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Department of Environmental Studies

THESIS COMMITTEE PAGE

The undersigned have examined the thesis entitled:

Influences of forest edges and human activities on the dry season ranging patterns of chimpanzees (*Pan troglodytes schweinfurthii*) in Nyungwe National Park, Rwanda

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May 2018

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Influences of forest edges and human activities on the dry season ranging patterns of chimpanzees (*Pan troglodytes schweinfurthii*) in Nyungwe National Park, Rwanda

> A Thesis Presented to the Department of Environmental Studies Antioch University New England

> > In Partial Fulfillment of the Requirements for the Degree of Master of Science

> > > By Enathe Hasabwamariya May 2018

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ABSTRACT

Great apes, our closest biological relatives are threatened globally by the increasing anthropogenic pressures on their habitat. The major threats to the eastern chimpanzees (Pan troglodytes schweinfurthii) are hunting for bush meat and illegal trade in chimpanzee infants, habitat loss or fragmentation and disease transmission (IUCN, 2010). Nyungwe National Park (NNP), Rwanda has a population of chimpanzees that face several threats, including hunting for bushmeat, habitat degradation from forest fires and human-wildlife conflicts, and much of these impacts are concentrated at forest edges. The main objectives of this research were to assess the use of forest edges by chimpanzees along the border of NNP and determine the influence of human activities on chimpanzee ranging patterns. My assistants and I set five transects inside the forest perpendicular to the forest edges in the vicinity of Gisovu in the north of NNP, and five transects parallel to the forest edges outside the forest. We recorded chimpanzee signs along those transects, and GPS waypoints were taken for each sign recorded. Vegetation sampling was done to identify habitat types along the edges (0-500m) and in the forest interior (500-1000m). In total 100 signs of chimpanzees were recorded, 67 signs near forest edges (0-500m), and 37 signs in the forest interior (500-1000m). I found a significant difference between the number of chimpanzee signs in forest edges and chimpanzee signs in forest interior (Binom. Test, 100, 0.6, p=0.01). There was no significant relationship between density, basal area of nesting trees and chimpanzee distribution, however, there was a tendency toward a positive or a negative relationship depending on the tree species present. I found a significant positive relationship between fruit availability and chimpanzee distribution. Outside the park, chimpanzees were recorded destroying people's beehives. This research is one of the first studies done in Gisovu area and contributes to the

understanding of the behavioral ecology of chimpanzees and their interactions with the surrounding human-dominated environment.

Keywords: buffer zones, human-primate conflict, ranging patterns

INTRODUCTION

About 60% of the world's estimated 660 primate taxa are threatened with extinction, and more than 75% have declining populations due to human pressure (Estrada, 2017). Growing human population and the resulting anthropogenic pressures such as habitat fragmentation are the strongest threats to primates living in tropical forests. Recent studies have shown that long-term deforestation is responsible for 46% of fragmented tropical forests (Estrada, 2016). Fragmented habitat leads to the formation of forest edges. Forest edges lead to exposure to many threats from the surrounding environment, and these threats are known as edge effects, which exacerbate habitat degradation and thus affect the behavioral ecology of species living in those fragmented habitats (Lenz et al., 2014).

Chimpanzees are classified as endangered by the International Union for Conservation of Nature (Oates et al., 2009) as is the eastern subspecies, *P. t. schwenfurthii* (Wilson et al., 2009). Eastern chimpanzees range from southeastern Central Africa Republic (CAR) through northern Democratic Republic of Congo (DRC) to the western regions of the countries of Eastern Africa (Uganda, Tanzania, Rwanda, Burundi and Southeast Sudan (Plumptre, 2010). Chapman (2006) found that most chimpanzee habitat is found in anthropogenically disturbed habitat mosaics of farmland, human settlements, and forest fragments, which expose the animals to different threats. In a rapidly changing environment and increasing edge habitat, effective conservation of great apes requires the understanding of their ranging and habitat selection patterns (Terada et al., 2015).

According to the International Union for Conservation of Nature (IUCN), the major threats to the Eastern chimpanzees are hunting for bush meat illegal trade in chimpanzee infants, habitat loss or fragmentation and disease transmission (IUCN, 2010). Nyungwe National Park (NNP), a tropical montane forest in Rwanda, has a population of chimpanzees which face several challenges including hunting for bush meat, forest fires, buffer zone management and crop raiding (Crawford, 2012). Considering that Nyungwe is surrounded by a very high human population density (Masozera et al., 2004), there is a need to understand how people and wildlife interact for effective conservation. My research focuses on both ecological and non-ecological factors influencing chimpanzee ranging patterns around the edges of Nyungwe.

Among different communities of chimpanzees living in Nyungwe, the chimpanzees of the northern Gisovu region have not been well studied. Chimpanzees in Nyungwe have been observed using forest edges, especially searching honey from local people's beehives in the buffer zone (Kamenya, personal communication), but no systematic research has documented this. Information about how chimpanzees use the edges and buffer zone are particularly relevant as the Rwandan Government has contracted a British-based company (The New Forest Company) to harvest the pine buffer around Nyungwe; the buffer was originally aimed at reducing contact between wildlife and humans (Gross-Camp et al., 2015). Previous studies found that chimpanzees in Nyungwe prefer pine over other types of buffers, and thus clearing pine buffer would reduce chimpanzee access to additional habitat, food resources and nesting sites which could lead to some local extinction of the species. (Martino, 2015; Kubwimana, 2013; Kaplin unpublished data). It is very important for both the park and any entities interested in harvesting the buffer zone to understand chimpanzee habitat selection in order to improve conservation and use best practices for buffer zone management.

This study evaluates the influence of forest edges on chimpanzee ranging patterns. The objectives of this study were to 1) assess the use of forest edges by chimpanzees, 2) determine ecological factors that influence the use of forest edges by chimpanzees and 3) determine the influences of human activities on the ranging patterns of chimpanzees at forest edges. My research questions are: 1) Does the distribution of chimpanzees vary as a function of proximity to forest edges? 2) How do ecological factors such as forest type, food and nesting tree availability influence chimpanzee's use of forest edges? 3) How do human activities such as beekeeping around park boundaries influence the distribution of chimpanzees at the forest edges?

Background

Edge effects

Edges are the results of abrupt transitions caused by forest fragmentation that separate two adjacent ecosystems. They are considered ubiquitous aspects of human disturbance to forest landscapes (Chapman, 2006). Edge effects are described as conditions that influence species distribution, richness and behavior following complex causal mechanisms (Leopold, 1933). During forest fragmentation, organisms of the interior forest are exposed to the conditions of different surrounding ecosystems (Murcia, 1995). Edges affect the organisms inside the forest by causing changes in biotic and abiotic conditions. However, which species are affected by the edge and how they are affected can vary widely as some species are more vulnerable to forest edges than others. For example, research has found that for many species, responses to edge penetration are detected at 300 meters, while others are detected at 600 meters; however, others species show no edge response (Lenz et al, 2014). For example, Lehman et al. (2006) found lemurs were distributed in three broad categories: (1) "edge-tolerant", for species that have their highest densities near forest edge, (2) "edge-intolerant" for species that avoid forest edges, and (3) "omnipresent" representing species that show little or no response to edge and matrix conditions.

Species living in the forest edge face many challenges including harsh environmental and climatic conditions such as wind, fire, increased predation rates, and invasive species. Laurence et al. (1997) found that at forest edges, the wind intensity can be high and cause reduction in fruit crops and so become hard for primates to survive there. Despite all the challenges and risks presented by the edges, chimpanzees and many other primates have been shown to increase their use of forest edges. In this study, I explore attributes of chimpanzee habitat adjacent to forest edges. I also observe the anthropogenic activities in the matrix outside the forest and evaluate their relationship with chimpanzee distribution outside the park.

Why chimpanzees?

Chimpanzees are the closest biological relatives to humans, and they are considered as an umbrella species for conservation because of their important ecosystem role as seed dispersers (Gross-Camp & Kaplin, 2005; Lambert, 2010). Eastern chimpanzees are listed as endangered (Oates et al., 2009). They occur at relatively low densities and require large areas to maintain viable populations, therefore, are thought to be particularly vulnerable to habitat fragmentation (Plumptre et al., 2010). As important contributors to forest regeneration, chimpanzees facilitate the wide distribution of seeds through the consumption of large quantities of fruit, and they have a tendency to swallow and not masticate large seeds (Gross-Camp & Kaplin, 2005). It was found that they disperse many different seeds compared to other primate species (Lambert, 2010). Due to increasing fragmentation, it is important to understand the role of primates as effective dispersers, especially for large-bodied primates like chimpanzees (Bufalo et al., 2016).

Chimpanzee tourism plays an important economic role as a source of revenue to the local communities living around Nyungwe and the country in general (RDB, 2012), and so to increase park visitation and revenue, the government of Rwanda is committed to promoting Nyungwe as a

tourism destination. Previous research in Nyungwe reported that chimpanzees and other frugivore species prefer areas adjacent to pine buffer more than tea buffer (Martino, 2015; Kubwimana, 2013; Kaplin unpublished data), and so I chose to look at the use of forest edges near pine buffer and other anthropogenic activities that may influence chimpanzee movement.

Chimpanzee ranging and feeding ecology in relation to forest edges

While much work has been done on changes in animal abundance at forest edges (Ewers and Didham 2006), there has been less work focused on the response to edges by primates (Ukizintambara, 2010; Mark et al., 2012; Magrash et al.2013, Martino et al. unpublished). Considering that chimpanzees are territorial, food availability and intercommunity relations will strongly define their territory use and size as well as their location at forest edges (Krief et al., 2014).

Primates do not choose feeding and sleeping sites randomly; in fact, research has shown that there are a lot of reasons why chimpanzees prefer certain areas where they feed or nest, especially in risky areas such as at forest edges. For example, in Kalinzu Forest, Uganda, chimpanzees mostly used forest edges as feeding and nesting sites, but this only happened when those edges offered other food resources like insects or when there were crops in the farmlands outside the forest. This happened mostly during the season of food or fruit scarcity (Furuichi et al., 2004). Ndimulingo (2007) found that the combination of tree species composition, size and density within chimpanzee home ranges in each site and nest sites can reflect food distribution if chimpanzees sleep where they feed during the day.

Studies show that fruit availability in tropical forests is highly seasonal (Kaplin et al., 1998; Chapman et al., 2005). During fruit scarcity, chimpanzees tend to expand their foraging ranges (Fawcett 2000; Morgan and Sanz 2006; Tutin et al., 1997), which can cause them to come into greater contact with forest edges, and they may sometimes end up feeding on crops from the surrounding agricultural farms (Hockings et al., 2010).

Forest boundaries often have distinctive vegetation structure, resource availability, and animal abundance in comparison to the forest interior (Kremsater & Bunnell, 1999). At forest edges, tree heights typically decline while shrubby vegetation increases (Kremsater & Bunnell, 1999), which may facilitate feeding by some animal species. Forest edges can offer increased insect biomass (Malcolm, 1994) which can influence primate ranging. Grow et al. (2013) showed that pygmy tarsiers (*Tarsius pumilis*) mitigated the decrease of insects at high altitudes by adjusting their ranging near forest edges. Edges also increased light penetration for night time navigation (Kremsater & Bunnell, 1999), which makes edges good foraging habitat for nocturnal and insectivorous primates (Lehman, 2010). This could also explain the unusual behavioral adaptation of foraging during the night that was discovered in chimpanzees ranging in Kibale National Park,Uganda (Krief, 2014).

In general primates with different diets should respond to forest edges differently. This means that if insects are more abundant near the forest edges, insectivorous primates may become more tolerant to forest edges compared to species that don't consume insects (Lehman et al., 2006; Corbin, 1995). Folivorous primates may be attracted to forest edges, if the quality of nutrients in the leaves at the forest edges is higher than the leaves of trees inside the forest (Lehman et al., 2006). In Bwindi Impenetrable National Park, Uganda, Ukizintambara (2010) found that the abundance of food species including farmers' crops at forest edges influenced the behaviors of l'hoesti' monkeys (*Allochrocebus lhoesti*).

Relationship between the type of matrix and forest edges

Forest edges are surrounded by different types of matrix and it is important to consider their role and influence on the ecological behaviors of species inside the forest. A matrix includes the landscape surrounding the forest, and typically can consist of different land uses and vegetation types such as secondary forests serving as buffer zones and farmlands. Knowing the impact of a surrounding matrix on a forest will increase our understanding of chimpanzee use of forest edges and interaction with humans. Ecologically, it was found that the matrix near forests can ameliorate some of the ecological effects of edges by increasing or decreasing the frequency of edge effect (Filloy et al., 2010; Zurita & Bellocq, 2012; Martino, 2015). If the matrix is similar to the forest, it can support species distribution and support biodiversity and ecosystem function within the forest (Fisher et al., 2006).

The survival of species depends on the type of land use around forests. For example, Ukizintambara (2010) found that l'Hoesti monkeys living at forest edges in Bwindi Impenetrable National Park, Uganda, consumed food from adjacent agricultural farmers, putting them at risk of mortality due to retribution from farmers. In Bwindi Impenetrable National Park, Uganda, gorillas were found ranging in community lands outside the forest not because of the lack of food inside the forest but because of the better quality of food outside the forest (Seiler et al., 2014). In NNP, Rwanda, chimpanzees used the surrounding matrix of pine buffer more frequently that other buffer types, likely due to the structure and composition of the buffer zones; chimpanzees used pine buffer for nesting sites and access to foraging opportunities more frequently compared to tea buffer zone (Kaplin, 2013 unpublished data; Kubwimana, 2013; Martino, 2015).

Primates can benefit from living at forest edges due to the availability and diversity of food at the edges and this is mostly observed during periods of food and fruit trees scarcity. However, it is important to note that while forest edges can provide good food sources and nesting sites for some species, they can also be a source of tension between humans and wildlife due to crop raiding, which can trigger major threats to their survival.

Risks at forest edges: disease transmission and human-wildlife conflicts

As human populations grow, parks become further isolated, and measuring and managing edge effects may be crucial to achieving conservation objectives. Human-wildlife conflict is neither new nor a rare issue, but through extensive transformation of natural habitats, an increasing number of wildlife species are forced at the forest edges in close proximity with humans, thereby, intensifying that conflict. Anthropogenic changes in fragmented landscapes at forest edges can be associated with increased disease levels in primates. For example, in Kibale National Park, Uganda, Chapman et al. 2006 found that for two primate species, red colobus (*Piliocolobus tephrosceles*) and black and white colobus (*Colobus guereza*), the groups that lived on the edges had higher risk of infectious diseases compared to the individuals of the groups that lived in the forest interior. Goldberg et al. (2008) also found that humans living near forest fragments had *Escherichia coli* bacteria that was 75% more similar to bacteria from primates in those fragments than to bacteria from primates in nearby undisturbed forests.

Habitat degradation in forest fragments has been related to increases in stress in primates (usually assessed by fecal glucocorticoids), which can have a negative effect on immune function (Sapolsky, 2002). Chimpanzees may also have higher stress levels along the edge when feeding on raided food rather than wild food. For example, chimpanzees vocalized less and showed higher frequency of signs of anxiety, including rough self-scratching in the presence of people during crop raiding in Bossou, Guinea (Hockings et al., 2007). In Bwindi Impenetrable NP, Uganda, l'Hoesti monkeys spent more time and energy being vigilant, rather than socializing (Ukizintambara, 2010), and the same was observed in chimpanzees in Kibale National Park, Uganda (Chapman, 2006; Krief et al., 2014).

Increasing forest edge conflicts

The current rate of forest destruction and fragmentation is resulting in increasingly prevalent human–wildlife conflicts along forest edges adjacent to protected areas. In fact, conflicts between people and wildlife have increased substantially around protected areas during the past decade because of increasing human populations and their activities, including expanding settlements, agriculture, livestock husbandry, deforestation, charcoal burning, tourism, and research (Mlengeya, 2005). Crop raiding by chimpanzees can be seasonal. For example, in Bossou, Republic of Guinea during periods of fruit scarcity chimpanzees stayed at forest edges in order to raid crops and sometimes attacked children at forest borders near small roads or trails, which resulted in human intolerance toward chimpanzees (Hockings, 2009). In western Uganda, humans have claimed to kill chimpanzees due to crop raiding (Krief et al., 2014). In Nyungwe National Park, primate species living at forest edges are exposed to threats including high human disturbances and illegal activities like poaching and collecting fire wood (Kubwimana, 2013). This study will help us to better understand the role played by human activities around NNP, in chimpanzees ranging at the edges of the forest.

2. METHODOLOGY

Site description

This study took place in the northern part of Nyungwe National Park (NNP), Rwanda called Gisovu. Nyungwe National Park is a mountainous rainforest in southwestern Rwanda, located between 2°15'-2°55'S, 29°00'-29°30'E at the southern border of Rwanda and Burundi; the park

connects with Kibira National Park, Burundi. It has a surface of 1015 km². NNP is part of the Albertine Rift biodiversity hotspot (Mittermeier et al., 2004), and has very high species diversity, including thirteen species of primates and about 260 bird species. The elevation ranges between 1600 to 2900 m. A major dry season occurs between July and August, and a minor dry season takes place between December and January. It is surrounded by a high human population density. The majority of people who live around NNP are poor and their livelihood in some cases depends on resources inside the forest. They rely on the forest for resources like firewood collection, livestock and agricultural activities, but the search for resources sometimes results into poaching activities. Poaching is a problem in Nyungwe and has resulted in the extinction of some species including forest elephant (*Loxondata africana*) and forest buffalo (*Syncerus coffer nanus*) (Gapusi et al., 2010).

In order to improve the conservation management of NNP, an official buffer zone (about 100 km²) was demarcated around parts of the park in 1969 with a threefold objective: to set up a clear demarcation of the limits of the park, to provide woody products for timber and energy and to create jobs for rural communities (Plumptre et al., 2004, Gross-Camp et al., 2012). There are three types of buffer zones present around NNP at this time, pine tree, eucalyptus tree. My study was specifically conducted in the northern part of the park, called Gisovu. The number of chimpanzees in this community is estimated to be between 25-30 individuals and they range on the surface of 50km² (JGI, 2013, unpublished report). Chimpanzees in Gisovu are not well habituated and had no tourist visitations during the time of my study.

Nyunwe national Park is surrounded by a very high human density of around 300-400 people/km², and 90% of these inhabitants are subsistence farmers (Masozera and Alavalapati 2004; Gross-Camp et al. 2015). Gisovu is located in one of the poorest districts in the country, and the

residents in this village heavily rely on subsistence farming, beekeeping and planting eucalyptus for charcoal production. The Gisovu tea factory also creates some seasonal jobs for local people. Beekeeping is done in cooperatives, but it is threatened by chimpanzees during the harvest time. Every day during the harvest season, some members of the cooperative must be obliged to guard the beehives from destruction by raiding chimpanzees. (pers. obs)

Data collection

For a period of three months, from June 15th until September 4th 2017, data on chimpanzee signs were collected inside and outside Nyungwe National Park. During this study, data were collected on presence and location of chimpanzee nests, feces and vocalizations in order to estimate frequency and distribution of chimpanzees relative to the forest edge. Data were also collected on vegetation composition at the edges and the forest interior within the chimpanzee home range.

Forest Edge use and Forest Interior

To document chimpanzee use of forest edges, I used five transects perpendicular to forest edges, running from the edge into the forest interior to locate and document chimpanzee forest use relative to the forest edge. A GPS unit was used to locate the start and end point of each transect and location of chimpanzee sign (Plumptre & Reynolds, 1997). Each transect was 1km long, and every 20 meters I marked the transect in order to know the location along it. Thus, inside the forest, five transects were set at regular intervals of 250 meters running perpendicular from the forest edge towards the forest interior. I visited transects every three weeks, and I noted every chimpanzee sign (nests, feces, vocal and other signs) for a total of 15 sampling sessions. Along the transects, I also recorded the presence and abundance of fruits eaten by chimpanzees.

Vegetation Sampling

Vegetation sampling was done to identify the forest type, as well as the composition and abundance of trees used by chimpanzees and to compare their distribution at the forest edge and in the forest interior. Sampling was done along the forest edge, defined at 0-50 meters from forest edge, and between 950-1000m (far from the edge). Circular plots of five meter radius were randomly located within forest edges, where I recorded tree species and diameter at breast height (DBH). I also put 10 circular plots of five-meter radius each in the forest interior (950-1000 m) to identify vegetation type (Martino, 2015). The location along the edge for plot sampling was randomly selected. Within each circular plot, the DBH of all trees \geq 10cm was measured and identified to species. To sample trees with a DBH of less than 10cm, inside the circular plot, four quadrats of $2m^2$ each were used to sample saplings and treelets.

Fruit abundance sampling

I sampled fruit phenology of top fruit species eaten by chimpanzees, based on what is already known about chimpanzee diet in Nyungwe NP (Taylor, unpublished report). Fruit abundance was estimated at the forest edge and the interior using a simple availability sampling method (Zhang *et al*, 1995). Along the perpendicular transects, while sampling for chimpanzee sign, I observed any fruits on the ground, noted the species and at what distance from the edges the fruits were found using a GPS or meter tape. I looked two meters to either side of the transect for fruit availability both on the ground and in the trees. Fruits were recorded with presence and absence at three different levels of abundance. The categories of abundance were: 0 (no fruit available), 1 (very few; fruits could be counted); 2 (few), 3 (a lot of fruits; fruits could be counted) and 4 (fruits were very abundant that we could not count them one by one).

Determining chimpanzee presence outside the park

To understand the influence of human activities on chimpanzee use of forest edges, five transects of one kilometer long each were set parallel to and just outside the forest edge at Gisovu. Due to the complexity of edges around the park in Gisovu, to have the transects parallel to the park, the first transect was at about 500 meters away from the forest edges, in the pine buffer. Each transect was visited once in a month when signs of chimpanzees and human activities (roads, houses, farmlands, particular crops, beehives) and the distance at which they were observed from forest edges and from the transects were recorded. GPS points were taken wherever chimp signs were found.

Data analysis

All statistical analyses were performed in R Studio software (RStudio team, 2015). To determine chimpanzee use of forest edges, ArcGIS 10.3.1 software was used to map chimpanzee distribution at different distances from the forest edge. A binomial test was used to determine if there was a significant difference between the number of chimpanzees that used forest edges (0-500m), and chimpanzees that used forest interior (500-1000m). The sampling effort was the same between the two areas.

Regarding the type of vegetation, a logistic regression was performed to determine if there was a relationship between the density and basal area of chimpanzee nesting trees and chimpanzee distribution at the edges and in the forest interior. The same test was done to see if there was any relationship between fruit availability and chimpanzee distribution. Regarding the interaction between chimpanzee and human activities, ArcGIS 10.3.1 was used to map and analyze chimpanzee distribution and land use types around the park, where chimpanzees were observed.

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3. RESULTS

Chimpanzee use of forest edges and forest interior

During this study, five transects of 1 km each, perpendicular to the forest edges were visited every three weeks. A total of 100 chimpanzee signs were recorded inside the park, including chimpanzee nests, feces and vocal signs, and sometimes chimpanzees were observed directly (Figure 1). Sixty-three chimpanzee signs were found near the forest edges (0-500m), and another 37 signs were found far from the forest edges (500-1000m) (Figure 2).

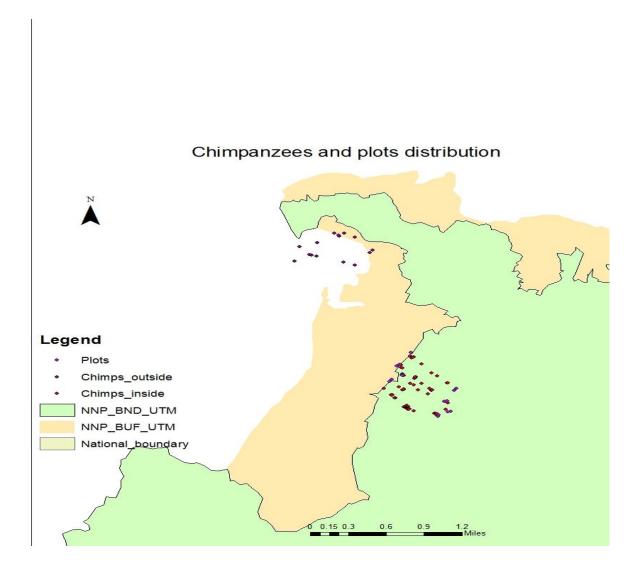


Figure 1: Map of chimpanzee signs and vegetation plots distribution in and outside Nyungwe National Park, Rwanda. NNP_BND: Nyungwe National Park Boundary, NNP_BUF_UTM: Nyungwe Buffer Zone.

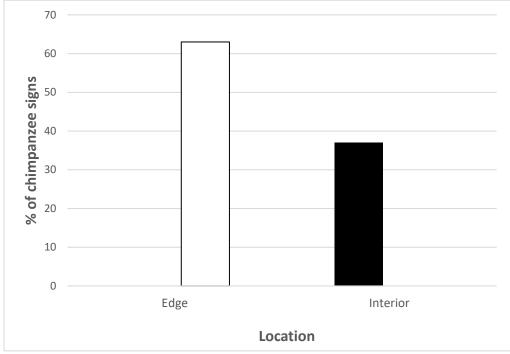


Figure 2: Frequency of chimpanzee distribution along forest edge (0-500m) versus forest interior (500-1000m) in Gisovu, NNP, Rwanda.

I found a significant difference in distribution of chimpanzee at forest edge and forest interior (binom. test (100, 0.6, p=0.01)).

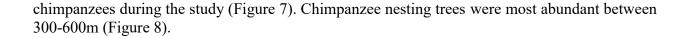
Ecological Factors influencing chimpanzee distribution

Vegetation sampling

In total, 26 large trees species (DBH>10cm) were recorded at the forest edges and forest interior. One of the most dominant species at the edges were *Galiniera saxiflaga*, an understory species, while *Macaranga kilimandscharica*, an early successional tree species, dominated the forest interior. A total of 49 saplings (DBH<10cm) were recorded at forest edges and forest interior. The most dominant saplings at the forest edges were *Galiniera Saxiflaga*, and *Mimilopsis arborescens*, both understory species, while the forest interior were dominated by *Syzigium guineense* and *Macaranga kilimandscharica*.

Comparison of large trees diameter sizes at forest edges versus forest interior

Overall, the study site was dominated by large trees with a diameter size between 10-40 cm. Forest edges were dominated by trees with a DBH between 10-20cm (Figure 3), while the forest interior was dominated by trees with a DBH between 40-60cm (Figure 4). *Carapa grandiflora* was the most common tree species observed to be used for making nests by



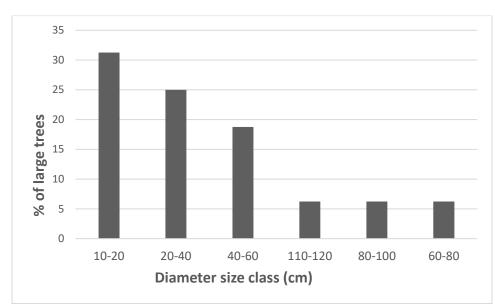


Figure 3: The diameter size class of large trees (DBH>10cm) at forest edges in Gisovu, NNP, Rwanda.

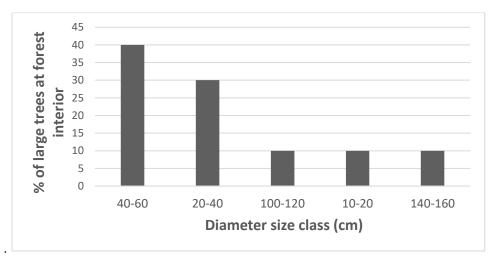


Figure 4: Diameter size class of large trees (DBH>10cm) in the forest interior in Gisovu, NNP, Rwanda.

Distribution of small trees/saplings at forest edges versus forest interior

Overall, trees with a DBH of less than 10cm were abundant both at the edge and forest interior.

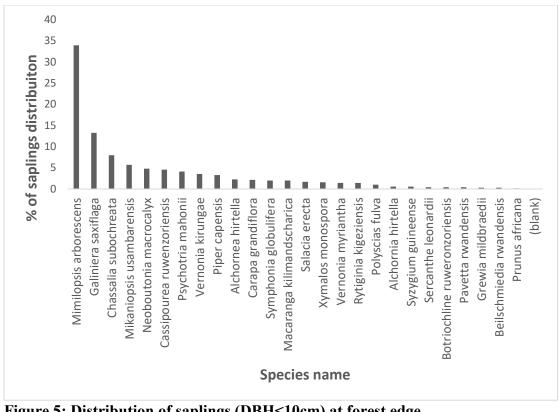


Figure 5: Distribution of saplings (DBH<10cm) at forest edge

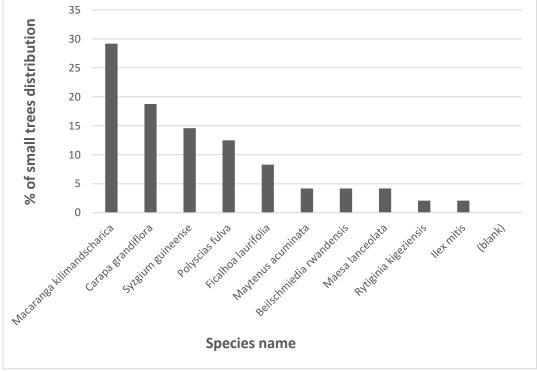


Figure 6: Distribution of saplings (DBH<10cm) in forest interior

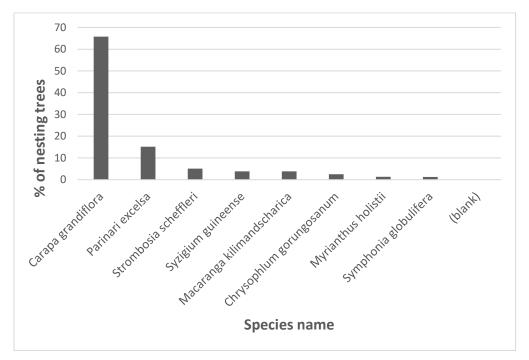


Figure 7: Top 10 chimpanzee nesting tree species

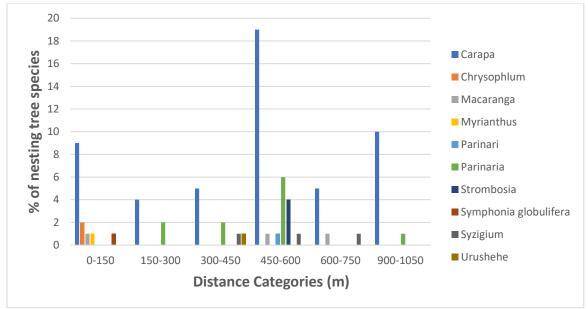


Figure 8: Chimpanzees nesting trees species at different distances

Table 1: Densities of chimpanzee most commonly observed nesting tree species at the edge and in forest interior.

| Nesting tree species | Density at the | Density in interior |
|----------------------|----------------|---------------------|
| | edge | forest |

| Carapa grandiflora | 1.92 | 1.48 | |
|----------------------------|------|-------|--|
| Chrysophyllum rwandensis | 0 | 0 | |
| Macaranga kilimandscharica | 1.8 | 12.3 | |
| Myrianthus holistii | 0 | 0 | |
| Parinaria excelsa | 0 | 0.37 | |
| Strombosia scheffleri | 0 | 0 | |
| Symphonia globulifera | 1.77 | 1.25 | |
| Syzigium guineense | 0.5 | 27.46 | |
| Overall Density | 5.5 | 42.88 | |
| | | | |

Relationship between nesting tree densities, basal area and chimpanzee distribution

I found that there is no significant relationship between chimpanzee signs and tree species (density) however, there were tendency toward positive or negative relationships depending on the species. Chimpanzee nests showed a positive relationship with *Carapa grandiflora and Symphonia globurifera* (Figure 9 & Figure 11), while chimpanzee nests showed a negative relationship with density of *Macaranga kilimandscharica* and *Syzigium guineense* (Figure 10 &Figure 12). Chimpanzee nests showed a positive relationship with fruit abundance (Figure 13).

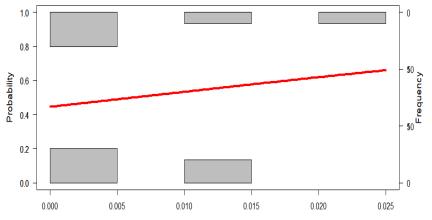


Figure 9: The relationship between density of *Carapa grandiflora* and chimpanzee distribution in Gisovu, NNP, Rwanda

Coefficients:

Estimate Std. Error z value Pr (>|z|) (Intercept) 0.002366 0.553185 0.004 0.997 CDEN -0.264105 36.339155 -0.007 0.994 AIC: 31.726

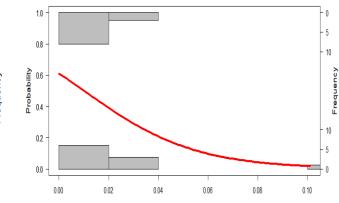


Figure 10: Relationship between density of *Macaranga kilimandscharica* and chimpanzee distribution in Gisovu, NNP, Rwanda

Coefficients:

| Estimate Std. Error z value $Pr(z)$ | | | | | | |
|---------------------------------------|---------|----|-------|----------|-----|-------|
| (Intercept) | 0.4506 | 0. | 5500 | 0.819 | 0.4 | 413 |
| MDEN | -44.705 | 4 | 36.08 | 394 -1.2 | 39 | 0.215 |

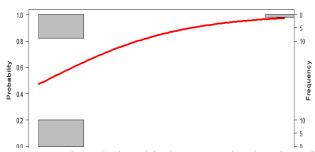


Figure 11: The relationship between the density of *Symphonia globulifera* and chimpanzee distribution in Gisovu, NNP, Rwanda

Coefficients:

Estimate Std. Error z value Pr(>|z|) (Intercept) -0.1098 0.4610 -0.238 0.812 SYMBA 0.1368 0.2275 0.601 0.548

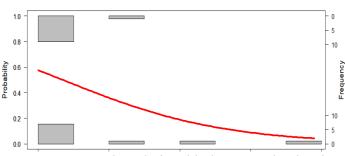


Figure 12: The relationship between the density of *Syzigium guineense* and chimpanzee distribution in Gisovu, NNP, Rwanda

Coefficients: Estimate Std. Error z value Pr(>|z|) (Intercept) 0.3056 0.4995 0.612 0.541 SYZDEN -88.0888 74.6852 -1.179 0.238

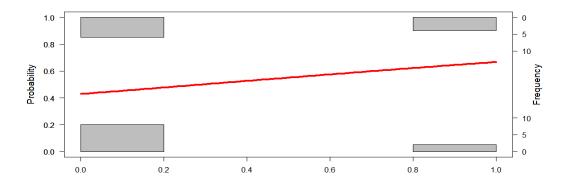


Figure 13: The relationship between fruit abundance and sign of chimpanzees in Gisovu, NNP, Rwanda

Coefficients:

Estimate Std. Error z value Pr(>|z|) (Intercept) -0.2877 0.5401 -0.533 0.594 FRUITS.AV 0.9808 1.0206 0.961 0.337 *AIC*: 30.76

4. DISCUSSION

Chimpanzee use of forest edges

Chimpanzee signs were frequently observed at forest edges. Chimpanzees used edges for different activities including nesting, feeding and travelling. Previous research found that some fruit eating primates are attracted to forest edges (Ukizintambara, 2010; Albert et al., 2014), but this can present risk of increased mortality, creating an ecological trap (Schlaepfer et al.,2002; Battin, 2004; Ukizintambara, 2010, Martino, 2015). The edges in Gisovu are surrounded by a pine and eucalyptus buffer zone. The type of matrix surrounding a forest can influence species' use of forest edges. Pine buffer is structurally similar to NNP and can provide chimpanzees with nesting habitat (Kaplin, 2013 unpublished data; Kubwimana, 2013; Martino, 2015). The pine buffer may also facilitate chimpanzees to go out of the forest to search for food to compensate what they lack, especially during periods of food scarcity. I observed chimpanzees passing through the pine buffer

to go outside to harvest honey from local people's beehives. The exposure to the outside environment makes forest edges very different and ecologically important to some species inside the forest. In particular, if we consider the unhabituated chimpanzees of Gisovu, under the pine canopy, their visibility is high, and they can assess their security and move further into the edge of the park.

Previous research found that road systems increase edge effects by altering the composition of vegetation at the forest edges (Ali et al., 2005; Jönsson et al., 2007), and this was also found in Nyungwe (Elias, 2005). Chimpanzees in Gisovu used a road to travel when outside the park boundary. Between the park and the buffer zone in this study site there is a main road that separates the park from the buffer zone, and it is used by rangers, researchers and local people working in the park. During this study, we recorded a lot of chimpanzee feces in the road, which coincides with Hockings et al. (2006) who found that chimpanzees (*Pan troglodytes verus*) in Bossou, Guinea cross roads to reach foraging sites.

Ecological factors influencing chimpanzee distribution

The aim of this study was to determine the influence of nesting and food tree density on chimpanzee use of forest edges and interior based on frequency of chimpanzee signs. I found no significant relationships between density of trees used for nests, basal area of those trees and chimpanzee sign distribution at the forest edge and forest interior. However, there was a tendency toward a positive or negative relationship depending on the species of tree. A lack of significant relationship between tree density, basal area and chimpanzee distribution may be due to a small dataset from the vegetation sampling.

Relationship between nesting tree densities, basal area and chimpanzee distribution

The size of trees in a given landscape determines the capacity of that landscape to support some primate species and nesting materials for nest construction (Ndimuligo et al., 2007). In this study small trees (less than 10cm DBH) were more frequent, with dominant species at the edges composed of saplings and shrubs such as *Galiniera saxifraga* and *Mimulopsis arborescens*. Large trees were mainly found between 300-600 meters from the forest edge, which is also the area where I found many chimpanzee nests. Previous research found that the seed dispersers of large seeded trees avoid forest edges (Martino, 2015), which can explain the lack of large trees at the forest edges. The density of *Macaranga kilimandscharica* was negatively related to chimpanzee distribution. This may be due to the fact that *Macaranga kilimandscharica* is an indicator of early successional forest (or a previously disturbed forest), contrary to *Carapa grandiflora*, which is an indicator of a late successional forest or undisturbed forest.

Relationship between fruit availability and chimpanzee distribution

I found a positive relationship between fruit availability and chimpanzee distribution. This finding coincides other studies, suggesting that the availability of fruit influenced the distribution of primates at forest edges or interior (Bortolamiol et al., 2014; Seil et al., 2018). Chimpanzees are mainly frugivorous, thus fruit availability inside the forest is expected to influence their ranging patterns (Hockings & Humle, 2009; Hockings et al., 2009; McLennan, 2013). During fruit scarcity, chimpanzees tend to expand their foraging ranges (Fawcett 2000; Morgan and Sanz 2006; Tutin et al., 1997), which can cause them to come into greater contact with forest edges, and they may feed on crops from the surrounding agricultural farms (Hockings et al., 2010). This may explain why chimpanzees in Gisovu were found ranging outside the park during the dry season if fruit availability was low.

Influences of human activities around the park on chimpanzees

Chimpanzee signs were found in the pine and eucalyptus buffer zone right at the edge of the park. I was able to record chimpanzee trails, and feces. I also found chimpanzee feces in the road next to the park. The presence of chimpanzee signs on the road may be related to the presence of *Myrianthus species* fruit trees along the road with ripe fruits (pers. obs). From my observations, the main food that took chimpanzees outside the forest at Gisovu during this study was honey from beehives placed by people for honey production based on direct observation and/or informal discussions with people. They also go outside the park to get insects such as beetles from dead trees in the eucalyptus or pine buffer zones. There are many eucalyptus trees around the park just outside the boundary. Although no study has been done on chimpanzees use of *Eucalyptus* in Gisovu, other studies have shown that chimpanzees and gorillas go outside the forest to consume eucalyptus bark because it contains high amounts of sodium (Rode et al., 2003).

Previous research found that land-use practices in areas bordering the parks plays an important role in human-wildlife conflicts for several primate species (Naughton- Treves *et al.*,1998; Saj *et al.*,2001; Yihune, Bekela& Tefera,2009). In this study I also found a lot of beehives destroyed by chimpanzees in the zone outside the forest between 300-500 meters from the park boundary. Beehives and other farms were put right up to the edge of buffer zone, potentially causing higher risks of crop raiding from wild animals leaving the park. Further research is needed to understand the extent of beehive raiding.

Influence of landscape

Previous studies showed that the distance at which primates can travel beyond park boundaries to raid crops is between 200-400 meters (Seil *et al.* 2014). However, in this study, I found that chimpanzees can even go beyond 700 meters outside the park to do crop raiding. The study site, Gisovu, is very hilly with steep slopes, many *Eucalyptus* trees, and beehives placed in trees next to the park's buffer zone. The park boundary is curved in the region of the study and it may be easy for chimpanzees to scan for available crops, beehives and presence of people from above. This may also explain why chimpanzee were able to destroy beehives and travel as far as up to 1000m from the park boundary.

Finally, it is important to note that although the pine buffer plays an ecological role in mitigating some negative edge effects from penetrating into the forest, pine can also act as an extension for animals to prepare for early intrusion into people's farms. A recent study by Fitzgerald et al. (2018) found that the topography and type of landscape has an influence on chimpanzee ranging outside the forest. Chimpanzees have sophisticated mental mapping capability which can allow them to perceive their surroundings at the level of individual trees and forest patches (Normand & Boesch, 2009; Normand et al., 2009). During informal interviews, local people mentioned that they believe that chimpanzees in Gisovu wait in the buffer zone scanning the area, before they go to destroy beehives.

5. CONCLUSION

Chimpanzee signs were frequently found along the forest edge in this study, suggesting they are frequently using this area of the forest as part of their home range. As human populations grow, parks will become further isolated, and measuring and managing edge effects may be crucial to achieving conservation objectives. A recent study showed that chimpanzees adjust their movement strategies as food availability changes (Reyna-Hurtado et al, 2018), thus it is very crucial to better understand primate socioecological behaviors and the main attractions outside the forest. In Gisovu, beehives were raided by chimpanzees outside the park (pers. obs). Beekeeping is one of the main activities that generate income in Gisovu, so better beekeeping practices could reduce human-chimpanzee conflicts in Gisovu.

People around the park at Gisovu appear to be tolerant toward chimpanzees and baboons crop raiding activities. During informal interviews, community members mentioned that due to crop raiding by chimpanzees and baboons, they have stopped cultivating in the fields around the park. They also mentioned that the Rwanda Development Board (RDB), an institution in charge of the parks, provides farmers with compensation fees for every crop damaged by wildlife, which increased people's tolerance toward chimpanzees and other crop-raiders. However, due to the severity of crop damage by chimpanzees in Gisovu, there is a need for a sustainable solution and more studies are needed to understand this problem.

The limited time frame for this study was a limitation and, in the future, more data should be collected over a larger area and for longer duration to consider other factors such as seasons, elevation and type of landscape to better understand chimpanzee ranging patterns in and outside Nyungwe. Using technologies such as GIS and remote sensing could also help to better understand how different land use types in the surrounding matrix around Nyungwe National Park influence chimpanzee movement outside the park. This information will help park managers reduce or prevent chimpanzee-human conflicts. Lastly, it is important that Nyungwe park management devote resources to understand the ecological causes of human-wildlife conflict around Nyungwe, so as to find ways to mitigate and eventually prevent these conflicts.

6. REFERENCE CITED

- Ali, J., Benjaminsen, T. A., Hammad, A. A., & Dick, Ø. B. (2005). The road to deforestation: An assessment of forest loss and its causes in Basho Valley, Northern Pakistan. *Global Environmental Change*, 15(4), 370-380.
- Arakwiye, B. (2014). *Mapping and modeling edge effects in response to matrix types around Nyungwe National Park, Rwanda: Implications for protected areas conservation* (Master's thesis). Antioch University New England, Keene, NH.
- Ban, S. D., Boesch, C., & Janmaat, K. R. (2014). Taï chimpanzees anticipate revisiting high-valued fruit trees from further distances. *Animal cognition*, 17(6), 1353-1364.
- Boesch, C., & Boesch, H. (1984). Mental map in wild chimpanzees: an analysis of hammer transports for nut cracking. *Primates*, *25*(2), 160-170.
- Bortolamiol, S., Cohen, M., Potts, K., Pennec, F., Rwaburindore, P., Kasenene, J., ... & Krief, S. (2014). Suitable habitats for endangered frugivorous mammals: small-scale comparison, regeneration forest and chimpanzee density in Kibale National Park, Uganda. *PloS one*, 9(7), e102177.
- Bufalo, F. S., Galetti, M., & Culot, L. (2016). Seed Dispersal by Primates and Implications for the Conservation of a Biodiversity Hotspot, the Atlantic Forest of South America. *International Journal of Primatology*, 37(3), 333-349.

Calder, W. (1984). Size, function, and life history. Cambridge, MA: Harvard University Press.

Chapman, C. A., Wasserman, M. D., Gillespie, T. R., Speirs, M. L., Lawes, M. J., Saj, T. L., & Ziegler, T. E. (2006). Do food availability, parasitism, and stress have synergistic effects on red colobus populations living in forest fragments? *American Journal of Physical Anthropology*, 131(4), 525-534.

- Chapman, C. A., Speirs, M. L., Gillespie, T. R., Holland, T., & Austad, K. M. (2006). Life on the edge: gastrointestinal parasites from the forest edge and interior primate groups. *American Journal of Primatology*, 68(4), 397-409.
- Corbin, G. D., & Schmid, J. (1995). Insect secretions determine habitat use patterns by a female lesser mouse lemur (Microcebus murinus). *American Journal of Primatology*, 37(4), 317-324.
- Crawford, A. (2012). Conflict-Sensitive Conservation in Nyungwe National Park: Conflict analysis. *International Institute for Sustainable Deelopement Report*.
- Elias, N. Y. A. N. D. W. I. (2005). Road Edge Effect on Forest Canopy Structure and Epiphyte Biodiversity in a Tropical Mountainous Rainforest Nyungwe National Park, Rwanda (Doctoral dissertation, MSc. Thesis, International Institute for Geo-Information Science and Earth Observation, Netherlands).
- Estrada, A., & Coates-Estrada, R. (1996). Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. *International journal of primatology*, *17*(5), 759-783.
- Estrada, A., Raboy, B. E., & Oliveira, L. C. (2012). Agroecosystems and primate conservation in the tropics: a review. *American Journal of Primatology*, *74*(8), 696-711.
- Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Di Fiore, A., ... & Rovero, F. (2017). Impending extinction crisis of the world's primates: Why primates matter. *Science Advances*, *3*(1), e1600946
- Filloy, J., Zurita, G. A., Corbelli, J. M., & Bellocq, M. I. (2010). On the similarity among bird communities: Testing the influence of distance and land use. *Acta Oecologica*, 36(3), 333-338.

- Fitzgerald, M., Coulson, R., Lawing, A. M., Matsuzawa, T., & Koops, K. (2018). Modeling habitat suitability for chimpanzees (Pan troglodytes verus) in the Greater Nimba Landscape, Guinea, West Africa. *Primates*, 1-15.
- Furuichi, T., & Hashimoto, C. (2004). Botanical and topographical factors influencing nesting-site selection by chimpanzees in Kalinzu Forest, Uganda. *International Journal of Primatology*, 25(4), 755-765.
- Gapusi R. J., Rushemuka P., Nkundimana V. (2010). Quarry restoration of natural vegetation in Nyungwe National Park. 14(38p.
- Goldberg, T. L., Gillespie, T. R., Rwego, I. B., Estoff, E. L., & Chapman, C. A. (2008). Forest fragmentation as cause of bacterial transmission among nonhuman primates, humans, and livestock, Uganda. *Forest*, 14(9),1375-1382.
- Gross-Camp., Kaplin, BA (2005). Chimpanzee (*Pan troglodytes*). Seed Dispersal in an Afromontane Forest: Microhabitat Influences on the Post Dispersal Fate of Large Seeds. Biotropica 37(4): 641–649.
- Gross-Camp, N. D., & Kaplin, B. A. (2011). Differential seed handling by two African primates affects seed fate and establishment of large-seeded trees. *Acta Oecologica*, *37*(6), 578-586.
- Gross-Camp, N. D., Martin, A., McGuire, S., & Kebede, B. (2015). The privatization of the Nyungwe National Park Buffer Zone and implications for adjacent communities. *Society* & *Natural Resources*, 28(3), 296-311.
- Grow, N., Gursky, S., & Duma, Y. (2013). Altitude and forest edges influence the density and distribution of pygmy tarsiers (Tarsius pumilus). *American journal of primatology*, 75(5), 464-477.

- Hockings, K., & Humle, T. (2009). *Best practice guidelines for the prevention and mitigation of conflict between humans and great apes* (No. 37). Gland, Switzerland: IUCN.
- Hockings, K. J., Anderson, J. R., & Matsuzawa, T. (2006). Road crossing in chimpanzees: a risky business. *Current Biology*, 16(17), R668-R670.
- Hockings, K. J., Yamakoshi, G., Kabasawa, A., & Matsuzawa, T. (2010). Attacks on local persons by chimpanzees in Bossou, Republic of Guinea: long-term perspectives. *American journal* of primatology, 72(10), 887-896.
- Jönsson, M. T., Fraver, S., Jonsson, B. G., Dynesius, M., Rydgård, M., & Esseen, P. A. (2007). Eighteen years of tree mortality and structural change in an experimentally fragmented Norway spruce forest. *Forest Ecology and Management*, 242(2-3), 306-313.
- Junker, J., Blake, S., Boesch, C., Campbell, G., Toit, L. D., Duvall, C., ... & Ganas-Swaray, J. (2012). Recent decline in suitable environmental conditions for African great apes. *Diversity and Distributions*, 18(11), 1077-1091.
- Kaplin, B. A., & Moermond, T. C. (1998). Variation in seed handling by two species of forest monkeys in Rwanda. *American Journal of Primatology*, 45(1), 83-101.
- Kremsater L, Bunnell FL. 1999. Edge effects: theory, evidence and implications to management of western North American forests. In: Rochelle JA, Lehmann LA, Wisniewski J, editors.Forest fragmentation: wildlife and management implications. Leiden, the Netherlands: Brill. 117–153
- Krief S, Cibot M, Bortolamiol S, Seguya A, Krief J-M, Masi S (2014) Wild Chimpanzees on the Edge: Nocturnal Activities in Croplands. PLOS ONE | www.plosone.org October 2014, Volume 9, Issue 10 e109925.

- Kubwimana, J.P 2013. Assessment of Matrix and Edges Effects on chimpanzee habitat and behavioral ecology in Nyungwe National Park (Master's thesis). The University of Rwanda, Kigali, Rwanda.
- Kumara, H. N., & Singh, M. (2004). Distribution and abundance of primates in rain forests of the Western Ghats, Karnataka, India and the conservation of Macaca silenus. *International Journal of Primatology*, 25(5), 1001-1018.
- Lambert, J. E. (2010). Primate seed dispersers as umbrella species: a case study from Kibale National Park, Uganda, with implications for Afrotropical forest conservation. American Journal of Primatology; 73(1):9-24.
- Lambshead, P.J.D., Paterson, G.L.J., Gage, J.D. (1977). Bio Diversity professional beta. The natural History Museum & The Scottish Association for Marine Science. http://www.nhm.ac.uk/zoology/bdpro
- Laurance, W. F., & Yensen, E. (1991). Predicting the impacts of edge effects in fragmented habitats. *Biological conservation*, 55(1), 77-92.

Laurance, W. F., Ferreira, L. V., Rankin-de Merona, J. M., & Laurance, S. G. (1998). Rain forest fragmentation and the dynamics of Amazonian tree communities. Ecology, 79(6), 2032-2040.

Lehman, S. M., Rajaonson, A., & Day, S. (2006). Edge effects and their influence on lemur density and distribution in southeast Madagascar. *American Journal of Physical Anthropology*, *129*(2), 232-241.

Lindenmeyer, D. B., & Fischer, J. (2006). Habitat fragmentation and landscape change. *An Ecological and Conservation Synthesis*, 8.

Martino, R. M. (2015). Matrix and Edge Effects on the Maintenance of Ecological Function in an Afromontane Protected Area (Doctoral dissertation). Antioch University New England, Keene, NH.

- Masozera, M.K. (2002). Socio-economic impact analysis of the conservation of Nyungwe Forest Reserve, Rwanda (Master's thesis). University of Florida, Gainesville, FL.
- McLennan, M. R., & Hockings, K. J. (2014). Wild chimpanzees show group differences in selection of agricultural crops. *Scientific reports*, *4*, 5956.
- Murcia, C. (1995). Edge effects in fragmented forests: implications for conservation. *Trends in* ecology & evolution, 10(2), 58-62.
- Ndimuligo Sood A. (2007). Assessment of chimpanzee (Pan troglodytes) population and habitat in Kwitanga forest, western Tanzania (Master's thesis). University of Witwatersrand, Johannesburg, South Africa.
- Normand, E., & Boesch, C. (2009). Sophisticated Euclidean maps in forest chimpanzees. *Animal Behaviour*, 77(5), 1195-1201.
- Normand, E., Ban, S. D., & Boesch, C. (2009). Forest chimpanzees (Pan troglodytes verus) remember the location of numerous fruit trees. *Animal cognition*, *12*(6), 797-807.
- Seiler, N., & Robbins, M. M. (2016). Factors influencing ranging on community land and crop raiding by mountain gorillas. *Animal Conservation*, 19(2), 176-188.
- Seiler, N., Boesch, C., Stephens, C., Ortmann, S., Mundry, R., & Robbins, M. M. (2018). Social and ecological correlates of space use patterns in Bwindi mountain gorillas. *American journal of primatology*, e22754.

- Sih, A., Ferrari, M. C., & Harris, D. J. (2011). Evolution and behavioural responses to humaninduced rapid environmental change. *Evolutionary Applications*, 4(2), 367-387.
- Oates JF, Tutin CEG, Humle T, Wilson ML, Baillie JEM, Balmforth Z, Blom A, Boesch C, Cox D, Davenport T, Dunn A, Dupain J, Duvall C, Ellis CM, Farmer KH, Gatti S, Greengrass E, Hart J, Herbinger I, Hicks C, Hunt KD, Kamenya S, Maisels F, Mitani JC, Moore J, Morgan BJ, Morgan DB, Nakamura M, Nixon S, Plumptre AJ, Reynolds V, Stokes EJ, Walsh PD. 2008. Pan troglodytes. In: IUCN 2009. *IUCN Red List of Threatened Species*. Version 2009.2, hwww.iucnredlist.orgi, Downloaded on 08 December 2009.
- Olupot, W. (2004). *Edge effect on trees and large mammal distribution*. In Olupot W., Boundary edge effects in Bwindi Impenetrable National park. A report. Institute of Tropical Forest Conservation. Uganda. Pp 127-186.
- Pienkowski, M. W., Watkinson, A. R., Kerby, G., Naughton-Treves, L., Treves, A., Chapman, C.,
 & Wrangham, R. (1998). Temporal patterns of crop-raiding by primates: linking food availability in croplands and adjacent forest. *Journal of Applied Ecology*, 35(4), 596-606.

Reyna-Hurtado, R., Teichroeb, J. A., Bonnell, T. R., Hernández-Sarabia, R. U., Vickers, S. M., Serio-Silva, J. C., ... & Stephens, D. (2017). Primates adjust movement strategies due to changing food availability. *Behavioral Ecology*.

Rode, K. D., Chapman, C. A., Chapman, L. J., & McDowell, L. R. (2003). Mineral resource availability and consumption by colobus in Kibale National Park, Uganda. *International Journal of Primatology*, *24*(3), 541-573.

RStudio Team (2015). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL <u>http://www.rstudio.com/</u>.

- Rwanda Development Board (2010). *Nyungwe National Park Management Plan 2012-2021*. Rwanda: Rwanda Development Board.
- Junker, J., Blake, S., Boesch, C., Campbell, G., Toit, L. D., Duvall, C., ... & Ganas-Swaray, J. (2012). Recent decline in suitable environmental conditions for African great apes. *Diversity and Distributions*, 18(11), 1077-1091.
- Plumptre, A. J. (2010). *Eastern Chimpanzee (Pan Troglodytes Schweinfurthii): Status Survey and Conservation Action Plan, 2010-2020.* Gland, Switzerland: IUCN.
- Plumptre, A. J., & Reynolds, V. (1997). Nesting behavior of chimpanzees: implications for censuses. *International Journal of Primatology*, 18(4), 475-485.
- Seiler, N., & Robbins, M. M. (2015). Factors influencing ranging on community land and crop raiding by mountain gorillas. *Animal Conservation*, 19(2), 176-188.
- Terada, S., Nackoney, J., Sakamaki, T., Mulavwa, M. N., Yumoto, T., & Furuichi, T. (2015).
 Habitat use of bonobos (Pan paniscus) at Wamba: Selection of vegetation types for ranging, feeding, and night-sleeping. *American journal of primatology*, 77(6), 701-713.
- Treves, (1997). Self-protection in Primates (Dissertation). Harvard University, Cambridge, MA.
- Ukizintambara, T. (2010). Forest Edge Effects on the Behavioral Ecology of L'Hoest's Monkey (Cercopithecus lhoesti) in Bwindi Impenetrable National Park, Uganda (Doctoral dissertation). Antioch University, Keene, NH.
- Wilson, M. L., & Wrangham, R. W. (2003). Intergroup relations in chimpanzees. *Annual Review* of Anthropology, 32(1), 363-392.

