan, S., Barelli, C., & Rovero, F. (2019). Effects of anthropogenic disturbance on primate density at the landscape scale. *Conservation Biology*, *33*(4), 873–882.

- Chapman, C. A., & Chapman, L. J. (2000). Constraints on group size in red colobus and red-tailed guenons: examining the generality of the ecological constraints model. *International Journal of Primatology*, 21(4), 565–585. https://doi.org/10.1023/A:1005557002854
- Chapman, C. A., Chapman, L. J. C. J., Naughton-Treves, L. C., Lawes, M. J., & Mcdowell, L. R. (2004). Predicting folivorous primate abundance: validation of a nutritional model. American Journal of Primatology, 62(2), 55–69. https://doi.org/10.1002/ajp.20006
- Chapman, C. A., & Peres, C. (2001). Primate conservation in the new millennium: the role of scientists. *Evolutionary Anthropology*, (10), 16–33. https://doi.org/10.1002/1520-6505(2001)10:1<16::AID-EVAN1010>3.0.CO;2-O
- Clark, A., Conklin, N., Hunt, K., Hauser, M., Etot, G., Wrangham, R., & Obua, J. (1993). The value of figs to chimpanzees. *International Journal of Primatology*, 14. https://doi.org/10.1007/BF02192634
- Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science*, *199*(4335), 1302 LP 1310. https://doi.org/10.1126/science.199.4335.1302
- Dominy, N. J., Yeakel, J. D., Bhat, U., Ramsden, L., Wrangham, R. W., & Lucas, P. W. (2016). How chimpanzees integrate sensory information to select figs. *Interface Focus*, 6(3), 20160001. https://doi.org/10.1098/rsfs.2016.0001
- Doran, D. (1997). Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Taï chimpanzees. *International Journal of Primatology*, *18*(2), 183–206. https://doi.org/10.1023/A:1026368518431
- Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-duque, E., Fiore, A. Di, ... Baoguo, L. (2017). Impending extinction crisis of the world's primates: why primates

- Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34(1), 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419
- Foerster, S., Zhong, Y., Pintea, L., Murray, C. M., Wilson, M. L., Mjungu, D. C., & Pusey, A. E. (2018). Feeding habitat quality and behavioral trade-offs in chimpanzees: A case for species distribution models. *Behavioral Ecology*, 27(2016), 1004–1016. https://doi.org/10.1093/beheco/arw004
- Fruth, B., Tagg, N., & Stewart, F. (2018). Sleep and nesting behavior in primates: a review. American Journal of Physical Anthropology, 166(3), 499–509. https://doi.org/10.1002/ajpa.23373
- Fuller, J. L., Foster, D. R., McLachlan, J. S., & Drake, N. (1998). Impact of human activity on regional forest composition and dynamics in Central New England. *Ecosystems*, 1(1), 76–95. https://doi.org/10.1007/s100219900007
- Garriga, R. M., Marco, I., Casas-Díaz, E., Acevedo, P., Amarasekaran, B., Cuadrado, L., & Humle, T. (2019). Factors influencing wild chimpanzee (*Pan troglodytes verus*) relative abundance in an agriculture-swamp matrix outside protected areas. *PloS One*, *14*(5), e0215545–e0215545. https://doi.org/10.1371/journal.pone.0215545
- Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve.

 **Animal Behaviour Monographs*, 1, 161–311. https://doi.org/10.1016/S0066-1856(68)80003-2
- Goodall, J. (1962). Nest building behavior in the free ranging chimpanzee. *Annals of the New York Academy of Sciences*, 102, 455–468. https://doi.org/10.1111/j.1749-

- Hackel, J. D. (1999). Community conservation and the future of Africa's wildlife. *Conservation Biology*, 13(4), 726–734. https://doi.org/10.1046/j.1523-1739.1999.98210.x
- Hansen, M. C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., ... Townshend, J. R. G. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, *342*(6160), 850 LP 853. https://doi.org/10.1126/science.1244693
- Hanski, I. (2011). Habitat loss, the dynamics of biodiversity, and a perspective on conservation. *AMBIO*, 40(3), 248–255. https://doi.org/10.1007/s13280-011-0147-3
- Hernandez-Aguilar, R. A. (2009). Chimpanzee nest distribution and site reuse in a dry habitat: implications for early hominin ranging. *Journal of Human Evolution*, *57*(4), 350–364. https://doi.org/https://doi.org/10.1016/j.jhevol.2009.03.007
- Hernandez-Aguilar, R. A., Moore, J., & Stanford, C. B. (2013). Chimpanzee nesting patterns in savanna habitat: environmental influences and preferences. *American Journal of Primatology*, 75(10), 979–994. https://doi.org/10.1002/ajp.22163
- Herrera, J. P., Wright, P. C., Lauterbur, E., Ratovonjanahary, L., & Taylor, L. L. (2011). The effects of habitat disturbance on lemurs at Ranomafana National Park, Madagascar. *International Journal of Primatology*, 32(5), 1091–1108. https://doi.org/10.1007/s10764-011-9525-8
- Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2012). Socioecological adaptations by chimpanzees, *Pan troglodytes verus*, inhabiting an anthropogenically impacted habitat. *Animal Behaviour*, 83(3), 801–810. https://doi.org/10.1016/j.anbehav.2012.01.002
- Hockings, K. J., McLennan, M. R., Carvalho, S., Ancrenaz, M., Bobe, R., Byrne, R. W., ... Hill, C. M. (2015). Apes in the anthropocene: flexibility and survival. *Trends in Ecology &*

- Humle, T., Boesch, C., Campbell, G., Junker, J., Koops, K., Kuehl, H. & Sop, T. (2016). Pan troglodytes ssp. Verus. The IUCN Red List of Threatened Species 2016: e.T15935A102327574.
- Itoh, N., & Nakamura, M. (2015). Diet and feeding behaviour. In Mahale Chimpanzees: 50 Years of Research, M. Nakamura, K. Hosaka, N. Itoh, & K. Zamma (Eds.), pp. 227–245. Cambridge University Press. https://doi.org/10.1017/CBO9781107280533
- Junker, J., Blake, S., Boesch, C., Campbell, G., Toit, L. D., Duvall, C., ... Kuehl, H. S. (2012).
 Recent decline in suitable environmental conditions for African great apes. *Diversity and Distributions*, 18(11), 1077–1091. https://doi.org/10.1111/ddi.12005
- Köster, N., Kreft, H., Nieder, J., & Barthlott, W. (2013). Range size and climatic niche correlate with the vulnerability of epiphytes to human land use in the tropics. *Journal of Biogeography*, 40(5), 963–976. https://doi.org/10.1111/jbi.12050
- Kouakou, C. Y., Boesch, C., & Kuehl, H. (2009). Estimating chimpanzee population size with nest counts: validating methods in Taï National Park. *American Journal of Primatology*, 71(6), 447–457. https://doi.org/10.1002/ajp.20673
- Kühl, H. S., Boesch, C., Kulik, L., Haas, F., Arandjelovic, M., Dieguez, P., ... Kalan, A. K. (2019). Human impact erodes chimpanzee behavioral diversity. *Science*, *363*(6434), 1453 LP 1455. https://doi.org/10.1126/science.aau4532
- Kühl, H. S., Sop, T., Williamson, E. A., Mundry, R., Brugière, D., Campbell, G., ... Boesch, C. (2017). The critically endangered Western chimpanzee declines by 80%. *American Journal of Primatology*, 79(9), e22681. https://doi.org/10.1002/ajp.22681
- Last, C., & Muh, B. (2013). Effects of human presence on chimpanzee nest location in the

- Lebialem-Mone Forest landscape, Southwest Region, Cameroon. *Folia Primatologica*, 84(1), 51–63. https://doi.org/10.1159/000346305
- Leendertz, F. H., Lankester, F., Guislain, P., Néel, C., Drori, O., Dupain, J., ... Leroy, E. M. (2006). Anthrax in Western and Central African great apes. *American Journal of Primatology*, 68(9), 928–933. https://doi.org/10.1002/ajp.20298
- Lôbo, D., Leão, T., Melo, F. P. L., Santos, A. M. M., & Tabarelli, M. (2011). Forest fragmentation drives Atlantic forest of Northeastern Brazil to biotic homogenization. *Diversity and Distributions*, 17(2), 287–296. https://doi.org/10.1111/j.1472-4642.2010.00739.x
- Marshall, A. J., & Wrangham, R. W. (2007). Evolutionary consequences of fallback foods. International Journal of Primatology, 28(6), 1219. https://doi.org/10.1007/s10764-007-9218-5
- McCarthy, M. S., Lester, J. D., & Stanford, C. B. (2017). Chimpanzees (*Pan troglodytes*) flexibly use introduced species for nesting and bark feeding in a human-dominated habitat. *International Journal of Primatology*, 38(2), 321–337. https://doi.org/10.1007/s10764-016-9916-y
- McLennan, M. R., Spagnoletti, N., & Hockings, K. J. (2017). The implications of primate behavioral flexibility for sustainable human–primate coexistence in anthropogenic habitats. *International Journal of Primatology*, 38(2), 105–121. https://doi.org/10.1007/s10764-017-9962-0
- Moore, D. L., & Vigilant, L. (2013). A population estimate of chimpanzees (*Pan troglodytes schweinfurthii*) in the Ugalla region using standard and spatially explicit genetic capture recapture methods. *American Journal of Primatology*, 76, 335–346. https://doi.org/10.1002/ajp.22237

- Morgan, D., Mundry, R., Sanz, C., Ayina, C. E., Strindberg, S., Lonsdorf, E., & Kühl, H. S. (2018). African apes coexisting with logging: comparing chimpanzee (*Pan troglodytes troglodytes*) and gorilla (*Gorilla gorilla gorilla*) resource needs and responses to forestry activities. *Biological Conservation*, 218, 277–286. https:// doi. org/ https:// doi. org/ 10. 1016/j.biocon.2017.10.026
- Moyer, D., Plumptre, A. J., Pintea, L., Hernandez-Aguilar, A., Moore, J., Stewart, F. a., ... Mwangoka, M. (2006). Surveys of chimpanzees and other biodiversity in Western Tanzania. Report to the US Fish and Wildlife Service. The Jane Goodall Institute, Wildlife Conservation Society, UCSD. Http://Ugalla.Ucsd.Edu/Objetos/Herwcsta.Pdf, 65.
- Naiman, R. J., Decamps, H., & Pollock, M. (1993). The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications*, 3(2), 209–212. https://doi.org/10.2307/1941822
- Nakamura, M. (2015). Home range. In Mahale chimpanzees: 50 Years of Research, M. Nakamura, K. Hosaka, N. Itoh, & K. Zamma (Eds.), pp. 94–105. Cambridge University Press. https://doi.org/10.1017/CBO9781107280533
- Nakamura, M., Corp, N., Fujimoto, M., Fujita, S., Hanamura, S., Hayaki, H., ... Zamma, K. (2013). Ranging behavior of Mahale chimpanzees: a 16 year study. *Primates; Journal of Primatology*, *54*(2), 171–182. https://doi.org/10.1007/s10329-012-0337-z
- Nakamura, M., Hosaka, K., Itoh, N., & Zamma, K. (2015). Mahale Chimpanzees: 50 Years of Research. Cambridge University Press. https://doi.org/10.1017/CBO9781107280533
- Newton-Fisher, N. E. (1999). The diet of chimpanzees in the Budongo Forest Reserve, Uganda. African Journal of Ecology, 37(3), 344–354. https://doi.org/10.1046/j.1365-2028.1999.00186.x
- Nishida, T. (1968). The social group of wild chimpanzees in the Mahale Mountains. *Primates*, 9,

- Nishida, T. (2012). Chimpanzees of the Lakeshore: natural history and culture at Mahale. Cambridge University Press. https://doi.org/10.1017/CBO9781139059497
- Nishida, T., & Uehara, S. (1983). Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*): long-term record from the Mahale Mountains, Tanzania. *African Study Monographs*, *3*, 109–138. https://doi.org/10.14989/67987
- Ogawa, H., Idani, G., Moore, J., Pintea, L., & Hernandez-Aguilar, A. (2007). Sleeping parties and nest distribution of chimpanzees in the savanna woodland, Ugalla, Tanzania. *International Journal of Primatology*, 28(6), 1397–1412. https://doi.org/10.1007/s10764-007-9210-0
- Ogawa, H., Yoshikawa, M., & Idani, G. (2013). The population and habitat preferences of chimpanzees in non-protected areas of Tanzania. *Pan Africa News*, 20(1), 1–5. https://doi.org/10.5134/177626
- Piel, A. K., Cohen, N., Kamenya, S., Ndimuligo, S. A., Pintea, L., & Stewart, F. A. (2015a).
 Population status of chimpanzees in the Masito-Ugalla ecosystem, Tanzania. *American Journal of Primatology*, 77(10), 1027–1035. https://doi.org/10.1002/ajp.22438
- Piel, A. K., Lenoel, A., Johnson, C., & Stewart, F. A. (2015b). Deterring poaching in Western Tanzania: The presence of wildlife researchers. *Global Ecology and Conservation*, *3*, 188–199. https://doi.org/10.1016/j.gecco.2014.11.014
- Piel, A. K., Strampelli, P., Greathead, E., Hernandez-Aguilar, R. A., Moore, J., & Stewart, F. A. (2017). The diet of open-habitat chimpanzees (*Pan troglodytes schweinfurthii*) in the Issa valley, Western Tanzania. *Journal of Human Evolution*, 112, 57–69. https://doi.org/10.1016/j.jhevol.2017.08.016

- Piel, A., & Stewart, F. (2014). Census and conservation status of chimpanzees (*Pan troglodytes schweinfurthii*) across the Greater Mahale Ecosystem. *Report submitted to the The Nature Conservancy*, USA, 74.
- Pintea, L. (2012). Modeling potential conflict between agricultural expansion and biodiversity in the Greater Mahale Ecosystem, Tanzania. *Report submitted to Africa biodiversity collaborative group. http://www.abcg.org/action/document/show?document_id=357*
- Plumptre, A. J., & Reynolds, V. (1996). Censusing chimpanzees in the Budongo Forest, Uganda. *International Journal of Primatology*, 17(1), 85–99. https://doi.org/10.1007/BF02696160
- Plumptre, A. J., & Reynolds, V. (1997). Nesting behavior of chimpanzees: implications for censuses. *International Journal of Primatology*, 18(4), 475–485. https://doi.org/10.1023/A:1026302920674
- Plumptre, A. J., Rose, R., Nangendo, G., Williamson, E. A., Didier, K., Hart, J., ... Bennett, E. (2010). Eastern chimpanzee (*Pan troglodytes schweinfurthii*): status survey and conservation action plan 2010–2020. *International Union for the Conservation of Nature* (*IUCN*). Gland, Switzerland.
- Rands, M. R. W., Adams, W. M., Bennun, L., Butchart, S. H. M., Clements, A., Coomes, D., ... Vira, B. (2010). Biodiversity conservation: challenges beyond 2010. *Science*, *329*(5997), 1298 LP 1303. https://doi.org/10.1126/science.1189138
- Rist, J., Milner-Gulland, E. J., Cowlishaw, G., & Rowcliffe, J. M. (2009). The Importance of hunting and habitat in determining the abundance of tropical forest species in Equatorial Guinea. *Biotropica*, *41*(6), 700–710. https://doi.org/10.1111/j.1744-7429.2009.00527.x
- Rothman, J. M., Pell, A. N., Dierenfeld, E. S., & Mccann, C. M. (2006). Plant choice in the construction of night nests by gorillas in the Bwindi Impenetrable National Park, Uganda.

- Sabo, J., Sponseller, R., Dixon, M., Gade, K., Harms, T., Heffernan, J., ... Welter, J. (2005). Riparian zones increase regional species richness by harboring different, not more, species. *Ecology*, 86, 56–62. https://doi.org/10.1890/04-0668
- Sanz, C., Morgan, D., Strindberg, S., & Onononga, J. R. (2007). Distinguishing between the nests of sympatric chimpanzees and gorillas. *Journal of Applied Ecology*, 44(2), 263–272. https://doi.org/10.1111/j.1365-2664.2007.01278.x
- Sarkar, S., Pressey, R. L., Faith, D. P., Margules, C. R., Fuller, T., Stoms, D. M., ... Andelman, S. (2006). Biodiversity conservation planning tools: present status and challenges for the future. *Annual Review of Environment and Resources*, 31(1), 123–159. https://doi.org/10.1146/annurev.energy.31.042606.085844
- Shapiro, S. S., & Wilk, M. B. (1965). An analysis of variance test for normality (complete samples). *Biometrika*, 52(3–4), 591–611. https://doi.org/10.1093/biomet/52.3-4.591
- Stevenson, P. R. (2001). The relationship between fruit production and primate abundance in Neotropical communities. Biological Journal of the Linnean Society, 72, 161–178. https://doi.org/10.1006/bijl.2000.0497
- Stewart, F. A., Piel, A. K., & McGrew, W. C. (2011). Living archaeology: artefacts of specific nest site fidelity in wild chimpanzees. *Journal of Human Evolution*, *61*(4), 388–395. https://doi.org/https://doi.org/10.1016/j.jhevol.2011.05.005
- TAWIRI. (2018). Tanzania chimpanzee conservation action plan 2018-2023. *Tanzania Wildlife Research Institute*. http://tawiri.or.tz/wp-content/uploads/2018/07/Tanzania-Chimpanzee-Conservation-Action-Plan-2018.pdf.
- Teleki, G. (1989). Population status of wild chimpanzees (Pan troglodytes) and threats to

- survival. In Understanding chimpanzees, G. H. Paul and A. M. Linda (eds.), pp.312–353. Harvard University Press, Cambridge. ISBN 9780674183858
- Watts, D. P., Potts, K. B., Lwanga, J. S., & Mitani, J. C. (2012a). Diet of chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda, 1. Diet composition and diversity. *American Journal of Primatology*, 74(2), 114–129. https://doi.org/10.1002/ajp.21016
- Watts, D. P., Potts, K. B., Lwanga, J. S., & Mitani, J. C. (2012b). Diet of chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda, 2. Temporal variation and fallback foods. *American Journal of Primatology*, 74(2), 130–144. https://doi.org/10.1002/ajp.21015
- Wilfred, P., & MacColl, A. (2014). The pattern of poaching signs in Ugalla Game Reserve, Western Tanzania. *African Journal of Ecology*, 52(4), 543–551. https://doi.org/10.1111/aje.12161
- Wilkinson, D. M. (1999). The disturbing history of intermediate disturbance. *Oikos*, 84(1), 145–147. https://doi.org/10.2307/3546874
- Willig, M. R., & Presley, S. J. (2018). Biodiversity and disturbance. In The encyclopedia of anthropocene, D. A. Dellasala & M. I. Goldstein (Eds.), pp. 45–51. Elsevier. https://doi.org/https://doi.org/10.1016/B978-0-12-809665-9.09813-X
- Wrangham, R. W., Chapman, C. A., Clark-Arcadi, A. P., & Isabirye-Basuta, G. (1996). Social ecology of Kanyawara chimpanzees: implications for understanding the costs of great ape groups. In *Great Ape societies*. (pp. 45–57). New York, NY, US: Cambridge University Press. https://doi.org/10.1017/CBO9780511752414.006
- Yoshikawa, M., & Ogawa, H. (2015). Diet of savanna chimpanzees in the Ugalla area, Tanzania. *African Study Monographs*, *36*(September), 189–209. https://doi.org/10.14989/200275

- Yoshikawa, M., Ogawa, H., Sakamaki, T., & Idani, G. (2008). Population density of Chimpanzees in Tanzania. *Pan Africa News*, *December*, 2008, 15(2). https://doi.org/10.5134/143497
- Yuh, Y. G., Dongmo, Z. N., N'Goran, P. K., Ekodeck, H., Mengamenya, A., Kuehl, H., ... Elvis, T. (2019). Effects of land cover change on Great Apes distribution at the Lobéké National Park and its surrounding forest management units, South-East Cameroon. A 13 year time series analysis. *Scientific Reports*, 9(1), 1445. https://doi.org/10.1038/s41598-018-36225-2

APPENDICES

Appendix 1: A list of chimpanzee plant feeding species documented in the Masito-Ugalla ecosystem based on direct observations and the compiled diet lists from Issa Valley, Gombe, and Mahale Mountains National Park (Goodall 1968; Nakamura et al., 2015; Nishida & Uehara 1983; Piel et al., 2017)

S/n.	Local name	Scientific name	Growth form
1	Bhufila	Annona senegalensis	Tree
2	Bhufulu	Vitex doniana	Tree
3	Bhungogolo	Multidentia crassa	Tree
4	Bhunkukuma	Grewia flavescens	Shrub
5	Bhusantu	Ximenia americana	Shrub
6	Bhusungunimba	Flacourtia indica	Shrub
7	Buhono	Pseudospondias microcarpa	Tree
8	Bwaje	Strychnos spinosa	Tree
9	Ighoghola	Aspilia mossambicensis	Herb
10	Igongo	Sclerocarya birrea	Tree
11	Ijubilha	Baphia capparidifolia	Liana
12	Ikolyoko 1	Voacanga africana	Tree
13	Ikolyoko 2	Tabernaemontana pachysiphon	Tree
14	Ikome	Strychnos pungens	Tree
15	Ikonjogholo	Oncinotis tenuiloba	Liana
16	Ikubilha	Ficus sur	Tree
17	Ikuku 1	Ficus sonderi	Tree
18	Ikuku 2	Ficus sycomorus	Tree
19	Ikuku 3	Ficus glumosa	Tree
20	Ikusu	Uapaca kirkiana	Tree
21	Ilombo	Saba comorensis	Liana
22	Isomang'ombe	Blepharis buchneri	Herb
23	Iswe	Pennisetum purpureum	Grass
24	Itambuka	Dalbergia malangensis	Liana
25	Itesa	Commelina africana	Herb

26	Itungulu	Aframomum mala	Herb
27	Kabamba	Julbernadia globiflora	Tree
28	Kabhumbu	Lannea schimperi	Tree
29	Kafunampasa	Albizia glaberrima	Tree
30	Kagera 1	Brachystegia microphylla	Tree
31	Kagera 2	Brachystegia sp	Tree
32	Kagobhole	Ziziphus abyssinica	Tree
33	Kahefu	Celtis africana	Tree
34	Kahembegwasya	Thevetia peruviana	Herb
35	Kajimonsole	Ficus sp	Tree
36	Kakubhabholo	Sterculia tragacantha	Tree
37	Kakusufikinyia	Uapaca guineensis	Tree
38	Kampandampanda	Canthium burtii	Shrub
39	Kamwibi	Psydrax parviflora	Tree
40	Kankolokombe	Ficus asperifolia	Climber
41	Kankundu	Strychnos madagascariensis	Tree
42	Kansonsokemba	Hewittia sp	Climber
43	Kantapansima	Toddalia asiatica	Liana
44	Kasolyo	Garcinia huillensis	Tree
45	Lingogha	Leea guineensis	Herb
46	Linkumbwe	Clerodendrum schweinfurthii	Herb
47	Linselele	Smilax anceps	Herb
48	Linsilu	Pteridium aquilinum	Herb
49	Lintonga	Strychnos cocculoides	Tree
50	Lujongololo 1	Artabotrys monteiroae	Climber
51	Lujongololo 2	Uvaria angolensis	Liana
52	Lujongololo 3	Monanthotaxis poggei	Liana
53	Lukosho	Ampelocissus abyssinica	Climber
54	Lulobhe	Uapaca nitida	Tree
55	Lulumasha	Pycnanthus angolensis	Tree
56	Lulyolwakanga	Margaritaria discoidea	Shrub

57	Lulyolwakape	Psychotria peduncularis	Herb
58	Lumpululu	Ceropegia sp	Herb
59	Luntafwanengwa 1	Keetia venosa	Shrub
60	Luntafwanengwa 2	Keetia guenzii	Shrub
61	Luntafwanengwa 3	Keetia ferruginea	Shrub
62	Lusanda	Phoenix reclnata	Palm
63	Lusisi	Tamarindus indica	Tree
64	Mhefu	Trema orientalis	Tree
65	Mhololo	Ficus lutea	Tree
66	Mjimo	Ficus thonningii	Tree
67	Mjonso	Vernonia amygdalina	Tree
68	Mkibugwesimbwa	Cordia millenii	Tree
69	Mkobegana	Ficus ottoniifolia	Tree
70	Mkoma	Brachystegia bussei	Tree
71	Mkombelonda	Tarenna pavettoides	Tree
72	Mkote	Phyllanthus reticulatus	Shrub
73	Mkubwa	Hexalobus monopetalus	Tree
74	Mkuni	Pleurostylia africana	Tree
75	Mlama	Combretum molle	Tree
76	Mlembela	Anthonotha noldeae	Tree
77	Mlulu	Ficus artocarpoides	Tree
78	Mlyansekesi	Synsepalum brevipes	Tree
79	Mninga	Pterocarpus angolensis	Tree
80	Mnyenye	Brachystegia boehmii	Tree
81	Mpatwe	Paullinia pinnata	Climber
82	Mpila	Landolphia owariensis	Liana
83	Mpongolela	Deinbollia fulvotomentella	Tree
84	Msabasaba 1	Syzygium guineense	Tree
85	Msabasaba 2	Syzygium cordatum	Tree
86	Msakansaka	Bauhinia thonningii	Tree
87	Mshindwi	Anisophyllea boehmii	Tree

88	Msomombo	Tinospora caffra	Climber
89	Msongati	Diplorhynchus condylocarpon	Tree
90	Msubhu	Dombeya rotundifolia	Tree
91	Mtimpu	Antidesma venosum	Tree
92	Mtobho	Azanza garckeana	Tree
93	Mtulu	Brachystegia spiciformis	Tree
94	Mtunu	Harungana madagascariensis	Tree
95	Mubhula	Parinari curatellifolia	Tree
96	Mwako	Julbernadia unijugata	Tree
97	Mwenje	Pterocarpus tinctorius	Tree
98	Ntalali	Vitex mombasae	Tree
99	Ntutami	Ficus cyathistipula	Tree
100	Omoji	Costus afer	Herb
101	Sihama	Dioscorea sp	Climber
102	Sitalya	Zanha africana	Tree

RESEARCH OUTPUTS

- 1. Research article "Anthropogenic disturbance and chimpanzee (*Pan troglodytes*) habitat use in the Masito-Ugalla ecosystem, Tanzania", published in the **Journal of Mammalogy**, under **Oxford University Press**. The journal operates under the flagship publication of the American Society of Mammologists.
- 2. Poster Presentation "Do anthropogenic activities impact chimpanzee foraging plant species and nesting tree selection in the Masito-Ugalla ecosystem, Tanzania".





Anthropogenic disturbance and chimpanzee (*Pan troglodytes*) habitat use in the Masito-Ugalla Ecosystem, Tanzania

SIMULA P. MAIJO, *, ALEX K. PIEL, AND ANNA C. TREYDTE

Tanzania Wildlife Research Institute, Box 661, Arusha, Tanzania (SPM)

School of Life Sciences and Bio-engineering, The Nelson Mandela African Institution of Science and Technology, Box 447, Tengeru, Arusha, Tanzania (SPM, ACT)

Department of Anthropology, University College of London, 14 Taviton St, Bloomsbury, London WC1H OBW, United Kingdom (AKP)

GMERC, LTD, Box 66, Kigoma, Tanzania (AKP)

Agroecology in the Tropics and Subtropics, University of Hohenheim, Stuttgart 70599, Germany (ACT)

The habitat quality of chimpanzee (*Pan troglodytes*), including the availability of plant food and nesting species, is important to ensure the long-term survival of this endangered species. Botanical composition of vegetation is spatially variable and depends on soil characteristics, weather, topography, and numerous other biotic and abiotic factors. There are few data regarding the availability of chimpanzee plant food and nesting species in the Masito-Ugalla Ecosystem (MUE), a vast area that lies outside national park boundaries in Tanzania, and how the availability of these resources varies with human disturbance. We hypothesized that chimpanzee plant food species richness, diversity, and abundance decline with increasing human disturbance. Further, we predicted that chimpanzee abundance and habitat use is influenced negatively by human disturbance. Published literature from Issa Valley, Gombe, and Mahale Mountains National Parks, in Tanzania, was used to document plant species consumed by chimpanzees, and quantify their richness, diversity, and abundance, along 32 transects totaling 63.8 km in length across four sites of varying human disturbance in MUE. We documented 102 chimpanzee plant food species and found a significant differences in their species richness (H = 55.09, P < 0.001) and diversity (H = 36.81, P < 0.001) across disturbance levels, with the moderately disturbed site exhibiting the highest species richness and diversity. Chimpanzees built nests in 17 different tree species. The abundance of nesting tree species did not vary across survey sites (H = 0.279, P > 0.964). The least disturbed site exhibited the highest encounter rate of chimpanzee nests/km, with rates declining toward the highly disturbed sites. Our results show that severe anthropogenic disturbance in MUE is associated with the loss of chimpanzee plant food species and negatively influences chimpanzee habitat use, a relationship that threatens the future of all chimpanzee populations outside national parks.

Key words: anthropogenic disturbance, habitat use, nests, species abundance, species diversity, species richness

Habitat loss and overexploitation of natural resources are major challenges for biodiversity conservation (Rands et al. 2010). These processes are driven mainly by human poverty and increasing human population size, which, when combined, result in overdependence on nature, thus threatening wildlife (Hackel 1999). Increasing human population sizes and encroachment on wildlife habitat are the core incitement of human–wildlife conflicts, habitat fragmentation and loss, and associated biodiversity loss in most areas (Brooks et al. 2002; Fahrig 2003;

Hanski 2011). A number of primate species, including chimpanzees (*Pan troglodytes*), inhabit human-impacted landscapes (Hockings et al. 2012, 2015; Bryson-Morrison et al. 2016, 2017), following the continuous contraction of their natural ranges as a result of human encroachment. To understand how chimpanzees will persist in human encroached landscapes, we need to assess the relationship between chimpanzee habitat degradation and the availability of resources used by this species.

^{*} Correspondent: maijocmla@yahoo.com

The availability and quantity of food resources in chimpanzee habitat is one of the primary factors that drives chimpanzee abundance and distribution (Stevenson 2001; Foerster et al. 2018). Hence, as the density of food resources declines, chimpanzee range tends to increase to compensate for reduced food availability (Baldwin et al. 1982). Alternatively, chimpanzees might instead consume more nutrient-poor foods (Doran 1997; Basabose 2005), which may reduce their fitness and survival. Chimpanzees are omnivorous and feed on fruits, leaves and other plant parts, vertebrates, and invertebrates, as well as on inorganic substances (i.e., termite mound soil and rocks-Goodall 1968; Nishida and Uehara 1983; Newton-Fisher 1999; Nishida 2012; Watts et al. 2012a, 2012b; Itoh and Nakamura 2015; Piel et al. 2017). Notwithstanding, chimpanzees predominantly depend on plant matter, especially ripe fruits, which constitute the majority of their diet (Goodall 1968; Nishida 1968; Nishida and Uehara 1983; Nakamura et al. 2013).

In addition to food resources, the availability of nesting sites is another key factor influencing chimpanzee presence, abundance, and distribution (Carvalho et al. 2015). Nesting is a daily behavior in all great ape species (Goodall 1968; Fruth et al. 2018). All weaned great apes, including chimpanzees, build night nests for sleeping, occasionally build daytime nests for resting, and rarely re-use nests (Goodall 1962; Rothman et al. 2006). Although any woody species is a potential nesting site, chimpanzees nest nonrandomly wherever the behavior has been studied (Basabose and Yamagiwa 2002; Hernandez-Aguilar 2009; Stewart et al. 2011; Last and Muh 2013). Chimpanzee nests, therefore, are a good proxy for chimpanzee presence (Hernandez-Aguilar et al. 2013) and reveal chimpanzee habitat use as well as population density and trends (Kühl et al. 2017). Indeed, most approaches for estimating wild chimpanzee populations rely on nest counts (Plumptre and Reynolds 1997; Bonnin et al. 2018). In some areas, chimpanzees occur at low densities and thus nest counts are impracticable over a large area. Nevertheless, recent work using drones (Bonnin et al. 2018) demonstrates the effectiveness of nest counts for population size estimates in wild chimpanzees.

Chimpanzee populations are declining rapidly (Junker et al. 2012), threatened by habitat loss, poaching, disease, and the pet trade (Leendertz et al. 2006; Hockings et al. 2015; Kühl et al. 2017, 2019). In Tanzania, eastern chimpanzees (P. t. schweinfurthii) are distributed across the western region (TAWIRI 2018), with an estimated total population of less than 2,500 individuals (Moyer et al. 2006; Piel and Stewart 2014). More than 75% of the current population lives outside national parks (Piel et al. 2015a). Chimpanzee numbers outside national parks have significantly declined in the 2000's (Yoshikawa et al. 2008; Ogawa et al. 2013) and a significant subpopulation is found in the Masito-Ugalla Ecosystem (MUE; Fig. 1; Moore and Vigilant 2013; Piel et al. 2015a). Surveys across MUE in 2012 revealed a density of 0.1 individuals/km² (Piel et al. 2015a), and a total population of about 288 individuals, or > 10% of Tanzania's chimpanzees.

Studies on the relationship between disturbance and primate populations have been conducted on a number of species. Chapman

and Chapman (2000) found that anthropogenic disturbance affected the abundance and group size of red colobus and red-tailed guenons in Kibale National Park, Uganda. Cavada et al. (2019) described the relationship between anthropogenic disturbance and the density of arboreal primate species in the Udzungwa Mountains of Tanzania and showed that disturbance negatively affected primate density. Herrera et al. (2011), examining the effects of disturbance on lemurs at Ranomafana National Park, Madagascar, found that anthropogenic disturbance did not always have deleterious effects on primates. The variation in lemur abundance was related to diet (i.e., feeding guilds) rather than disturbance, with frugivorous species more prone to population declines than folivores or insectivores. Moreover, anthropogenic disturbance not only affects primate densities but also their behaviors (Kühl et al. 2019). In most environments where nonhuman primates coexist with people, primates exhibit behavioral flexibility, including dietary adjustments, to survive (McCarthy et al. 2017; McLennan et al. 2017).

There are a number of studies that described chimpanzee diet across western Tanzania (Table 1). However, the only two studies that described chimpanzee diet in MUE were undertaken in the Issa Valley, and at Nguye and Bhukalai sites. Based on chimpanzee diet studies across western Tanzania, Yoshikawa and Ogawa (2015) found a proportion (range: 20–39%) of the identified chimpanzee plant food species to overlap between Nguye, Bhukalai, Gombe, and Mahale Mountains. For example, of 100 plant food species identified in Nguye and Bhukalai, 39% of the plant food species also were consumed by the Mahale chimpanzees, and 33% by the Gombe chimpanzees. Out of 198 plant food species identified in Mahale Mountains National Park, Nguye and Bhukalai chimpanzees consumed 20%, and of 147 plant food species identified in Gombe National Park, Nguye and Bhukalai chimpanzees consumed 22%.

While Balcomb et al. (2000) found a positive relationship between the density of fleshy fruit trees and chimpanzee density measured across six sites in Kibale Forest, Uganda, a similar study on plant food availability and habitat disturbance has yet to be carried out at MUE, where anthropogenic disturbance is high (Plumptre et al. 2010; Wilfred and MacColl 2014). Increasing threats from agricultural expansion, settlements, cattle herding, annual fires, logging, and poaching have been reported in the region and threaten chimpanzee habitat. Given the rate of disturbance across MUE in western Tanzania and the direct result disturbance has on chimpanzees and population-specific cultures (Kühl et al. 2019), a clearer understanding of the relationship between habitat disturbance, resource availability, and chimpanzee abundance is required.

In this study, we compared the availability of chimpanzee plant food and nesting species across four areas within MUE to investigate whether human disturbance levels are associated with chimpanzee plant food species, nesting tree species, and chimpanzee abundance. Following Morgan et al.'s (2018) model of assessing the impact of human activities on great apes and their habitat, we quantified the extent of human disturbance in MUE and related the levels of human disturbance to chimpanzee abundance and resources. We hypothesized first, that chimpanzee plant food species richness, diversity, and abundance, decline

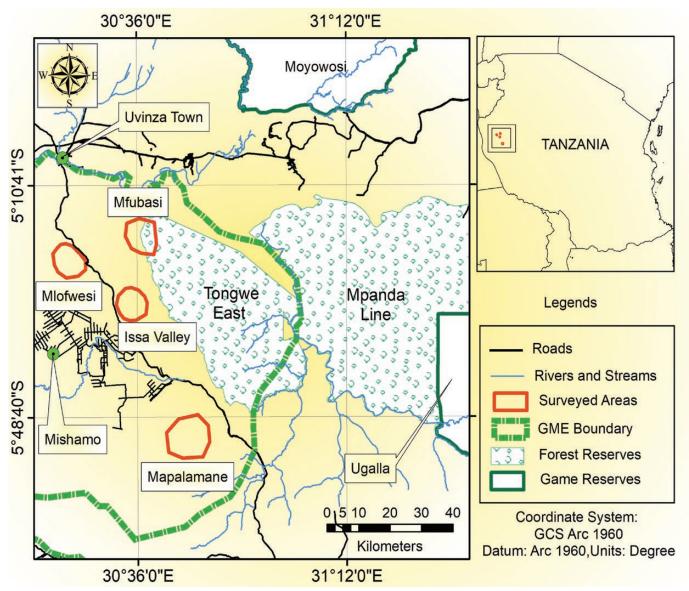


Fig. 1.—Map of the four survey sites located in the Masito-Ugalla Ecosystem, western Tanzania.

Table 1.—Chimpanzee diet data summarized from western Tanzania communities. Indirect and direct refer to observation methods (indirect methods used fecal analyses and food remains; direct methods used observations through focal follows).

Site	Vegetation	Method	# Fecal samples	# Species consumed	Reference
Issa Valley	Open habitat	Indirect	810	69	Piel et al. (2017)
Nguye and Bhukalai	Open habitat	Indirect	465	100	Yoshikawa and Ogawa (2015)
Mahale	Forested	Direct	NA	198	Nishida and Uehara (1983)
Gombe	Forested	Direct	NA	147	Wrangham (1975)

with increasing human disturbance. Second, that chimpanzee abundance—as inferred from nest counts—would be negatively associated with human disturbance: we predicted that nest counts would be high in areas of low or no human disturbance.

MATERIALS AND METHODS

This study was carried out in the MUE at four sites (Issa Valley, Mfubasi, Mlofwesi, and Mapalamane; Fig. 1) during the wet season from February to May, 2019. MUE is a region located

in western Tanzania and forms a part of the Greater Mahale Ecosystem (GME), covering an area of 5,756 km² (Piel et al. 2015a). The region is a biodiversity-rich habitat (Moyer et al. 2006) and is protected partly as the Tongwe Forest Reserves (TFRs). Major threats to the region include agriculture, which represents the main economic income source for people (Mwageni et al. 2015), illegal logging, livestock grazing, bush fires, and poaching (Plumptre et al. 2010; Pintea 2012; Wilfred and MacColl 2014). Wilfred and MacColl (2014) reported on the pattern of illegal natural resource exploitation in

Ugalla, western Tanzania, and found poaching, logging, and bushmeat hunting, to be the dominant illegal activities.

Elevation across MUE ranges from 900 to 1,800 masl, with average annual temperatures from 11°C to 35°C (Piel et al. 2015a) and average annual rainfall between 900 and 1,400 mm, mainly falling between November and April (Piel et al. 2015b). The ecosystem is characterized by five different vegetation types: (1) miombo woodland, dominated by *Brachystegia* spp. and Julbernardia spp., interspersed with (2) seasonally inundated grasslands, (3) rocky outcrops, as well as (4) evergreen riparian and (5) thicket riverine forests (Piel et al. 2017). Open woodland (i.e., more open miombo woodland) is reported as wooded grassland in this study. Issa Valley, Mfubasi, Mlofwesi, and Mapalamane vary in protection status. Issa Valley and Mfubasi are located in Tongwe East Forest Reserve, Mlofwesi is located in Tongwe West Forest Reserve, and Mapalamane is located in Mishamo Village Forest, a lower level protection status from the TFRs, which are District forest reserves. Despite the difference in protection status, all the sites experience anthropogenic activities. Issa Valley has an established long-term research presence, which has been shown to deter some human activities (Piel et al. 2015b). In contrast, Mfubasi, Mlofwesi, and Mapalamane, all have experienced extensive disturbance over the last 10 years (Piel and Stewart 2014).

To survey chimpanzee plant food species, we laid out eight 2-km-long transects radially around a center point established in each study site. We walked approximately 1 km away from the center point before starting transects, covering different vegetation types. In some cases, we walked for more than 1 km until a particular vegetation type was reached. That is, the start point of transects depended on the availability of a particular vegetation type and the direction followed the extension of such vegetation type. Because riparian forests rarely are sited along cardinal directions, we followed these forests regardless of the cardinal direction. Along each transect, we established 10 vegetation plots of 25 m \times 25 m each, with 200 m between plots, summing up to 199,375 m² (0.199 km²) of the total sampled vegetation plot area across survey sites. We did not conduct vegetation plots in cultivated areas. Since most of MUE is miombo woodland with few strips of riparian forest and very few patches of wooded grassland, we used stratified sampling to have sufficient representation of chimpanzee plant food species. The vegetation plots covered wooded grassland, riparian forest, and miombo woodland. A total of 6 (2%) vegetation plots were sampled in wooded grassland, 137 (43%) in riparian forest, and 176 (55%) in miombo woodland. Published literature (Goodall 1968; Wrangham 1975; Nishida and Uehara 1983; Nakamura et al. 2015; Piel et al. 2017) was used to document chimpanzee plant food species (Supplementary Data SD1). In each plot, we documented and counted all known chimpanzee plant food species and determined their growth form and diameter at breast height (DBH).

We inferred chimpanzee abundance from chimpanzee nest presence (Plumptre and Reynolds 1997; Kouakou et al. 2009; Bonnin et al. 2018) and identified nesting tree species. Chimpanzee nests visible along and from transects were

counted and recorded, and we established a 10-m radius around any nest to document nearby nests. Chimpanzee nest number served as a proxy for chimpanzee abundance as our sample size did not warrant further analyses using DISTANCE to calculate population density (Buckland et al. 2001). Using nest counts as a proxy measure for population density has known limitations. For instance, nest age and nest production rate (both of which influence density calculations) can vary by region and season. However, previous work in Tai Forest, Cote d'Ivoire, that tested the reliability of nest counts with known population sizes demonstrated nest counts as an effective method to document wild chimpanzee population sizes and confirmed that the method produced reasonable density estimates (Kouakou et al. 2009).

To quantify anthropogenic disturbance, we documented human activities that interrupted the natural state of chimpanzee habitat. We recorded different human activities based on visible signs along transects and in vegetation plots (Table 2). All signs, e.g., cattle bomas, houses, farms, etc., within 50 m of transects and plots were documented. We used the presence of houses and people to count households. Agricultural activity was determined based on the presence of cultivated fields and areas cleared for cultivation, and the number of different farms based on farm demarcations; visible cattle herds and bomas represented livestock grazing. When more than one sign of different human activities was observed in a single location, e.g., logging on farms, beekeeping on farms, etc., we recorded only the major activities that were presumed to cause the greatest impact on chimpanzee habitat, regardless of the others. In general, we recorded type, frequency, and location, of each event of illegal human activity and assumed that each recorded activity had a different impact on chimpanzee habitat. Based on the presumed impact, we assigned impact scores following Morgan et al. (2018) between 1 (lowest impact) and 5

Table 2.—Human activities recorded across Masito-Ugalla Ecosystem (MUE) with respective weight of destructive impacts (impact score) on chimpanzee habitat. Impact scores of a particular human activity were based on the extent of disturbance the activity is likely to pose on chimpanzee habitat.

Human activities	Signs for identification	Impact score
Agriculture	Cultivated fields	5
	Cleared areas for farming	5
Beekeeping	Commercial beehives	1
	Illegal beehives	2
	Debarking tree for beehives	2
Harvesting medicinal plants	Peeling of tree barks	1
	Digging for tree roots	1
Livestock grazing	Cattle herds	3
	Cattle bomas	4
Logging	Logging sites	4
	Cut logs	2
	Logging stumps	2
Poaching	Snares	1
	Encountered poachers	2
Settlement	Households	4
Small fires	Burnt vegetation	3

(highest impact) to all types of human activities observed across MUE (Table 2).

We computed the frequency of anthropogenic evidence by using encounter rates of the signs per kilometer walked. Following Morgan et al. (2018), we multiplied the weighted impact scores by the frequency of encounters of each sign and then summed an overall measure of severity of disturbance per site. Based on the disturbance measure, we placed survey sites into four categories, i.e., least disturbed, mildly disturbed, moderately disturbed, and highly disturbed sites (Table 3).

We calculated chimpanzee plant food species richness by counting the total number of plant food species in each vegetation plot and then determined Shannon–Wiener diversity indices. We defined chimpanzee plant food abundance as the total number of individual plant species with DBH > 10 cm per site. Based on the hypothesis that chimpanzee plant food species richness, diversity, and abundance, decline with increasing human disturbance, we averaged the values and compared the intersite values across disturbance categories.

To determine if the data were normally distributed, we carried out a Shapiro-Wilk test followed by a Levene's test for homogeneity of variances (Shapiro and Wilk 1965). We used a Kruskal-Wallis test with Dunn's post hoc test to compare the variation of chimpanzee plant food species richness, diversity, and abundance, among and within sites as the data sets were non-normal. We also compared chimpanzee plant food species richness, diversity, and abundance across vegetation types. We converted chimpanzee nest number into nests/km walked in each survey site and related these proportions

Table 3.—Encounter rates of human activities per km walked in each survey site and the severity of disturbance calculated by multiplying the weighted impact scores and the frequency of encounters of each human activity and then summed as an overall measure of severity of human disturbance. The values indicate the rate of encounter of a particular human activity per km walked in different survey sites. Last row on the bottom show severity of disturbance (=Severity).

Severity	Issa Valley	Mfubasi	Mlofwesi	Mapalamane
Cultivated fields	0.00	0.00	0.00	2.00
Cleared areas for farming	0.00	0.00	0.00	0.31
Commercial beehives	0.00	0.00	2.06	0.00
Illegal beehives	0.06	0.81	3.56	0.44
Debarking tree for beehives	0.00	0.06	0.75	0.00
Peeling of tree barks	0.06	0.00	0.06	0.00
Digging for tree roots	0.00	0.00	0.00	0.13
Cattle herds	0.00	0.31	0.13	0.63
Cattle bomas	0.00	0.13	0.06	0.50
Logging sites	0.13	0.31	0.81	0.19
Cut logs	0.00	0.44	0.69	0.00
Logging stumps	0.00	0.25	1.13	0.19
Snares	0.19	0.00	0.38	0.00
Encountered poachers	0.00	0.13	0.00	0.00
Households	0.00	0.00	0.00	2.88
Burnt vegetation	0.31	0.00	0.13	0.00
Severity of disturbance	29	77	294	465
Disturbance category	Least disturbed	Mildly disturbed	Moderately disturbed	Highly disturbed

to disturbance categories. We carried out all statistical analyses in Paleontological Statistics software (PAST Version 3.20—Hammer et al. 2001) and for all statistical tests, statistical significance was set at P = 0.05.

RESULTS

The types and frequency of anthropogenic activities differed across survey sites and disturbance categories (Table 3). At Issa Valley (the least disturbed site), anthropogenic signs were old and we observed no active signs during the survey. In Mfubasi (the mildly disturbed site), we documented recent signs of livestock activities, beekeeping, poaching, and logging. At Mlofwesi (the moderately disturbed site) we found evidence of active logging, poaching signs, livestock grazing, illegal beekeeping, and commercial beekeeping. In Mapalamane (the highly disturbed site), we observed predominantly active agricultural activities, numerous settlements, and livestock activities. Mapalamane was inhabited with people in established settlements and contained cleared land for cultivation of corn (Zea mays), cassava (Manihot esculenta), tobacco (Nicotiana tabacum), cotton (Gossypium sp.), sunflower (Helianthus sp.), beans (Phaseolus vulgaris), and other crops.

Logging and illegal beekeeping were present across all four survey sites in MUE. Logging threatened *Pterocarpus angolensis* and *P. tinctorius* tree species. The latter species is an important food source for chimpanzees (Piel et al. 2017). We observed cut logs of both species in Mfubasi and Mlofwesi sites. We recorded seven locations of already cut logs (range: 1–4 logs) in Mfubasi and 11 locations (range: 1–6 logs) in Mlofwesi. Mlofwesi had a slightly but not significantly higher mean of cut logs 3.1 (3.1, SE = 0.5) than Mfubasi 2.1 (2.1, SE = 0.4; t = 1.049, P = 2.119). Illegal beekeeping threatened *J. globiflora* and *B. speciformis* because local people debark these tree species to make local beehives. These two tree species provide chimpanzees with food (Piel et al. 2017) and are important tree species used in nesting.

We documented a total of 102 potential chimpanzee plant food species that occurred within MUE (Supplementary Data SD1). Of these plant species, most were trees (62%), followed by herbs (12%), shrubs (9%), lianas (8%), climbers (7%), and grasses and palm trees (1% each). Chimpanzee plant food species richness differed significantly among sites with different disturbance levels (H = 55.09, P < 0.001; Fig. 2), with Mlofwesi and Mapalamane exhibiting the highest richness values. These two sites also exhibited higher chimpanzee plant food diversity compared to the other two (H = 36.81, P < 0.001; Fig. 3). Chimpanzee plant food abundance (i.e., trees, shrubs, and liana species with DBH > 10 cm) did not differ significantly across sites (H = 2.477, P = 0.478). Riparian forest exhibited chimpanzee plant food species richness that was nearly twice that of wooded grassland (H = 33.58, P < 0.001; Fig. 4). Chimpanzee plant food diversity did not differ significantly across vegetation types (H = 1.334, P = 0.513); however, chimpanzee plant food abundance (i.e., trees, shrubs, and liana, species with DBH > 10 cm)

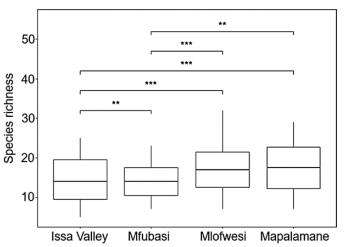


Fig. 2.—Variation in average chimpanzee plant food species richness across the four sites of different disturbance levels in the Masito-Ugalla Ecosystem (MUE). The averages were calculated from vegetation plots (n=80 in Issa Valley, 80 in Mfubasi, 79 in Mlofwesi, and 80 in Mapalamane). Issa Valley = least disturbed site, Mfubasi = mildly disturbed site, Mlofwesi = moderately disturbed site, and Mapalamane = highly disturbed site. The line in the box represents the median and the box the upper and lower quartile, each representing 25% of data scores. Whiskers are variability of data scores outside the upper and lower quartiles, and points represent outliers. **P < 0.01, and ***P < 0.001, based on a Kruskal–Wallis test.

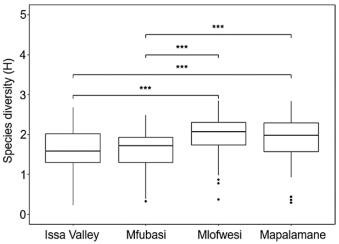


Fig. 3.—Variation in average chimpanzee plant food diversity across the four sites of different disturbance levels in the Masito-Ugalla Ecosystem (MUE). The averages were calculated from vegetation plots (n=80 in Issa Valley, 80 in Mfubasi, 79 in Mlofwesi, and 80 in Mapalamane). Issa Valley = least disturbed site, Mfubasi = mildly disturbed site, Mlofwesi = moderately disturbed site, and Mapalamane = highly disturbed site. The line in the box represents the median and the box the upper and lower quartile, each representing 25% of data scores. Whiskers are variability of data scores outside the upper and lower quartiles, and points represent outliers. ***P < 0.001 based on a Kruskal–Wallis test.

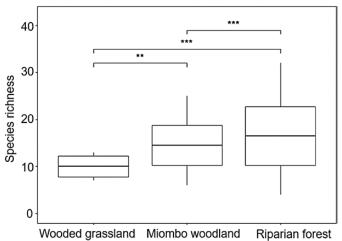


Fig. 4.—Variation in average chimpanzee plant food species richness across vegetation types. The averages were calculated from vegetation plots (n = 6 in wooded grassland, 176 in miombo woodland, and 137 in riparian forest). The line in the box represents the median and the box the upper and lower quartile, each representing 25% of data scores. Whiskers are variability of data scores outside the upper and lower quartiles, and points represent outliers. **P < 0.01, and ***P < 0.001 based on a Kruskal–Wallis test.

was higher in miombo woodland compared to riparian forest and wooded grassland (H = 9.163, P < 0.01).

The encounter rates of the number of chimpanzee nests (i.e., nests/km) differed significantly between sites with different disturbance levels. The least disturbed site had the highest encounter rate of chimpanzee nests (8.5 nests/km); encounter rates declined considerably toward the highly disturbed site (1.5 nests/km). Seventeen different plant species comprised the trees in which all nests were built (Table 4). The abundance of the identified nesting plant species did not vary significantly across sites (H = 0.279, P > 0.964). Brachystegia boehmii and J. unijugata were the most frequently used nesting species.

DISCUSSION

In this study, we compared four sites in the MUE area of western Tanzania to investigate the relationship between anthropogenic disturbance and chimpanzee abundance as well as the availability of chimpanzee plant food species (i.e., species richness, diversity, and abundance) and nesting tree species in each of the sites. In contrast to our hypothesis that chimpanzee plant food species richness, diversity, and abundance decline with increasing human disturbance, our results indicate that chimpanzee plant food species richness and diversity increased with increasing human disturbance, while abundance did not.

Table 4.—Average, minimum, maximum, and the sum as well as relative proportions of number of nests observed per plant species that chimpanzees selected for nesting across all survey sites within Masito-Ugalla Ecosystem.

Nesting plant species	Min	Mean	Max	Sum	%
Albizia adianthifolia	3	3	3	3	1.5
Albizia glaberrima	1	1	1	1	0.5
Brachystegia boehmii	1	7.4	16	67	33
Brachystegia bussei	1	2.3	3	7	3.4
Brachystegia microphylla	1	2	3	6	3
Brachystegia sp.	2	2	2	4	2
Brachystegia speciformis	1	3.7	8	11	5.4
Combretum molle	2	2.7	4	8	3.9
Julbernadia globiflora	1	1.7	2	5	2.5
Julbernadia unijugata	1	2.6	7	49	24
Markhamia obtusifolia	2	2.5	3	5	2.5
Parinari curatellifolia	1	1	1	1	0.5
Pericopsis angolensis	2	2	2	2	1
Psydrax parviflora	2	2	2	2	1
Pterocarpus tinctorius	2	3	4	6	3
Syzygium guineense	1	2.3	3	14	6.9
Uapaca guineensis	1	2	4	12	5.9

However, at the site with the highest level of human disturbance both species richness and diversity declined slightly.

Our results are consistent with the intermediate disturbance theory, which suggests that species richness and diversity may increase with disturbance in a particular habitat (Connell 1978; Wilkinson 1999; Catford et al. 2012), provided that the extent of disturbance is neither too low nor too severe. Moderate disturbance in a particular habitat creates unstable environments of low competitive exclusion between co-occurring species and, therefore, supports high species richness and diversity (Willig and Presley 2018). In contrast, high disturbance interrupts and eliminates many species in plant communities, resulting in plant communities dominated by few tolerant species, a situation that may result in taxonomic homogenization (Lôbo et al. 2011). The intermediate disturbance theory might explain why Mlofwesi, with moderate disturbance, exhibited higher values of chimpanzee plant food species richness and diversity compared to sites of relatively low disturbance such as Issa Valley and Mfubasi. Mfubasi, Mlofwesi, and Mapalamane have all experienced extensive disturbance over the last 10 years (Piel and Stewart 2014) and the latter had the highest occurrence of human activities of severe negative influence (e.g., agriculture and settlement) on chimpanzee habitat, which might have influenced the decline of plant food species richness and diversity. Our results suggest that more individual plant species are lost in areas of severe human disturbance than in areas of low human disturbance. This is in agreement with Köster et al. (2013), who reported that environmental conditions in disturbed habitats do not support a variety of tree species because few tree species have the capacity to establish in these habitats.

Moreover, our results show that human disturbance has not yet had an influence on the abundance of chimpanzee plant food and nesting tree species. This is in contrast to Fuller et al. (1998), who found that human disturbance resulted in changes to forest composition and plant species abundance in New England, United States, which granted was carried out in New

England–Acadian forest habitat, rather than Tropical forest. In the present study, we did not set up vegetation plots in cultivated fields and in areas cleared for farming, as these activities only were observed in one of the four survey sites. However, we observed signs of selective logging, livestock grazing, and unsustainable beekeeping practices in all survey sites. Since livestock grazing has no immediate effect on the abundance of woody plant species (with the exception of cattle bomas, which also were not sampled for vegetation plots), selective logging and debarking of trees for making beehives, resulting in the death of the affected woody plant species, has potentially the largest influence on chimpanzee plant food and nesting tree abundance. Selective logging threatened P. angolensis and P. tinctorius. Illegal beekeeping threatened J. globiflora and B. speciformis because local people around MUE debark these tree species to make local beehives using the bark. However, all these activities often are selective toward certain preferred woody species, and initially do not impact abundance of plant species (Brown and Gurevitch 2004). The selective nature of these activities may explain why the abundance of chimpanzee plant food and nesting tree species did not differ across survey sites with different human disturbance levels.

Furthermore, we found that riparian forests had significantly higher chimpanzee plant food species richness compared to miombo woodlands and wooded grasslands. Sabo et al. (2005) revealed that riparian habitats do not harbor higher number of species, but rather support significantly different species from neighboring upland habitats (i.e., habitats along the sides of a river that are slightly higher in elevation and do not contain surface water). In the case of this study, upland habitats were denoted by miombo woodlands and wooded grasslands. High plant species richness in riparian forests has been considered an indication of high levels of biodiversity (Naiman et al. 1993). An array of plants comprising herbs, grasses, lianas, vines, shrubs, and trees, grow in riparian forests, as was observed in this study. Therefore, riparian forests are of major conservation concern due to the support these habitats provide for a large number of species (Sabo et al. 2005). In addition, these habitats can act as corridors between isolated habitats and play important roles in facilitating movement and migration of animals, providing shelter and maintaining biodiversity (Naiman et al. 1993). Despite the importance and ecological relevance of riparian forests, human encroachment through agricultural activities is an important threat to these habitats in MUE. During this study, we observed people establishing farms along the riverbanks in the highly disturbed survey site (Mapalamane), thereby encroaching and diminishing the quality of these habitats. In this study we were not able to quantify the extent to which these habitats have been reduced or even disappeared; however, future studies that integrate remote sensing easily could calculate reliable estimates (see Hansen et al. 2013). While riparian forests are more threatened by farming activities, miombo woodlands and wooded grasslands are threatened by logging, debarking of trees for local beehives, and livestock activities.

We also hypothesized that chimpanzee abundance is influenced negatively by human disturbance and predicted that nest counts would be high in areas of low or no human disturbance. Our results indicate that as human disturbance levels increase. there is a decrease in chimpanzee abundance despite resources being plentiful and more diverse in moderately disturbed sites. Based on our results, we argue that resource availability is not the only factor driving chimpanzee population size in moderately disturbed sites. Our results can be explained in the context of the deterring effect from human presence and activities. This argument is supported by Garriga et al. (2019), who revealed that in the Moyamba district in southwestern Sierra Leone, the presence and the proximity of humans through roads available in chimpanzee habitats negatively influenced chimpanzee relative abundance and their distribution due to the risks associated with the likelihood of encountering people. Our results also are consistent with those of Bryson-Morrison et al. (2017), who showed that chimpanzees in a human-dominated landscape of Bossou, Guinea, preferred habitat types both with low human presence and abundant food availability. As reported by Bryson-Morrison et al. (2017), Bossou chimpanzees preferred to travel, rest, and socialize in areas with low human-induced pressure. Our results suggest that human disturbance in chimpanzee habitat may affect chimpanzee spatial and temporal distribution, regardless of resource availability, i.e., feeding tree species in our case. However, not all human activities increase chimpanzee vulnerability to anthropogenic disturbance. Some studies suggest that chimpanzees can tolerate human disturbance such as agriculture, settlements, and low levels of hunting (Rist et al. 2009; Brncic et al. 2015). This argument is similar to that of Garriga et al. (2019), who found that at larger spatial scales, settlements and human presence did not influence chimpanzee relative abundance. Yet, at a temporal level, they found that chimpanzees tended to reduce their activity at midday when human activity was more prevalent, indicating a certain degree of temporal divergence.

Although we were not able to assess chimpanzee behavior in relation to human disturbance, we acknowledge that chimpanzees may adjust behaviorally to disturbance. Kühl et al. (2019) argued that human disturbance in chimpanzee habitat not only influences critical resources for chimpanzee survival, but also erodes behavioral diversity. Some anthropogenic features are likely to influence chimpanzee behavioral activities (e.g., feeding, nesting, grouping, etc.) in response to human encounters and pressures exerted in their habitats (Brncic et al. 2015; Bryson-Morrison et al. 2016; McLennan et al. 2017). In support of this argument, Yuh et al. (2019) found that chimpanzees avoid nesting in frequently disturbed areas, similar to what may be occurring in MUE. Although chimpanzees are behaviorally flexible and are able to exploit human-influenced habitats (Hockings et al. 2012, 2015; Bryson-Morrison et al. 2016, 2017), anthropogenic activities, especially those that affect habitat integrity, threaten their survival.

Based on our findings, we encourage conservation planners and researchers to conduct extensive regular surveys to examine changes in chimpanzee critical resources over time in relation to levels of anthropogenic disturbance. Researchers should set up gradient studies of proximity to large settlements to examine thresholds for change in wildlife densities. Furthermore,

additional effort should be employed to survey large areas and collect sufficient data that will allow for DISTANCE sampling rather than just nest counts. This will enable conservation planners to understand the causative relationships (i.e., effects of anthropogenic activities on chimpanzee resources and abundance), and opt for appropriate conservation actions to conserve the MUE, an important habitat for chimpanzees living outside national parks in western Tanzania.

ACKNOWLEDGMENTS

This work was supported by the Greater Mahale Ecosystem Research and Conservation (GMERC) Project. SPM received additional support from the Rufford Foundation (grant no. 27075-1). We thank the Tanzania Wildlife Research Institute (TAWIRI), the Commission for Science and Technology (COSTECH), and Mpanda District Council, for granting permission to conduct this study. We are thankful to field assistants and to the botanist, Yahya Abeid, who helped with identification of plant species. The UCSD/Salk Center for Academic Research and Training in Anthropogeny (CARTA) supports long-term research in the Issa Valley.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online

Supplementary Data SD1.—A list of chimpanzee plant food species documented in the Masito-Ugalla Ecosystem based on direct observations and the compiled diet lists from Issa Valley, Gombe, and Mahale Mountains National Parks (Goodall 1968; Wrangham 1975; Nishida and Uehara 1983; Nakamura et al. 2015; Piel et al. 2017).

LITERATURE CITED

- BALCOMB, S. R., C. A. CHAPMAN, AND R. W. WRANGHAM. 2000. Relationship between chimpanzee (*Pan troglodytes*) density and large, fleshy-fruit tree density: conservation implications. American Journal of Primatology 51:197–203.
- Baldwin, P. J., W. C. McGrew, and E. G. Tutin. 1982. Wideranging chimpanzees at Mt. Assirik, Senegal. International Journal of Primatology 3:367–385.
- Basabose, A. K. 2005. Ranging patterns of chimpanzees in a montane forest of Kahuzi, Democratic Republic of Congo. International Journal of Primatology 26:33–54.
- BASABOSE, A. K., AND J. YAMAGIWA. 2002. Factors affecting nesting site choice in chimpanzees at Tshibati, Kahuzi-Biega National Park: influence of sympatric gorillas. International Journal of Primatology 23:263–282.
- Bonnin, N., C. A. Van Andel, T. J. Kerby, K. A. Piel, L. Pintea, and A. S. Wich. 2018. Assessment of chimpanzee nest detectability in drone-acquired images. Drones 2:17.
- Brncic, T., B. Amarasekaran, A. McKenna, R. Mundry, and H. S. Kühl. 2015. Large mammal diversity and their conservation in the human-dominated land-use mosaic of Sierra Leone. Biodiversity and Conservation 24:2417–2438.
- Brooks, T. M., ET AL. 2002. Habitat loss and extinction in the hotspots of biodiversity. Conservation Biology 16:909–923.

- BROWN, K. A., AND J. GUREVITCH. 2004. Long-term impacts of logging on forest diversity in Madagascar. Proceedings of the National Academy of Sciences of the United States of America 101:6045–6049.
- Bryson-Morrison, N., T. Matsuzawa, and T. Humle. 2016. Chimpanzees in an anthropogenic landscape: examining food resources across habitat types at Bossou, Guinea, West Africa. American Journal of Primatology 78:1237–1249.
- Bryson-Morrison, N., J. Tzanopoulos, T. Matsuzawa, and T. Humle. 2017. Activity and habitat use of chimpanzees (*Pan troglodytes verus*) in the anthropogenic landscape of Bossou, Guinea, West Africa. International Journal of Primatology 38:282–302.
- Buckland, S., D. Anderson, K. Burnham, J. Laake, D. Borchers, and L. Thomas. 2001. Introduction to distance sampling: estimating abundance of biological populations. Oxford University Press. Oxford, United Kingdom.
- Carvalho, J. S., C. F. Meyer, L. Vicente, and T. A. Marques. 2015. Where to nest? Ecological determinants of chimpanzee nest abundance and distribution at the habitat and tree species scale. American Journal of Primatology 77:186–199.
- CATFORD, J. A., ET AL. 2012. The intermediate disturbance hypothesis and plant invasions: implications for species richness and management. Perspectives in Plant Ecology, Evolution and Systematics 14:231–241.
- CAVADA, N., S. TENAN, C. BARELLI, AND F. ROVERO. 2019. Effects of anthropogenic disturbance on primate density at the landscape scale. Conservation Biology 33:873–882.
- CHAPMAN, C. A., AND L. J. CHAPMAN. 2000. Constraints on group size in red colobus and red-tailed guenons: examining the generality of the ecological constraints model. International Journal of Primatology 21:565–585.
- CONNELL, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302–1310.
- DORAN, D. 1997. Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Taï chimpanzees. International Journal of Primatology 18:183–206.
- FAHRIG, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515.
- FOERSTER, S., ET AL. 2018. Feeding habitat quality and behavioral trade-offs in chimpanzees: a case for species distribution models. Behavioral Ecology 27:1004–1016.
- FRUTH, B., N. TAGG, AND F. STEWART. 2018. Sleep and nesting behavior in primates: a review. American Journal of Physical Anthropology 166:499–509.
- FULLER, J. L., D. R. FOSTER, J. S. McLACHLAN, AND N. DRAKE. 1998. Impact of human activity on regional forest composition and dynamics in central New England. Ecosystems 1:76–95.
- GARRIGA, R. M., ET AL. 2019. Factors influencing wild chimpanzee (*Pan troglodytes verus*) relative abundance in an agriculture-swamp matrix outside protected areas. PLoS ONE 14:e0215545.
- GOODALL, J. M. 1962. Nest building behavior in the free ranging chimpanzee. Annals of the New York Academy of Sciences 102:455–467.
- GOODALL, J. 1968. The behaviour of free-living chimpanzees in the Gombe Stream Reserve. Animal Behaviour Monographs 1:161–311.
- HACKEL, J. D. 1999. Community conservation and the future of Africa's wildlife. Conservation Biology 13:726–734.
- Hammer, Ø., D. Harper, and P. Ryan. 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4:1–9.
- Hansen, M. C., et al. 2013. High-resolution global maps of 21st-century forest cover change. Science 342:850–853.
- HANSKI, I. 2011. Habitat loss, the dynamics of biodiversity, and a perspective on conservation. Ambio 40:248–255.

- HERNANDEZ-AGUILAR, R. A. 2009. Chimpanzee nest distribution and site reuse in a dry habitat: implications for early hominin ranging. Journal of Human Evolution 57:350–364.
- HERNANDEZ-AGUILAR, R. A., J. MOORE, AND C. B. STANFORD. 2013. Chimpanzee nesting patterns in savanna habitat: environmental influences and preferences. American Journal of Primatology 75:979–994.
- HERRERA, J. P., P. C. WRIGHT, E. LAUTERBUR, L. RATOVONJANAHARY, AND L. L. TAYLOR. 2011. The effects of habitat disturbance on lemurs at Ranomafana National Park, Madagascar. International Journal of Primatology 32:1091–1108.
- HOCKINGS, K. J., ET AL. 2015. Apes in the Anthropocene: flexibility and survival. Trends in Ecology & Evolution 30:215–222.
- HOCKINGS, K. J., J. R. ANDERSON, AND T. MATSUZAWA. 2012. Socioecological adaptations by chimpanzees, *Pan troglodytes verus*, inhabiting an anthropogenically impacted habitat. Animal Behaviour 83:801–810.
- ITOH, N., AND M. NAKAMURA. 2015. Diet and feeding behaviour. Pp. 227–245 in Mahale chimpanzees: 50 years of research (M. Nakamura, K. Hosaka, N. Itoh, and K. Zamma, eds.). Cambridge University Press. Cambridge, United Kingdom.
- JUNKER, J., ET AL. 2012. Recent decline in suitable environmental conditions for African great apes. Diversity and Distributions 18:1077–1091.
- KÖSTER, N., H. KREFT, J. NIEDER, AND W. BARTHLOTT. 2013. Range size and climatic niche correlate with the vulnerability of epiphytes to human land use in the tropics. Journal of Biogeography 40:963–976.
- KOUAKOU, C. Y., C. BOESCH, AND H. KUEHL. 2009. Estimating chimpanzee population size with nest counts: validating methods in Taï National Park. American Journal of Primatology 71:447–457.
- KÜHL, H. S., ET AL. 2017. The critically endangered western chimpanzee declines by 80%. American Journal of Primatology 79:e22681.
- KÜHL, H. S., ET AL. 2019. Human impact erodes chimpanzee behavioral diversity. Science 363:1453–1455.
- Last, C., and B. Muh. 2013. Effects of human presence on chimpanzee nest location in the Lebialem-Mone Forest land-scape, Southwest Region, Cameroon. Folia Primatologica 84:51–63.
- LEENDERTZ, F. H., ET AL. 2006. Anthrax in Western and Central African great apes. American Journal of Primatology 68:928–933.
- Lôbo, D., T. Leão, F. P. L. Melo, A. M. M. Santos, and M. Tabarelli. 2011. Forest fragmentation drives Atlantic forest of northeastern Brazil to biotic homogenization. Diversity and Distributions 17:287–296.
- McCarthy, M. S., J. D. Lester, and C. B. Stanford. 2017. Chimpanzees (*Pan troglodytes*) flexibly use introduced species for nesting and bark feeding in a human-dominated habitat. International Journal of Primatology 38:321–337.
- McLennan, M. R., N. Spagnoletti, and K. J. Hockings. 2017. The implications of primate behavioral flexibility for sustainable human–primate coexistence in anthropogenic habitats. International Journal of Primatology 38:105–121.
- MOORE, D. L., AND L. VIGILANT. 2013. A population estimate of chimpanzees (*Pan troglodytes schweinfurthii*) in the Ugalla region using standard and spatially explicit genetic capture-recapture methods. American Journal of Primatology 76:335–346.
- MORGAN, D., ET AL. 2018. African apes coexisting with logging: comparing chimpanzee (*Pan troglodytes troglodytes*) and gorilla (*Gorilla gorilla gorilla*) resource needs and responses to forestry activities. Biological Conservation 218:277–286.

- MOYER, D., ET AL. 2006. Surveys of chimpanzees and other biodiversity in Western Tanzania. Report to the US Fish and Wildlife Service. The Jane Goodall Institute, Wildlife Conservation Society, UCSD. http://pages.ucsd.edu/~jmoore/publications/HernandezEtAl2006WCSTanz.pdf. Accessed 23 November 2019.
- MWAGENI, N., R. S. SHEMDOE, AND R. KIUNSI. 2015. Assessment of changes in provision of forest ecosystem goods and services and benefit sharing mechanisms in the Ugalla-Masito Ecosystem: a case of Ilagala and Karago villages in Kigoma Region, Tanzania. International Journal of Biodiversity 7:290–298.
- NAIMAN, R. J., H. DECAMPS, AND M. POLLOCK. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications 3:209–212.
- NAKAMURA, M., ET AL. 2013. Ranging behavior of Mahale chimpanzees: a 16 year study. Primates 54:171–182.
- NAKAMURA, M., K. HOSAKA, N. ITOH, AND K. ZAMMA. 2015. Mahale chimpanzees: 50 years of research. Cambridge University Press. Cambridge, United Kingdom.
- Newton-Fisher, N. E. 1999. The diet of chimpanzees in the Budongo Forest Reserve, Uganda. African Journal of Ecology 37:344–354.
- NISHIDA, T. 1968. The social group of wild chimpanzees in the Mahale Mountains. Primates 9:167–224.
- NISHIDA, T. 2012. Chimpanzees of the lakeshore: natural history and culture at Mahale. Cambridge University Press. Cambridge, United Kingdom.
- NISHIDA, T., AND S. UEHARA. 1983. Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*): long-term record from the Mahale Mountains, Tanzania. African Study Monographs 3:109–138.
- OGAWA, H., M. YOSHIKAWA, AND G. IDANI. 2013. The population and habitat preferences of chimpanzees in non-protected areas of Tanzania. Pan Africa News 20:1–5.
- PIEL, A. K., N. COHEN, S. KAMENYA, S. A. NDIMULIGO, L. PINTEA, AND F. A. STEWART. 2015a. Population status of chimpanzees in the Masito-Ugalla Ecosystem, Tanzania. American Journal of Primatology 77:1027–1035.
- PIEL, A. K., A. LENOEL, C. JOHNSON, AND F. A. STEWART. 2015b. Deterring poaching in western Tanzania: the presence of wildlife researchers. Global Ecology and Conservation 3:188–199.
- PIEL, A. K., AND F. A. STEWART. 2014. Census and conservation status of chimpanzees (*Pan troglodytes schweinfurthii*) across the Greater Mahale Ecosystem. Report submitted to The Nature Conservancy. Washington, D.C.
- PIEL, A. K., P. STRAMPELLI, E. GREATHEAD, R. A. HERNANDEZ-AGUILAR, J. MOORE, AND F. A. STEWART. 2017. The diet of open-habitat chimpanzees (*Pan troglodytes schweinfurthii*) in the Issa Valley, western Tanzania. Journal of Human Evolution 112:57–69.
- PINTEA, L. 2012. Modeling potential conflict between agricultural expansion and biodiversity in the Greater Mahale Ecosystem, Tanzania. Report to Africa Biodiversity Collaborative Group, The Jane Goodall Institute. http://www.abcg.org/action/document/show?document_id=357. Accessed 2 November 2019.
- PLUMPTRE, A. J., ET AL. 2010. Eastern chimpanzee (*Pan troglodytes schweinfurthii*): status survey and conservation action plan 2010–2020. International Union for the Conservation of Nature (IUCN). Gland, Switzerland.
- PLUMPTRE, A. J., AND V. REYNOLDS. 1997. Nesting behavior of chimpanzees: implications for censuses. International Journal of Primatology 18:475–485.

- RANDS, M. R. W., ET AL. 2010. Biodiversity conservation: challenges beyond 2010. Science 329:1298–1303.
- RIST, J., E. J. MILNER-GULLAND, G. COWLISHAW, AND J. M. ROWCLIFFE. 2009. The importance of hunting and habitat in determining the abundance of tropical forest species in Equatorial Guinea. Biotropica 41:700–710.
- ROTHMAN, J. M., A. N. PELL, E. S. DIERENFELD, AND C. M. McCANN. 2006. Plant choice in the construction of night nests by gorillas in the Bwindi Impenetrable National Park, Uganda. American Journal of Primatology 68:361–368.
- SABO, J., ET AL. 2005. Riparian zones increase regional species richness by harboring different, not more, species. Ecology 86:56–62.
- SHAPIRO, S. S., AND M. B. WILK. 1965. An analysis of variance test for normality (complete samples). Biometrika 52:591–611.
- STEVENSON, P. R. 2001. The relationship between fruit production and primate abundance in Neotropical communities. Biological Journal of the Linnean Society 72:161–178.
- STEWART, F. A., A. K. PIEL, AND W. C. McGREW. 2011. Living archaeology: artefacts of specific nest site fidelity in wild chimpanzees. Journal of Human Evolution 61:388–395.
- TAWIRI (TANZANIA WILDLIFE RESEARCH INSTITUTE). 2018. Tanzania chimpanzee conservation action plan 2018–2023. Tanzania Wildlife Research Institute. Arusha, Tanzania. http://tawiri.or.tz/wp-content/uploads/2018/07/Tanzania-Chimpanzee-Conservation-Action-Plan-2018.pdf. Accessed 6 November 2019.
- Watts, D. P., K. B. Potts, J. S. Lwanga, and J. C. Mitani. 2012a. Diet of chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda, 1. Diet composition and diversity. American Journal of Primatology 74:114–129.
- Watts, D. P., K. B. Potts, J. S. Lwanga, and J. C. Mitani. 2012b. Diet of chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo, Kibale National Park, Uganda, 2. Temporal variation and fallback foods. American Journal of Primatology 74:130–144.
- WILFRED, P., AND A. MACCOLL. 2014. The pattern of poaching signs in Ugalla Game Reserve, western Tanzania. African Journal of Ecology 52:543–551.
- WILKINSON, D. M. 1999. The disturbing history of intermediate disturbance. Oikos 84:145–147.
- WILLIG, M. R., AND S. J. PRESLEY. 2018. Biodiversity and disturbance. Pp. 45–51 in The Encyclopedia of the Anthropocene (D. A. Dellasala and M. I. Goldstein, eds.). Elsevier. Amsterdam, The Netherlands.
- Wrangham, R. W. 1975. Behavioural ecology of chimpanzees in Gombe National Park, Tanzania. Ph.D. dissertation, Cambridge University. Cambridge, United Kingdom.
- YOSHIKAWA, M., AND H. OGAWA. 2015. Diet of savanna chimpanzees in the Ugalla Area, Tanzania. African Study Monographs 36:189–209.
- Yoshikawa, M., H. Ogawa, T. Sakamaki, and G. Idani. 2008. Population density of chimpanzees in Tanzania. Pan Africa News 15:17–20.
- Yuh, Y. G., et al. 2019. Effects of land cover change on Great Apes distribution at the Lobéké National Park and its surrounding Forest Management Units, South-East Cameroon. A 13 year time series analysis. Scientific Reports 9:1445.

Submitted 11 March 2020. Accepted 27 July 2020.

Associate Editor was Rafael Reyna.

Do anthropogenic activities impact chimpanzee foraging plant species and nesting tree selection in the Masito-Ugalla ecosystem, Tanzania

TAWRIAT

Simula P. Maijo1,2,3,*, Alex K. Piel4,5, Anna C. Treydte2

¹Tanzania Wildlife Research Institute, Box 661, Arusha, Tanzania ²The Nelson Mandela African Institution of Science and Technology, Box. 447, Tengeru, Arusha, Tanzania. ³Mahale-Gombe Wildlife Research Centre, Box 1053, Kigoma, Tanzania ⁴School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool, United Kingdom ⁵Greater Mahale Ecosystem Research and Conservation, Box 60118, Dar es Salaam, Tanzania *Corresponding author. email: sim



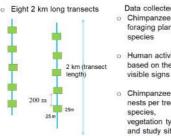
INTRODUCTION

Anthropogenic activities in the Masito-Ugalla ecosystem (MUE) in Western Tanzania include expansion of human settlements and farms and increasing livestock numbers, resulting in human encroachment on chimpanzee habitat. Little is known about chimpanzee foraging plant species available in the MUE and how forage plant species and nesting trees are influenced by human activities. We compared the availability of chimpanzee forage plant species across areas of varying intensities of human disturbances and across different vegetation types. We predicted that chimpanzees prefer nesting in areas of low human disturbances and areas with abundant food resources



Fig. 1: The eastern chimpanzee (Pan troglodytes schweinfurthii) - photo by Camille Giuliano

MATERIAL AND METHODS **Data collection**



- Data collected Chimpanzee foraging plant
- o Human activities based on the visible signs
- nests per tree species. vegetation types and study sites



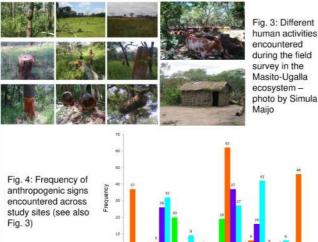
Fig. 2: Sampling sites for chimpanzee foraging plant species and nesting plant species

RESULTS

Anthropogenic signs

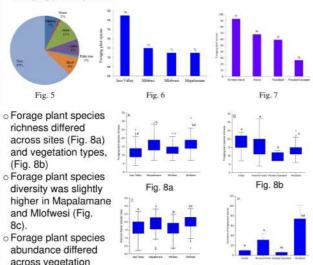
Table 1. Encounter rates of different signs of human activities along eight 2 km long transects laid out in each study site during data collection

Human activities	Issa Valley	Mapalamane	Mfubasi	Mlofwesi
Agriculture	0	2.3	0	0
Beekeeping	0.1	0.3	1.6	2
Fire	1.3	0	0	0.6
Harvesting medicinal plants	0.1	0.1	0	0.1
Livestock grazing	1.2	3.9	2.3	1.7
Logging	0.1	0.9	1	2.6
Posching	0.2	0	0.1	0.4
Settlement	0	2.9	a	0



Chimpanzee foraging plant species

o We identified a total of 102 plant species as preferred chimpanzee foraging plant species



Damage on foraging plant species

types (Fig. 8d)

o Forage species were logged for timber, debarked for beehives, burnt and marked by poachers and livestock keepers

Fig. 8c

- o Pterocarpus angolensis and Pterocarpus tinctorius logging
- o Julbernadia globiflora and Brachystegia speciformis debarking

Chimpanzee nesting tree selection

- o In total, 203 chimpanzee nests were observed across study sites. Issa Valley, the least disturbed site, had higher number of nests compared to sites with high human disturbance levels (Fig. 9a)
- o We found 92 nests (45%) in riverine forests, 85 nests (42%) in miombo woodland, and 26 nests (13%) in forest patches (Fig. 9b).
- o Masito-Ugalla chimpanzees used 17 tree species for nesting, with Brachystegia boehmii and Julbernadia unijugata being highly preferred
- o Considering the proportional cover of different vegetation types in the MUE, riverine forests were significantly preferred for nesting

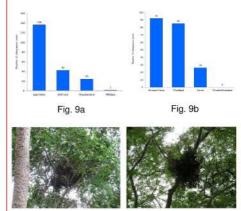


Fig. 10: Chimpanzee nests - photo by Simula Maijo

CONCLUSION

- o Chimpanzees living in open-habitat such as MUE have narrower diets than those of forestdwelling chimpanzees such as in Gombe & Mahale Mountains National Parks
- o Riverine forests and forest patches provide important foraging grounds for chimpanzees, highlighting the chimpanzees' need for diverse vegetation types and landscape heterogeneity
- o An increasing rate of human encroachment in MUE influences habitat destruction and, thus, diminishes habitat suitability
- o The growing trend of human activities threatens the continued existence of the eastern chimpanzee across the MUE
- o We conclude that severely impacted sites and vegetation types from anthropogenic activities are less preferred by chimpanzees than undisturbed areas
- o Areas that contained many foraging plant resources were preferred for nesting

ACKNOWLEDGMENTS



Fig. 8d

