Shared Landscapes: A Biosocial Analysis for Primate Conservation

by

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Abstract

Currently, 66% of primate species are facing threats of extinction, and 74% are experiencing declining populations. Many primate populations inhabit increasingly anthropogenic environments. Therefore, effects such as habitat loss and proximity to humans and human settlements are being studied in an effort to understand the ways in which primates cope with changing environments. As primate-human relationships intensify, understanding the anthropogenic modifications primate habitats are facing, how primates respond to these modifications, and how humans might alleviate or exacerbate anthropogenic effects is a prerequisite to designing and implementing conservation strategies. My research aims to contribute to the conservation of primates and primate habitats by focusing on the interrelatedness of primate-human relationships that emerge in shared landscapes. My study concentrates on two geographically and phylogenetically distant, yet socio-ecologically similar taxa: spider monkeys (genus *Ateles*) and chimpanzees (*Pan troglodytes*). I analyse primatological field studies and integrate literature from historical ecology and ethnoprimatology to present a more nuanced understanding of underlying human social and cultural factors that contribute to anthropogenic modifications in primate habitats. I argue the value of primatological field studies can be enriched by historical, ecological, and ethnographic literature, as these concepts take into account past and present interactions between primates and humans, and the landscapes in which they live. My analysis reveals that spider monkeys and chimpanzees are remarkable in their abilities to adapt to their behaviour to anthropogenic modifications. However, colonial pressures, population growth and density, global demand for forest resources, and the subsequent commercialization these resources, as well as locals' varying and changing perceptions toward primates and primate-inhabited forests can both encourage and inhibit behavioural adaptations.

Key words
Primatology, ethnoprimatology, historical ecology, anthropogenic, landscapes, conservation, spider monkey, chimpanzee

Table of Contents

INTRODUCTION

Topic and Problem

Extinction and regional extirpation are threatening non-human primates (hereafter referred to as primates) worldwide. According to current International Union for Conservation of Nature (IUCN) data, 66% of primate species are facing threats of extinction, and 74% are experiencing declining populations (https://www.iucnredlist.org/). Accordingly, issues of conservation have become the major focus of primatological literature. Many species of primates inhabit increasingly anthropogenic environments (Gonzalez-Zamora et al. 2015; Hockings et al. 2012). Therefore, effects such as habitat loss and proximity to humans and human settlements have been studied in an effort to understand the ways in which primates cope with changing environments. This research is essential because humans have impacted nearly every environment on earth. Therefore, it is increasingly irrelevant to study primates as if they have not been affected by human activity (Fuentes 2012; Maldonado and Waters 2020). Moreover, as human populations increase, and as human settlements expand, primate-human relationship will continue to intensify. Thus, understanding the anthropogenic modifications primate habitats are facing, how primates respond to these modifications, and how humans might alleviate or exacerbate anthropogenic effects is a prerequisite to designing and implementing conservation strategies (Bicca-Marques et al. 2019; Bowie et al. 2021; Campbell 2008; Garcia del Valle et al. 2020; Hickey et al. 2013; Hill and Webber 2010; Hockings et al. 2012; McLennan and Hill 2012; Rimbach et al. 2014).

Research and Argument

My research aims to contribute to the conservation of primates, and primate habitats. Primates and humans have been influencing, sharing, and relying on the same landscapes and resources for millennia (Carey 2009; Fuentes 2012). Therefore, my research focuses on the interrelatedness of primate-human relationships that emerge in shared landscapes. As the overwhelming majority of primates inhabit tropical and subtropical forests, my research is situated within these landscapes (https://www.iucnredlist.org/). Specifically, I am interested in primate behavioural plasticity in anthropogenically modified environments, as well as the historical and social factors contributing to these modifications. I analyse these concepts by concentrating on two geographically and phylogenetically distant, yet socio-ecologically similar taxa: spider monkeys (genus *Ateles*) and chimpanzees (*Pan troglodytes*). I argue that the value of primatological field studies can be enriched by considering historical, ecological, and ethnographic insights, as these perspectives take into account past and present interactions between primates and humans, and the landscapes in which they live. I analyse primatological field studies and integrate concepts from historical ecology and ethnoprimatology to illuminate how historical and social factors contribute to anthropogenic modifications in primate habitats. I illustrate how a more holistic and longitudinal look at issues facing primate conservation can provide new understandings of the anthropogenic modifications occurring in primate habitats. I hope that these novel perspectives generate innovative research questions and areas of study, and ultimately inspire alternative approaches to primate conservation.

My research has been guided by the following questions:

1. How does behavioural plasticity enable spider monkeys and chimpanzees to navigate anthropogenic modifications in their habitats?

2. How do social and historical factors influence local views and treatment toward these primates?
3. How do these perspectives alleviate or exacerbate anthropogenic pressures on primates?
4. How can primates and humans move forward and co-exist in a sustainable (or a mutually beneficial) manner?

Overview

In the first section, I provide the contextual framework in which my analysis takes place. I discuss the biological, ecological, and social importance of primates. I then provide an overview of anthropogenic modifications occurring in primate habitats. This is followed by a brief statement on the language that has influenced my research process, and the intentional language choices I have made throughout my writing. I conclude this section with my rationale for choosing spider monkeys and chimpanzees as model taxa for investigating behavioural plasticity in changing environments.

In the second section, I explain my methodology. I discuss the anthropological sub-fields and concepts that have informed and guided my research. I then describe how I carried out my analysis, and outline the literature that has formed the basis of my study.

In the third section, I present my analytical discussion. Here, I provide brief introductory overviews of spider monkey and chimpanzee phylogeny, behaviour, life history, and conservation status. I then summarize behavioural studies on both taxa inhabiting anthropogenic landscapes. After this, I integrate concepts from historical ecology and ethnoprimatology in an effort to explore the interrelations between primates and humans in shared landscapes. I reflect on how primates and humans use shared landscapes, how they navigate and adapt to each other's presence, and what factors enable or inhibit sustainable co-existence. Moreover, I demonstrate

how the value of primatological field studies can be enriched by applying literature that considers the historical and social interactions between primates and humans.

Finally, I conclude with a brief discussion on the themes that have emerged from my analysis. Here, I highlight the value of a longitudinal and holistic approach to primate conservation and the significance of my research.

Context and Framework

Why Do We Need Primates?

Primates are biologically, ecologically, and culturally significant. As they are our closest living relatives, primates offer valuable insight into our evolutionary history. Human behaviour, cognition, cooperation, sociality, tool use, and communication, as well as numerous other traits, all, to varying degrees, have roots in our primate ancestry. Therefore, studying the behaviour of our non-human relatives has the potential to provide a glimpse into how similar traits evolved in our own species. Additionally, while ethically debatable, primates have furthered medical research regarding various illnesses, as well the evolutionary processes of parasites and pathogens that pose risks to humans (Estrada et al. 2017; Garcia del Valle et al. 2020).

Primates are also crucial to maintaining diverse and sustainable ecosystems. Like all living organisms, primates contribute to environmental biodiversity and promote species richness. Moreover, because the overwhelming majority of primates live in tropical and sub-tropical forests (Dew 2008; Chaves et al. 2011; https://www.iucnredlist.org/), their feeding ecology and geographic distributions are vital for the long-term sustainability of these forests, and for the humans that inhabit them. Primates facilitate forest regeneration by pollinating and dispersing seeds. Their relatively large body sizes compared to other seed dispersers such as

birds, enables primates to ingest and disperse large seeds (Andersen et al. 2018; Chaves et al. 2011; Dew 2008). Notably, primates have been found to disperse the seeds of fruits that humans themselves forage and consume. In effect, primates' feeding ecology promotes forest biodiversity and sustainability, as well as contributes to human livelihoods (Andersen et al. 2018, Estrada et al. 2017; Gonzalez-Zamora et al. 2015, Pinto-Marroquin and Serio-Silva 2020).

Finally, in various societies, primates are culturally significant beings. From family pets which are incorporated into kinship relations to embodiment of both benign and malevolent forest spirits, primates have a rich history in various human cultures. Primates have been used in the telling of creation stories and folklore that have been passed down for generations. Moreover, primates have assisted humans in navigating the shared landscapes. They have served as guides for anticipating weather phenomena, and in hunting expeditions for Indigenous communities (Maldonado and Waters 2020; Pinto-Marroquin and Serio-Silva 2020). Primates are biologically, ecologically and culturally significant animals that contribute to the understanding of our own species, promote diverse and sustainable ecosystems, and enrich human culture.

What do Anthropogenic Modifications Look Like in Primate Habitats?

For the purposes of my study, anthropogenic modifications include both direct and indirect human-induced changes to environments in which primates live. Anthropogenic modifications that directly impact primate livelihoods include legal and illegal trade, as well as hunting. Primates are increasingly threatened by local and global demand. Accordingly, trade is one of the leading activities threatening primates today (https://www.iucnredlist.org/). Primates are removed from their natural habitat to be traded for various reasons, including biomedical research, traditional medicine, zoos, and the pet trade (Estrada et al. 2017). Additionally, hunting primates for bushmeat is a major threat to primate survival (Estrada et al. 2017;

https://www.iucnredlist.org/). However, it is important to note that not all of these anthropogenic modifications represent equally intense threats for primates. For instance, keeping primates as pets ranges from traditional Indigenous practices, wherein pet primates are cherished and incorporated into kinship relations, to global trade networks of exotic and illegal pets (Pinto-Marroquin and Serio-Silva 2020).

Similarly, hunting ranges from traditional and Indigenous subsistence-based practices to global-scale commercialization (Estrada et al. 2017; Garcia del Valle et al. 2020; Pinto-Marroquin and Serio-Silva 2020). Forms of traditional subsistence hunting are generally considered to be more sustainable and of lower intensity, whereas commercialized hunting claims significantly higher numbers of primate casualties (Douglas and Alie 2014; Estrada et al. 2017; Garcia del Valle et al. 2020; Maldonado and Waters 2020). In short, there is great variation in the effects that trade and hunting have on primates. However, such direct modifications to primate livelihoods also occur alongside indirect modifications that affect primate habitats.

Indirect anthropogenic modifications of primate habitats take the form of deforestation and forest degradation. These activities vary in intensity from pre-colonial forms of anthropogenic land management to extreme resource extraction operations, such as mining, oil and gas drilling, logging, and agriculture. Moreover, population growth and human expansion, as well as civil unrest, contribute to the decline in the quality of forests in which primates reside (Estrada et al. 2017). Deforestation and degradation reduce food and resource availability, decrease suitable range, and ultimately eliminate plant and animal biomass (Bolt et al. 2020; McCarthy et al. 2017; McLennan et al. 2020). Additionally, deforestation results in forest fragmentation. This serves to increase forests edges, which further results in poorer habitat

quality, increased tree mortality, and overall forest degradation (Bolt et al. 2020). Unfortunately, both indirect and direct modifications frequently work in conjunction to alter primate-inhabited landscapes.

Resource extraction, human expansion, and civil unrest often exacerbate the primate trade and hunting practices described above. Large-scale resource extraction operations in remote forested areas often increase demand for bushmeat, as humans working and living in these regions rely on it for nourishment (Estrada et al. 2017). Furthermore, worksites require roads for access, which are constructed through forested habitats. This not only results in deforestation and degradation, but enables hunters to more easily access primates in their natural habitats (Estrada et al. 2017). Additionally, civil conflict often intensifies both income and food insecurity. This increases the need for alternative sources of income, such as commercialized bushmeat hunting, and increases demand for bushmeat itself. Moreover, bombs, land mines, and chemical warfare also serve to deforest and degrade primate habitats (Douglas and Alie 2014; Estrada et al. 2017). Evidently, anthropogenic modifications occurring in primate habitats are varied and complex.

Language

As discussed, anthropogenic modifications affecting primates and primate habitats vary greatly in form and intensity. This variation has informed and influenced my research and writing and process, as well as the overall way in which I have come to view anthropogenic modification. My research aims to contribute to the conservation of primates and primate habitats by examining primate behavioural plasticity in response to anthropogenic modifications in its varying forms. As such, I believe it is important to acknowledge and convey this variation in my writing, particularly regarding the language I used to describe anthropogenic activity. Words are

powerful in that they not only communicate information, but they influence *how* one thinks about the information being conveyed (Wolf 1994).

It is not uncommon to see terms, such as 'disturbance', 'human-dominated', 'degradation' throughout conservation literature. While disturbed, human-dominated, and degraded habitats certainly exist, not all modifications are necessarily detrimental to primates, as these terms would imply. My research considers a variety of anthropogenic actions and intensities. Therefore, I have chosen to label anthropogenic activities as 'modifications,' as this term can be thought of, and understood, as a more neutral, and all-encompassing, description of human activity in primate habitats.

Spider Monkeys and Chimpanzees as Model Taxa to Investigate Anthropogenically Modified Habitats

Spider monkeys are neotropical primates found throughout Central and South America, and chimpanzees are found in the equatorial forests of West and Central Africa (Bowie et al. 2021; Campbell 2008; Hickey et al. 2013; Hicks et al. 2013). Though they are distantly related, both taxa exhibit socioecological similarities. Shared characteristics include large multi-male/multi-female communities, male philopatry with female dispersal, a predominantly frugivorous diet, and a high degree of fission-fusion dynamics (Aureli et al. 2008; Di Fiore et al. 2008; Gonzalez-Zamora et al. 2015; Rimbach et al. 2014; Rodrigues 2017).

Social organization plays a vital role in studies analysing behavioural responses to habitat modification. 'Fission-fusion' is used to describe a social system wherein group members 'fission' into smaller subgroups and 'fusion' into larger subgroups according to available resources. It is considered a highly flexible and adaptable, but relatively rare, social system among primates (Aureli et al. 2008; Rimbach et al. 2014). The flexibility of fission-fusion social

dynamics has served as the foundation of research for primates living in, coping with, and adapting to, environmental modifications (Aureli et al. 2008; Campbell 2008).

Within the framework of fission-fusion dynamics, flexible and varied dietary responses to habitat modification have also received considerable attention from researchers. This is the case for spider monkeys and chimpanzees, as they are highly frugivorous primates (Di Fiore et al. 2008; Pinto-Marroquin and Serio-Silva 2020). Compared to more folivorous diets, fruit is more energetically dense; however, it is more spatially and temporally variable, and therefore requires more strategic foraging. Habitat destruction and degradation have been said to reduce fruit availability, thus increasing costs associated with frugivorous diets (Gonzalez-Zamora et al. 2015). The fission-fusion social dynamic is often understood as a response strategy in that it reduces the risk of competition over resources (Bolt et al. 2020; Rimbach et al. 2014). Therefore, fission-fusion social organization may be especially adaptive in environments experiencing a reduction in available food resources (McLennan et al. 2020; Rimbach et al. 2014; Rodrigues 2017). Given their diverse and widespread ranges, flexible social organizations, and highly frugivorous diets, spider monkeys and chimpanzees are highly suited for a comparative analysis on behavioural plasticity in response to habitat modifications. (Campbell 2008; Hockings et al. 2012)

METHODOLOGY

Anthropological Subfields

My study uses existing scholarly publications from three interrelated, but often segregated, subfields of anthropology: primatology, ethnoprimatology, and historical ecology. In its broadest sense, Primatology is the scientific study of human and non-human primates. I am interested in non-human primate behavioural plasticity in anthropogenic environments. Therefore, my

analysis specifically incorporates primatological field studies carried out in wild settings, as this research is crucial to understanding primate behaviour, and in determining how primates respond to anthropogenic modifications in their habitats. Ethnoprimatology is defined as the "theoretically and methodologically interdisciplinary study of the multifarious interactions and interfaces between humans and other primates" (Fuentes 2012, 103). For my analysis, enthnoprimatology provides insight into local views and perceptions towards primates with which humans share land and resources. Historical ecology is defined as the "transdisciplinary research program concerned with the interactions through time between societies and environments and the consequences of these interactions for understanding the formation of contemporary and past cultures and landscapes" (Isendahl 2016, 130). For my study, historical ecology provides a longitudinal lens through which to understand how societies and environments have interacted to shape past and contemporary landscapes wherein primates and humans live sympatrically. Furthermore, I incorporate additional scholarship I deem appropriate and relevant to investigating social and cultural factors pertaining to primates and humans in shared landscapes.

Methods and Approach

My methodological approach is a combination of systematic and exploratory. For my analysis, I specifically selected literature that explicitly identifies as being carried out in anthropogenic habitats. I chose publications that incorporate anthropogenic terms, such as "fragment," "disturbance,", "human-dominated," and "anthropogenic." However, it is important to note that studies which refrain from incorporating anthropogenic terms in their titles have also likely been carried out in anthropogenically modified environments. This is supported by primatological literature which repeatedly states that it is increasingly impossible to carry out field studies on

primates that have not been affected by anthropogenic activity (Fuentes 2012; Isendahl 2016). Nevertheless, my study reviews the following publications:

- "Behavioral and Physiological Responses to Fruit Availability of Spider Monkeys Ranging in a Small Forest Fragment" by Rimbach et al. (2014).
- "Female Spider Monkeys (Ateles geoffroyi) Cope with Anthropogenic Disturbance Through Fission-Fusion Dynamics" by Rodrigues (2017).
- "Forest fragments become farmland: Dietary Response of wild chimpanzees (*Pan troglodytes*) to fast-changing anthropogenic landscapes" by McLennan et al. (2020).
- "Chimpanzees (*Pan troglodytes*) flexibly use introduced species for nesting and bark feeding in a human-dominated habitat" by McCarthy et al. (2017).

For each publication, I review and evaluate the duration of the study, how the data were collected, habitat or range size, as well as how anthropogenic modifications are established and presented. I systematically analyse similarities and differences between studies to draw out salient points. With these points, I then employ an exploratory approach wherein I integrate ethnoprimatology and historical ecology literature to present a more nuanced understanding of underlying human social and cultural factors that contribute to anthropogenic modifications in primate habitats.

ANALYTICAL DISCUSSION

What are Spider Monkeys?

Spider monkeys are wide-ranging neotropical primates found from Mexico to Bolivia. Spider monkeys are members of the genus *Ateles* (Collins 2008; Di Fiore et al. 2008). While taxonomy and phylogenies have been debated and revised on several occasions, most recent molecular data

supports seven distinct species: *Ateles geoffroyi; Ateles belzebuth; Ateles paniscus*; *Ateles hybridus*; *Ateles marginatus*; *Ateles fusciceps*; and *Ateles Chamek.* Depending on the publication, there are up to 16 additional subspecies (Morales-Jimenez et al. 2015; https://www.iucnredlist.org/). Spider monkeys are easily recognizable by their long limbs, acrobatic abilities and charismatic disposition. Labelled "ripe fruit specialists," spider monkeys prefer high canopy rainforests with high fruit abundance. Their prehensile tail functions as a fifth limb while they swing through trees. Additionally, their reduced, or vestigial thumb, and elongated phalanges enables spider monkeys to travel through the canopy more efficiently (Di Fiore et al. 2008). Spider monkeys' large body size, lengthy gestation periods, high levels of post-natal parental care, and long interbirth intervals make them especially vulnerable to extinction and regional extirpation (Campbell and Gibson 2008; Dew 2008). Sadly, spider monkeys are one the most endangered genera of primates. The most recent IUCN data states that six out of seven species of spider monkeys are endangered or critically endangered, and that all seven species have declining populations (Dew 2008; https://www.iucnredlist.org/)

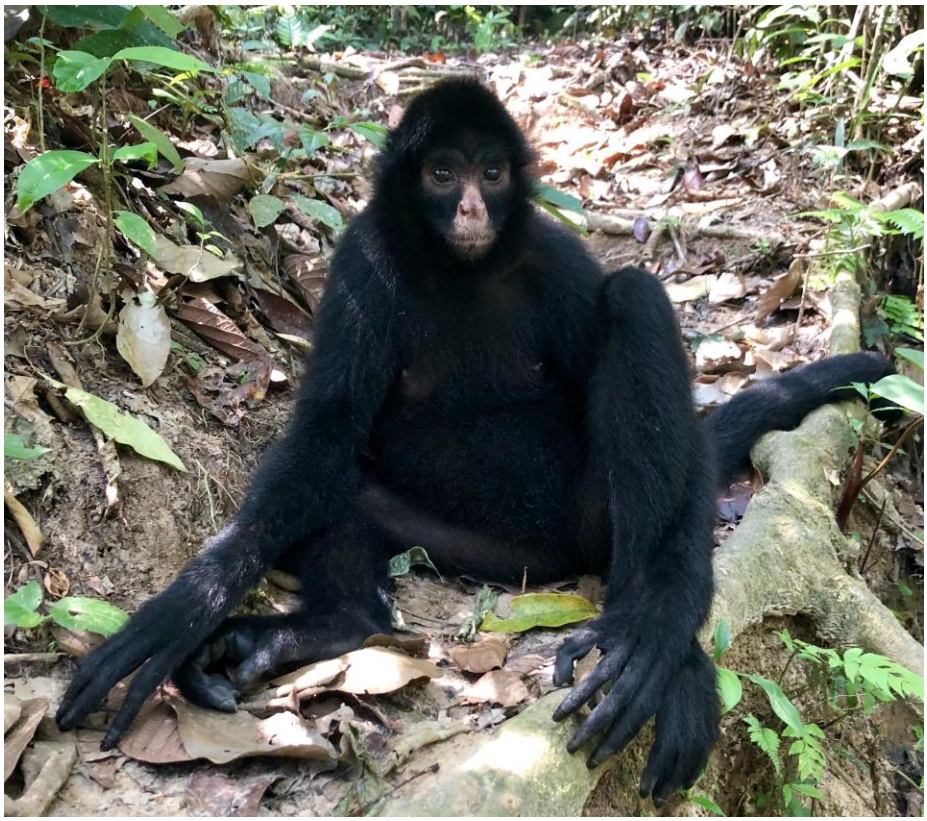

Figure 1. Image of a spider monkey (*Ateles chamek*) named Micaela exhibiting atypical terrestrial behaviour as a result of the illegal pet trade. That Micaela can live a free, but provisioned, lifestyle after living several years inside a small urban household exemplifies behavioural plasticity and adaptation to anthropogenic modifications. Note the characteristically long limbs, elongated phalanges, and prehensile tail. Photo by Lindsey Warshawski.

Biosocial Analysis of Spider Monkeys Inhabiting Anthropogenically Modified Habitats

A study carried out by Rodrigues (2017) on a population of spider monkeys in a small fragment in Costa Rica looked at females' responses to anthropogenically modified habitats. Rodrigues (2017) examined subgroup size, fecal glucocorticoid metabolites as an indicator for stress levels, activity budgets, diet composition, as well as fruit availability as factors contributing to fission-fusion. In terms of diet, five species of fruit made up nearly 90% of these spider monkeys' diet, with Pílon (*Hyeronima* spp.) comprising 38.2%. The study found that subgroup size was significantly smaller during periods of low fruit availability, and larger during periods of fruit abundance. Analyses also concluded that fruit abundance had no effect on glucocorticoid levels.

These results support the hypothesis that spider monkeys reduce the size of their foraging group in response to reduced resources, which may, in turn, mitigate physiological stress signals. These behavioural responses may be viewed as a strategy adopted to minimize the risk of intra-group confrontations over resources, and to cope with habitat modifications.

Conversely, a similar study looking at two populations of spider monkeys ranging in a small forest fragment in Colombia found varied results. Like Rodrigues (2017), Rimbach et al. (2014) collected data on subgroup size, fecal glucocorticoid metabolites, feeding behaviour, and fruit availability. However, Rimbach et al. (2014) found smaller subgroups and higher glucocorticoid levels during periods of high fruit availability. Unlike Rodrigues (2017), Rimbach et al. (2014) also collected data on aggression between individuals, and found that aggression rates were higher during periods of high fruit availability. These results do not conform to the typical fission-fusion grouping patterns, and the authors suggest that this study group may be less effective at mitigating variation in available resources.

While both Rodrigues (2017) and Rimbach et al. (2014) collected their data over relatively long periods of time, 15 months and 22 months respectively, the study locations varied in several ways. Rodrigues' (2017) study was carried out in a comparatively large area of 1000 hectares, with two spider monkey groups ranging within the area. The study group ranged in the lower half, but the size of their range is never quantified. In comparison, the size of Rimbach et al.'s (2014) study site was 65 hectares, and also contained two groups of spider monkeys. Even without detailed quantification of individual group's range size, the fragment studied by Rodrigues (2017) in Costa Rica is substantially larger than that of Rimbach et al.'s (2014). Additional differences include high seasonal variation and a high prevalence of primate-hunting at Rimbach et al.'s (2014) study site, whereas Rodrigues' (2017) site in Costa Rica is

characterized by low seasonality with few natural, and no human, predators. Rodrigues (2017) classifies the study fragment as anthropogenically modified based on the presence of roads and resource extraction, crop-foraging, and fluctuating researcher and tourist presence. Conversely, Rimbach et al. (2014) provide no comparable data; however, the stark contrast in fragment size between the two study sites remains noteworthy. Varied results between these studies, which were carried out in different regions, illustrate the adaptive nature of primate behavioural plasticity. However, this variation also highlights the need to explore additional factors that influence habitat modification, which in turn may affect primate behavioural responses.

One notable difference between these studies, and possible limitation is that Rodrigues' (2017) examined only female responses to anthropogenically modified habitats. Excluding males from the analysis limits the amount of data collected and may restrict the applicability of the results; however, there is value in focusing on female's behaviour. Socio-ecological theory posits that females distribute themselves according to available resources and that males arrange themselves according to reproductive females. Moreover, reproduction in sexually reproducing species is limited by females. While males are anatomically able to sire a near-unlimited amount of offspring, they are limited by females' reproductive ability to gestate and nurse a limited number of offspring (Dammhahn & Kappler 2009). Thus, because male behaviour is closely tied to female behaviour and reproduction, conservation approaches may be able to understand, and therefore contribute to, species survival by paying particular attention to female behaviour and distribution. This in turn affects successful reproduction, along with population growth and sustainability.

While both Rodrigues' (2017) and Rimbach et al.'s (2014) study sites vary considerably in size, 1000 and 65, respectively, both sites are characterized as "fragmented.". Rodrigues

(2017) bases this characterization according to an anthropogenic classification system put forth by McKinney (2015), whereas Rimbach et al. (2014) provide no such classification. However, given the sizeable difference between the sizes of both study sites, it is not unreasonable to describe a 65-hectare site as fragmented, when a 1000-hectare site is also described as fragmented based on an established classification system. However, neither study provides a benchmark for what these landscapes were like before their current fragmentary states. An exploration of local ecological history can illuminate social and environmental changes through time that have contributed to the anthropogenic modification of these landscapes.

Historical Ecology of Anthropogenic Modifications in Spider Monkey Habitats

A significant finding from Rodrigues (2017) is that Pílon (*Hyeronima* spp.) was the most commonly consumed fruit for this study group, as it made up 38.2% of these spider monkeys' diet. Rodrigues (2017) describes the study site as a secondary, disturbed mosaic forest, made up of harvestable monocultures, including species of *Hyeronima*, which are locally known as Pílon. While native from Mexico to Argentina, Pílon is an anthropogenically introduced monoculture to this region of Costa Rica (Redondo-Brenes 2007; Rodrigues 2017). High growth rates, and the ability to grow in degraded soil, has rendered Pílon one of the most common trees used for forest regeneration in Costa Rica (Gonzalez and Fisher 1994; Moulaert et al. 2002). In the early 20th century, Costa Rica experienced a rapid increase in deforestation. From 1940 to 1990, forested landscape declined from 75% to 29% (Nygren 1995). This intense anthropogenic activity was the result of global, largely U.S, demand for tropical hardwoods, beef, as well as cash crops, such as coffee and sugarcane (Carey 2009; Nygren 1995). However, in the 1980s Costa Rica introduced extensive reforestation programs. Initially, exotic species, such as *Eucalyptus* spp., were planted. However, as the benefits of using native trees, such as Pílon (*Hyeronima* spp.), came to light,

these soon became favoured, and were widely planted across Costa Rica (Gonzalez and Fisher 1994; Moulaert et al. 2002; Redondo-Brenes 2007). As Rodrigues' (2017) study reveals, Pílon plantations are a crucial component of spider monkey ecology.

The rapid deforestation that led to widespread planting of Pílon was likely detrimental to spider monkey populations, as these primates are largely understood to require large areas of primary canopy forest (Collins 2008). However, that spider monkeys persist in this region today suggests they are capable of adapting to certain levels of anthropogenic modification. That Pílon is a canopy tree and produces edible fruits, makes this tree species particularly suited for spider monkey habitats (Gonzalez and Fisher 1994; Moulaert et al. 2002, Redondo-Brenes 2007). The choice to use Pílon for forest regeneration projects likely increased this group of spider monkeys' ability to adapt to these particular anthropogenic modifications. However, at the same time, this highlights the notion that different organisms have different ecological needs. A species of tree that is well-suited for one taxa, may not be as well-suited for another. Therefore, this illustrates the need for a holistic understanding of how anthropogenic modifications occur, and how they affect various organisms when designing conservation strategies.

In addition to the relatively recent 20th-century economic demand for foreign goods, colonial, and pre-colonial anthropogenic activities have also shaped landscapes over time. Humans have a long history of inhabiting neotropical environments. The arrival of European colonizers in 1492 is often portrayed as the beginning of significant anthropogenic modification throughout the Americas (Carey 2009; Stahl 2009; Stahl 2015). In particular, the Amazon rainforest is frequently perceived to have been a pristine, untouched, 'natural' landscape until this time. However, emerging research regarding neotropical historical ecology and archaeology supports extensive pre-Columbian agriculture, human migration, and the introduction of species,

including primates, into new environments (Carey 2009; Isendahl 2016; Stahl 2009; Stahl 2015). Pre-colonial Indigenous populations engaged in sophisticated land management and domestication practices to encourage productivity. While these practices varied in complexity, they undoubtedly influenced and shaped present-day landscapes, and the behavioral strategies of primates that inhabit them. However, the arrival of European colonizers likely intensified anthropogenic modifications throughout the neotropics. An exploration of ethnoprimatological literature can illuminate how views and treatment toward primates have evolved over time, and how they have ultimately influenced anthropogenic modifications in primate habitats.

Ethnoprimatology of Anthropogenic Modifications in Spider Monkey Habitats

Regarding the anthropogenic modifications occurring at both Rodrigues' (2017) and Rimbach et al.'s (2014) study sites, one important difference between the two is the prevalence of primate-hunting pressures at Rimbach et al.'s (2014) site in Colombia. Indigenous peoples have relied on bushmeat, including that of primates, for millennia. However, relatively recent historical events have rendered traditional subsistence practices in some regions unsustainable.

Ethnoprimatological research in the Colombian Amazon by Maldonado and Waters (2020) found that Indigenous sedentarism played a significant part in the depletion of local wildlife. As colonialism has corralled formerly nomadic Indigenous peoples into small restricted settlements, their hunting grounds have also been reduced. While some Indigenous populations have historically targeted spider monkeys for bushmeat due to their large size, and preference as pets, the relatively recent restrictions in hunting territory are driving regional extirpation of them and other species of primates. Moreover, sedentary lifestyles and the consequent narrowing of geographic locations from where resources are obtained, is detrimental to the humans who share landscapes with primates (Maldonado and Waters 2020). For example, Indigenous groups in

Ecuador had to re-locate entire villages due to the depletion of large game species. Additionally, meat scarcity in Brazil and Venezuela lead to sociopolitical issues and intra-village conflict, and ultimately resulted in communities fissioning and relocating. This suggests that euro-centric colonial oppression which forced Indigenous peoples to abandon traditional subsistence practices have resulted in the over-exploitation of forest resources, and are underlying factors threatening primate extinction.

At the same time, ethnoprimatological research regarding perceptions and uses of primates reveals that hunting and consuming primate meat varies by region, and between communities (Maldonado and Waters 2020; Pinto-Marroquin and Serio-Silva 2020). Some societies throughout Central and South America continue to rank spider monkeys amongst the most nutritional, and economically valuable, primates. Accordingly, certain Indigenous communities continue to hunt and eat primates as a primary form of subsistence. Additionally, in some circumstances, spider monkey meat is a sought-after commodity that is served in modern restaurants (Pinto-Marroquin and Serio-Silva 2020). In contrast, some Indigenous communities abstain from hunting and eating primates for various reasons. Ethnoprimatological research by Maldonado and Waters (2020) reveals how traditional taboos against consuming primates contribute to species survival. The Tikuna Indigenous peoples of Colombia hold beliefs that certain animals represent either gentle or malevolent spirits and should therefore never be hunted (Maldonado and Waters 2020). In contrast, Indigenous peoples inhabiting Amazonian regions of Venezuela and Brazil regularly consume spider monkeys, as their cosmology dictates that these animals are there for their consumption (Urquiza-Haas et al. 2020). Additionally, community restrictions are imposed against the hunting of various species of primates due to physical and behavioural similarities to humans, and because of primates' roles as seed dispersers and

contributors to forest regeneration. Notably, some Indigenous communities are aware of the declining populations of spider monkeys in particular and have therefore imposed hunting restriction as a result (Maldonado and Waters 2020; Pinto-Marroquin and Serio-Silva 2020). Overall, ethnoprimatological research details the variation in attitudes and perspectives humans have towards hunting and consuming primates. This research underscores the importance of consulting with local Indigenous peoples' regarding hunting traditions and practices when designing conservation approaches.

Hunting not only directly jeopardizes individual and species survival, but it often works in conjunction with the legal and illegal pet trade. Ethnoprimatological research reveals that spider monkeys are one of the most common taxa targeted for the pet trade (Duarte-Quiroga and Estrada 2003; Pinto-Marroquin & Serio-Silva 2020). Among Indigenous Popoluca peoples in Mexico, spider monkeys were once the preferred primate pet, as they are considered easy to tame and to care for. However, since exotic pets were made illegal, the majority of Popoluca peoples no longer keep primates as pets (Pinto-Marroquin and Serio-Silva 2020). Conversely, large urban centers continue to fuel the demand for illegal pets, and threaten spider monkey populations. Ethnographic research by Duarte-Quiroga and Estrada (2003) surveyed 179 households with pet primates in Mexico City. While 12 species were recorded, 67% of pets were spider monkeys. Empathy for primates was the primary reason owners sought pet primates. Most owners attempted to provide their pet primates with loving care, and treated them as if they were members of the family. However, captive spider monkeys are often plagued with respiratory and intestinal illnesses from inadequate housing and diet. Additionally, many pet primates are subject to household accidents, such as poison or alcohol ingestion, and stove or electrical burns. Duarte-Quiroga and Estrada's (2003) research suggests that potential primate-pet owners' empathy can

be the target of education regarding the detrimental effects of primate ownership. Educating potential owners on the dangers that urban households pose to primates may serve to reduce the demand for pet primates.

Not only are pet primates removed from their communities and habitat, but mothers are often killed for bushmeat, and juveniles are kept to be sold into the illegal pet trade. Therefore, the pet trade also disproportionally targets reproductive females, which are critical for sustaining primate populations and species' survival. While certain Indigenous populations throughout the neotropics undoubtedly keep pet primates, the comparatively large populations of city centers, urban demand for pet primates, and the fact that many primates die during transit to city markets, continue to threaten primate populations (Duarte-Quiroga and Estrada 2003; Maldonado and Waters 2020; Pinto-Marroquin and Serio-Silva 2020).

Rodrigues (2017) and Rimbach et al. (2014) have demonstrated that spider monkeys are able to adapt their feeding ecology and ranging behaviours to persist in small anthropogenically modified forest fragments. My research has built on these findings by integrating literature from historical ecology and ethnoprimatology. Spider monkeys, among other fauna, likely experienced negative effects from extreme deforestation resulting from global demand for forest land and resources. However, reforestation initiatives using Pílon (*Hyeronima* spp.) have provided anthropogenic food sources for these primates. Additionally, the colonial process which resulted in the intensification of land management combined with the conversion from nomadic to sedentary lifestyles for Indigenous peoples have depleted forest resources and contributed to regional extirpation of local primates. However, Indigenous awareness of declining populations of spider monkeys likely alleviates some pressures from these anthropogenic modifications. However, urban demand for pet spider monkeys also threatens populations by particularly

targeting reproductive females. Despite the pressures this demand places on primate populations, there is an opportunity to educate potential owners on the dangers and detrimental effects that primate ownership has on individual primates, and on wild populations. With this, my research illustrates how analysing historical and social factors can contribute to primate conservation.

What are Chimpanzees?

Chimpanzees have a wide and diverse geographic range. Across Equatorial Africa, chimpanzees inhabit forests and mosaic savannah-woodland environments (Kalan et al. 2020). Taxonomically, all chimpanzees belong to *Pan troglodytes*, though various sub-species have been debated. Chimpanzees are not monkeys, but are one of four species of apes. Moreover, they are our closest living relatives. Humans' close evolutionary relationship with chimpanzees has served as the foundation of decades of research regarding their biology, behaviour, and ecology. Chimpanzees are renowned for their cognitive abilities, including extensive and culturally variable tool-use behaviours, including algae and termite fishing, accumulative stone-throwing, and water dipping (Boesch et al. 2020). However, chimpanzees exhibit slow life histories. Their relatively large body size, long gestation periods, high levels of parental care, and lengthy interbirth intervals have rendered them extremely vulnerable to extinction and regional extirpation. Accordingly, the most recent IUCN data lists *Pan troglodytes* as endangered (https://www.iucnredlist.org/).

Figure 2. Image of two chimpanzees (*Pan troglodytes*) feeding on anthropogenically introduced jackfruit in the fragmented forests between Budongo and Bugoma forest reserves in Western Uganda. That these chimpanzees have incorporated non-native fruit into their diets exemplifies behavioural plasticity and adaptation to anthropogenic modifications. Photo from by McLennan et al. (2019:Pg 10)

Biosocial Analysis of Chimpanzees Inhabiting Anthropogenically Modified Habitats

A study on Bulindi chimpanzees inhabiting fragmented forest between Budongo and Bugoma forest reserves in Western Uganda by McLennan et al. (2019) looked at changes in feeding ecology in relation to rapid deforestation. The authors compared diet and fragment size between two study periods. The study concluded that forest fragment size, and thus suitable chimpanzee habitat, were drastically reduced by 80% between the two study periods. Reduced diet diversity and overall fruit consumption were also shown; however, there was an increase in cultivated fruit consumption. The authors suggest that the increase in consumption of agricultural fruits is a response to deforestation of the chimpanzee's habitat as an extensive amount of fruiting trees

were cleared from habitat fragments. Therefore, the fruits that chimpanzees relied on for sustenance were no longer available.

In order to study change in diet and fragment size over time in these study populations, McLennan et al. (2019) carried out and compared two longitudinal studies. The first study period took place over 19 months from June 2006 to January 2008. The second study period took place over 21 months from January 2014 to December 2015. The study community's documented home range spanned 21 km^2 and was deemed anthropogenically modified based on the absence of continuous forest and the presence of forest fragments, agricultural fields, villages, roads, and trading centers. Anthropogenic modifications were further established as deforestation between study periods was systematically quantified based on tracking and mapping of chimpanzee ranging habits using handheld GPS. During the first study period, six fragments ranging from 14 to 50 hectares were identified as main forest fragments. McLennan et al. (2019) surveyed these fragments again during the second study period and found that total fragment hectares decreased from 121.6 to 26.0 hectares between study periods. In effect, these Bulindi chimpanzees lost 78.6% of their forest habitat in a period of seven to eight years. The extent of anthropogenic modification in this region served as a foundation to investigate changes in local chimpanzee's dietary ecology.

Fecal analyses, food traces, and direct feeding observations were used to look at dietary changes between study periods one and two. During the first study period, McLennan et al. (2019) collected fecal samples continuously over a 13-month period. In total, 1436 samples were analysed. Conversely, during the second study period, fecal samples were not collected continuously, but were taken from January to April 2014, September to November 2014, March to June 2015, and October to December 2015. From study period one to two, there was a decline

in the amount of fruit present in chimpanzee feces, which suggests chimpanzees ate more non-fruit foods, such as foliage and piths, after the extensive deforestation. During the first study period, figs (*Ficus* spp.) were the most commonly eaten fruit; however, consumption of this dietary staple declined by nearly half in the second study period. This coincided with an overall decline in diet diversity, but with an increase in the presence of cultivated fruits found in chimpanzee feces. Most notably, cultivated jackfruit which was not identified in fecal samples from the first study period, became an obvious dietary staple in the second study period. In addition to fecal analysis, trace foods and direct feeding observations were used to supplement fecal data. Because the chimpanzees were not habituated during the first study, these data were not statistically analysed. Nevertheless, these data provide insight into changes in feeding behaviour across study periods.

Perhaps the greatest strength of McLennan et al.'s (2019) study is that it established a baseline to study and quantify deforestation and dietary changes over time for this community of chimpanzees. Importantly, the data are comparable as the study looked at the same community of chimpanzees and used identical methods to survey forest clearance and to analyse fecal samples for two study periods seven years apart. Despite the chimpanzees being habituated by the second study period, the authors retained fecal sampling as their primary form of data collection for both studies. This approach was most plausible given that direct feeding behaviour observations were comparably minimal prior to habituation. With this longitudinal and comparable data, the authors effectively establish what they term 'rapid deforestation' in this region, which enables them to explore how this community of chimpanzees altered their feeding ecology in response to these conditions.

Research by McCarthy et al. (2017) also looked at chimpanzees inhabiting fragmented forest between Budongo and Bugoma forest reserves in Western Uganda. The study looked at chimpanzee feeding ecology and nesting behaviour in response to fragmented and anthropogenic forest habitats. McCarthy et al. (2017) systematically collected data on nesting behaviour, and opportunistically on feeding habits. Nest locations were surveyed and mapped using GPS. Researchers recorded the species of tree in which the nests resided, the general habitat type, and the type of nest (i.e. ground, composite, reused). The study found evidence of widespread nesting in non-native tree species. The chimpanzees regularly nested in eucalyptus, guava, cocoa, and Caribbean pine trees. Evidence of ground nests, nest reuse, and composite nest construction was also found. The study also reports novel evidence of chimpanzees feeding on eucalyptus bark. The authors suggest these behaviours may result from a lack of suitable trees in their anthropogenically modified habitat.

Both McLennan et al. (2019) and McCarthy et al. (2017) carried out their studies in the same unprotected and fragmented forest area between the Budongo and Bugoma forest reserves in Western Uganda. The study region is relatively small, as McCarthy et al. (2017) state that the fragmented forest between these two reserves is approximately 40 km by 30 km. McLennan et al. (2019) systematically quantify the range of their study community as declining from 121.6 to 26.0 hectares. McCarthy et al. (2017) reference a 2013 study by Hansen et al., and state a range of 643 hectares for two populations of chimpanzees on which they collected data. Though the range for McCarthy et al.'s (2017) study is for two chimpanzee communities, the difference in range(s) size between the two studies is considerable.

While both McLennan et al.'s (2019) and McCarthy et al.'s (2017) studies share certain similarities, they differ in several respects. McLennan et al. (2019) and McCarthy et al. (2017)

both refer to population density, more than 150 persons per km^2 and 113.3 per km^2 respectively, to convey anthropogenic activity. McCarthy et al. (2017) also point out that the population growth rate in Uganda sits at 3.8%, which globally, is one of the highest. McLennan et al. (2019) established a benchmark for the deforestation that their study community endured over a seven- to eight-year period, whereas, McCarthy et al. (2017) established anthropogenic modifications by providing Ugandan and United Nations census statistics for human subsistence and commercial agricultural practices, reliance on fuelwood, and forest coverage decline from 1990 to 2010. An additional difference between the two studies is the length of the data collection periods. McCarthy et al. (2017) collected data for 12 months, while McLennan et al. (2019) collected data over 19 months for the first study period, and 21 months for the second. However, both data collection periods encompass seasonal changes in vegetation that occur throughout the year in this region (McLennan et al. 2019).

McLennan et al.'s (2019) study essentially carried out two identical studies seven years apart to establish a benchmark for anthropogenic modification, which is a significant advantage of their study. However, considering the close geographic proximity and similar population densities, it is not unreasonable to extend similar rates of anthropogenic modifications to the area in which McCarthy et al. (2017) carried out their study. Combined, these studies effectively explore behavioural plasticity regarding feeding, ranging, and nesting behaviours of chimpanzees, and provide valuable insight into how chimpanzees respond to anthropogenically introduced flora. Together, they suggest that chimpanzees inhabiting fragmented forests in Western Uganda have adapted their feeding ecology and nesting behaviour to anthropogenic activity. However, the value of these studies can be enriched with an exploration of causal factors surrounding these anthropogenic modifications.

Historical Ecology of Anthropogenic Modifications in Chimpanzee Habitats

Both studies are carried out in the same, relatively small, area; however, one striking aspect of McCarthy et al.'s (2017) study that is not discussed by McLennan et al. (2019) is the presence of eucalyptus plantations throughout the region. While these chimpanzees were seemingly able to adapt to introduced eucalyptus trees, the prevalence of these plantations merits further consideration. An exploration of social and historical factors surrounding these plantations can offer a more nuanced understanding of the anthropogenic modifications occurring in Western Uganda.

Eucalyptus (*Eucalyptus* spp.), though primarily native to Australia, and to a lesser extent New Guinea, the Philippines, and Indonesia, is the most widely planted tree genus across the world today. This is largely due to the fact that Eucalyptus trees exhibit high growth rates, and are generally adaptable to varied soil and climate conditions (Bayle 2019; Turnbull 1999). Fuelwood is the primary source of energy for developing countries across Africa, Latin America, and Asia. Given that it is fast-growing and relatively easy to manage, Eucalyptus trees are often viewed as the solution to ever-increasing fuelwood demands across developing tropical and sub-tropical regions. Eucalyptus trees are planted and used for fuelwood in place of indigenous species, thus preserving natural forests (Bayle 2019; Sassen et al. 2015; Specht et al 2015, Turnbull 1999). In order to support the overwhelming majority of Ugandans who rely on fuelwood as their primary energy source, natural forests have been cleared and replaced with monoculture eucalypt plantations (McCarthy et al. 2017). Globally, present-day Uganda has one of the highest population growth rates. Together, the high population of people dependent on fuelwood and a growing population, are contributing factors to the deforestation of native species, and subsequent introduction of non-native species, such as *Eucalyptus* spp. In addition

to this exploration of demand for forest resources, an historical approach regarding how populations and ecologies have evolved over time allows for a more nuanced understanding of anthropogenic modifications in this region.

Watkins (2009) presents an historical view of the evolution of anthropogenically modified forests in Western Uganda. Nineteenth-century British colonial rule was largely responsible for a shift to more intense forest resource extraction and anthropogenic modification in Uganda. Prior to colonization, the Budongo Forest region in Uganda (Formerly Bunyoro Kingdom) was sparsely inhabited and minimal forest resources were harvested. Forest edges were burned to control tsetse fly infestations and to promote forest expansion. However, British officials discontinued these practices. Instead, they removed indigenous tree species, including *Ficus* spp., which is a dietary staple for chimpanzees (McLennan et al. 2020). While favoured chimpanzee foods were not specifically targeted in this process, these modifications were likely detrimental for chimpanzee foraging and feeding behaviours. Cash crops were introduced, and Indigenous trees were replaced with exotic species better suited for timber. Fuelled by international demand for tropical hardwoods, the timber industry in the Budongo region became the largest in Uganda, which served to encourage immigration to the region, which in turn intensified anthropogenic modifications in this forest region (McLennan et al. 2020; Watkins 2009). This example underscores the importance of viewing anthropogenic modifications through a wider lens. Evidently, modern-day resource extraction and anthropogenic activities are rooted in historical colonial practices and globalization. These practices completely changed the way local people live their lives, and continue to modify chimpanzee habitats today.

Ethnoprimatology of Anthropogenic Modifications in Chimpanzee Habitats

Bulindi chimpanzees were able to adjust to severe anthropogenic modifications by adapting nesting habits as well as by incorporating eucalyptus bark and cultivated fruit into their diet. However, these behavioural responses are harming primate-human relationships in that they are contributing to local peoples' increasingly ambivalent attitudes toward chimpanzees. Deforestation of natural species for monoculture eucalypt plantations resulted in the clearance of Indigenous fruiting trees. This included a chimpanzee dietary favorite, *Ficus* spp. As chimpanzee habitats underwent modification, and figs became increasingly unavailable, new dietary sources were required.

McLennan et al. (2019) and McCarthy et al. (2017) found that chimpanzees responded to deforestation by incorporating cultivated foods into their diet. However, ethnoprimatological research by McLennan and Hill (2012) in this same region highlights emerging fear and ambivalence toward chimpanzees as a result of their dietary adaptations. During interviews with villagers, locals stated that they see and hear chimpanzees more often than they used to. They also feared chimpanzees, and considered them to be dangerous animals. Notably, the majority of villagers interviewed said they believed that the chimpanzees' behaviour, and locals' attitudes toward them, have changed over time. These changing perspectives are largely due to chimpanzees raiding cash crops and an increase in human-directed aggression (McLennan and Hill 2012). There are understandably limits to the amounts of crop losses and aggression local populations can tolerate. However, if deforestation and population growth continue, one can expect that the frequency of confrontational chimpanzee-human interactions will only continue to increase. This suggests that if humans are unable to tolerate chimpanzees' behavioural

adaptations to anthropogenic modifications, their adaptations may in fact be maladaptive in the long term.

The majority of individuals interviewed by McLennan and Hill (2012) expressed unfavorable attitudes toward local chimpanzees; however, variation in perceptions persists to some extent. Ethnographic research by Hill and Webber (2010) surrounding the Budongo forest reserve reveals that locals perceive chimpanzees as "gentle" and "disciplined" when feeding on cultivated crops. This contrasts with views of other crop-foraging primates, such as baboons, which are reported to be more wasteful and destructive. In this instance, more favourable attitudes towards chimpanzees appear to be relative to the presence and behaviour of other species of primates. This suggests that local attitudes and perceptions toward chimpanzees are not static, but are dynamic and varied. Furthermore, these ethnographic findings underscore the importance of taking a more holistic look at underlying factors which influence sentiments towards chimpanzees.

I have argued that ethnoprimatology serves to enrich primate behavioural field studies by presenting locals' views and attitudes towards sympatric populations of primates. However, because primate behavioural ecology is tied to the environment, ethnographic research regarding how local peoples' perceptions of forests habitats can also be of value. Primates and humans are intricately connected and dependent on one another in that they both contribute to, and rely on, forest resources (Fuentes 2012). Watkins (2009) research in Western Uganda reveals a disconnection between locals' perceptions toward chimpanzees and the forests. In general, local villagers want to protect the surrounding forests, and strive toward sustainable forest use. However, these sentiments juxtapose the majority of villagers from McLennan and Hill's (2012) study who expressed that chimpanzees should be collected and re-located elsewhere. While some

locals maintained there were advantages to living alongside chimpanzees, the majority expressed that intervention was warranted. Therefore, this suggests that many villagers in Western Uganda may not view chimpanzees as an integral and necessary component of the forest, when in fact they are essential ecosystem participants, and are needed for forest regeneration and biodiversity. This biodiversity not only sustains chimpanzees, but also sustains the humans which rely on these landscapes.

McLennan et al. (2019) and McCarthy et al. (2017) have demonstrated that chimpanzees are remarkable in their abilities to adapt to fast-changing anthropogenic environments. I have built on this research by integrating historical and ethnographic concepts. Historical ecology provides insight into how these changes came about, and what continues to fuel them. Specifically, local demand for fuelwood, attempts to preserve indigenous tree species by introducing Eucalyptus plantations, along with colonial processes and global demand for forest resources, continue to modify chimpanzee habitats today. Additionally, ethnoprimatology highlights the notion that human perceptions and attitudes toward chimpanzees are mixed. However, it also suggests that if anthropogenic modifications continue, behavioural adaptations may not sustain chimpanzees in the long term. Furthermore, there is opportunity to educate local populations on the benefits chimpanzees bring to the forests on which humans rely. This, combined with the fact that locals' perceptions and attitudes are varied and change over time, suggests that the prospect of sustainable co-existence of primates and humans is still possible. In the end, my analysis emphasizes the importance and value of examining primate conservation from multiple angles.

CONCLUSION

Throughout this thesis, I have integrated studies from field primatology with concepts from historical ecology and ethnoprimatology to illustrate the value of a longitudinal and holistic approach to primate conservation. My analysis has revealed some common themes regarding anthropogenic modifications in both spider monkey and chimpanzee habitats. Broadly, it has revealed underlying processes which continue to influence anthropogenic modifications of primate habitats across the neotropics and equatorial Africa. Colonial processes have altered Indigenous subsistence strategies, and increased population densities. These processes have in turn served to increase demand for, and commercialization of, forest resources. At the same time, these processes overlap with locals' views and attitudes towards the primates with which they share land and resources. My analysis has demonstrated how these perceptions are fluid and highly variable between and within regions. Therefore, this underscores the need to consider and incorporate locals' perceptions towards primates and primate habitats when designing conservation initiatives. My analysis has revealed that, while spider monkeys and chimpanzees are extraordinary in their abilities to adapt their behaviour to sometimes extreme anthropogenic modifications, there are also limitations to these adaptations.

To conclude, my thesis provides a longitudinal and holistic look at the underlying historical and social factors regarding anthropogenic modifications in primate habitats. This research is significant because, as I have illustrated, historical, ecological, and social trends are continuing to intensify primate-human relationships in shared landscapes. This reinforces the need for primate conservation which takes into account the multitude of factors that affect primates and their habitats. The notion of integrating historical, social, and ethnographic research to address primate conservation is not new (Fuentes 2012). However, I believe it is underutilised,

as this kind of integrated methodology has the potential to generate new understandings, and therefore alternative approaches to primate conservation. With this, I welcome and encourage scholars to join me in approaching primate conservation through a wider lens.

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