#### Regis University

# [ePublications at Regis University](https://epublications.regis.edu/)

Regis University Student Publications<br>(comprehensive collection)

Regis University Student Publications

Spring 2018

# MS Environmental Biology Capstone Project

Elizabeth Sheehan Regis University

Follow this and additional works at: [https://epublications.regis.edu/theses](https://epublications.regis.edu/theses?utm_source=epublications.regis.edu%2Ftheses%2F879&utm_medium=PDF&utm_campaign=PDFCoverPages)

## Recommended Citation

Sheehan, Elizabeth, "MS Environmental Biology Capstone Project" (2018). Regis University Student Publications (comprehensive collection). 879. [https://epublications.regis.edu/theses/879](https://epublications.regis.edu/theses/879?utm_source=epublications.regis.edu%2Ftheses%2F879&utm_medium=PDF&utm_campaign=PDFCoverPages)

This Thesis - Open Access is brought to you for free and open access by the Regis University Student Publications at ePublications at Regis University. It has been accepted for inclusion in Regis University Student Publications (comprehensive collection) by an authorized administrator of ePublications at Regis University. For more information, please contact [epublications@regis.edu](mailto:epublications@regis.edu).

# MS ENVIRONMENTAL BIOLOGY CAPSTONE PROJECT

by

Elizabeth A. Sheehan

A Project Presented in Partial Fulfillment of the Requirements for the Degree Masters of Science in Environmental Biology

> REGIS UNIVERSITY May, 2018

# MS ENVIRONMENTAL BIOLOGY CAPSTONE PROJECT

by

Elizabeth A. Sheehan

has been approved

May, 2018

# APPROVED:



# Table of Contents





 $iv$ 

# TABLES AND FIGURES

# Chapter 3, List of Tables

<span id="page-5-1"></span><span id="page-5-0"></span>

# Chapter 3, List of Figures

<span id="page-5-2"></span>

# <span id="page-6-0"></span>CHAPTER 1. LITERATURE REVIEW: IMPACTS OF NATURAL VERSUS ANTHROPOGENIC EDGES ON WILDLIFE POPULATIONS

Widespread deforestation is a leading cause of biodiversity loss (Sanchez-Azofeifa et al. 2003). Community stability is closely tied to a region's level of biodiversity (Tilman 1999). Due to the effects of deforestation, forest fragmentation – breaking up of forest into small disconnected patches which increases the edge to interior ratio – creates new biological obstacles for the resident species, including edge effects (Broadbent et al. 2008). Edge effects are when established boundaries around forest fragments allow for newly introduced biotic and abiotic conditions to impact the forest (Schwitzer 2011). Additionally, forest edges are expanding inwards, thereby decreasing the size of forest fragments either by natural (i.e. rivers, habitat changes, etc.) or anthropogenic causes (i.e. deforestation to create roads, logging, etc.) (Gascon et al. 2000). Once a forest edge is established, extreme protective measures must be enforced in order to keep the fragment at its original size (Gascon et al. 2000). However, once introduced, edge effects rarely ever allow a forest fragment to grow in size; because of the changes at the edge, these effects are never completely reversed (Gascon et al. 2000). Overall, compared to natural edges, anthropogenic edges have greater negative effects on wildlife populations, specifically concerning species richness and density, survival, predator-prey relationships and reproduction, including the different areas and forest layers of the fragment they reside in. Therefore, conservation planning must be adjusted accordingly to account for these greater negative effects caused by anthropogenic edges as compared to natural edges.

Neither flora nor fauna are independently affected by edges. Edges create a distinct boundary around these fragments, which causes varying levels of light, wind, moisture and temperature to produce an amplified effect on the fragment itself, producing a microclimate at the edge (Chen et al. 1999; Hardt et al. 2013). Once a fragment edge is firmly established, the fragment will continue to shrink in size, thereby increasing the edge effects (Gascon et al. 2000). Regeneration of vegetation at the edge is vital to protect the interior of the forest fragment from microclimate changes at the edge (Gascon et al. 2000). Since forest fragments are often surrounded by privately-owned or government-owned agricultural lands (Tabarelli et al. 2008), anthropogenic edges do not allow for regeneration to occur due to the presence of human structures, so this fragility at the new edge of anthropogenic-caused fragments never subsides. This level of permanent susceptibility allows pioneer species and turnover events (the disappearance of a species from a community, allowing new species to invade) to occur at increased rates in anthropogenic edges as compared to natural edges (Murcia 1995). Therefore, the reasons behind the origins of forest fragments edges matter; anthropogenic edges generate additional impacts on wildlife compared to natural edges (Murcia 1995). These additional effects (i.e. increased levels of light, noise and disturbance) should be considered when developing conservation management plans for forest fragments; treating the conservation of natural forest fragments identical to anthropogenically-created forest fragments will fail to properly address these different effects.

While anthropogenic fragments have negative effects on animals (Murcia 1995), natural edges still introduce obstacles for wildlife. The change of habitat from the interior of the fragment to the edge decreases vegetation levels in natural edges, altering the natural habitat of animals who reside in the fragment (Murcia 1995). Additionally, bodies of water that form a natural edge impede travel between habitats and decrease the available space and resources for wildlife (Murcia 1995). If a habitat specialist species relies solely on the presence of trees and a

natural edge is established between a forest and a prairie, resources are again limited at the edge. Therefore, conservation planning needs to examine the origin of forest fragmentation, as anthropogenic edges might be harder to cross or further limit resource availability compared to natural edges. An animal might be unable to travel through or around a human-made structure that is constantly emitting sound whereas the animal might easily be able to cross a river. Multiple species, including birds, can be affected by anthropogenic edges.

Anthropogenic edges negatively affected bird population density in Alberta, Canada (Bayne et al. 2008). Researchers measured the abundance of *Zonotrichia albicollis, Dendroica coronate* and *Vireo olivaceus* in varying distances from noise-generating compressor stations established at anthropogenic edges in a boreal forest. The level, location and timespan of sounds coming from anthropogenic edges are important factors on several song bird species, as bird population density increased with distance away from anthropogenic edges due to the difference in sound levels (Bayne et al. 2008). Such resulting impacts of anthropogenic edges play an important role which might not exist or be as obvious with a natural edge. Sounds created by construction, traffic and other human activity are not necessarily a constant presence in natural forest fragments. Therefore, these additional disturbances more negatively impact bird populations in anthropogenic forest fragments compared to those bird populations residing in natural forest fragments (Bayne et al. 2008). Human-created sound is a factor that must be considered when creating conservation plans at anthropogenic edges. Permits establishing noiselevel limits would aid in lessening the impacts in an anthropogenic forest fragment for avian populations.

Anthropogenic edges also directly affect the food sources of avian populations, specifically through decreasing fragment size and abiotic factors, such as light (Galetti et al. 2003). By measuring the number of pecks on evenly-distributed fake fruit, researchers studied foraging patterns of various bird populations between the interior and edge of an anthropogenically-induced (clear-cut) forest fragment in Southeast Brazil. More fruit was "consumed" in the edge than the interior, which was attributed to increased light levels in the edge. Anthropogenic edges decreased vegetation levels at the edge, allowing more light into the edge, letting birds find fruit more easily. More fruit was consumed in larger anthropogenicallyinduced fragments as compared to smaller fragments (Galetti et al. 2003). These results indicate that smaller anthropogenically-induced fragments negatively impact foraging patterns of birds and changing levels of abiotic factors at anthropogenic edges also alter the ways in which birds obtain food. Wildlife populations' foraging preferences could also further decrease the vegetation levels at the edge, increasing fragility and susceptibility of the anthropogenic fragment at the edge.

Bird populations are also affected by natural edge impacts. Researchers in Argentina used mist-nets to sample bird populations, measuring 74 bird species' abundance and richness (de Casenave et al. 1998). Bird species abundance and richness increased in the edge (where the forest fragment is replaced by meadows) compared to the interior while successional avian species were only present in the edge (de Casenave et al. 1998). Additionally, avian insectivores that eat "short-flight" and bark-living insects are more abundant in the interior, while birds that prey on "long-flight" insects are more abundant in the edge (de Casenave et al. 1998). This means that birds who prey upon certain insects are now limited according to the habitat availability of their prey between the edge and interior. Since the opportunity for vegetation regrowth is higher in natural edges compared to anthropogenic edges (Murcia 1995), the impact on food availability for wildlife populations between edge and interior is longer-lasting in

anthropogenic edges than natural edges, as these insects are limited by specific habitat. Conservation efforts should take into account not just the species they are trying to protect in forest fragments, but also the prey that the species consumes and how that prey is also affected by edges. Conservation efforts would benefit by taking more extreme measures in anthropogenically-edged forests than naturally-edges fragments, as the effects to wildlife populations are worse in the former.

Wildlife in other kinds of habitat in addition to forest fragments are also more negatively affected by anthropogenic edges than natural edges. In Southeastern Ontario, Canada, for example, the presence of roads negatively affected species richness within wetlands for birds, reptiles, amphibians and plants (Findlay & Houlahan 1997). Researchers found that the edge impacts created by roads measured as far as 2 kilometers from the wetland (Findlay & Houlahan 1997). In addition, forest cover leading up to the anthropogenic edge from the wetland interior positively increased mammal, reptile and amphibian species richness (Findlay & Houlahan 1997). Similarly, increased light levels created by decreasing canopy and litter cover at silvicultural edges (the practice of regenerating, tending and harvesting forests) negatively affected fourteen salamander species in Maine (Demaynadier & Hunter 1998). Salamander population abundance significantly increased within increasing proximity to the interior, away from clear-cut edges (Demaynadier & Hunter 1998). In naturally-bordered wetlands surrounded by pastures, population abundance in frogs was mostly impacted by seasonality (Schlaepfer & Gavin 2001). During the wet season, frog population abundance increased in the interior compared to the edge, while decreasing in the dry season (Schlaepfer & Gavin 2001). Fragment size and distance to the edge did not significantly affect five species of leaf-litter frog (*Eleutherodactylus)* population abundances in a forest fragment naturally-bordered by pastures in Las Cruces, Costa Rica (Schlaepfer & Gavin 2001). These studies suggest that compared to naturally-fragmented habitat, anthropogenic edges more strongly affect amphibian populations. Therefore, when establishing conservation plans for anthropogenic forest fragments compared to natural fragments, the impact of human-induced effects on the abiotic factors already present at the edge must be realized.

Anthropogenic edges also negatively impact the interactions between wildlife populations. Researchers applied radio telemetry to the native leopard (*Panthera pardus)*  population in the protected habitat of Phinda-Mkhuze Complex (P.M.C.) located in South Africa (Balme et al. 2010). Hunting caused higher rates of leopard mortality at the anthropogenic edge (formed by surrounding villages and fencing) than the interior (Balme et al. 2010). While the establishment of the reserve positively affected the leopard population overall, anthropogenic edges around the reserve weakened the P.M.C.'s ability to protect the leopard population (Balme et al. 2010). Because leopards are a carnivorous, predatory species, the ability of a reserve to protect this population has a top-down effect on the populations they prey upon. By preying on lower species within the food chain and keeping prey populations from overproducing, predators help stabilize the ecological balance of habitats. The increased mortality predators face from anthropogenic edges (due to events such as hunting, logging and clear-cutting) negatively alters this predator-prey balance (Rodewald et al. 2011). Policies put in place to ban the hunting of these populations would greatly decrease the mortality rates of animals living in anthropogenically-created forest fragments.

Ultimately, compared to natural edges, anthropogenic edges have a greater negative effect on wildlife populations (Balme et al. 2010; Bayne et al. 2008; de Casenave et al. 1998; Demaynadier & Hunter 1998; Findlay & Houlahan 1997; Galetti et al. 2003; Murcia 1995;

Schlaepfer & Gavin 2001). While both types of edge have an impact on the species within forest fragments, anthropogenic edges introduce additional factors that are not present in natural edges, such as additional noise, human-built structures, manmade obstacles and an increased rate of mortality (Murcia 1995; Rodewald et al. 2011). These factors further impede a population's ability to successfully reproduce in an anthropogenic edge and interfere in predator-prey relationships between populations (Rodewald et al. 2011). Anthropogenic impacts such as increased sound and the construction of human facilities may also exaggerate natural events and abiotic factors. Deforestation and harvesting of forest resources can alter the light levels and canopy cover of a forest, thereby changing the habitat of animal populations (Demaynadier & Hunter 1998). Because there is a lower level of vegetation growth at anthropogenic edges compared to natural edges (Murcia 1995), this change in habitat at anthropogenic edges creates longer-lasting effects than those seen in natural edges.

Since anthropogenic edges have a larger negative effect on wildlife populations compared to natural edges, management plans and conservation efforts to preserve any species residing in fragmented habitat should address these differences and adjust efforts accordingly. Future conservation planning for both natural and anthropogenically-induced forest fragments must consider edge effects and their negative impacts on wildlife populations. However, the conservation measures implemented at anthropogenically-induced forest fragments should reflect these more negative effects, whether that be through employing stricter environmental policy laws, permitting or additional funding. Wildlife populations living in anthropogenically-edged fragments would benefit from bans on hunting and deforestation, which are some additional threats these populations face compared to living in a naturally-edge forest fragment (Rodewald et al. 2011. Permits restricting noise levels and human construction are also further examples that

would aid in protecting these populations. Multiple options are available for policymakers to employ in order to reduce anthropogenic impacts on wildlife; anthropogenic forest fragments must be given more protection and attention in order to address the additional impacts they create compared to natural forest fragments.

- <span id="page-14-0"></span>Balme, G. A., Slotow, R. O. B., & Hunter, L. T. (2010). Edge effects and the impact of nonprotected areas in carnivore conservation: leopards in the Phinda–Mkhuze Complex, South Africa. *Animal Conservation*, *13*(3), 315-323.
- Bayne, E. M., Habib, L., & Boutin, S. (2008). Impacts of chronic anthropogenic noise from energy‐sector activity on abundance of songbirds in the boreal forest. *Conservation Biology*, *22*(5), 1186-1193.
- Broadbent, E. N., Asner, G. P., Keller, M., Knapp, D. E., Oliveira, P. J., & Silva, J. N. (2008). Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biological Conservation*, *141*(7), 1745-1757.
- de Casenave, J. L., Pelotto, J. P., Caziani, S. M., Mermoz, M., & Protomastro, J. (1998). Responses of avian assemblages to a natural edge in a Chaco semiarid forest in Argentina. *The Auk*, 425-435.
- Chen, J., Saunders, S. C., Crow, T. R., Naiman, R. J., Brosofske, K. D., Mroz, G. D., ... & Franklin, J. F. (1999). Microclimate in forest ecosystem and landscape ecology: variations in local climate can be used to monitor and compare the effects of different management regimes. *BioScience*, *49*(4), 288-297.
- Demaynadier, P. G., & Hunter, M. L. (1998). Effects of silvicultural edges on the distribution and abundance of amphibians in Maine. *Conservation Biology*, *12*(2), 340-352.
- Findlay, C. S., & Houlahan, J. (1997). Anthropogenic correlates of species richness in southeastern Ontario wetlands. *Conservation Biology*, *11*(4), 1000-1009.
- Galetti, M., Alves-Costa, C. P., & Cazetta, E. (2003). Effects of forest fragmentation, anthropogenic edges and fruit colour on the consumption of ornithocoric fruits. *Biological Conservation*, *111*(2), 269-273.
- Gascon, C., Williamson, G. B., & da Fonseca, G. A. (2000). Receding forest edges and vanishing reserves. *Science*, *288*(5470), 1356-1358.
- Hardt, E., Pereira-Silva, E. F., Dos Santos, R. F., Tamashiro, J. Y., Ragazzi, S., & Lins, D. B. D. S. (2013). The influence of natural and anthropogenic landscapes on edge effects. *Landscape and Urban Planning*, *120*, 59-69.
- Murcia, C. (1995). Edge effects in fragmented forests: implications for conservation. *Trends in Ecology & Evolution*, *10*(2), 58-62.
- Rodewald, A. D., Kearns, L. J., & Shustack, D. P. (2011). Anthropogenic resource subsidies decouple predator–prey relationships. *Ecological Applications*, *21*(3), 936-943.
- Sanchez-Azofeifa, G. A., Daily, G. C., Pfaff, A. S., & Busch, C. (2003). Integrity and isolation of Costa Rica's national parks and biological reserves: examining the dynamics of landcover change. *Biological Conservation*, *109*(1), 123-135.
- Schlaepfer, M. A., & Gavin, T. A. (2001). Edge effects on lizards and frogs in tropical forest fragments. *Conservation Biology*, *15*(4), 1079-1090.
- Schwitzer, C., Glatt, L., Nekaris, K. A. I., & Ganzhorn, J. U. (2011). Responses of animals to habitat alteration: an overview focusing on primates. *Endangered Species Research*, *14*(1), 31-38.

Stewart, B. P., Nelson, T. A., Laberee, K., Nielsen, S. E., Wulder, M. A., & Stenhouse, G.

(2013). Quantifying grizzly bear selection of natural and anthropogenic edges. *The Journal of Wildlife Management*, *77*(5), 957-964.

- Tabarelli, M., Lopes, A. V., & Peres, C. A. (2008). Edge-effects drive tropical forest fragments towards an early‐successional system. *Biotropica*, *40*(6), 657-661.
- Tilman, D. (1999). The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, *80*(5), 1455-1474.

# <span id="page-17-0"></span>CHAPTER 2 GRANT PROPOSAL: COMPARING GROUP SIZE AND SEX RATIOS OF *C. CAPUCINUS* BETWEEN NATURAL AND ANTHROPOGENIC EDGES IN A COSTA RICAN FOREST FRAGMENT

## Abstract

<span id="page-17-1"></span>Deforestation negatively impacts wildlife populations, specifically through the establishment of forest fragments – the breaking up of forest into small disconnected patches which increases the edge to interior ratio. Forest fragments are either created naturally or by anthropogenic causes. While both exhibit negative impacts on wildlife populations, anthropogenic edges may more negatively impact an animal population's group size and sex ratio, which are vital to a population's reproductive success and survival. The purpose of this research project is to gain insight into the effects of both natural and anthropogenic forest edges on white-faced capuchin's (*Cebus capucinus*) group size and sex ratio. The research will be conducted at La Suerte Biological Field Station (LSBFS) in Costa Rica, under the guidance of Dr. Amy Schreier. It is hypothesized that vegetation richness and tree diameter at breast height (DBH) are higher in natural edges compared to anthropogenic edges, creating varying levels of food sources and habitat. Therefore, I predict that *C. capucinus* will have smaller group sizes and less even sex ratios in the anthropogenic edge compared to the natural edge because of the limited DBH and tree species richness present in the anthropogenic edge. I will record the number and sex of individuals in a group within a twenty-meter radius. This research will help to increase the understanding of the negative effects of forest edges and deforestation on animal populations. It will be the first of its kind within this study site and will have implications for conservation globally.

## Background/Rationale/Significance

<span id="page-18-0"></span>Widespread deforestation is a leading cause of biodiversity loss (Sanchez-Asofiefa et al. 2003). Community stability is closely tied to a region's level of biodiversity, including plant species richness, disturbance levels and nutrient supply (Tilman 1999). Forest fragmentation – breaking up of forest into small disconnected patches which increases the edge to interior ratio – creates new ecological obstacles for the resident species, including edge effects (Broadbent et al. 2008).

Edge effects occur when boundaries established around forest fragments allow introduced biotic (plants and animals) and abiotic (factors such as sunlight and temperature) conditions to impact the forest (Schwitzer et al. 2011). By creating a distinct boundary around these fragments, varying levels of light, wind, moisture and temperature have an amplified effect on the fragment, creating a microclimate (Chen et al. 1999). Fragments are especially susceptible to invasion from foreign or generalist species from the bordering territory, furthering the possibility of promoting an ecological shift within the environment (Laurance et al. 1998). Once a fragment edge is firmly established, it can lead to the recession of the fragment itself, thereby increasing the edge effects while simultaneously decreasing the size of the forest fragment, either by natural or anthropogenic causes (Gascon et al. 2000). Naturally-occurring events, such as extreme weather (i.e. a hurricane that destroys part of a forest) or bodies of water bordering a fragment establish natural edges (Broadbent et. al 2008). Conversely, human-induced activity, such as the construction of buildings or clear-cutting of forest for logging, forms anthropogenic edges (Broadbent et. al 2008). Compared to natural edges, anthropogenic edges may more negatively affect wildlife populations residing in forest fragments (Wade et. al 2003). Therefore, I will

investigate these effects on white-faced capuchin monkeys (*Cebus capucinus)* in a Costa Rican forest fragment.

Natural edges can still present obstacles for wildlife (Malcolm 1994). Edge effects decrease vegetation at the edge of a forest fragment, altering the natural habitat of animals who reside in the fragment (Broadbent et. el 2008). Natural edges negatively affect various wildlife populations including several amphibian species (Schlaepfer & Gavin 2001) and mantled howler monkeys (*Alouatta palliata)* (Schwitzer et al. 2011). Specifically, the cerro utyum rubber frog (*E. podiciferus)* and the chiriqui rubber frog (*E. cruentus)* populations are more abundant in the interior than the edge (where fragments are surrounded by natural pastures and ponds) (Schlaepfer & Gavin 2001) and mantled howler monkeys face significantly higher levels of mortality through the establishment of natural edges (i.e. bodies of water, such as a river) due to natural disasters (Schwitzer et al. 2011). Therefore, it is important to study how natural edges affect other primate populations to determine any additional possible threats that might also exist.

Anthropogenic edges may also pose threats to wildlife populations. Since forest fragments are often surrounded by privately-owned or government-owned agricultural lands (Tabarelli et al. 2008), anthropogenic edges often do not allow for regeneration to occur due to the presence of human structures, so this fragility at the new edge of anthropogenicallyestablished fragments never subsides. Anthropogenic edges also negatively affect group sizes and sex ratios of certain wildlife species. For example, the presence of roads negatively affected the sex ratios of multiple turtle species, as females experienced higher mortality rates by crossing these roads to lay their eggs in ponds separated by anthropogenic edges (Aresco 2005). Additionally, Mbora et al. (2009) found that mangabey *(Cercocebus galeritus*) groups were

smaller in anthropogenic habitat compared to natural habitat. Smaller group sizes may negatively affect foraging success and survivability of a population by decreasing an individual's ability to find food (Mbora et al. 2009).

Edge effects also likely negatively affect capuchin monkey populations (Fedigan & Jack 2001). A neotropical monkey, *C. capucinus* lives in troop sizes of roughly twenty individuals with a higher proportion of females than males (a sex ratio of 3:1) (Fedigan  $\&$  Jack 2011) and employ a flexible foraging strategy (Phillips 1995). Philips (1995) reported that as the diameter at breast height (DBH) of fruiting trees increased, so did foraging party size. Thus, *C. capucinus*  modify their group size according to the availability of fruiting trees. Because it is hypothesized that there are lower DBH levels present at anthropogenic edges compared to natural edges (Schreier pers. comm.), it is likely that *C. capucinus* will gather in smaller groups at anthropogenic edges compared to natural edges.

Females stay within their birth group while males disperse between groups at sexual maturity (Jack & Fedigan 2004). The number of *C. capucinus* males within a group significantly alters the reproductive success of both sexes: more males in a group increases female reproductive success while fewer males increase individual male reproductive success (Fedigan & Jack 2011). Additionally, groups with fewer males are at greater risk of takeovers by outside males and thus increased infanticide (Fedigan & Jack 2011). *C. capucinus* consumes different types of food according to sex: males forage more strenuously in shorter time periods while females spend more time foraging; males acquire larger, higher-quality prey while females obtain smaller, lesser-quality prey (Rose 1994). It is then likely that there will be more females overall in both types of edges but there will be more males in anthropogenic edge than natural edges within groups due to decreased food availability at the anthropogenic edge as females

spend more time foraging than males (Phillips 1995). Studying these edge effects on sex ratios within a population is important to determine future reproductive success and population survivability within fragments containing only natural edges compared to forest fragments with anthropogenic edges (Aresco 2005).

The La Suerte Biological Field Station (LSBFS) in Costa Rica is a forest fragment containing both natural and anthropogenic edges (Garber et al. 2010). Established in the early 1990's, LSBFS encompasses 150 hectares of lowland neotropical rainforest, and is home to a multitude of flora and fauna. It is separated into two patches linked by a corridor. Cattle ranches and agricultural plantations surround both patches, culminating in clear anthropogenic borders (Malcolm 1994). The La Suerte River runs through the property, creating a natural edge. We hypothesize that tree species richness and DBH are both higher in the interior of the fragment compared to the anthropogenic edges and researchers are currently investigating this (Schreier pers. comm.). These varying levels of tree density and plant resources in the natural edges versus the anthropogenic edges may create an ecological strain on the species residing within this fragment. However, little is known about how anthropogenic and natural edges impact *C. capucinus* populations at LSBFS. Therefore, my research goal is to examine how anthropogenic and natural edges impact *C. capucinus* group sizes and sex ratios at LSBFS.

As part of its mission statement, Regis University asks its students to think critically in the search for truth and values. During my visit to LSBFS in the summer of 2017, I developed an appreciation for the impacts of forest fragmentation and edge effects on the *C. capucinus*  population. By thinking critically and searching for the truth through my research, I will be able to educate the public about deforestation and its negative impacts on wildlife. As human-induced impacts on forest fragments are occurring on a global scale, my findings can aid in the

understanding of these effects. This study will be the first of its kind to explore the impacts of anthropogenic edges compared to natural edges on *C. capucinus* group size and sex ratio at LSBFS*.* This research is necessary to evaluate the potential threats this population faces within the LSBFS forest fragment and to determine how the natural and anthropogenic edges might impact reproductive success of *C. capucinus* groups.

## Purpose and Specific Aims

<span id="page-22-0"></span>The aim of this research is to examine how anthropogenic and natural edges affect the group sizes and sex ratios of *C. capucinus* at the La Suerte Biological Field Station (LSBFS) in Costa Rica. Anthropogenic edges have a stronger negative effect on other wildlife populations than natural edges (Wade et. al 2003), affecting group size and sex ratios disproportionately (Schwitzer et al. 2011). Natural edges are at a lower risk of further degradation and may provide more opportunity for vegetation regrowth compared to anthropogenic edges (Wade et. al 2003). As edge effects naturally limit food resources, it is important to research these effects on primate populations who live in habitat containing both types of edges within the same fragment (like LSBFS). Therefore, I predict that *C. capucinus* will have smaller group sizes in the anthropogenic edge compared to the natural edge because of the hypothesized lower DBH and tree species richness present in the anthropogenic edge (Schreier pers. comm.). Furthermore, I predict that *C. capucinus* will have sex ratios with more females in the natural edges compared to the anthropogenic edges due to the higher food availability in the former. Collectively, testing these hypotheses will aid in determining how anthropogenic and natural edge impacts influence *C. capucinus'* group sizes and sex ratios.

#### Methods

#### *Study Site*

<span id="page-23-1"></span><span id="page-23-0"></span>I will conduct my research at La Suerte Biological Field Station (LSBFS) in Costa Rica (10°26'N, 88°47'W) from May 22 to August 22, 2018. At 150 hectares, the site contains both primary and secondary forest (Pruetz and Leasor 2002). This neotropical rainforest fragment includes two patches connected by a corridor. A clear anthropogenic edge has been established due to the surrounding cattle ranches and banana and pineapple plantations (Garber et al. 2010). The La Suerte River runs through the property, acting as a natural edge. Both edges are defined as extending 100 meters towards the interior from the border of the edge (Schreier et al. 2016). Several primate species inhabit the area, including white-faced capuchins (*Cebus capucinus*), Geoffrey's spider monkeys (*Ateles geoffroyi*) and mantled howler monkeys (*Alouatta palliata). C. capucinus* group sizes at LSBFS are roughly twenty individuals and there are at least two groups within the forest fragment (Pruetz & Leasor 2002). These primates have acclimated to human observation as they have been studied since the early 1990s (Garber et al. 2010).

#### *Data Collection*

<span id="page-23-2"></span>I will compare *C. capucinus* group size and sex ratios between the anthropogenic edge and natural edge to test my hypothesis of higher group sizes and more even sex ratios in the natural edges compared to the anthropogenic edges. In the early morning, I will locate a group of *C. capucinus* and follow them as long as possible, counting and recording the number of individuals within the group. I will count from the leftmost individual to the rightmost individual in a twenty-meter radius of the centermost focal individual once every twenty minutes, as well as record the sex (male or female) of each individual in that twenty-meter radius. If I am unable to follow a group at any point during sampling, I will continue to search for that same group up to

one hour. If I still cannot find that group after one hour of searching, I will locate another group of *C. capucinus.* I will sample monkeys in both the natural and anthropogenic edges of the forest. To accurately assign the groups to either type of edge, I will use a handheld GPS unit to collect the GPS location of a group of *C. capucinus* once every hour, as the groups move between both types of edges*.* Additionally, since groups move between both edges, recording individuals within a twenty-meter radius allows me to measure group cohesion between the edges. Maintaining a measure of a twenty-meter radius accounts for the group as a collective unit as they travel; without applying this type of control, it is possible for the group counts to be skewed as they move between both types of edges, which could give false results. At the end of collection, I will plot these GPS locations onto a map of the field site to determine which points are in the natural and anthropogenic edges. I will calculate the mean group size and sex ratio for both natural and anthropogenic edges and conduct t-tests to determine if differences in group size and sex ratio are statistically significant between the natural and anthropogenic edges. I will also analyze the data using generalized linear models to determine any possible variable effects (such as dependency between edge type and group size) that might influence the group sizes and sex ratios. Significance level is  $p < 0.05$ .

## Work Plan

<span id="page-24-0"></span>May 22, 2018: Arrive at La Suerte, Costa Rica

May 23 – August 22, 2018: Field Data Collection

August 22, 2018: Depart Costa Rica

September 2018: Data Analysis

October – December 2018: Project Write-Up for publication and conference presentations.

April 2019: Presentation at URSC Symposium and American Association of Physical

Anthropologists annual meeting

#### References

- <span id="page-26-0"></span>Aresco, M. J. (2005). The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. *Biological Conservation,* 123(1), 37-44.
- Broadbent, E. N., Asner, G. P., Keller, M., Knapp, D. E., Oliveira, P. J., & Silva, J. N. (2008). Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biological Conservation*, *141*(7), 1745-1757.
- Chen, J., Saunders, S. C., Crow, T. R., Naiman, R. J., Brosofske, K. D., Mroz, G. D., ... & Franklin, J. F. (1999). Microclimate in forest ecosystem and landscape ecology: variations in local climate can be used to monitor and compare the effects of different management regimes. *BioScience*, *49*(4), 288-297.
- Fedigan, L. M., & Jack, K. (2001). Neotropical primates in a regenerating Costa Rican dry forest: a comparison of howler and capuchin population patterns. *International Journal of Primatology*, *22*(5), 689-713.
- Fedigan, L. M., & Jack, K. M. (2011). Two girls for every boy: the effects of group size and composition on the reproductive success of male and female white-faced capuchins. *American journal of Physical Anthropology*, *144*(2), 317-326.
- Garber, P. A., Molina, A., & Molina, R. L. (2010). Putting the community back in community ecology and education: the role of field schools and private reserves in the ethical training of primatologists. *American Journal of Primatology*, *72*(9), 785-793.
- Gascon, C., Williamson, G. B., & da Fonseca, G. A. (2000). Receding forest edges and vanishing reserves. *Science*, *288*(5470), 1356-1358.
- Jack, K. M., & Fedigan, L. (2004). Male dispersal patterns in white-faced capuchins, *Cebus capucinus*: Part 2: patterns and causes of secondary dispersal. *Animal Behaviour*, *67*(4), 771-782.
- 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.
- Malcolm, J. R. (1994). Edge effects in central Amazonian forest fragments. *Ecology*, *75*(8), 2438-2445.
- Mbora, D. N., Wieczkowski, J., & Munene, E. (2009). Links between habitat degradation, and social group size, ranging, fecundity, and parasite prevalence in the Tana River mangabey (*Cercocebus galeritus*). *American Journal of Physical Anthropology*, *140*(3), 562-571.
- Phillips, K. A. (1995). Resource patch size and flexible foraging in white-faced capuchins (*Cebus capucinus*). *International Journal of Primatology*, *16*(3), 509-519.
- Pruetz, J. D., & Leasor, H. C. (2002). Survey of three primate species in forest fragments at La Suerte Biological Field Station, Costa Rica. *Neotropical Primates*, *10*(1), 4-9.
- Rose, L. M. (1994). Sex differences in diet and foraging behavior in white-faced capuchins (*Cebus capucinus*). *International Journal of Primatology*, *15*(1), 95-114.
- Sánchez-Asofeifa, G. A., Daily, G. C., Pfaff, A. S., & Busch, C. (2003). Integrity and isolation of Costa Rica's national parks and biological reserves: examining the dynamics of landcover change. *Biological Conservation*, *109*(1), 123-135.
- Schlaepfer, M. A., & Gavin, T. A. (2001). Edge effects on lizards and frogs in tropical forest fragments. *Conservation Biology*, *15*(4), 1079-1090.
- Schreier, A. L., Franco, M. D., Barton, M., Pryor, N. P., & Barrickman, N. L. (2016). A preliminary examination of genetic diversity in mantled howler monkeys (*Alouatta palliata*) in a fragmented forest in Costa Rica. *American Journal of Physical Anthropology,* 159 Supp., 283-284.
- Schwitzer, C., Glatt, L., Nekaris, K. A. I., & Ganzhorn, J. U. (2011). Responses of animals to habitat alteration: an overview focusing on primates. *Endangered Species Research*, *14*(1), 31-38.
- Tabarelli, M., Lopes, A. V., & Peres, C. A. (2008). Edge effects drive tropical forest fragments towards an early-successional system. *Biotropica*, *40*(6), 657-661.
- Tilman, D. (1999). The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, *80*(5), 1455-1474.
- Wade, T., Riitters, K., Wickham, J., & Jones, K. B. (2003). Distribution and causes of global forest fragmentation. *Conservation Ecology*, *7*(2).

# Prior URSC Awards

<span id="page-28-1"></span><span id="page-28-0"></span>I have previously applied for and received an URSC award in spring semester, 2017.

# Budget Justification







# URSC Project Budget Justification Narrative

<span id="page-30-0"></span>Please describe each item you listed in the budget table. The description should enable reviewers to understand a) how the cost of each item was computed, and b) how the budget items relate to your project objectives.

# *Supplies*

<span id="page-30-1"></span>Rite in the Rain Notebooks: Waterproof notebooks are required for data collection at La Suerte Biological Field Station because of the high amount of rainfall. Calculated using online pricing from Amazon.com.

Bug Spray: Calculated using online pricing from Amazon.com, required to repel mosquitos and other insects in the field.

Binoculars: Calculated using online pricing from L.L.Bean stores, required to view and identify primates in the field. These will be provided for me through the Regis University Biology Department.

<span id="page-30-2"></span>Research Assistant(s): N/A

## *Other*

Flight: Roundtrip between Denver, CO, and San Jose, Costa Rica. Calculated using online ticket prices acquired from Travelocity.com. Required for travel to La Suerte Biological Field Station

in Costa Rica. I will pay for this flight through outside sources, using a grant awarded for this research by the National Science Foundation.

Hotel: Required for my first night in San Jose, Costa Rica when I arrive. I will stay at Hotel Mi Tierra Casa Blanca near the San Jose airport. Price calculated using past field season rates. I don't need a hotel on my last night because I will be traveling directly from the field site to the airport.

Room and Board at La Suerte: The student price for room and board is \$20 per day. I will be staying at La Suerte for 90 days and thus the total cost is \$1800.00 which will be paid using funds from the grant awarded to me by the National Science Foundation.

Food: I will be staying in San Jose, Costa Rica the first night of the trip and will need to purchase food during that day in town. Breakfast is included with the hotel and thus I will need to purchase only lunch and dinner; food in San Jose is relatively inexpensive. I will also need to purchase food on the last day that I travel from the field site to the San Jose airport.

Transportation from field site to San Jose Airport: The taxi from the field site to the Cariari bus station is \$25.00. The bus from Cariari bus station to the San Jose airport is \$3.50. I don't need to pay for transportation to the field site on the first day as I am traveling with Dr. Schreier's field course.

## <span id="page-31-0"></span>**Total amount requested from URSC: \$116.80**

## Relevance to Current Coursework

This research builds on my current graduate research at Regis University about the impacts of edge effects on social cohesion and activity budgets of mantled howler monkeys at LSBFS. I will continue this research after I graduate, assisting Dr. Schreier on her research of investigating the influence of forest fragmentation on primate behavior and ecology. Using skills I have obtained from my classes in the Regis University Master's program in Environmental Biology, I am adequately prepared to carry out this research. These skills include GIS mapping from my Ecological Application of GIS class, statistical analysis from my Biostatistics class and the knowledge about animal behavior from my Advanced Behavioral Ecology class. Ultimately, my goal is to obtain a PhD in Biology and continue conducting academic research on animal

populations centering on behavior and physiology. Completing this research will allow me to gain further experience in this field.

# <span id="page-33-0"></span>CHAPTER 3 JOURNAL MANUSCRIPT: SOCIAL COHESION VARIES BY SEX BUT NOT BY FOREST ZONE AMONG MANTLED HOWLER MONKEYS (*ALOUATTA PALLIATA)* IN A COSTA RICAN FOREST FRAGMENT

## Abstract

<span id="page-33-1"></span>Social cohesion – proximity among individuals – provides primates with better access to food resources. Little is known about how primate social cohesion varies by sex in different forest zones. Due to their higher energetic demands of reproduction, females should prioritize feeding more highly than males and forest interior is expected to have higher food abundance than the edge. Therefore, we hypothesized that as a group, individuals would be more cohesive in the interior than the edge. Additionally, we hypothesized that females would be more cohesive in the interior than the edge while male cohesion would not vary by forest zone. We tested this hypothesis in *Alouatta palliata* at the La Suerte Biological Research Station, a fragmented forest in Costa Rica. We compared the number of nearest neighbors within 5m of focal subjects in the edge and interior as well as the distance to the focal individual's nearest neighbor from May-August 2017. As a group, the effect of forest zone was not different for male and female *A. palliata.* However, between sexes, females on average had significantly more nearest neighbors in the interior (1.22) than males (0.83). Females were also significantly closer to their nearest neighbors in both the interior  $(1.27m)$  and the edge  $(1.07m)$  compared to males  $(2.50m, 2.81m,$ respectively). These results suggest that while *A. palliata* social cohesion varies by sex, this population is able to cope with anthropogenic edge effects.

## Introduction

<span id="page-34-0"></span>Widespread deforestation exacerbates species loss due to habitat destruction (Sanchez-Azofeifa et al., 2003). Species loss negatively influences community stability, which consequently depresses a region's level of productivity (Tilman, 1999). Further effects of deforestation also include increased disturbance regimes and decreased herbivory levels and plant species richness (Haddad et al., 2015). Anthropogenic deforestation reduces the overall size of a forest, thereby decreasing animal population residency time within the forest while simultaneously increasing isolation levels (Haddad et al., 2015). Specifically, anthropogenic deforestation often results in forest fragmentation (Haddad et al., 2015). Forest fragmentation the breaking up of forest into small disconnected patches, or zones - increases the edge to interior ratio (Broadbent et al., 2008). This fragmentation creates new ecological pressures for the resident species, including increased edge effects (Broadbent et al., 2008).

Edge effects are a change in abiotic conditions that alters ecological processes at the forest edge (Schwitzer, 2011). The altered levels of light, wind, moisture and temperature around the boundary cause edge effects on the fragment itself creating a microclimate (Chen et al., 1999). Additionally, these newly created forest fragments are especially susceptible to invasion from foreign or generalist species from the surrounding matrix, which can promote an ecological shift within the environment (Laurance et al., 1998). For example, *Cheirogaleus major*  population densities decreased in edge habitat due to increased ambient temperatures compared to the interior zone of Madagascar forest fragments (Lehman et al., 2006). Similarly, Kirika et al. (2008) reported that local forest disturbance decreased frugivorous species densities within a forest which consequently decreased seed dispersal rates. Once a fragment edge is firmly established, the forest patch can decrease further in size, causing edge effects within that

fragment to intensify (Gascon et al., 2000). This intensification can further affect the behavior and survival of animals that reside within the forest fragment.

Specifically, social cohesion levels are an important consideration in examining these differences in edge effects in forest fragments. Social cohesion – the proximity between individuals – is vital to primate interaction, and enhances access to food, range defense, information exchange and learning (Garber & Kowalewski, 2011). Mantled howler monkeys (*Alouatta palliata)* live in multi-male, multi-female groups of 15-20 individuals (Bezanson, 2008). Bezanson (2008) reports that *A. palliata* will segregate into smaller subgroups; this social cohesion drives daily activities of individuals within subgroups that can influence the survival of the entire population. Wang and Milton (2003) reported that female grouping aids in female social relationships which thereby shapes the structure of male social relationships and reproduction efforts. Social cohesion is therefore a key aspect of daily life and important for survival (Wang & Milton, 2003).

Fragmentation and edge effects may negatively influence social cohesion among primates; by diminishing patch size through deforestation, food availability decreases while anthropogenic pressures increase (Arroyo-Rodriguez & Diaz, 2009). For example, diademed sifakas (*Propithecus diadema)* living in a forest fragment in Madagascar were less socially cohesive (measured by the number of nearest neighbors within a 5m and 10m radius) compared to sifakas inhabiting non-fragmented forests (Irwin, 2006). *A. palliata* arrange themselves according to the availability of resources within fragments, with smaller, more dispersed subgroups in areas with lower food availability (Chapman, 1990). With respect to deforestation, social cohesion levels decrease within groups of *A. palliata* after habitat destruction occurs: in

areas of destruction compared to pre-destruction, group sizes of *A. palliata* decreased along with increased female emigration and death rates (Clarke et al., 2002).

While little is known about how social cohesion varies between forest zones, sex differences may influence the levels of social cohesion both among individuals of the same sex and individuals of the opposite sex. By sex, male and female fitness are limited by different factors (Trivers, 1972). Males are limited by the number of females within a population, while females are limited by the availability food (Trivers, 1972). Since females bear the energetic cost of gestation and lactation, food availability is vital to their reproductive success (Trivers 1972). As plant species richness has been shown to decrease from the interior to the edge of a forest fragment (Haddad et al., 2015) females may be more spatially limited within fragments than males. Therefore, I expect female *A. palliata* to be more social cohesive than males within the interior. Furthermore, Clarke et al. (1990) report that shortly after being weaned, female *A. palliata* are more sociable with other males and females, whereas infant males actively avoid social interactions with other males while reacting oppositely towards adult females. I examined the relationship of social cohesion between sex and forest zones at the La Suerte Biological Field Station (LSBFS) in Costa Rica.

The LSBFS in Costa Rica is a forest fragment surrounded by commercial banana and pineapple plantations, as well as grazing pastures that establish a clear anthropogenic edge around the property (Garber et al., 2010). Varying levels of vegetation richness and density exist around the property (Malcom, 1994). Recent vegetation surveys at LSBFS show that mean tree species richness and DBH (diameter at breast height) is higher in the interior of the fragment compared to the edges (Bolt et al., 2018). These results indicate that more food resources exist in the interior compared to the edge at LSBFS. These varying levels of tree density, food resources

and available habitat in the edge versus interior may create additional pressure on mantled howler monkeys residing at the edge of this fragment. Very little is known about how fragmentation influences *A. palliata's* social cohesion at LSBFS and how social cohesion differs between sexes in each forest zone. Therefore, my research goal is to examine how *A. palliata's* social cohesion patterns vary by sex between the edge and interior of this fragmented forest habitat. I predict that as a group, *A. palliata* will be more socially cohesive in the forest interior compared to the edge. Furthermore, I predict that female *A. palliata* will be more socially cohesive in the interior than the edge at LSBFS, while males will show no difference in social cohesion between forest zones, because females are more dependent upon the availability of food, while males are more limited by the presence of females. Lastly, I predict that regardless of forest zone, females will exhibit higher social cohesion than males, as females are burdened with the reproductive processes of gestation and lactation, as well as caring for offspring; these responsibilities make it advantageous for females to have high social cohesion levels, as well as to avoid predators.

#### Methods

#### *Study Site*

<span id="page-37-1"></span><span id="page-37-0"></span>Research was conducted at La Suerte Biological Field Station (LSBFS) in Costa Rica (10°26'N, 88°47'W) from May through August, 2017. At 150 hectares, the site contains both primary and secondary forest (Pruetz and Leasor, 2002). This neotropical rainforest fragment includes two patches connected by a corridor (Figure 1). A clear edge has been established due to the presence of surrounding cattle ranches and banana and pineapple plantations (Garber et al., 2010). Recent vegetation surveys conducted at LSBFS show that mean tree species richness and DBH are higher in the interior of the fragment compared to the edge (Bolt et al., 2018). Several

primate species inhabit the area, including white-faced capuchins (*Cebus-capucinus)*, Geoffrey's spider monkeys (*Ateles-geoffroyi)* and several groups of *A. palliata*. These primates have acclimated to human observation, as they have been studied since the early 1990s (Garber et al., 2010).



Figure 1: Map of La Suerte Biological Field Station property

# *Data Collection*

<span id="page-38-0"></span>I compared *A. palliata* social cohesion patterns between the edge and interior to test my hypothesis that females will be more socially cohesive in the interior than the edge and that males will not differ in cohesion between forest zones. I conducted scan sampling on focal individuals, recording data every 2 minutes for 30-minute sampling periods (Altmann, 1974). In order to obtain information on social cohesion, at each 2-minute interval I recorded the sex and age-class (infant, juvenile, or adult) of the focal individual's nearest neighbor (Andren, 1994) and estimated the distance in meters between the focal individual and the nearest neighbor. I also recorded the number of individuals within a 5-meter radius of the focal individual. I sampled random individuals in both edge and interior zones of the forest after physically locating troops of mantled howler monkeys. The edge zone was defined as being within 100m of the boundary of the forest fragment (Bolt et al., 2018). In order to accurately assign an individual to edge and interior observations, I used a handheld GPS unit to collect the latitudinal and longitudinal coordinates at the start of each 30-minute sample. I then plotted these GPS locations onto a map of the field site using ArcGIS to determine which individuals were in each forest zone. Overall, 573 thirty-minute focal samples were recorded and of those samples, I had 336 scans of unsexed adults, 4,404 scans of adult females, 3,312 scans of adult males and 854 scans of juveniles.

#### *Data Analysis*

<span id="page-39-0"></span>I calculated the mean distance between focal individuals and their nearest neighbor, and the mean number of individuals within a 5-meter radius in the edge and in the interior by sex. I then compared social cohesion by sex between the edge and interior. I fit generalized linear mixed models (GLMM) to assess the relationship between the number of nearest neighbors and distance to the nearest neighbor as a function of forest zone and the sex of the focal individual and their interaction. The GLMM used either a Gaussian distribution (distance to nearest neighbor) or a Poisson distribution (number of nearest neighbors). I also included a random effect per each focal individual to uniquely classify each 30-minute sample, as the monkeys themselves were not individually identified during sampling. I then applied generalized linear hypotheses tests to determine whether differences in activity and social cohesion between the edge and interior were statistically significant ( $\alpha$  = 0.05). All analyses were performed using R 3.3.1 (R Core Team, 2016), specifically using the lme4 (Bates & Maechler, 2015) and multcomp packages (Hothorn, Bretz & Westfall, 2008).

## Results

<span id="page-40-0"></span>Contrary to my prediction, the howler monkeys were, on average, equally close to their nearest neighbors in the interior and the edge. Although the median distance(m) to an individual's nearest neighbor in the interior (1.44, CI:1.21-1.72) was marginally higher than the distance to neighbors in the edge (1.43, CI:1.16-1.77), these differences were not statistically significant ( $p = 0.99$ ). Similarly, on average, individuals had more nearest neighbors within 5m of an individual in the edge (0.98, CI:0.79-1.21) versus interior (0.90, CI:0.76-1.08), but these differences were also not statistically significant ( $p = 0.76$ ).

Contrary to my prediction that female social cohesion would vary by forest zone while males would not, neither females ( $p=0.97$ ) nor males ( $p=0.84$ ) significantly differed in the mean number of neighbors by forest zone (Fig. 2). Females had an average of 1.22 (95% CI: 0.95- 1.55) neighbors in the interior and 1.12 (95% CI: 0.81-1.54) in the edge. Males had an average of 0.83 (95% CI: 0.58-1.18) neighbors in the interior and 0.70 (95% CI: 0.51 – 0.95) in the edge.



*Figure. 2: Mean number of neighbors within 5m by sex in forest edge and interior. While neither sex showed significant differences by forest zone, between sexes, females did have significantly more nearest neighbors than males in the interior (p=0.001) while differences in the edge were not significant (p=0.19).* 

Similarly, there were no significant differences in the median distance to nearest neighbors by forest zone for males ( $p=0.95$ ) or females ( $p=0.77$ ) (Fig. 3). Females' median distance to their nearest neighbor was 1.27m in the interior (95% CI:1.00-1.61) and 1.07m in the edge (95% CI:0.79-1.48), but this difference was not significant ( $p=0.77$ ). Likewise, male's median distance to the nearest neighbor was not significantly different (p=0.97) between the edge (2.81m, 95% CI: 2.00-3.97) and the interior (2.50m, 95% CI: 1.83-3.43).

In the interior, females were more socially cohesive than males because they had significantly more neighbors ( $p = 0.001$ ) and were closer to their nearest neighbors ( $p = 0.001$ ). In terms of distance to nearest neighbors, males' median distance to their nearest neighbor was 2.50m in the interior (95% CI: 1.83-3.42), compared to females' 1.27m (95% CI:1.00-1.61). In the edge, males' median distance to their nearest neighbor was 2.72m (95% CI: 1.90-3.87) while females' median distance to their nearest neighbor was 0.98m (95% CI: 0.69-1.38), the difference of which was also significant ( $p = < 0.001$ ). Raw counts indicating the sex of the closest neighbor for both males and females indicated that females preferred to be nearest to other females, while males preferred to nearest to females (Table 1).

<b>Focal Individual</b>	<b>Nearnest Neighbor</b>	<b>Nearest Neighbor Count</b>
<b>Adult Male</b>	<b>Adult Female</b>	1201
	Adult Male	214
<b>Adult Female</b>	<b>Adult Female</b>	870
	<b>Adult Male</b>	626

*Table 1: Raw count of nearest neighbors by sex for both male and female mantled howler monkeys.*



*Fig. 3: Median distance to nearest neighbor by sex and forest zone. Neither sex showed significant differences in the median distance to their nearest neighbors between edge and interior, although, females were significantly closer than males to their nearest neighbors in both forest zones.*

# **Discussion**

<span id="page-42-0"></span>While deforestation and human-induced fragmentation largely negatively impact primate populations, groups within a species may exhibit different responses to fragmentation in the same forest fragment (Schwitzer et al., 2011). Negative impacts of habitat loss include the creation of small forest patches, which are negatively correlated with anthropogenic pressure and positively related to food availability (Arroyo-Rodriguez & Diaz, 2009). Furthermore, plant species richness and the density of larger trees were reportedly lower in smaller patch sizes, thereby reducing foraging opportunities (Arroyo-Rodriguez & Diaz, 2009). Due to this, Arroyo-Rodriguez & Diaz (2009) reported that edge effects resulting from forest fragmentation may negatively impact howler monkey social cohesion levels. However, at LSBFS, *A. palliata* social

cohesion levels as an entire population weren't significantly affected by forest zone but rather only by sex in both forest zones.

Therefore, I cannot support my first hypothesis that predicted higher overall social cohesion of howler monkeys in the interior versus the edge. Social cohesion did not vary by forest zone for *A. palliata,* suggesting that anthropogenic edge effects have little influence on social cohesion levels at LSBFS. Recent results from population surveys at LSBFS show that *A. palliata* individuals did not exhibit preferences in either forest zone (Bolt et al, 2018). It is possible, then, that this lack of anthropogenic impact extends to overall social cohesion as well. As social cohesion measurements consist of sampling groups of individuals within close proximity to one another, if *A. palliata* did not exhibit a preference between forest zones in population surveys, one would not expect social cohesion levels to vastly differ between forest zones either. The mantled howler monkeys residing at LSBFS may have also adjusted to the anthropogenic disturbances around the forest edge and are thereby less affected by forest fragmentation than I previously hypothesized. Similarly, *Hylobates lar* and *Presbytis melalophos*  exhibited no change in home range after selective logging was conducted in their habitat which Johns (1986) attributed to an ability to adjust foraging strategies based on changes in resource availability. Since social cohesion aids in a primate's ability to obtain resources and I did not observe differences in social cohesion level due to edge effects, my results suggest that this foraging flexibility extends to the social behavior of *A. palliata* (Garber & Kowalewski, 2011).

Long-term studies have reported that the level of intensity of anthropogenic disturbances on primate communities also plays a role: less-intense anthropogenic effects (specifically, logging practices) on primate populations were proven to have less impact compared to highintensity effects (Chapman et al., 2000). Similarly, the phenology cycles of fruiting trees

commonly consumed by black-and-white ruffled lemurs are more negatively impacted by intense disturbances (such as heavy logging) compared to moderate disturbances (like selective logging) (Balko & Underwood, 2005). It is possible that the severity of edge effects at LSBFS are not as intense compared to other forest fragments or that the anthropogenic disturbances are not as severe as previously suspected. While the ability of local citizens to cross LSBFS borders remains possible, the surrounding plantations are well-established edges. Additionally, as LSBFS remains a protected forest fragment, deforestation beyond its borders is strictly prohibited, which may help to alleviate anthropogenic influence within the fragment.

Surprisingly, with regard to my second hypothesis that female social cohesion would vary by forest zone while males' would not, neither sex showed significant differences in the number of neighbors or the distance to their nearest neighbor between forest zones. This would suggest that *A. palliata* social cohesion levels of neither sex at LSBFS are affected by the existing anthropogenic edge effects. Similarly, Strier (1989) reported that while patch occupancy time in a fragmented forest was positively correlated to the size of fruit patches, neither males nor females showed significant differences in their feeding styles (males preferred to only feed with males while females preferred to feed alone). While little research exists comparing male and female primate social cohesion with respect to anthropogenic edge effects, my results exhibit a lack of edge effects on either male or female social cohesion.

Indeed, sex is in fact the main determinant of social cohesion levels of *A. palliata* at LSBFS and differences in the life histories of male and female primates might help to explain this finding. As Trivers (1972) explains, females are limited by food resources while males are limited by the availability of females. Other primates exhibit these same energetic demands by sex: Wrangham & Smuts (1980) reported that female chimpanzees will focus the majority of

their energy on foraging while males will forego foraging events in order to participate in mating opportunities. Furthermore, direct infant care by males occurs in fewer than 5 percent of all mammalian species (Van Schaik et al., 1996). These results all suggest that females are limited by their long gestation periods and lactation, as they can only successfully birth healthy offspring with an adequate supply of high-quality food. Most importantly, the risk of predation forces females to group together (Sterck et al., 1997). It is therefore clearly advantageous for females to have high social cohesion levels no matter the forest zone, due to increased foraging success and predator avoidance. Oppositely, as male social cohesion is driven less by these reasons but more so by mating opportunities, their social cohesion levels might differ from females'. Unlike female, males would not benefit from grouping together with other males, as doing so would create direct competition for mating access to females between multiple males (Dobson, 1982). This means that males would achieve better mating opportunities by searching for females without other males present, consequently establishing lower social cohesion between them compared to females. So, it is no surprise that sex influences social cohesion levels and that females are more socially cohesive than males at LSBFS, regardless of forest zone. Additionally, my finding that males preferred to socialize with females while females preferred other females supports previous research also observing this pattern of higher female social cohesion compared to males.

In conclusion, social cohesion levels of howler monkeys residing at LSBFS are affected by sex rather than the surrounding anthropogenic edge effects. This would indicate that in fact, the anthropogenic edge effects are not as far-reaching as previously suspected. For *A. palliata,*  this positive result indicates their resiliency to survive the effects of deforestation and forest fragmentation. Future research on this topic would add to our understanding of how primate

social cohesion is affected by sex. While still unexpected, my results indicate that this population's social cohesion is unaffected by edge effects and therefore provides positive insight into the resiliency of primate social cohesion to forest fragmentation.

#### References

- <span id="page-47-0"></span>Altmann, J. (1974). Observational study of behavior: sampling methods*. Behaviour*, 49(3), 227- 266.
- Andren, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review*. Oikos*, 71(3), 355-366.
- Arroyo-Rodriguez, V., Americo D. Dias, P. (2009). Effects of habitat fragmentation and disturbance on howler monkeys: a review. *American Journal of Primatology*, 72(1), 1-16.
- Balko, E. A., & Brian Underwood, H. (2005). Effects of forest structure and composition on food availability for *Varecia variegata* at Ranomafana National Park, Madagascar. *American Journal of Primatology*, *66*(1), 45-70.
- Bates, D., Maechler, M., Bolker, B., Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1-48.[<doi:10.18637/jss.v067.i01>](http://dx.doi.org/10.18637/jss.v067.i01).
- Bezanson, M., Garber, P.A., Murphy, J.T., Premo, L.S. (2008). Patterns of subgrouping and spatial affiliation in a community of mantled howling monkeys *(Alouatta palliata). American Journal of Primatology*, 70(3), 282-293.
- Bolt, L.M., Schreier, A.L., Voss, K.A., Sheehan, E.A., Barrickman, N.L., Pryor, N.P., & Barton, M.C. (2018). The influence of anthropogenic edge effects on primate populations and their habitat in a fragmented rainforest in Costa Rica. *Primates* (accepted) DOI: 10.1007/s10329-018-0652-0
- Broadbent, E.N. Asner, G.P., Keller, M., Knapp, D.E., Oliveira, P.J.C., Silva, J.N. (2008). Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biological Conservation,* 141(7), 1745-1757.
- Chapman, C. A., Balcomb, S. R., Gillespie, T. R., Skorupa, J. P., & Struhsaker, T. T. (2000). Long‐term effects of logging on African primate communities: a 28‐year comparison from Kibale National Park, Uganda. *Conservation Biology*, *14*(1), 207-217.
- Chapman, C.A. (1990). Ecological constraints on group size in three species of neotropical primates. *Folia Primatoligica,* 55(1), 1-9.
- Chen, J., Saunders, S.C., Crow, T.R., Naiman, R.J., Brosofske, K.D., Mroz, G.D., Brookshire, B.L., Franklin, J.F. (1999). Microclimate in forest ecosystem and landscape ecology: variations in local climate can be used to monitor and compare the effects of different management regimes*. BioScience*, 49(4), 288-297.
- Clarke, M. R., Collins, D. A., & Zucker, E. L. (2002). Responses to deforestation in a group of mantled howlers (*Alouatta palliata)* in Costa Rica. *International Journal of Primatology,*  23(2), 365-381.
- Clarke, M. R. (1990). Behavioral development and socialization of infants in a free-ranging group of howling monkeys (*Alouatta palliata). Folia Primatologica,* 54(1-2), 1-15.
- Dobson, F. S. (1982). Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour*, *30*(4), 1183-1192.
- Garber, P. A., & Kowalewski, M. K. (2011). Collective action and male affiliation in howler monkeys (*Alouatta caraya*). In *Origins of Altruism and Cooperation* (pp. 145-165). Springer, New York, NY.
- Garber, P.A., Molina, A., Molina, R.L. (2010). Putting the community back in community ecology and education: the role of field schools and private reserves in the ethical training of primatologists. *American Journal of Primatology,* 72, 785-793.
- Gascon, C., Williamson, G.B., Fonseca, G.A.B. (2000). Receding forest edges and vanishing reserves*. Science*, 288(5470), 1356-1358.
- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., ... & Cook, W. M. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, *1*(2), e1500052.
- Hothorn, T., Bretz, F., and Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal,* 50(3), 346--363.
- Irwin, M.T. (2006). Living in forest fragments reduces group cohesion in diademed sifakas (*Propethicus diadema*) in eastern Madagascar by reducing food patch size. *American Journal of Primatology*, 69(4), 434-447.
- Johns, A. D. (1986). Effects of selective logging on the behavioral ecology of West Malaysian primates. *Ecology*, *67*(3), 684-694.
- Kirika, J., Farwig, N., & Bohning‐Gaese, K. (2008). Effects of local disturbance of tropical forests on frugivores and seed removal of a small‐seeded afrotropical tree. *Conservation Biology*, *22*(2), 318-328.
- Laurance, W.F., Ferreira L.F., Rankin-De Merona J.M., Laurance S.G., Hutchings R.W., & Lovejoy, T.E. (1998). Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. *Conservation Biology*, 12(2), 460-464.
- Lehman, S. M., Rajaonson, A., & Day, S. (2006). Lemur responses to edge effects in the Vohibola III Classified Forest, Madagascar. *American Journal of Primatology*, *68*(3), 293-299.
- Malcom, J.R. (1994). Edge effects in central Amazonian forest fragments. *Ecological Society of America*, 75(8), 2438-2445.
- Pruetz, J.D., Leasor, H.C. (2002). Survey of three primate species in forest fragments at La Suerte Biological Field Station, Costa Rica. *Neotropical Primates,* 10(1), 4-9.
- R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.
- Sanchez-Azofeifa, G.A., Daily G.C., Pfaff A., & Busch, C. (2003). Integrity and isolation of Costa Rica's national parks and biological reserves: examining the dynamics of landcover change. *Biological Conservation*, 109(1), 123-135.
- Schwitzer, C., Glatt, L., Nekaris K., & Ganzhorn, J. (2011). Responses to animals to habitat alteration: an overview on focusing on primates. *Endangered Species Research*, 14(1), 31-38.
- Sterck, E. H., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, *41*(5), 291- 309.
- Strier, K. B. (1989). Effects of patch size on feeding associations in muriquis (*Brachyteles arachnoides*). *Folia Primatologica*, *52*(1-2), 70-77.
- Tilman, D. (1999). The ecological consequences of changes in biodiversity: a search for general principles. *Ecological Society of America*, 80(5), 1455-1474.
- Trivers, R. (1972). *Parental investment and sexual selection* (Vol. 136, p. 179). Cambridge, MA: Biological Laboratories, Harvard University.

Van Schaik, C. P., & Paul, A. (1996). Male care in primates: does it ever reflect paternity*? Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews*, 5(5), 152-156.

- Wang, E., Milton, K. (2003). Intragroup social relationships of male *Aloutta palliata* on Barro Colorado Island, Republic of Panama*. International Journal of Primatology*, 24(6), 1227- 1243.
- Wrangham, R. W., & Smuts, B. B. (1980). Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. *Journal of Reproduction and Fertility. Supplement*, 28(1), 13-31.

# <span id="page-52-0"></span>CHAPTER 4 ENVIRONMENTAL STAKEHOLDER ANALYSIS: PRESERVING COSTA RICAN RAINFOREST: BATTLING DEFORESTATION THROUGH THE EYES OF MULTIPLE STAKEHOLDERS

The Costa Rican rainforest has been exploited by humans for many years (Sader & Joyce, 1988). After World War II, Costa Rica experienced a four-fold increase in human population while simultaneously eradicating roughly 50% of the nation's rainforests (Rosero-Bixby  $\&$ Palloni, 1998). By the 1980s, only the rainforest territories in the mountainous regions were left untouched by human use (Sader & Joyce, 1988). Between 1991 and 2001, it was estimated that anthropogenic deforestation depletes roughly 4% of the nation's rainforests every year (Sanchez-Azofeifa et al., 2001). Some of the most common uses of cleared forest land are for agricultural use, specifically cattle grazing and fruit crops (Andam et al., 2008). However, parts of the Costa Rican rainforest have since been placed under legal protection in the form of wildlife, biological and forest reserves as well as national parks (Andam et al., 2008). Certain governmental policies already in place help to reduce deforestation rates but some policies omit certain public groups and stakeholders (de Camino Velozo, 2000). Costa Rican citizens, lawmakers, researchers and tourists and economically-poor residential citizens are the main stakeholders affected by deforestation. While the issue of deforestation is complex, with the proper access to information and funding, successfully decreasing deforestation rates is possible. All groups involved can benefit from employing local citizens (such as cattle ranchers and farmers) to conserve the rainforest, creating inclusive policies with incentives, regulating access to forests for tourists and researchers and establishing more national parks with sensitivity to location.

There are several stakeholders whose interests are associated with Costa Rican deforestation. One of the largest groups includes cattle ranchers and farmers who use deforested land to farm and graze cattle. This group values their livelihood and ability to make a profit with which to support their families. As such, these stakeholders' ability to conserve the rainforest comes second to their ability to conduct their businesses. Since 1950, the largest change to land use in Costa Rica has been from forests to pastures and agricultural land (de Camino Velozo, 2000). Between 1970 and 1983, low interest rate loans for cattle ranches combined with increased meat prices created a boom for cattle ranchers in Costa Rica (de Camino Velozo, 2000). However, since then, the growth potential of wood exportation is higher than that of cattle ranching; but cultural ties to cattle ranching prevent ranchers from switching to wood production (de Camino Velozo, 2000). Indeed, in the 1960's, large ranchers' associations successfully lobbied to increase governmental support of livestock farming while simultaneously loosening restrictions on deforestation (de Camino Velozo, 2000).

Plantations are even more profitable (experiencing a 15% higher profit margin) than cattle ranches (De Camino Velozo, 2000). De Camino Velozo (2000) suggests providing incentives for ranch owners to invest in existing secondary forests rather than subsidize natural forest regeneration. Knowing that wood plantations have 20% higher border prices – the import or export price of an economic commodity - than cattle ranches, this should incentivize citizens to practice forest regeneration over cattle ranching on forest soil (de Camino Velozo, 2000). However, enacting this solution would require the aid and funding of the Costa Rican government and its lawmakers, as they would be responsible for bringing this idea to fruition.

Lawmakers and national governments are two of the largest stakeholders concerned with the practice and prevention of deforestation. Their actions have a direct ability to affect other

stakeholders involved in the matter. This group values their ability to simultaneously serve the current population while preserving the nation's natural resources for future generations. Therefore, they would benefit by creating a compromise that is appealing to many Costa Rican citizens while finding a way to conserve the rainforest. While the Costa Rican government has implemented several successful policies intended to protect forest land, many are complex and only favor certain groups. For example, the 1979 Income Tax Deduction promoted the creation of wood plantations for profit rather than promote the conservation of natural forests (De Camino Velozo, 2000). However, while the original intent was meant for all citizens, only large landowners in Costa Rica pay income taxes and, therefore, smaller landowners did not benefit from this deduction (De Camino Velozo, 2000). The creation of national parks by the Costa Rican government has also greatly decreased deforestation, but Pfaff et al (2009) reports that the location of national parks influences their impact on deforestation. Parks that are closer to national roads and larger cities actually decrease deforestation rates better than those elsewhere (Pfaff et al., 2009). In addition, Andam et al. (2010) report that although most communities around national parks are very poor, (once researchers were able to control for possible data collection bias) the overall net impact actually decreased poverty by promoting local tourism and improving neighboring infrastructure. Therefore, lawmakers can help decrease deforestation by increasing the number of national parks with attention to chosen locations. In addition to benefitting local communities, national parks and protected lands also offer the chance for education, increased tourism and research.

One simple way that protected forests, which reduce deforestation and can benefit nations is by allowing researchers access to these places to further educate the public through their work. For example, La Suerte Biological Field Station (LSBFS) in Costa Rica is a field school operated by the Maderas Rainforest Conservancy (Pruetz and Leasor, 2002). Throughout the year, LSBFS is open to students and scientists around the world to come and study the flora and fauna of this Costa Rican rainforest. Additionally, LSBFS employs local citizens to maintain the property and host researchers, professors and students during their time at LSBFS (Maderas Rainforest Conservancy, n.d.). Research conducted in LSBFS and other protected forests contributes to knowledge about rainforest ecology and anthropogenic deforestation (Bolt et al., 2018), enabling the public and politicians to make better-informed decisions about conservation efforts against deforestation. These researchers value the opportunity to conduct research within Costa Rica's rainforests while also preserving the plant and animal populations that reside in the forests, as well as the rainforest and its inhabitants in and of themselves. Thus, they value conservation above other solutions or compromises.

Jacobsen and Robles (1992) report that employing local citizens in tourism programs enables the education of the public while reducing negative tourism impacts on the local wildlife. By increasing regulated access to nationally protected forests for researchers, students and tourists, Costa Rica is able to both create a monetary profit for its citizens and spread knowledge about the importance of decreasing deforestation. The last group of stakeholders that are pertinent to the issue of deforestation in Costa Rica are the economically-poor citizens of Costa Rica. They value their day-to-day ability to obtain basic human requirements such as food, clothing and shelter. Lawmakers and government officials would be hard pressed to ask a poor citizen to uphold the protection of the rainforest over their own basic needs. Additionally, while attracting tourists provides a monetary resource to the country of Costa Rica, the everyday responsibilities and motivation required to actively protect the rainforest must come from its native population. Therefore, while lawmakers and government officials should continue to

enforce laws that protect the rainforest, it would behoove those same officials to regard any possible cultural implications with sensitivity. A novel idea that might attract more native citizens to prevent deforestation would be to set aside a certain percentage of money earned from national tourism to aid in obtaining those basic needs that poor citizens require, thereby enabling them to focus on the protection of forests instead.

Ultimately, while Costa Rica is already a model country in terms of protecting forests and decreasing deforestation rates, there are still ways to further improve this effort. As the practice of cattle-ranching has less growth potential than that of wood plantations, citizens and the Costa Rican economy could potentially benefit from creating incentives for ranchers to operate plantations instead (de Camino Velozo, 2000). Furthermore, policies already enacted by the Costa Rican government do aid in reducing deforestation rates (de Camino Velozo, 2000). However, creating policies that ensure the involvement and inclusion of multiple interest groups would continue to reduce deforestation rates (de Camino Velozo, 2000). This could either be accomplished by monetarily incentivizing the public to change careers to those that help protect the forest or creating new policies that target previously-ignored groups, such as small landowners. Employing local citizens to work in the Costa Rican tourist business would allow the native public to learn more about deforestation and also educate foreign tourists about the importance of preserving forests (Jacobsen and Robles, 1992). Allowing regulated access to these protected areas for the public and researchers would aid in producing public knowledge about deforestation, similarly to studies conducted at LBSFS (Bolt et al., 2018). With the knowledge obtained from scientific studies conducted in protected forests along with increased funding, lawmakers who favor protecting Costa Rican forests and decreasing deforestation can enact better, more inclusive policies that include more citizens and members of the public.

Lastly, these citizens (specifically those of the poor, lower class) might be more enticed to aid in the prevention of rainforest deforestation if the Costa Rican government enacts policies with cultural sensitivity in mind while simultaneously providing a certain level of financial aid to these citizens. This thereby allows these valuable citizens to focus more on protecting the rainforests rather than simple day-to-day survival. Overall, I present a multitude of solutions with which to ensure the protection of Costa Rica rainforest but only because any one of these solutions alone would not suffice. It is only by providing opportunities to local citizens (both through employment and financial aid), creating inclusive, incentivized policies and regulating access to forests for both tourists and researchers will the country of Costa Rica be able to unite all stakeholders in the protection of its rainforests.

- <span id="page-58-0"></span>Andam, K. S., Ferraro, P. J., Pfaff, A., Sanchez-Azofeifa, G. A., & Robalino, J. A. (2008). Measuring the effectiveness of protected area networks in reducing deforestation. *Proceedings of the National Academy of Sciences*, *105*(42), 16089-16094.
- Andam, K. S., Ferraro, P. J., Sims, K. R., Healy, A., & Holland, M. B. (2010). Protected areas reduced poverty in Costa Rica and Thailand. *Proceedings of the National Academy of Sciences*, *107*(22), 9996-10001.
- Bolt, Laura M., Schreier, Amy L., Voss, Kristofor A., Sheehan, Elizabeth A., Barrickman, Nancy L., Pryor, Nathaniel P., and Barton, Matthew C. The influence of anthropogenic edge effects on primate populations and their habitat in a fragmented rainforest in Costa Rica. *Primates* (accepted) DOI: 10.1007/s10329-018-0652-0
- de Camino Velozo, R. (2000). *Costa Rica: forest strategy and the evolution of land use*. World Bank Publications.
- Jacobson, S. K., & Robles, R. (1992). Ecotourism, sustainable development, and conservation education: Development of a tour guide training program in Tortuguero, Costa Rica. *Environmental Management*, *16*(6), 701-713.
- Pfaff, A., Robalino, J., Sanchez-Azofeifa, G. A., Andam, K. S., & Ferraro, P. J. (2009). Park location affects forest protection: Land characteristics cause differences in park impacts across Costa Rica. *The BE Journal of Economic Analysis & Policy*, *9*(2).
- Pruetz, J. D., & Leasor, H. C. (2002). Survey of three primate species in forest fragments at La Suerte Biological Field Station, Costa Rica. *Neotropical Primates*, *10*(1), 4-9.
- (n.d). Maderas Rainforest Conservacy A conservancy established to promote conservation, protection and management of forests and jungles*.* Retrieved March 11, 2018, from http://maderasrfc.org/
- Rosero-Bixby, L., & Palloni, A. (1998). Population and deforestation in Costa Rica. *Population and Environment*, *20*(2), 149-185.
- Sader, S. A., & Joyce, A. T. (1988). Deforestation rates and trends in Costa Rica, 1940 to 1983. *Biotropica*, 20(1), 11-19.
- Sánchez-Azofeifa, G. A., Harriss, R. C., & Skole, D. L. (2001). Deforestation in Costa Rica: a quantitative analysis using remote sensing imagery. *Biotropica*, *33*(3), 378-384.