The Effects of Habitat Disturbance on the Populations of Geoffroy's Spider Monkeys in the Yucatan Peninsula

PhD thesis

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August 2017

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For the spider monkeys of the Yucatan Peninsula,
and all those dedicated to their conservation.

Acknowledgements

This thesis turned into the biggest project I have ever attempted and it could not have been completed without the invaluable help and support of countless people and organizations.

A huge thank you goes out to my supervisors Drs. Filippo Aureli and Gabriel Ramos-Fernández. Thank you for your guidance, friendship and encouragement, I have learnt so much and truly enjoyed this experience. This thesis would not have been possible without you and I am extremely proud of the results. Additionally, I would like to thank Filippo Aureli for all his help in organizing the logistics of field work. Your constant help and dedication to this project has been inspiring, and kept me pushing forward even when it was not always easy to do so, so thank you very much.

I would like to thank Dr. Martha Bonilla for offering me an amazing estancia at the INECOL. Your kind words have encouraged and inspired me throughout the past three years, and have especially helped me to get through the last few months. Thank you!

A big thank you to Drs. Colleen Schaffner and Jorge Morales Mavil for all your feedback and ideas over the past three years. Colleen, thank you for helping me to feel at home in Mexico and for all your support!

I very much look forward to continue working with all of you in the future!

I would like to thank the CONACYT for my PhD scholarship and the Instituto de Neuroetología for logistical, administrative and financial support. I would like to thank the Instituto de Ecologia, A.C. for the facilities provided. My field research was kindly funded by the National Geographic Society Young Explorers Grant and the PROCER grant of the CONANP. Additionally, I would like to thank National Geographic Society for inviting me to be part of the Young Explorers Meet-Up and introducing me to an amazing community of researchers and storytellers. I thank the European Federation of Primatology for the travel grant that enabled me to present my research at the European Federation of Primatology Conference in Rome in 2015. I also thank the Association of Tropical Biology and Conservation for the student scholarship to attend the annual meeting to be held in Merida in 2017.

I would like to thank the CONANP for allowing me to conduct field research in three protected areas. I would additionally like to thank Sandra Flores for all her encouragement and enthusiasm in this project. A huge thank you to Kathy Slater, Operation Wallacea and the team of Pronatura Peninsula Yucatan for logistical help in Calakmul and Santa Clara. I thank the residents of Los Arboles Tulum for allowing me to perform surveys and I hope they will continue to conserve the spider monkeys living there.

I would like to thank Drs. Vinicio Sosa Fernández, Roger Guevara Hernández, Salvador Mandujano Rodríguez, Sonia Antonieta Gallina Tessaro and Victor Arroyo Rodríguez for

invaluable advice and feedback on statistical and population analyses. I learnt a great deal from our conservations.

Karla Hernández Hernández without your hard work and dedication I would still be measuring trees today. Thank you for your friendship and all the great memories in the forest!

Braulio Pinacho Guendulain, thank you for introducing me to line transect surveys, accompanying me into the field, and helping me to train field asistants. I learnt so much!

Alfredo Dorantes Euán, thank you for your invaluable help in identifying tree species and answering my endless questions.

This project would not have been possible without the immense help and dedication of my field assistants. I would like to thank Juan Can Yam, Jorge Can Yam, Don Nemencio, Don Cirilo, Juan, Agusto, Eulogio and Macedonio Canul, and Anthony Denice for their help in Otoch M'aax yetel Kooh. In particular, I would like to thank Juan Can Yam for accompanying me on countless surveys. Thank you to Esteban Domínguez Bonilla and his family for accompanying me into the forest and opening their home up to me in Calakmul. Thank you to Adrian, Ricardo, Don Eutimio, Don Adumauro, Don Lorenzo Franco, Don Javier, Don Loretto, Manuel and Manuel for all your help in Bala'an K'aax and your continued commitment to conservation. It was extremely inspiring and a real joy to work there. I would especially like to thank Don Eutimio and Don Lorenzo Franco for allowing me to stay in their homes and to Doña Amalia for all the delicious meals. In Santa Clara I would like to thank Marcos and his family for helping me in the field.

A huge thank you goes to my family and friends for supporting me these past three years. Thanks to Amor Saldaña, Tania Palacios, Fay Moorland, Anthony Denice and Coral Rangel for all the laughs and good times in the field. A big thanks to my friends and lab mates in Xalapa for making my final year extremely memorable. In particular I want to thank Gonzalo Pinilla Buitrago for all your love and support these past two years. I hope we continue to create lots of great memories together.

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Abstract

Spider monkeys have long been vulnerable to the effects of anthropogenic disturbance due to their long gestation periods and inter-birth intervals, large home range requirements and the high reliance on ripe fruits in their diet. Yet, their high degree of fission-fusion dynamics could enable them to flexibly adjust to changes in their environment. Problematically, anthropogenic disturbance may cause large-scale habitat modification, often occurring at an accelerated pace compared to changes in the environment caused by natural processes, potentially preventing spider monkeys from adjusting to these changes. However, understanding how spider monkeys respond to habitat disturbance is complicated by the difficulty of surveying them. The aim of my project was to determine the effect of anthropogenic and natural habitat disturbance on Geoffroy's spider monkeys in the Yucatan Peninsula and to assess different methods to estimate their population densities. In Chapter 3, I evaluated potential factors affecting line transect surveys on individually-identified spider monkeys in Punta Laguna to determine the best method to survey spider monkeys. I found that aspects of survey design, such as the number of observers or time of day, do not affect the number of spider monkeys observed. Recounting of individuals during the same transect walk was rare and only occurred when transects were walked slowly, and can thus be minimized by walking transects at a speed similar to or faster than the monkeys. The comparison of population density estimates obtained with different methods to the actual density showed that some methods highly over- or under-estimate population density. In Chapter 4, I combined field data using the findings of Chapter 3 and data from Geographical Information Systems to determine the effects of anthropogenic and natural habitat disturbance and ecological factors on the population of

Geoffroy’s spider monkeys at four sites in the Yucatan Peninsula. I found that the number of spider monkeys is higher in areas where forest loss is lower and villages are farther away, but it is not affected by distance to roads. Additionally, the number of spider monkeys is higher in areas with greater basal area of feeding trees, especially *Brosimum alicastrum*, a preferred feeding tree. The distribution and abundance of spider monkeys in the Yucatan Peninsula is therefore influenced by both ecological factors and anthropogenic and natural habitat disturbance. Canopy height did not affect spider monkey numbers, suggesting that spider monkeys can use forests in different stages of regeneration. In Chapter 5, I performed surveys for a complete year in the southern section of the Otoch Ma’ax yetel Kooh protected area and compared population density estimates with those based on surveys carried out in the same area in 1997-98. Spider monkey population density was higher in mature forest than regenerating forest, suggesting that although spider monkeys use regenerating forest, they prefer mature forest. Importantly, I found that spider monkey population density remained relatively stable in mature forest and regenerating forest over time. Since slash-and-burn agriculture stopped within the protected area in 2002, and no forest fires have occurred in the southern section of the protected area, the forest has been left to regenerate. It is therefore likely that more suitable forest is available in the southern section of the protected area than in 1997-98. As the population density remained relatively stable in sampled mature and regenerating forest, the overall population of spider monkeys may have increased in the southern section of the protected area. Additionally, I found that changes in population size over time can be monitored using any of the tested methods to estimate population density. Overall, my thesis indicates that spider monkeys may be more flexible in their use of habitats and are more resilient to habitat disturbance than was previously thought. My findings have important conservation implications. Areas with a high abundance of spider monkey feeding trees, located far away from villages must be protected from forest loss to conserve spider monkey populations in the Yucatan Peninsula, and emphasis must be placed on promoting forest regeneration to increase the amount of available spider monkey habitat.

Chapter 1: General introduction

A population consists of individuals of the same species using the same area at a particular time. (Krebs, 1994). Populations are therefore difficult to identify in the field and many researchers resort to defining populations as the group of individuals occupying their study site. The stability of populations is determined by an interplay of mortality, natality, immigration and emigration of individuals (Krebs, 1994). Changes induced by biotic or abiotic factors in one of these processes may lead to increases or decreseases in population size. For instance, if mortality increases and birth rate decreases as a result of changes in food availability, the population declines when immigration and emigration remain stable. Likewise, when more individuals emigrate from the population than immigrate into it, population size decreases if natality and mortaility remain stable. Population size may remain stable if despite high mortaility, immigration into the population is also high (sink popualtions; Pilliam, 1988).

Population size is an important factor affecting time to extinction (Fagan and Holmes, 2006). Populations declining in size may experience an extinction vortex, in which biotic and abiotic factors (e.g. inbreeding) create a positive feedback, leading the population to extinction (Fagan and Holmes, 2006). Additionally, in many species the fitness of the individual may be reduced at smaller population sizes (Allee effect) due to difficulty in finding mates or cooperators for obligate cooperative breeders (Stephens and Sutherland, 1999; Courchamp et al., 2006). Group-living species may therefore be especially susceptible to Allee effects, which cause negative growth rates when populations are small and thereby drive smaller populations to extinction more quickly (Courchamp et al., 2006). Allee effects may be both directly or indirectly triggered by anthropogenic factors (Courchamp et al., 2006).

Metapopulations are populations made up of subpopulations separated in space, but connected through the dispersal of individuals (Forman, 1995; Hanksi, 1998). Clear examples of metapopulations are animal populations living fragmented landscapes, in which each population occupies a separate forest fragment. Dispersal is a key determinant of whether forest fragments are colonized by the species and may be limited by the distance between fragments (isolation distance) and the habitat surrounding forest fragments (matrix) (Saunders et al., 1991). The size and habitat quality of the fragment determine the probability of extinction of the local population (Forman, 1995). In metapopulations it is common that populations within some fragments may go extinct, and such fragments can be colonized at a later date as a result of a population boom in a different population. The amount of suitable habitat in the fragmented area determines the persistence of a metapopulation (Hanski, 1998).

1.1 Habitat disturbance

Habitat disturbance, a term commonly used in studies of ecology and conservation, refers to the modification of habitat due to human (anthropogenic habitat disturbance) or natural processes. When referring to habitat disturbance, most authors refer to one of three processes: deforestation, forest fragmentation and habitat degradation (Sodhi et al., 2009), also known as exogenous disturbances (McIntyre and Hobbs, 1999; Fischer and Lindenmeyer, 2007). Exogenous disturbances refer to disturbances that are novel and recent (McIntyre and Hobbs, 1999), and originated independently of the species' biology (Fischer and Lindenmeyer, 2007). Exogenous disturbances may cause changes to the composition, structure or ecosystem functioning of a habitat (McIntyre and Hobbs, 1999). Modifications to a species' habitat as a result of exogenous disturbances may cause alterations in the species' biology (endogenous disturbances); for example, changes in the size or location of home ranges. Endogenous habitat disturbances are therefore disturbances that have originated as part of the species' biology (Fischer and Lindenmeyer, 2007). Confusingly, the term habitat disturbance is often used to refer to a wide range of anthropogenic and natural drivers of environmental change. For instance, in the primatological literature habitat disturbance has been used as a term to refer to deforestation, logging (Chapman and Lambert, 2000; Remis and Jost Robinson, 2012), hunting (Aquino et al., 2012), and extraction of resources (Rovero et al., 2012). In this context, the expression anthropogenic habitat disturbance includes a range of human activities that modify the environment and directly or indirectly affect animals, including primates.

Agricultural expansion, including cattle farming and logging, and the expansion of infrastructure, are the leading causes of deforestation in the tropics (Geist and Lambin, 2002; Gibbs et al., 2010; Graesser et al., 2015). Problematically, tropical forests support a wide array of biodiversity and are home to the majority of primate species (Cowlishaw and Dunbar, 2000). In 2001, it was reported that primate range countries were annually losing 125,140 km^2 of forest equaling a loss of 32 million primates per year (Chapman and Peres, 2001). Although in the last decade rates of deforestation decreased (e.g., Brazil lost around 40,000 km^2/year of forest in 2003-2004 compared to under 20,000 km/year in 2011-2012; Hansen et al., 2013), it is still a mayor threat for tropical organisms (Morris, 2010). The process of deforestation not only reduces the overall land area of forest (Fahrig, 2003), but it often creates fragments of much smaller blocks of forest. Such forest blocks become isolated (Andrén, 1994; Fischer and Lindenmayer, 2007), surrounded by a matrix of altered or degraded habitat (Andrén, 1994; Arroyo-Rodríguez and Mandujano, 2009), which differs in habitat quality (Fischer and Lindenmeyer, 2007) through alterations in vegetation structure and composition (Hillers et al., 2008).

Secondary forests (forest regrowth after clearance; Guariguata and Ostertag, 2001) are the principal vegetation type in human-modified tropical landscapes (Arroyo-Rodríguez et al., 2015), and understanding how primates use such environments is increasingly important to develop successful conservation strategies. The recovery process of a forest after a disturbance event (e.g. hurricanes, fire, lightning, pathogens, herbivores, slash-and-burn agriculture, or logging), depends on a range of factors including seed dispersal (Holl, 1999, Ashton et al., 2001; van Nieuwstadt et al., 2001; Chazdon et al., 2009). Primates play a vital role in tropical ecosystems where they act as important seed dispersers (Chapman and Onderdonk, 1998; Levi and Peres, 2013; Arroyo-Rodríguez et al., 2015a), dispersing seeds over great distances and improving germination of seedlings when seeds pass through their guts (Chapman and Onderdonk, 1998; Levi and Peres, 2013). In the absence of seed dispersers, seeds fall to the ground under the parent tree and have lowered probabilities of survival, due to density dependence (Connell, 1971), or because they have not been separated from the fruit’s pulp (Chapman and Onderdonk, 1998; Levi and Peres, 2013). Large-bodied Neotropical primates such as spider monkeys (*Ateles* spp.) are important dispersers of medium-sized and large seeds (Stevenson et al., 2005; Stevenson and Aldana, 2008; Stevenson, 2011; Calle-Rendón et al., 2016). A recent study, however has indicated that removal of ateline primates from the Lacandona rainforest in south Mexico, did not affect the dispersal of large-seeded species (Chaves et al., 2015).

Aspects of forest structural complexity such as basal area, tree density, species richness, aboveground biomass and tree height may recover relatively quickly (40-95 years) after slash-and-burn agriculture as these areas are often well-connected and surrounded by large tracks of old-growth forest where seed dispersal is high, promoting regeneration (Aide et al., 2000; Chazdon 2003; Read and Lawrence, 2003; Chazdon et al., 2009; 2016; Dupuy et al., 2012). This suggests that arboreal species, such as spider monkeys, may use secondary forests relatively soon after they have been left to regenerate. Interestingly, the biomass of feeding tree species for three primates living in regenerating forest (due to pasture abandonment) increased linearly with forest age and over time primate species diversity recovered (Sorenson and Fedigan, 2000). Capuchin monkeys (*Cebus capucinus*) used the forest after 14-25 years of regeneration, followed by howler monkeys (*Aloutta palliata*; 30-60 years of regeneration) and spider monkeys (*A. geoffroyi*; 60-80 years of regeneration; Sorenson and Fedigan, 2000). However, difference in successional pathways (i.e. the sequence of temporal changes and population parameters determining vegetation composition and structure; Arroyo-Rodríguez et al., 2015b) and speed of forest regeneration will largely determine the likelihood of primates recolonizing the area. For example, forests in regeneration on an abandoned pasture may follow a different successional pathway than slash-and-burn agricultural lands, as the majority of trees are removed to allow cattle grazing.

Although forest structure recovers quickly, forest composition takes much longer to return to pre-disturbed levels (Aide et al., 2000; Chazdon, 2003; Chazdon et al., 2016).

For instance, in Indonesian mixed diptocarp forest used for slash-and-burn agriculture it may take 150-500 years for primary forest species to reestablish (Riswan et al., 1985). As food abundance is a key factor influencing primate abundance (Hanya and Chapman, 2013) forests' species composition may directly affect primate abundance. For instance, changes in forest composition directly affect primates by reducing the number of feeding trees and dormitories (often large primary forest tree species), and may cause changes in primate activity budget, home-range size and diet (Arroyo-Rodríguez and Dias, 2010), as animals are forced to range over larger distances in search of food. For specialist species, such as spider monkeys, the change in forest species composition after a disturbance event may prevent or slow down recolonization of the area. Monitoring of primate populations both within mature and secondary forest are vital to understand the conservation challenges facing these species.

1.2 Flexibility in response to habitat change

Although the effect of habitat disturbance on primates has been widely studied in relation to forest fragmentation (Estrada and Coates Estrada, 1996; Onderdonk and Chapman, 2000; Benchimol and Peres, 2013), information is lacking on how primates cope with and adapt to living in degraded habitats. The degree of behavioral flexibility determines whether members of a given species are able to persist in habitats experiencing anthropogenic or natural disturbance. Behavioral flexibility refers to an animals' ability to change its behavior in response to a changing environment (Nowak et al., 2013). Behavioral flexibility is positively correlated with brain size, favoring flexibility in primate species (van Schaik, 2013). However, as many primates have long life-histories and low population growth rates, it is hypothesized that they may go extinct once a critical level of habitat change has occurred (van Schaik, 2013). For example, howler monkeys (*Alouatta* spp.) are considered highly flexible as they are found in a wide range of human modified landscapes such as shade coffee plantations (McCann et al., 2003), cacao plantations (Muñoz et al., 2006), and eucalyptus plantations (Bonilla-Sánchez et al., 2012), whereas the absence of often sympatric spider monkeys suggests that they are have a lower threshold of habitat change. The speed with which primates can change their behaviors to mirror changes in the environment depends on the degree of human influence. For instance, primates living in close proximity to humans adjust their behavior rapidly (Hockings et al., 2015).

Behavioral flexibility benefits individuals living in habitats experiencing anthropogenic or natural disturbance. For example, orangutans (*Pongo* spp.) and Pitheciins take advantage of new forest strata by becoming more terrestrial (Barnett et al, 2012; Ancrenaz et al, 2014). Howler monkeys (*A. pigra*) reduce the number of energetically expensive behaviors such as agonistic behaviors in smaller forest fragments, thereby reducing the size of their behavioral repertoire (Rangel-Negrín et al., 2016). However, the long-term impact of reducing behaviors that are important in managing intra-group competition are not yet clear. Chimpanzees (*Pan troglodytes*) living in heavily hunted regions present another example of behavioral plasticity as they reduce the number of loud calls compared to chimpanzees living in areas where hunting levels are low (Hicks et al., 2013). Primates that are able to expand their trophic niche breath by changing their diet in response to anthropogenic or natural habitat disturbance may survive such disturbance events (Bicca-Marques, 2003; Chapman et al, 2003; Galat-Luong and Galat, 2005; Cristóbal-Azkarate and Arroyo-Rodríguez, 2007). For example, folivorous black-and-gold howler monkeys (*A. caraya*) supplement their diet by predating on bird nests in impoverished environments (Bicca-Marques et al., 2009). Likewise, diademed sifakas (*Propithecus diadema*) living in forest fragments consume mistletoe (*Bakarella clavata*) year-round instead of seasonally as they do in continuous forests due to the reduction of fruiting tree species in fragments (Irwin, 2007, 2008). However, immediate responses to habitat disturbance may not guarantee long-term survival. In the case of the diademed sifakas, individuals living in fragments had lower body mass (Irwin, 2007) and decreased physiological health (Irwin et al., 2010a). Additionally, the level of frugivory (Johns and Skorupa, 1987) and diet specialization is an important factor in determining whether primates are able to persist in forest fragments (Abondano and Link, 2012). Species with highly specialized diets (i.e., less flexible or intolerant species) are at a disadvantage when their habitats and food sources change and may not be able to respond to this change as rapidly as more generalist species (tolerant species; Meijaard et al., 2008).

Aside from flexibility in behaviors, such as feeding and locomotion, social flexibility may aid animals in adapting to changing habitats. The term fission-fusion dynamics refers to the temporal variation in the degree of spatial cohesion and individual membership in subgroups (Aureli et al., 2008). Species exhibiting high degrees of fission-fusion dynamics are common in a range of mammals and birds such as bats (*Myotis bechsteinii*, Kerth and König, 1999), dolphins (*Orcaella heinsohni*, Parra et al., 2011), elephants (*Loxodonta africana*, Archie et al., 2006) and primates (Lehmann et al., 2007). For example, spider monkeys and chimpanzees live in large communities in which all members rarely associate with each other at the same time (Symington, 1990). Instead, small subsets of individuals forage and travel together in subgroups. Spider monkeys and chimpanzees split into subgroups depending on the feeding tree size and the amount of fruit available (McFarland Symington, 1986). These subgroups change throughout the day in both size and composition (Goodall, 1986; Shimooka 2003; Asensio et al. 2009). The fissioning and fusing of subgroups can have several advantages. The formation of smaller subgroups permits the reliance on a patchily distributed food source, such as ripe fruit, through a reduction in competition between group members (Kummer, 1971; Korstjens et al., 2006; Asensio et al., 2008). Moreover, spider monkeys and chimpanzees minimize ranging costs by the fissioning and fusing of subgroups (Asensio et al., 2009; Lehmann et al., 2007).

The social flexibility provided by a high degree of fission-fusion dynamics means that the animals should be able to respond rapidly to environmental changes (Lehmann and Boesch, 2004). Interestingly, species such as spider monkeys and chimpanzees, exhibiting a high degree of fission-fusion dynamics, are often characterized as being highly susceptible to anthropogenic and naturally-occurring habitat disturbance (Ramos-Fernández and Wallace, 2008). For instance, *A. belzebuth* decreased their subgroup size after the start of seismic oil exploration in the Peruvian Amazon (Kolowski and Alonso, 2012). In contrast, no difference in brown spider monkey (*A. hybridus*) subgroup size was found between continuous forest and forest fragments in Colombia (Link et al., 2010). As outlined above, anthropogenic disturbance may cause large-scale habitat modification (e.g. forest loss), often occurring at an accelerated pace compared to changes in the environment caused by natural processes. It is unclear whether social flexibility aids response to such accelerated changes in the animals' environment. Although it is a short-term response, the social flexibility provided by a high degree of fission-fusion dynamics may allow animals to change in response to a disturbed environment by making foraging more efficient which in the longer term may keep population density stable despite the disturbance. There is indirect evidence that changes in foraging patterns can have such a consequence. For instance, population density of female red colobus monkey (*Procolobus rufomitratus*) did not differ in logged and unlogged areas of Kibale National Park, possibly due to female monkeys in logged areas feeding from more species and longer periosd than females in undisturbed areas (Milich et al., 2014). By changing subgroup size and composition in response to anthropogenic or natural disturbance, social flexibility may prevent a decline in population density (Kolowski and Alonso, 2012). For example, there was no effect of seismic oil exploration on number of spider monkey subgroups encountered but subgroup size significantly decreased when exploration began (Kolowski and Alonso, 2012). Changing subgroup size and composition as an immediate response to an anthropogenic or natural disturbance (as in the case of the red colobus monkeys: Milich et al., 2014 and spider monkeys: Kolowski and Alonso, 2012) can become a long-term adaptation to living in a changed environment. Behavioral flexibility may therefore promote responses that keep population density stable in the face of anthropogenic or natural habitat disturbance or that allow species to persist at lowered population densities.

By examining the response of animals to natural disasters we can learn how they may cope with other forms of disturbance. Hurricanes, a common phenomenon in the Yucatan Peninsula, cause large-scale damage to forests, especially younger successional stages (Bonilla-Moheno 2012). Although these young successional forests are not often used by atelines (Sorensen et al. 2000; Ramos-Fernández et al. 2003), changes in social structure, population density and diet of Neotropical monkeys have been reported in the aftermath of hurricanes (Pavelka et al. 2007; Behie & Pavelka 2005; Schaffner et al. 2012). Moreover, in the Yucatan Peninsula, spider monkey subgroup sizes were significantly smaller and fusion events less frequent after consecutive hurricanes Emily and Wilma (Schaffner et al., 2012), suggesting that a high degree of fission-fusion dynamics allows spider monkeys to adjust to changes in food sources. Additionally, diademed sifakas, a species with a low degree of fission-fusion dynamics, showed a lower social cohesion in fragmented forests as compared to continuous forests (Irwin, 2007). These inter-species differences illustrate that further investigation into the effects of different types of anthropogenic and natural habitat disturbance on species with varying degrees of fission-fusion dynamics is needed to understand the role of social flexibility in coping with habitat disturbance.

1.3 Spider monkey susceptibility to habitat disturbance

Spider monkeys (*Ateles*) are part of the subfamily Atelinae (Di Fiore et al., 2011), ranging from Southern Mexico to Northern Bolivia and are found on both sides of the Andes mountain range (Collins and Dubach, 2000). Males's home range are typically larger than females', who tend to restrict themselves to the core area of the group home range (McFarland Symington, 1988; Shimooka, 2005; Wallace, 2008a, b; Spehar et al., 2010; Asensio et al., 2015).

High levels of fission fusion dynamics may aid spider monkeys in coping with the effects of anthropogenic or natural habitat disturbance in the short term. However, aspects of their life history may limit their ability to change their behavior in the long term. Female spider monkeys have long inter-birth intervals, having an infant approximately every three years (McFarland Symington, 1988; Ramos-Fernández et al., 2003; Vick, 2008), which is longer than expected based on their weight (Chapman and Chapman, 1990). In addition, males and females take long to reach sexual maturity (i.e. 5-6 years, Vick, 2008). Spider monkeys are ripe fruit specialists (Klein and Klein, 1977; Weghorst, 2007; Di Fiore et al., 2008), which may leave them vulnerable to habitat change, as there is a negative correlation between species' survival rate as a result of fragmentation and percentage of fruit in the diet (Johns and Skorupa, 1987). Furthermore, spider monkeys have large home ranges and are almost completely arboreal (Campbell et al., 2005; Abondano and Link, 2012). Therefore, disturbance in their arboreal pathways can have negative effects on their movement patterns (Ramos-Fernández and Wallace, 2008). As a result of all of these factors, spider monkeys are among the slowest Neotropical primate species to recover from habitat disturbance (Sorenson and Fedigan, 2000). Additionally, habitat fragmentation is mostly coupled with anthropogenic activities to which spider monkeys are especially susceptible. Spider monkeys are favored meat in subsistence hunting (Freese et al., 1982; Mittermeier, 1991; Peres, 1990) and infants are often captured and kept as pets at the expense of their mothers' lives (Duarte-Quiroga and Estrada, 2003).

1.4 Primate conservation in Mexico

Mexico, part of the Mesoamerica biodiversity hotspot (Myers et al., 2000), is home to three species of primates: the mantled howler monkey (*Aloutta palliata*), the black howler monkey (*A. pigra*) and Geoffroy's spider monkey (*Ateles geoffroyi*). Protected areas and sites designated for the conservation of biodiversity cover 13% of forested area in Mexico (FAO, 2010), and have been increasing for the past 25 years (FAO, 2015; Figure 1.1). In addition, although annual rates of deforestation (largely the result of land conversion for pasture and cropland; Estrada et al., 2006) in Mexico remain high, they are steadily decreasing: 0.24 % for the period 2005-2010 and 0.1% between 2010-2015 (FAO, 2010; 2015; Aide et al., 2013; Figure 1.1). Yucatan in particular was one of the states with the highest levels of forest loss between 1976 and 2000 (Mas et al., 2004). The decrease in deforestation may in part be attributed to urbanization and resulting natural forest regeneration (Jacob et al., 2008). A priority setting exercise identified the Yucatan Peninsula as harboring some of the most important sites for primate conservation in Mexico (Tobón et al., 2012). *A. geoffroyi* and *A. pigra*, both classed as Endangered according to the International Union for the Conservation of Nature (IUCN; Cuarón et al., 2008; Marsh et al., 2008) occur throughout the Yucatan Pensinsula.

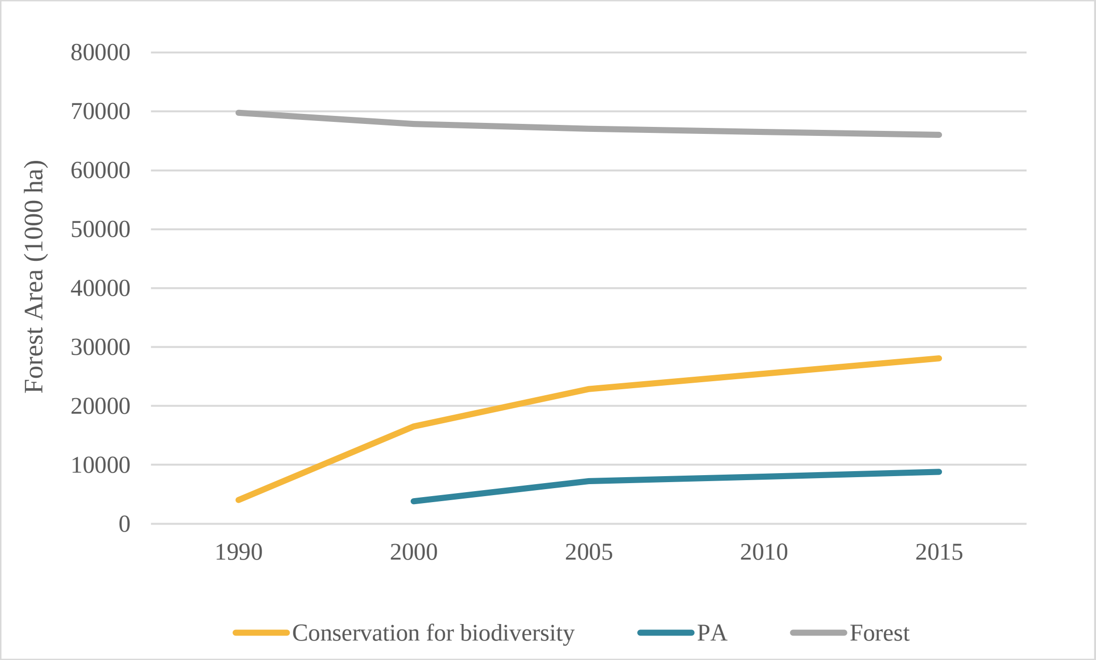

Figure 1.1. Amount of forest area lost, forest designated for conservation of biodiversity, and forest present within protected areas (PA) in Mexico between 1990 and 2015 (FAO, 2015).

Although the effects of natural and anthropogenic habitat disturbance on howler monkeys in Mexico have been intensively investigated (Estrada and Coates Estrada, 1996; Bicca-Marques, 2003; Arroyo-Rodríguez and Mandujano, 2006; Muñoz et al., 2006), there is a scarcity of similar studies that examine the consequence of such disturbance on spider monkey populations. Previous studies have examined the effects of fragmentation on spider monkey demography (Ramos-Fernández and Ayala-Orozco, 2003; Ramos-Fernández et al., 2003), sleep site use (Velázquez-Vázquez et al., 2015), and stress (Rangel-Negrin et al., 2009; Ordóñez-Gómez et al., 2016). Additionally, there have been investigations into the consequences of hurricanes and fragmentation on activity patterns and diet of spider monkeys (Chaves et al., 2011; Chaves et al., 2012; Schaffner et al., 2012). To date no studies have compared the effects of different types of habitat disturbance on spider monkey populations in Mexico. A country wide examination of human impact on mammalian biodiversity found frugivores such as spider and howler monkeys to be negatively correlated with a human settlement index, concluding that such species are sensitive to habitat degradation (Munguía et al., 2016). Studies examining overall vertebrate responses to disturbance in the Yucatan Peninsula found that species richness increased with a greater amount of forest cover in the surrounding matrix (Urquiza-Haas et al., 2010) and was affected by human population density (Urquiza-Haas et al., 2009). As human population density increased, the probability that sites were occupied by felids decreased. Interestingly, this trend was not found for primates; human population density did not affect the probability of neither spider nor howler monkeys occurring at a particular site (Urquiza-Haas et al., 2009). The lack of population information (population numbers, trends) associated with presence/absence surveys may make it too rough a measure of primate responses to anthropogenic disturbance, and emphasizes the need of more detailed research into the effects of habitat disturbance on primates.

Ramos-Fernández et al. (2013a) modeled the effects of climate change on the current and future distribution of spider monkeys in Mexico. The northeastern portion of the Yucatan Peninsula, currently an important refuge for spider monkeys, would lose suitability as a result of climate change, causing a shift in spider monkey distribution with those residing in the north-eastern portion of the Yucatan Peninsula disappearing and southern populations moving to south-central Mexico (Ramos-Fernández et al, 2013a). This change will likely increase the number of situations in which monkeys and humans come into contact and therefore potential conflict as the “Riviera Maya” tourism industry continues to expand. Human population density increased from 43.2 to 50.9 and 17.4 to 26.4 people per square kilometer between 2000 and 2010 in the state of Yucatan and Quintana Roo, respectively (INEGI 2000, INEGI 2010), due to the development of infrastructure resulting from the booming tourism industry (Urquiza-Haas et al., 2009). Human population density in the state of Quintana Roo is predicted to exceed the level tolerable by vulnerable species within the next 30 years (Urquiza-Haas et al., 2009). This tragic scenario seems likely, as more locations become popular tourist destinations. For example, the population of the fishing village of Puerto Morelos has increased from 892 people in 2000 (INEGI, 2000) to 9188 people in 2010 (INEGI, 2010) and there are plans to develop the area further. This is important as species distribution models have strongly predicted the occurrence of spider monkeys along the eastern coast of Quintana Roo (Vidal-García & Serio-Silva, 2010; Tobón et al., 2012), but survey data to corroborate their presence are outdated (Watts et al., 1986; Para Larra and Jorgenson, 1998; Serio-Silva et al., 2006; Ramos-Ferández et al., 2013a). As spider monkeys are especially susceptible to changes in their environment (Ramos-Fernández and Wallace, 2008), understanding their coping mechanisms to natural and anthropogenic habitat disturbance can help in the creation of management plans for this endangered primate (Cuarón et al., 2013).

1.5 Surveying spider monkeys

To get estimates of abundance (number of individuals in the population) or population density (number of individuals per unit area) scientists have surveyed spider monkeys using a range of methods. As spider monkeys (*Ateles* spp.) are a fast moving, arboreal primate (Di Fiore et al., 2011) that exhibit high levels of fission-fusion dynamics (Aureli et al., 2008), surveying them is notoriously difficult (Fedigan and Jack, 2001). Presence/absence surveys are quick and provide information on the distribution of a species (*A. geoffroyi*, Watts et al., 1986; Para Larra and Jorgenson, 1998; Méndez-Carvajal, 2013) and when combined with occupancy modeling can elucidate the factors that may affect presence in a certain area (*A. fusciceps fusciceps*, Spaan et al. in prep). Since opportunistic sampling and complete group counts are rare (Link et al., 2010), the most commonly used method to survey spider monkeys is line transects (Gonzalez-Kirchner, 1999; Weghorst, 2007; Aquino et al., 2012).

1.6 General objective

The aim of my research is to determine the effect of different types of anthropogenic and natural habitat disturbance on spider monkey populations in the Yucatan Peninsula and to assess different methods to estimate their population densities. The first objective is to determine the best method of performing line transect surveys for spider monkeys through analysis of how often and which assumptions of line transact sampling are violated given their high degree of fission-fusion dynamics and fast movement (Chapter 3). The second objective is to evaluate the effect of different types of anthropogenic and natural disturbance on spider monkey encounter rate and population density at the landscape scale (Chapter 4). The third objective is to evaluate change in spider monkey population density in the Otoch Ma’ax yetel Kooh Protected Area over an 18-year period (1997-98 vs. 2015-16), identifying the potential reasons for population changes (Chapter 5).

Chapter 2: General methods

2.1 Study sites

Study sites were selected based on the level (see section 4.1.1.2) and type of natural or anthropogenic habitat disturbance (i.e., ecotourism, forest regeneration as a result of forest fires and slash-and-burn agriculture, potential human-wildlife conflict, and construction). Study sites are located in the three states of the Yucatan Peninsula (Campeche, Quintana Roo and Yucatan; Figure 2.1).

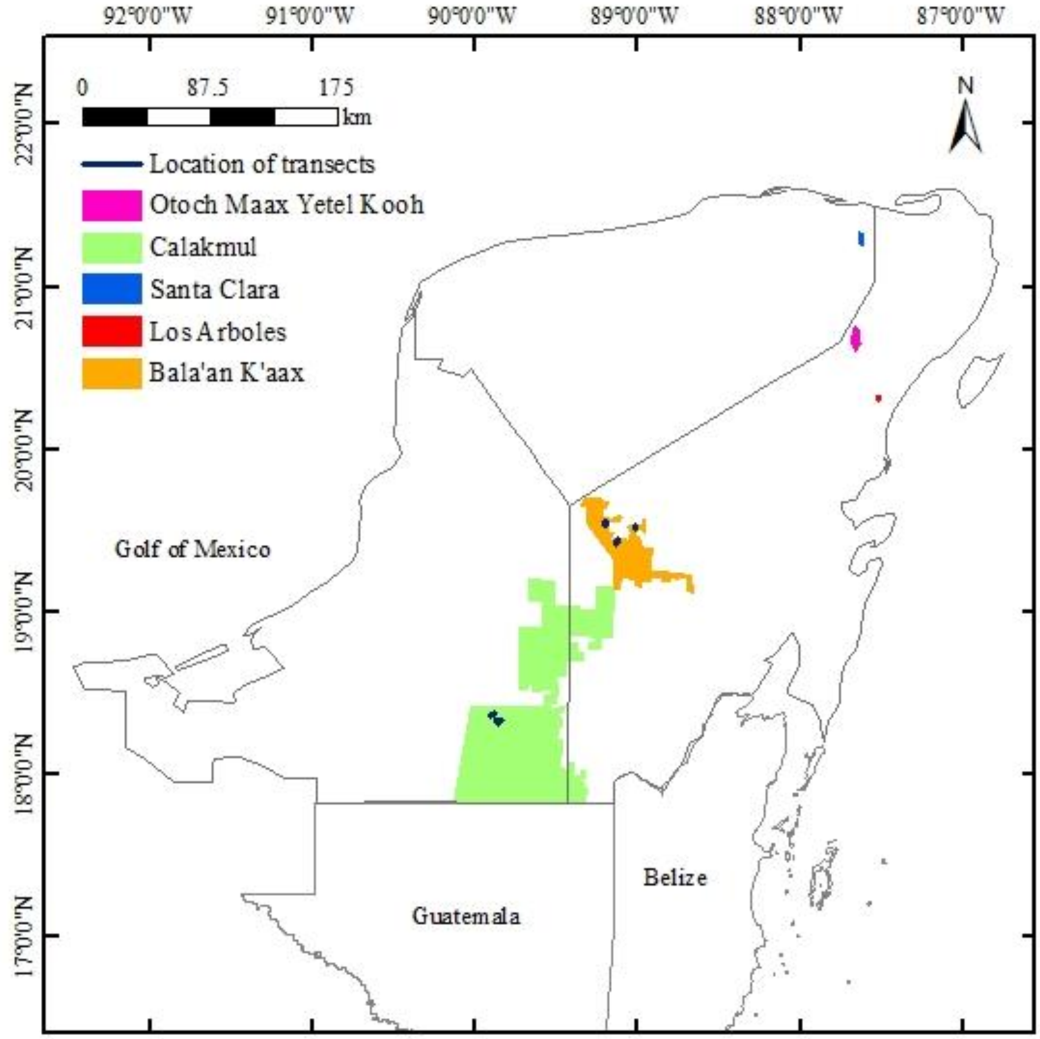

Figure 2.1. The location of study sites in the states of Campeche, Yucatan and Quintana Roo in the Yucatan Peninsula, Mexico.

2.1.1 Otoch Ma'ax yetel Kooh

Otoch Ma'ax yetel Kooh (OMYK; the house of the spider monkey and the puma in Yucatec Maya) Flora and Fauna Federal Reserve (20°38' N, 87°38' W, 14 m elevation, Figure 2.1), Yucatan, Mexico, was decreed a protected area in 2002 (García-Frapolli et al., 2007, 2009). The main goals of the protected area (as identified by the stakeholders) are to conserve biodiversity and improve the livelihood of the local people (Bonilla-Moheno and

García-Frapolli, 2012). Around 300 Yucatec Mayan people live in villages or small land-holdings in or around the reserve (García-Frapolli et al., 2007). The protected area consists of 5,367 hectares and includes old growth medium semi-deciduous forest and different degrees of regenerating forest due to historical practice of slash-and-burn agriculture (Ramos-Fernández et al., 2003). The slash-and-burn agriculture performed by the Yucatec Maya is referred to as milpa agriculture. Understory vegetation is removed, followed by burning of the remaining vegetation. The land is then farmed for 2-3 years, abandoned and left to regenerate for 20-30 years before it is farmed again (García-Frapolli et al., 2007). Principal crops grown on milpas include maize, beans, and chili (García-Frapolli et al., 2007). In a study carried out in 1999, approximately 700 hectares were occupied by old growth medium semi-deciduous forest and 2700 hectares consisted of 30-50-year-old successional forest (Ramos-Fernández et al., 2003). Between 1999-2003 3% of the reserve area consisted of milpas (García-Frapolli et al., 2007).

The protected area contains two preservation areas situated around the two major lakes, where activities are restricted to those that do not modify the habitat. The rest of the reserve constitutes multiple-use areas, which may be used for sustainable productive and extractive activities such as agriculture and apiculture (Bonilla-Moheno and García-Frapolli, 2012). However, forbidding the use of fire in the reserve has limited traditional slash-and-burn agriculture (Bonilla-Moheno and García-Frapolli, 2012). Some communities do gain economic benefit from the reserve. For instance, the Mayan community of Punta Laguna bordering the southern part of the reserve has been practicing eco-tourism for several decades (García-Frapolli et al., 2009; Bonilla-Moheno and García-Frapolli, 2012), but only since 2003 in a more structured form through the cooperative

Najil Tucha (the house of the spider monkey). Spider monkey investigations have been conducted since the mid-1990s (Ramos-Fernández et al., 2003). As a result of near constant human presence, the spider monkeys in Punta Laguna are fully habituated and individually recognized. Spider monkey population surveys have been done in the reserve in the past but have been restricted to certain areas and have not been carried out in the northern section of the reserve (Ramos-Fernández and Ayala-Orozco, 2003; Urquiza-Haas et al., 2010). For a list of tree species recorded on transects refer to Appendix 1.

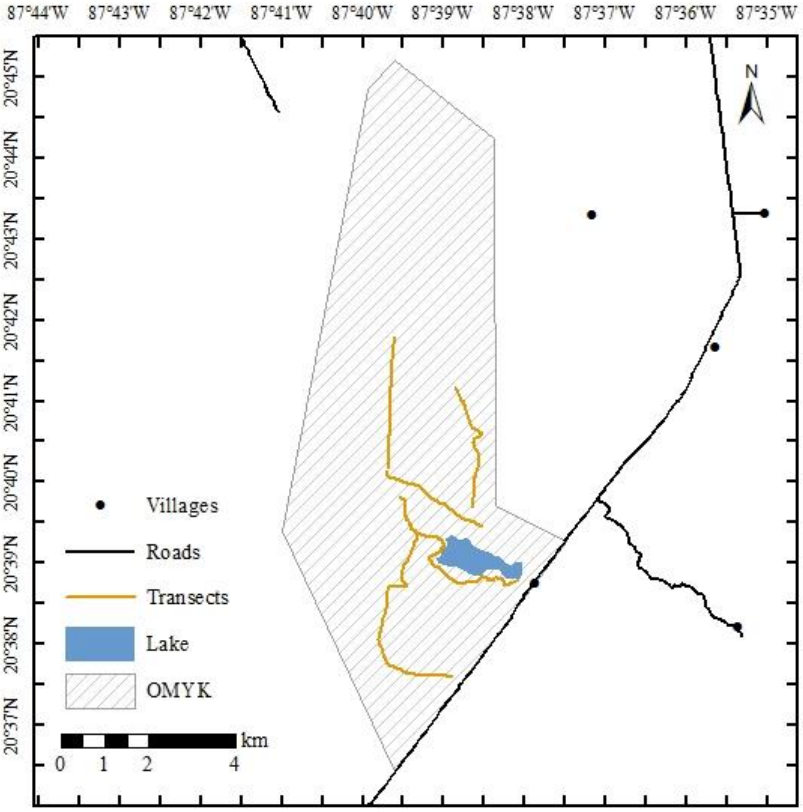

Figure 2.2. Otoch Ma'ax yetel Kooh Flora and Fauna protected area with the study transects.

Spider monkey population densities were calculated at 89.5 individuals per km^2 in the medium forest and 6.3 per km^2 for 30-50 years old regenerating forest (Ramos-

Fernández et al., 2003). Urquiza-Haas et al. (2010) found an encounter rate of 2.43 groups per 10 km. These surveys were carried out in 1997-1998 (Ramos Fernández, 2000a; Ramos-Fernández and Ayala-Orozco, 2003) and 2003-2004 (Urquiza-Haas et al., 2010).

I investigated the effect of forest regeneration on spider monkeys in OMYK. Interestingly, the reserve harbors forest in different stages of regeneration due to fire and slash-and-burn agriculture. A forest fire passed through the northern section of the reserve around 2011. The vegetation is therefore still in a very young stage of regeneration with the exception of small primary forest patches. Vegetation maps were constructed using satellite images by members of the research team determining the extent of the damage caused by the fire.

2.1.2 Calakmul

Calakmul Biosphere Reserve, Campeche (18°6′ 19.41″ N, 89°48′38.98″ W) in the southern Yucatan Peninsula was established in 1989. The biosphere reserve covers an area of 723,185ha and is the largest protected tropical forest in Mexico (García-Frapolli et al., 2009). Calakmul provided the most pristine habitat with the least anthropogenic or natural habitat disturbance, and only some degree of tourism. Spider monkey surveys in the reserve have been conducted in 2001-2002, but were restricted to the main Mayan ruins (Estrada et al., 2004) located at kilometer 60. The surveys found a population density of 17.2 individuals per km^2 (Estrada et al., 2004). For a list of tree species recorded on transects refer to Appendix 2.

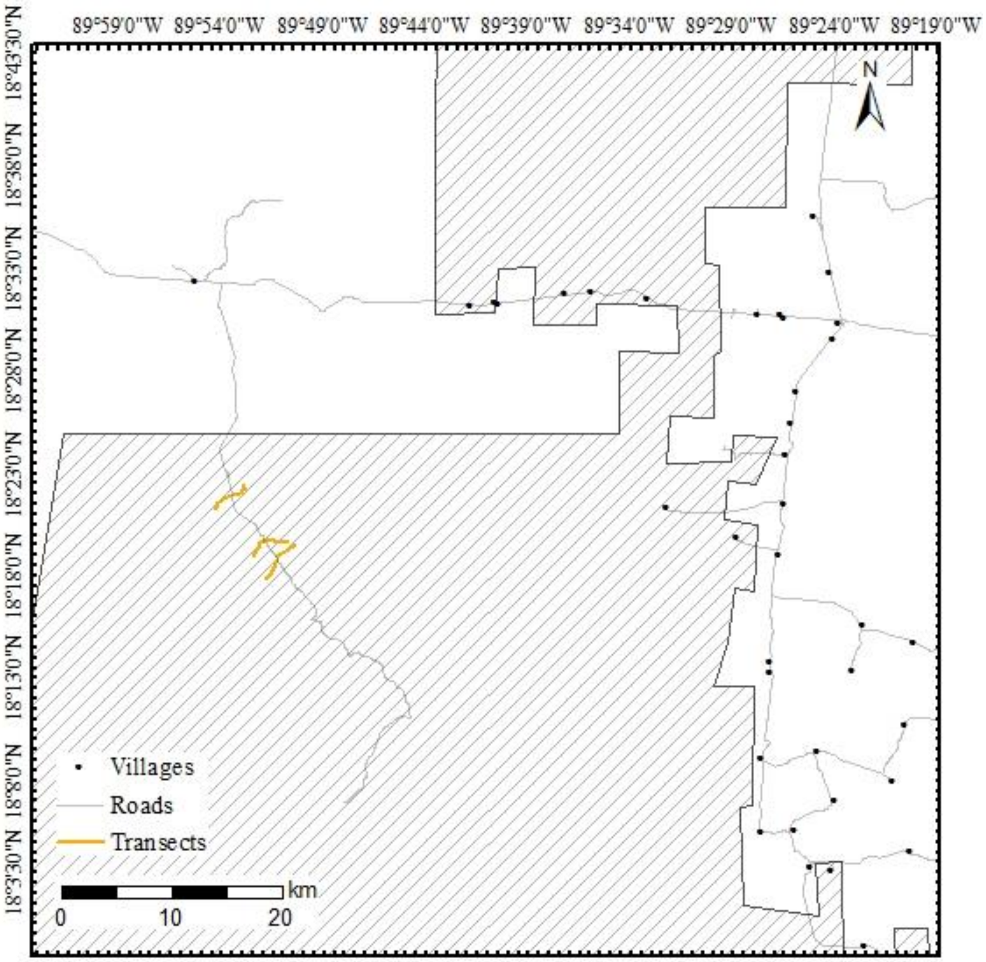

Figure 2.3. Biosphere reserve Calakmul with the study transects.

2.1.3 Los Arboles

Los Arboles Tulum (20°17'50.5''N, 87°30'59.1''W) is a residential housing development located about 14km from the city of Tulum, Quintana Roo on the Coba-Tulum highway. The 400-hectare area of primary forest is divided into 2-hectare plots (Figure 2.4). Owners are only allowed to build on 5% of their 2-hectare plots, using sustainable building materials. Only 25 of the 200 plots have completed residential homes. Spider monkey surveys have not previously been carried out at the site. For a list of tree species recorded on transects refer to Appendix 1.

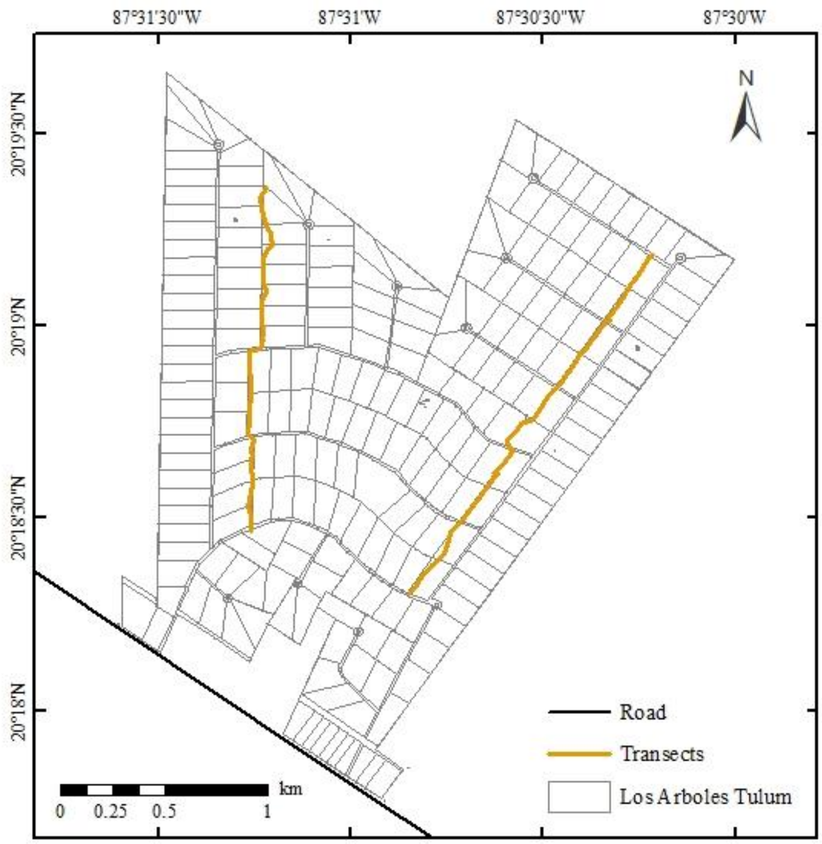

Figure 2.4. Los Arboles residential development with the study transects. The grey lines represent the boundaries between plots.

2.1.4 Bala’an K’aax

Bala’ax K’aax Flora and Fauna protected area (19°14’58”N, 89°20’30”W) covers an area of 128,390 hectares divided into a protected area and an area where sustainable activities may take place (Figure 2.5). Spider monkey surveys have not previously been carried out at the site. For a list of tree species recorded on transects refer to Appendix 3.

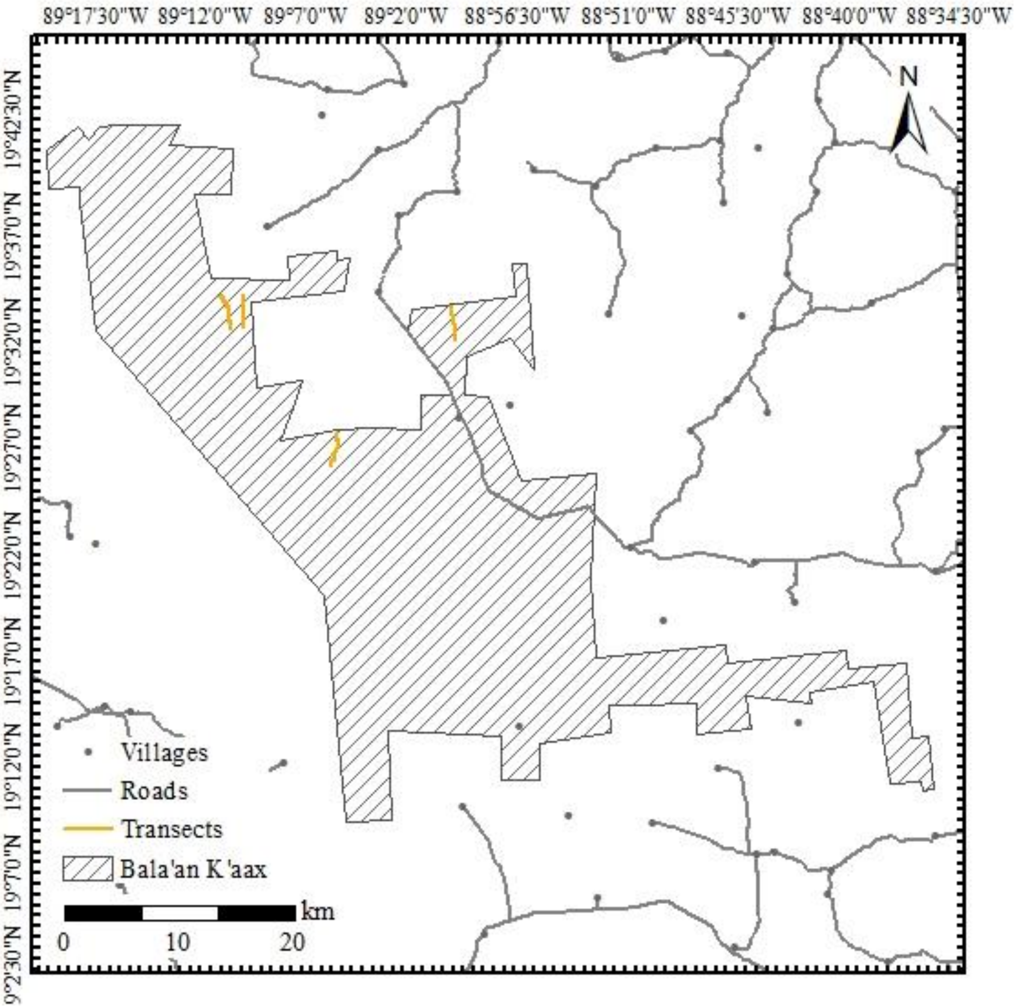

Figure 2.5. Bala’an K’aax Flora and Fauna protected area with the study transects.

2.1.5 Santa Clara

Santa Clara (21°16'15.4"N, 87°37'01.3"W), Yucatan is an ejido (Figure 2.6) located near the protected area of El Zapotal. Two forest fires passed through the area; the first around 20-30 years ago and the second around 8-10 years ago, burning down much of the forest of the ejido. These areas are now used for milpa and cattle farming, though several parts of the ejido have remained untouched since the forest fires. The only primary forest that remains is a 1 km^2 patch going 500 m outwards along both sides of the road leading from Colonia Yucatan to Nuevo Tescoco. The village of Santa Clara consists of a few houses along the road. In the past crop-raiding by the spider monkeys (e.g. feeding of fruit trees in the house backyards) was reported in the village. Currently, only 4-6 families live in the village of Santa Clara. Due to a lack of schooling and job opportunities, most families moved to the nearby cities of Colonia Yucatan and Tizimin in the village. The 1 km^2 fragment of primary forest that remains has been divided into 8 lots, which are currently for sale or have recently been sold.

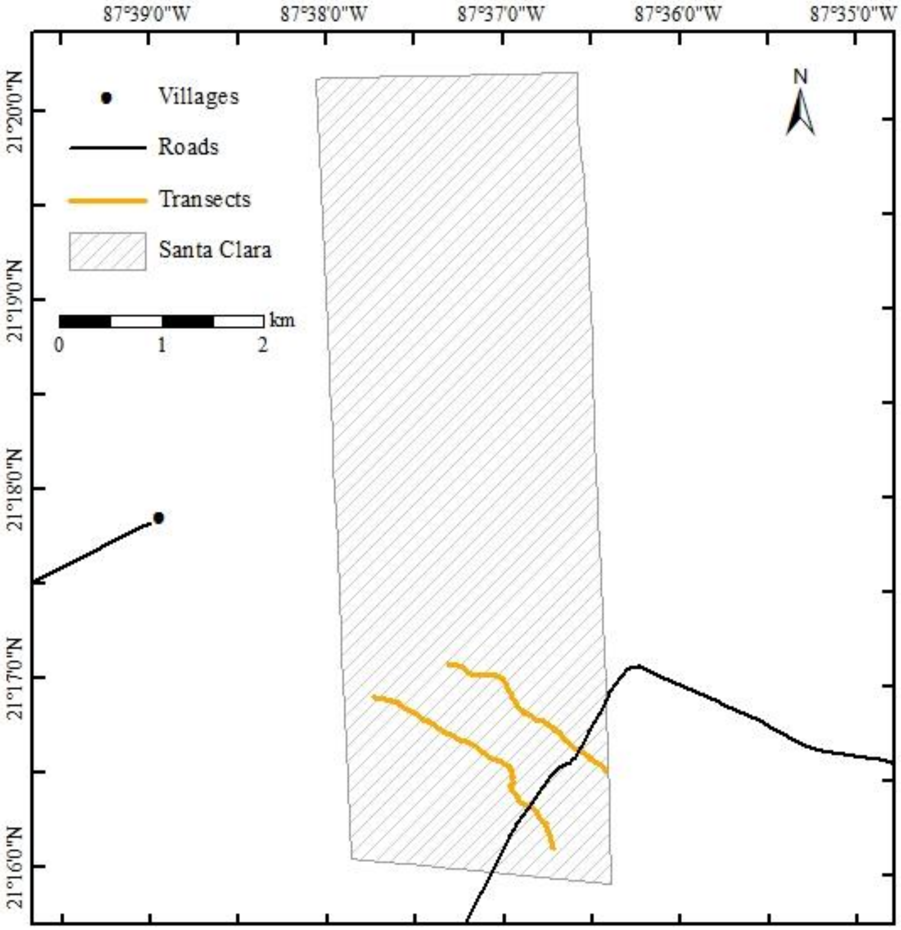

Figure 2.6. The ejido Santa Clara with the study transects.

I placed two transects in the ejido of Santa Clara (Figure 2.6). Both transects started in the village of Santa Clara passing through both mature forest and forest in differing stages of regeneration as a result of forest fires. Transect 1 was 2 km in length whilst transect 2 was 2.5 km in length. For a list of tree species recorded on transects refer to Appendix 4. Due to logistical constraints, I surveyed each transect in Santa Clara only 4 times. Therefore, data from Santa Clara was not used in any further analyses. In Santa Clara 3 spider monkeys were observed in 2 subgroups for a total survey effort of 14kms. The encounter rate of individual spider monkeys 0.21 individuals/km. Subgroup encounter rate 0.14 subgroups/km.

2.2 Data collection

2.2.1 Study design

Transects were marked using flagging tape at regular intervals (Anderson et al., 1979; Peres, 1999). Return walks were not counted as transect walks. New transects were cut at least one week before initial surveys were carried out to allow any animals that had fled to return (Peres, 1999). Transects were not cut more than 1 m wide but existing transects such as roads or paths may be wider than 1 m. Transect start time, date of survey, number of observers, and transect number/name were recorded prior to performing the survey. When monkeys were sighted during line transect surveys, I spent no more than 10 minutes collecting data on variables such as time of sighting, location (using a GPS), individual monkey age class, sex, activity, mode of detection (visual, audio, movement of the canopy), distance from the transect centerline to the individual, and compass bearing from the centerline to individuals sighted. Once a survey was completed, the time was recorded to determine the overall duration of the transect walk.

The size and composition of each encountered subgroup was recorded. I categorized independently-moving sighted monkeys into two age classes: adult and young. Adults are distinguished from young based on the size of the individual and facial coloration (Vick, 2008). Infants clinging to their mothers were not included in encounter rates or population density estimates as other studies of spider monkey population density only recorded independently-moving individuals (Weghorst, 2007).

Dense vegetation limits the use of rangefinders and measuring tapes to assess the distance from the centerline to the individual monkey. In those cases, I relied on visually estimating distances. Errors in estimating distances can substantially affect population density calculations, as observers may differ in their ability to estimate distances (Mitani et al., 2000) and to detect the survey species (Diefenbach et al., 2003). I performed all distance estimates and regular distance estimating exercises to minimize error in estimating distances to individual monkeys (see section 2.2.3). I calculated the monthly mean of the proportion of error ([actual distance - estimated distance]/ actual distance) for each 5 m distance class (0-5 m, 5-10 m, 10-15 m, etc.) based on distance estimating exercises done each month. I then multiplied the monthly mean proportion of error by the estimated perpendicular distances of sighted spider monkeys for the corresponding distance class and month, giving an output in meters, which was subtracted (when perpendicular distances were overestimated) or added (when perpendicular distances were underestimated) to the estimated perpendicular distances to obtain the corrected perpendicular distances.

2.2.2 Line transects

Conventional distance sampling is a survey method that accounts for detectability and visibility during surveys and can be applied to both line transects and point surveys

(Buckland et al., 2001). Line transect surveys are a population monitoring method in which straight lines are walked at set times and speeds recording all animals sighted above and along the transect centerline. During line transect surveys, perpendicular distance is measured from the transect centerline to the group or individual sighted (Peres, 1999; Buckland et al., 2010b; Plumptre et al., 2013; Figure 2.7). The decreasing probability of observing a group/individual with increasing distance from the transect centerline allows the estimation of the sample area (Marshall et al., 2008) and the estimation of the population density of that area (individuals per km^2).

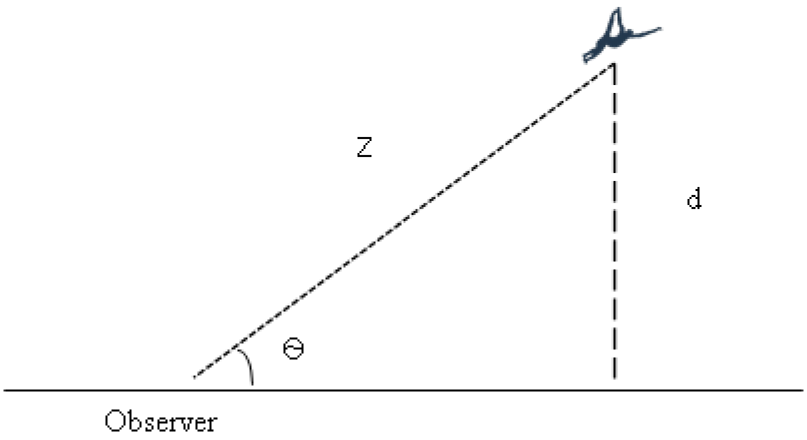

Figure 2.7. Measuring perpendicular distance (adapted from Greenwood and Robinson, 2006). The perpendicular distance from the transect centerline to the monkey (d) is calculated as d = ZsinΘ, where Z is the distance between the observer on the transect centerline and the monkey, and Θ is the sighting angle.

Conventional distance sampling uses the software DISTANCE (Thomas et al., 2010) to estimate population density. In order to run DISTANCE a minimum of 40 group/individual sightings per site are required (Peres, 1999), with a recommended number of sightings between 60 and 80 (Greenwood and Robinson, 2006; Plumptre et al., 2013). Such a large number of sightings can be difficult to obtain with species that are characterized by large home ranges, a high degree of fission-fusion dynamics and fast movements. Encounter rate (also referred to as relative density or relative abundance; Mitani et al., 2000) is the number of groups or individuals observed per km of transect walked. Encounter rate has fewer assumptions than conventional distance sampling and is thus less prone to error. The main assumption is that the number of animals recorded is a consistent proportion of the real population abundance (Norvell et al., 2003). Encounter rates do not use measurements of distance. In dense habitats range finders or measuring tapes are impractical and density estimates rely on estimated distances. Some studies found that observers greatly differed in their distance estimations (Mitani et al., 2000; Rovero et al., 2006), but not in the number of groups observed, the measure used to calculate encounter rates (Mitani et al., 2000). Encounter rates are generally only used as a population measure in habitats with the same characteristics (Teelen, 2007; Lwanga et al. 2011, with exceptions Nekaris et al., 2007; Urquiza-Haas et al., 2010) ensuring the same probability of detection resulting from similar levels of visibility during surveys (Norvell et al., 2003; Marshall et al., 2008). Several studies overcame differences in visibility between transect segments by excluding groups observed at distances greater than 40 m from the observer (Warner, 2002; Rovero & Struhsaker, 2007). However, Urquiza-Haas et al. (2010) found marginal differences in visibility for only 2 of 5 species when they compared mean perpendicular distances across sites in the Yucatan Peninsula. Therefore, I consider encounter rate to be an appropriate measure of primate populations in sites with different levels of visibility in the Yucatan Peninsula.

2.3 Data analysis

2.3.1 Generalized linear mixed models

Count data, like the number of sighted individuals, are discrete data as they can only be positive, and they often contain a large number of zeros. The large number of zeros limits the use of tests that assume a normal distribution of the data and the use of transformations to obtain normality. Count data commonly follow a Poisson distribution and are often overdispersed.

Generalized linear mixed models (GLMMs) are used when data are hierarchically structured (Rhodes et al., 2009), e.g. transects are nested within sites, and residuals are not normally distributed, such as count data. To ensure that no sources of error are introduced into the models, I tested for collinearity and spatial autocorrelation. Collinearity refers to the presence of a correlation between independent variables (Zuur et al., 2010). Collinearity between predictor variables can increase variance of regression coefficients (i.e., estimates of parameter variance), produce coefficients of the wrong sign or magnitude and produce models in which despite a large R^2 no variables are statistically significant (O'Brien, 2007). Collinearity between predictor variables complicates interpretation of results because it is difficult to separate the independent effects of each variable on the dependent variable (Rhodes et al., 2009; Freckleton et al., 2011). I used a variance inflation factor (VIF) to assess the collinearity between predictor variables. High VIF values of a variable indicate collinearity with the other variables (Sikkink et al., 2007). VIF values less than 3 suggest that predictor variables are independent of one another (i.e. no collinearity; Zuur et al., 2010). The variable with the highest VIF value is removed and the VIF analysis is rerun until all variables have VIF values less than 3.

Spatial autocorrelation refers to the amount of autocorrelation a variable has with itself as a function of its position in space (Negrete-Yankelevich and Fox, 2015). Spatial autocorrelation of the spider monkey sighting counts can occur between transect segments along the same transect as the distance between transect segments is smaller than the spider monkey home range (Rhodes et al., 2009), or between transects as they come from the same site. This is because residuals that are spatially closer to one another are more similar than those located farther from one another (Barelli et al., 2015). Spatial autocorrelation of the data was assessed using Moran's I test (Negrete-Yankelevich and Fox, 2015) in ArcGIS with the spatial autocorrelation function in the spatial statistics toolbox.

2.3.2 Estimating population density

Population density is calculated as a function of the total number of observations (N_t), total transect length (L_t) and effective strip width (ESW) (Struhsaker, 1981).

$$D = \frac{N_t}{2 \times ESW \times L_t}$$

The effective strip width is the distance from the transect centerline within which it is assumed that all monkeys have been detected (Struhsaker, 1981; Brugiere and Fleury, 2000). Several methods exist on how to calculate the effective strip width such as the King method (Meyler et al., 2012), the Kelker method (Struhsaker, 1981), the maximum perpendicular distance (MPD; Defler and Pintor, 1985; Chapman et al., 1988), and conventional distance sampling (CDS; Buckland et al., 2001; Buckland et al., 2010b). CDS commonly uses the software Distance (Thomas et al., 2010) to calculate population density (see section 2.2.2). In the MPD, the ESW is assumed to be the maximum perpendicular distance recorded during surveys (Chapman et al. 1988). In the Kelker method, the ESW is estimated through the visual inspection of histograms of the frequency of perpendicular distances (Chapman et al. 2000; Hassel-Finnegan et al. 2008; Meyler et al. 2012). I grouped perpendicular distances into bins of 4, 5, 6, 7, 8, 9, and 10 m. I then used the "fall-off distance" (FD), i.e., the distance at which the number of sighted individuals reduces dramatically (potentially due to problems of visibility) and beyond which it cannot be assumed that all animals present have been detected, to determine the number of sighted individuals and the area to include in the estimation of population density. I calculated population density using a FD of 50%, which was determined as the perpendicular distance bin that contained fewer than half the sighted individuals compared to the previous bin. As the Kelker method assumes that all individuals are detected with certainty within the ESW (Marshall et al. 2008; Campbell et al. 2016), I excluded individuals sighted outside of the ESW (and thus the FD) from the analysis (Struhsaker 1981; Chapman et al. 2000; Marshall et al. 2008). I selected the histogram that excluded the least number of sighted individuals after the 50% FD was applied.

CDS models the probability of detection as a function of the perpendicular distance $g(x)$ (i.e. the probability that an object at any particular distance x from the line is detected), assuming that all animals on the transect centerline are detected with certainty, i.e., $g(0) = 1$ (Buckland et al. 2001; Thomas et al. 2002). Therefore, the number of detections are expected to decrease with increasing distance from the transect centerline (Buckland et al. 2001; Campbell et al. 2016). The number of animals seen in the survey area is inversely related to the probability of detection required to calculate the number of animals recorded had the detection function equaled 1 at all perpendicular distances from the transect centerline (Burt et al. 2014). I fitted the distribution of perpendicular distances to the following key functions and adjustments in the software Distance 7.0 (Thomas et al. 2010): uniform key function with cosine adjustment, uniform key function with simple polynomial adjustment, hazard-rate key function with cosine adjustment, hazard-rate key function with simple polynomial adjustment, half-normal key-function with cosine adjustment, half-normal key-function with hermite polynomial adjustment (Buckland et al. 2001). I used the goodness of fit tests using Q-Q plots and Kolmogorov-Smirnov tests to assess the fit of the detection function to the data. Data heaping (i.e. a large number of observations of the same distances, which may occur when distances are estimated (Buckland et al. 2001) depends on bin size. After visually inspecting the Q-Q plots, I determined that there was no evidence of data heaping. To increase model robustness, I right-truncated 5% of the data (Buckland et al. 2001). I compared the models obtained using the Akaike information criterion (AIC) and chose the model(s) with the fewest parameters to determine the best fitting model (Buckland et al. 2001).

Chapter 3: Testing line transect surveys for fast-moving primates with high levels of fission-fusion dynamics

3.1 Introduction

Monitoring wildlife allows us to track populations over time, monitoring their welfare and extinction risk, and is thus central in conservation (Kühl et al., 2008). Population estimates are often the base of a wide range of different studies in the fields of ecology and biology. For instance, baseline data on population size are needed to make inferences on the effects of habitat disturbance on populations, the impact of disease or zoonoses, along with other aspects of animal biology (Kühl et al., 2008; Plumptre et al., 2013). Although wildlife surveys are of great significance, methods and analyses tend to vary, preventing the comparison between sites or years (Plumptre and Cox, 2006; Shanee and Shanee, 2011; Wich et al., 2016).

Population density, i.e., the number of groups or individuals per km^2, is the most popular measure used to monitor wildlife. However, population density may be affected by survey design, and recommendations that apply to one species cannot usually be universally applied to others. For this reason, several studies have aimed to test aspects of survey design in relation to population density estimates. The most common aspects include: the time at which the survey should be performed, the speed at which the observers should walk and the number of observers needed to obtain reliable estimates (Haus et al., 2009; Lee et al., 2014; Nekaris et al., 2014).

For diurnal primates, line transect surveys are often used to estimate population density, and are commonly performed in the morning and late afternoon (Peres, 1999;

Ingberman et al., 2009) as it is believed that primates are more likely to be encountered during periods of heightened activity (Chapman et al., 1988; Peres, 1999). For instance, the optimum time to survey gibbons (*Hylobates agilis*) is in the early morning (Lee et al., 2014). Conversely, howler monkeys (*Alouatta clamitans*) and sifakas (*Propithecus coquereli*) can be surveyed in the morning or afternoon as no differences in encounter rate (i.e., number of animals detected per km surveyed) and population density were found between the two times of day (Ingberman et al., 2009; Kun-Rodrigues et al., 2013). Studies of spider monkey activity budgets have shown that peak resting occurs around midday, with activity peaks in the early morning and late afternoon (Wallace, 2001). These peaks in activity correspond to peaks in encounter rate (Green, 1978), suggesting that these may be the ideal times to perform surveys. However, a recent study by Marsh et al. (2016) found no effect of time of day on spider monkey (*A. hybridus*) encounter rate.

Transects should be walked at a speed that allows the surveyor to detect the animals present and survey a large enough area (Ross and Reeve, 2003). Walking speed needs to avoid positive bias in population density when transects are walked slowly as more animals are detected closer to the transect centerline, and a negative bias in population density resulting from decreased detectability and increased evasive movement when transects are walked fast (Buckland et al., 2010b). For this reason, several studies have suggested that line transects aimed at surveying forest primates should be performed at speeds between 1-2 km/h (Peres, 1999; Ross and Reeve, 2003), however data to support this choice are often lacking. Recently, Nekaris et al. (2014) tested the effect of walking speed on slow loris (*Nycticebus javanicus*) encounter rate. Encounter rate decreased as walking speed increased, potentially the result of sighting lorises from greater distances when transects were walked slowly (Nekaris et al., 2014). Similarly, the mean number of bobwhite coveys (*Colinus virginianus*) seen per flight decreased with increased helicopter speed (Shupe et al., 1987). Contrastingly, studies on Atelines (*Ateles chamek* and *Lagotrix cana*) and river dolphins (*Inia geoffrensis boliviensis*) found no evidence of walking speed (1.5 km/hour vs. 2.0 km/hour) or boat speed on encounter rate (Iwanga and Ferrari, 2002; Aliaga-Rossel et al., 2006). These contrasting results suggest that walking speed may affect species differently and requires further investigation.

Line transect surveys are characteristically performed by a group of 1-2 observers, although, Peres (1999) recommends that transects are walked by only one observer. Several studies have used two observers with each observer monitoring a specific side of the transect (Defler and Pintor, 1985; Marshall et al., 2008), or one observer recording all animals observed close to or above the transect centerline (Marshall et al., 2008; Plumptre et al., 2013), while the other observer scans the transect sides. Studies examining the effect of the number of observers on encounter rate or population density estimates are limited. For instance, gibbon (*H. muelleri*) encounter rate did not differ between surveys performed by one or two observers (Nijman and Menkin, 2005). Large survey teams (i.e. more than three people) may cause more noise (Mathai et al., 2013), and therefore animals are more likely to flee before being detected. A study surveying primates in Vietnam conducted by two observers accompanied by 1-3 extra personal found the number of primate encounters to be independent of the size of the survey team (Haus et al., 2009). Thus, limited evidence suggests that the number of observers does not affect primate encounter rate (Romero et al., 2016).

3.1.1 Line transect assumptions

Line transect surveys are the most commonly used method to survey arboreal primates (Peres 1999; Hassel-Finnegan et al. 2008; Buckland et al. 2010b), and more specifically, *Ateles* spp. (Weghorst, 2007; Ravetta et al., 2009; Link et al., 2010; Aquino et al., 2012). The most basic output of line transect surveys is the encounter rate, i.e., the number of groups detected per km walked. Additionally, group density (number of groups per km^2) can be calculated by taking measures of the perpendicular distance from the transect centerline to the center of the group. Multiplying group density by the average group size gives the number of individuals per km^2 (i.e., individual density; Peres, 1999; Buckland et al., 2010b). Multiplying the population density (individual or group density) by the survey area gives an estimate of the number of individuals or groups inhabiting the area of interest. The ability to estimate the number of individuals or groups in an area makes line transect surveys an exceptionally important tool in conservation.

Line transect surveys are based on a series of assumptions (Buckland et al., 2010a; Buckland et al., 2010b; Ross and Reeve, 2011): 1) groups or individuals on or close to the survey line are detected with certainty; 2) groups or individuals are detected before they respond to the observer in the form of fleeing; 3) group sizes are recorded precisely and groups are not counted twice; 4) distances and angles from the line to the center of the group are measured accurately, and 5) a sufficient number of transect lines are randomly distributed in the survey area.

These assumptions may be difficult to meet when surveying animals exhibiting high degrees of fission-fusion dynamics and fast arboreal movement. The main problem is meeting the requirements of assumptions 2, 3 and 4. Violating the assumptions could lead to inaccurate estimates and is therefore of concern for conservation. The fast movement of spider monkeys enables them to flee from observers before the monkeys have been detected (assumption 2), which has been highlighted as a potential problem when surveying this species. One way to counter this potential problem is by walking at a speed that is faster than the commonly used 1 km/hour (Plumptre et al., 2013). The fast movement and high degree of fission-fusion dynamics of spider monkeys also makes it difficult to ensure that the same (sub)groups and/ or individuals are not counted multiple times (assumption 3). Despite this, to date no primate studies have aimed to investigate how commonly the same individual or group is detected at various points on the same transect.

As with many primates that move in widely spaced groups, it is difficult to determine the center of the group and thus it is challenging to measure the perpendicular distance from the line to the center of the group accurately (assumption 4, Buckland et al., 2010b; Bradford et al., 2014). To overcome this problem many studies have measured the distance from the observer to the first detected individual (*A. geoffroyi*, Gonzalez-Kirchner, 1999; *A. belzebuth*, Aquino et al., 2012; *Oreonax flavicauda*, Shanee and Shanee, 2011). However, the distance to the first detected individual is usually shorter than to the group center, as first detected individuals may hold peripheral positions in the group, causing inflated population density estimates (Buckland et al., 2010a). Additionally, several studies have used the animal to observer distance (AOD) instead of perpendicular distance. AOD is not based on statistical or theoretical frameworks and its use in determining primate population densities has therefore been repeatedly challenged (Plumptre and Cox, 2006; Hassel-Finnegan et al., 2008; Buckland et al., 2010a). A correction factor of group spread has been applied to improve population density estimates (Whitesides et al., 1988; Peres, 1999; Ferrari et al., 2010; Shanee and Shanee, 2011). However, the correction assumes that group spread is circular (Whitesides et al., 1988), whereas Plumptre (2000) demonstrated that group spread of several primate species is not stable, changing throughout the day and between months. Moreover, group spread is greater between 6:00-8:00, when surveys are often carried out (Plumptre, 2000). Using such a correction is therefore not appropriate for distance to first detected individual or to AOD of the group center. Another way to measure the distance to the group center is by considering only members that are visible at the time of the survey as group members. Perpendicular distance is then measured from the transect centerline to the center point of all the visible animals, assuming that all individuals in groups whose center is above the transect centerline are considered (Plumptre and Cox, 2006). A correction factor is then applied to control for the ability to detect larger groups more easily than smaller ones, especially with increasing distances from the line (Plumptre and Cox, 2006). However, using this method is not advisable as it likely leads to biased results, though the authors provide no reasons for this bias (Plumptre et al., 2013). Use of the first individual detected, AOD, and measuring to the center of visible animals are not applicable to species with high levels of fission-fusion dynamics as their groups are naturally highly spread out and subgroup patterns are continuously changing, thereby potentially biasing population density estimates.

Measuring perpendicular distances accurately (assumption 4) is imperative to obtain reliable population density estimates. Despite the availability of laser range-finders and measuring tapes, estimating distances by eye during line transect surveys remains common practice in primatology (Brugiere and Fleury, 2000; Hassel-Finnegan et al., 2008) as dense forest environments may prevent the use of laser range finders and measuring tapes when measurements need to be done quickly. Visually estimating distances has a high potential error, thereby introducing bias into population density estimates as perpendicular distances are not recorded accurately (Chapter 2, section 2.2.2). For instance, Buckland et al. (2010b) demonstrate that field assistants showed low accuracy in estimating distances, with only 24% of distances being estimated within 1 m and 59% within 2 m of the actual distance. Several studies have attempted to minimize bias by performing distance estimation training either before starting (Pruetz and Leasor, 2002), or at regular intervals throughout their survey. However, to date no studies have incorporated corrections for such bias into their calculations of population density.

3.1.2 Estimating population density

Population density estimates are often the base of a wide range of studies in ecology and conservation. However, methods for data collection and analysis of population density estimates from wildlife surveys vary, often preventing comparisons between sites or years (Plumptre and Cox 2006; Chapman et al., 2010; Shanee and Shanee 2011; Wich et al. 2016). Line transect surveys are the most commonly used method to survey mammals (Chiarello 2000), and estimate their population density, i.e., the number of groups or individuals per km^2 (Peres 1999; Hassel-Finnegan et al. 2008; Buckland et al. 2010).

Differences in effective strip width give different population density estimates as the survey area calculated by multiplying the effective strip width by the transected length increases or decreases with respect to the total number of observations, leading to over- or under-estimating population density (Struhsaker, 1981). For instance, although the King method has been advocated for spider monkeys (Link et al., 2010), in other primate species this method has provided inflated population density estimates (Meyler et al., 2012, Kun-Rodrigues et al., 2014).

Comparisons of population density estimates have found no differences between CDS and the Kelker method for a range of primate species including spider monkeys (Hassel-Finnegan et al., 2008; Link et al., 2010; Meyler et al., 2012, Kun-Rodrigues et al., 2014). Most studies use a modified t-test, the Z-test, to compare population density estimates between methods (Link et al., 2010; Kun-Rodrigues et al., 2014). Interestingly, seemingly large differences in population density estimates do not differ from one another statistically. For instance, Link et al. (2010) found no differences between the Kelker method and the CDS even though the CDS for capuchin monkeys (*Cebus albifrons*) gave population density estimates greater than 100% of the Kelker method (Kelker method: 56.3 vs. CDS: 116.6 individuals/km^2). Similarly, Meyler et al., (2012) found no significant difference between CDS and the Kelker method and confidence intervals overlapped (Kelker: 140.7 vs. CDS: 195.5 individuals/km^2 and Kelker: 179.1 vs. CDS: 264.9 individuals/km^2). In addition to using Z-tests, comparing population density estimates to an actual density estimate based on home range size and a known number of individuals in the population may also be an accurate method to compare population density estimates.

For group-living species such as most diurnal primates, using the group as the spatial unit of the population is advocated (Fleagle, 1998; Peres, 1999). Population density is thus calculated as group density times the average group size (Peres, 1999) Although for species with a high degree of fission-fusion dynamics, the subgroup can be used instead of the group (Peres, 1999), the average subgroup size is not a representative measure of the population. In species with high degrees of fission-fusion dynamics, subgroup size and composition changes throughout the day (Chapter 1, section 1.1) without reflecting population size (e.g., smaller subgroups do not reflect a smaller population size). Subgroup size is linked to food availability (Chapman et al., 1995, Pinacho-Guendulain and Ramos-Fernández, 2017), and average subgroup size differs between seasons (Hashimoto et al., 2003; Asensio et al., 2009), while group size stays the same. Average subgroup size is thus not a representative measure of average group size. Therefore, for species with high degrees of fission-fusion dynamics population density could be calculated better by using every individual animal encountered instead of the center of each subgroup (Buckland et al., 2010b), assuming that all individuals on or close to the transect centerline are recorded (Buckland et al., 2010b).

3.1.3 Aims and objectives

The aim of this chapter was to determine whether the assumptions for distance sampling are violated while surveying spider monkeys. Specifically, my objective was to determine the factors affecting spider monkey encounter rate and to evaluate which of several methods provides a population density estimate that is relatable to the actual density based on known population size and home range size of spider monkeys (cf. Chapman et al., 1988; Link et al., 2010). Additionally, I determined the effect of walking speed on population density estimates. I used the results to provide recommendations on how to best survey spider monkeys and other animals with a high degree of fission-fusion dynamics and fast arboreal movement.

3.1.2 Hypotheses and predictions

H 3.1 Time of day, number of observers and walking speed affect spider monkey encounter rate.

P 3.1.a. The encounter rate of spider monkeys is lower in transect walks performed at 10:01-14:00 compared to those performed at 6:00-10:00 and 14:01-18:00.

P 3.1.b. The number of monkeys encountered is higher when performing a survey with 2 or 3 observers compared than with 1 observer.

P 3.1.c. Spider monkey encounter rate is lower when transects are walked slowly.

H 3.2 The high degree of fission-fusion dynamics and fast movement of spider monkeys affects the frequency of recounting and accurate recording of detected individuals

P 3.2.a. The fast movement of spider monkeys leads to a high number of recounting the same individuals during the same transect walk.

P 3.2.b. The high degree of fission-fusion dynamics causes recounted individuals to be re-encountered in subgroups of differing size and composition.

P 3.2.c. Young individuals go unsighted more often than adult individuals.

H 3.3 The method used to calculate effective strip width affects population density estimates.

P 3.3.a. Population density estimates obtained from the Kelker method are less accurate than CDS when compared to the actual population density.

P 3.3.b. The density estimates obtained with the King method are the highest and therefore the least reliable when compared to the actual population density.

H 3.4 The speed at which a transect is walked affects population density estimates

P 3.4.a. Population density is overestimated when transects are walked slowly.

3.2 Method

3.2.1 Study site and subjects

Punta Laguna is a Mayan village bordering the Otoch Ma'ax yetel Kooh (OMYK) protected area where studies on spider monkey behavioral ecology have taken place over the past 20 years (see Chapter 2, section 2.1.1 for more information on the study site). The long-term study group of spider monkeys thus provides a unique opportunity to test line transect methodology as all monkeys are individually recognized, and current group size and home range size are known. For the purpose of my study 'young individuals' were defined as those older than 1 year but younger than 5 years, as infants less than 1 year still cling to their mother's bodies for large periods of time and may be obscured from view. Additionally, young less than 5 years old are found in the same subgroup as their mother (Vick, 2008). Individuals between 5 and 8 years old are usually considered subadults, being sexually mature, but not yet fully grown (Shimooka et al. 2008). As subadults can be difficult to distinguish from adults during surveys they were included in the adult class. Using these definitions, the study group consisted of 36 individuals older than 1 year: 5 adult males, 17 adult females and 14 young. The group included 11 mother-young dyads based on long-term demographic records.

3.2.2 Study design

I collected data between October 2014 and January 2015. Placement of transects were selected based on the area of the reserve that was highly used by the spider monkeys during the time of the study. One transect (919 m, Figure 3.1) was cut with the help of two assistants at the end of September 2014. The existing transect (919 m) was established a few years prior to the start of my study to perform twice-weekly phenological transect walks. The newly cut transect was opened to run in the same general direction as the existing transect and contains the same vegetation types as the existing transect in similar proportions. The vegetation of both transects consisted of mature forest (newly cut: 349 m and existing transect: 442 m) and regenerating forest in differing stages of regeneration. The existing transect also passed through an area of the reserve where ecotourism is practiced (417 m of transect), where the transect is wider than 1 m to accommodate a daily stream of tourists. As the number of monkey sightings in regenerating forest was very low for both transects, data from the different habitat types were pooled together per transect.

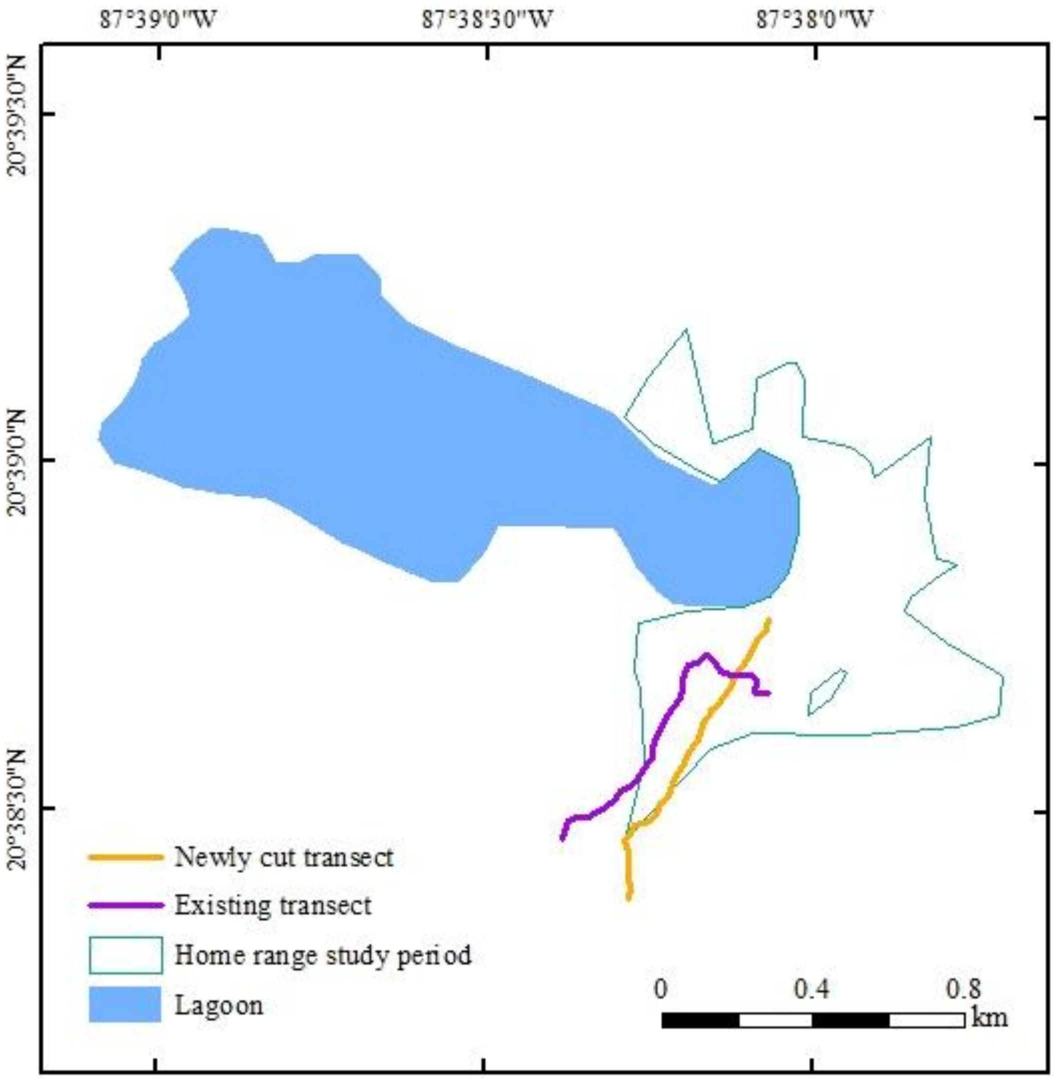

Figure 3.1. Home range of the study group of spider monkeys calculated for the study period.

Surveys were performed according to the line transect method (see section 2.2.1). Transects were walked at a speed of 1.0-2.0 km per hour. Surveys were performed twice daily for most survey days and the same transect was not walked more than three times per day. Transect walks were performed by one observer (always me), two observers (me with one assistant), and three observers (me with two assistants). Transect walks were performed in one of three time blocks covering all hours of the day in which spider monkeys are active (Table 3.1).

Table 3.1: The number of walks performed on each transect in relation to the number of observers and time block. The number of sighted monkeys is presented in brackets.

		Number of observers			**Time block**			
Transect type	**Transect length (km)**	1	2	3	6:00-10:00	10:01-14:00	14:01-18:00	Total
Newly cut	0.919	8(40)	35(75)	7(11)	23(84)	18(16)	9(26)	50(126)
Existing	0.919	7(3)	37(123)	8(28)	24(45)	16(54)	12(55)	52(154)
Total		15(43)	72(198)	15(39)	47(129)	34(70)	21(81)	102(280)

A 2-week pilot study was performed from the 1st to the 11th of October 2014 in which training in survey methodology was done. In particular, I was trained by highly knowledgeable local assistants, which have been following the monkeys for more than a decade, in identifying spider monkey age and sex classes and estimating sighting distances.

I recorded the subgroup size and composition during each spider monkey encounter and visually estimated the perpendicular distance from the transect centerline to all sighted individual monkeys. A correction was applied to the perpendicular distances (see section 2.2.3). During 2- and 3-observer transect walks I recorded the identity of all detected individuals with the help of local assistants trained in individually recognizing the study spider monkeys.

3.2.3 Data analysis

3.2.3.1 Spider monkey counts

I ran generalized linear models (GLM) to determine the effect of the predictor variables on each dependent variable (individual and subgroup counts). The predictor variables were the number of observers (1, 2 or 3), walking speed (continuous from 1.0 to 1.9 km/hour), and time of the day in which the survey was carried out (06:00-10:00, 10:01-14:00 or 14:10-18:00). Two sets of models were run with walking speed calculated in different ways. In one set of models walking speed was calculated including the time to record monkey sightings and in the other set walking speed excluded recording time. All VIF values were below 2 indicating that there was no collinearity between predictor variables (Rhodes et al., 2009; see section 2.3.1). Poisson distributions are commonly used to model count data (Richards, 2015). After checking for overdispersion (Buckley, 2015), I modeled individual counts and subgroup counts using negative binomial distributions. I created negative binomial GLMs using the glm.nb function of the package MASS (Ripley et al., 2013) in the program R v. 3.2.1 (R Core Team, 2016). I entered month and transect type (newly cut vs. existing trail) as control variables in all models to account for the potential effect of change in the distribution of food sources across months and repeat transect walks on the same transects. I compared the full models to null models including only the control variables (month and transect type) using a likelihood ratio test (Forstmeier & Schielzeth, 2011), with the anova function in R. I set statistical significance at $P<0.05$.

3.2.3.2 Line transect assumptions

I used the demographic data from the study group to determine when mothers or young were not observed in the encountered subgroup (i.e. they were missed) during 2-

and 3-observer transect walks (i.e. when a local assistant could individually recognize all encountered monkeys), because the corresponding young or mother was observed. I calculated the percentage of missed individuals per transect and age class by dividing the total number of missed individuals by the total number of individuals that should have been present in the encountered subgroups (i.e. all sighted and missed individuals) during all walks of one transect and multiplying this figure by 100.

I used the individual identity of the spider monkeys to determine when the same individual was observed multiple times during the same transect walk (recounted individuals) during 2- and 3-observer transect walks. I calculated the percentage of individuals that were recounted by dividing the total number of recounted individuals by the total number of individuals that were encountered and multiplying this figure by 100. To determine whether walking speed affects recounting individuals, transect walks were divided into slowly walked when walking speed was <1.5 km/h (n = 70) and fast walked when speed was >1.5 km/h (n = 32). I selected 1.5 km/h as previous line transect surveys of spider monkeys have been walked at speeds below or above 1.5 km/h (>1.5 km/hour: Cant, 1978; Iwanga and Ferrari, 2002; Ravetta and Ferrari, 2009; <1.5 km/hour: Weghorst, 2007; Link et al., 2010; Aquino et al., 2012; Kolowski and Alonso, 2012; Mendez-Carvajal, 2013).

3.2.3.3 Population density analyses

To compare population density estimates between methods, population density was estimated using the King method, maximum perpendicular distance, the Kelker method and CDS (see section 2.3.2). All 278 sighted individuals were included in the population density estimate for the King method and the maximum perpendicular distance. For the

Kelker method I grouped perpendicular distances into bins of 4-10 m and selected the histogram that excluded the least number of sightings; this histogram included 257 sighted individuals. For CDS 266 sighted individuals were included after right-truncation of 5% of perpendicular distances.

To determine the effect of walking speed on population density estimates, I calculated population density using the Kelker method and CDS for transects walked slowly (<1.5 km/hour) and fast (>1.5 km/hour). When transects were walked slowly 193 and 196 out of a total of 206 sighted individuals were included in analyses for the Kelker method and CDS, respectively. When transects were walked fast, 47 and 64 out of a total of 72 sighted individuals were included in analyses for the Kelker method and CDS, respectively.

3.2.3.4 Home range

Follows of spider monkey subgroups were conducted four days per week between the 1st of October 2014 and 29th of January 2015 by trained field assistants and students as part of a long-term behavior study. Upon encountering a subgroup, its location was marked using a Garmin GPS from approximately the center of the subgroup. Every subsequent 20 minutes a GPS point was similarly taken until the subgroup was lost or the shift for behavioral observations was completed. In total 981 GPS points were used to calculate the home range of the spider monkey group during the study period, which can be considered a large data set (i.e., >200 data points; Laver and Kelly, 2008; Pebsworth et al., 2012).

Home range was calculated using the adaptive-Local Convex Hull Method (LoCoH; Getz et al., 2007) by Sandra Smith Aguilar using the T-LoCoH package in R software platform (version 3.2.1). LoCoH was selected for its ability to detect natural boundaries as the spider monkeys in OMYK live along a lake (Figure 3.1). LoCoH constructs utilization distributions through the union of convex polygons related to each GPS point (subgroup location) and their *k* closest neighbours (Ramos-Fernández et al., 2013b). Distribution isopleths consist of sub-layers of convex polygons representing a certain proportion of the GPS points in the sample. For example, a 50% isopleth represents convex polygons that contain 50% of the GPS points (Ramos-Fernández et al., 2013b). Home range was defined as the 95% isopleth, a definition previously used in studies of various species (Laver and Kelly, 2008) including the spider monkeys of OMYK (Ramos-Fernández et al., 2013b), thereby ensuring comparability with other studies.

3.3 Results

3.3.1 Encounter rates

Between October 2014 and January 2015 I performed 102 transect walks (newly cut transect: 50; existing transect: 52), with a total survey effort of 93.74 km (newly cut transect: 45.95 km; existing transect: 47.79 km). I sighted 280 individuals (newly cut transect: 126; existing transect: 154) in 103 subgroups (newly cut transect: 48; existing transect: 55). The mean (±SE) size of encountered subgroups was 2.7±0.17 individuals; 2.7±0.28 individuals (range: 1-12) on the newly cut transect and 2.8±0.21 individuals (range: 1-6) on the existing transect.

Full-null model comparisons found that the predictor variables did not affect individual spider monkey counts including ($\chi^2 = 7.06$, df = 5, p = 0.22) or excluding the time to record individuals ($\chi^2 = 7.04$, df = 5, p = 0.22). Similarly, the predictor variables did not affect spider monkey subgroup counts including (χ^2 = 10.69, df = 5, p = 0.06) or excluding recording time (χ^2 = 10.62, df = 5, p = 0.06).

3.3.2 Line transect assumptions

During transect walks, when I was accompanied by an assistant that recognized the monkeys individually (i.e. transect walks with two and three observers), I observed a total of 237 spider monkeys older than 1 year in 89 subgroups including 115 adult females and 93 young. Recounting individuals was relatively rare, with only 5 monkeys reencountered during the same transect walks (3 on the newly cut transect, and 2 on the existing transect), which is 2.1% of the encountered monkeys in 3.3% of the encountered subgroups (3 of the 89 subgroups). In all 5 cases the subgroup composition changed between the first and second sighting. All 5 cases of recounting occurred when the transects were walked slowly (i.e. <1.5 km/h).

In total 2 adult females (1 on the newly cut transect and 1 on the existing transect) and 14 young over the age of 1 year (7 on each transect) were missed. The 2 missed adult females represented 1.7% of the encountered adult female monkeys (115 sighted and 2 missed), whereas the 14 missed young represented 13.1% of the encountered young (93 sighted and 14 missed). When transects were walked slowly 7 individuals were missed (2 adult females and 5 young) and 9 individuals (all young) were missed when transects were walked fast.

3.3.3 Population density

Transects were located in areas where spider monkeys were sighted during the same season in previous years to maximize sightings for methods testing. However, as spider monkey home ranges in OMYK change yearly (Ramos-Fernández et al., 2013b) and seasonally (Smith-Aguilar et al., 2016), parts of the transects ended outside of the study period home range, but were within the home range calculated for the entire 2014 (Figure 3.1). Between October 2014 and January 2015, 36 spider monkeys older than 1 year used a home range of 0.55 km^2 (Figure 3.1). The actual population density based on the home range size during the study period was therefore 65.4 individuals per km^2.

Population density estimates calculated using various methods to determine ESW (irrespective of walking speed) are presented in Table 3.2. The AIC values of two models run with CDS in the software Distance did not differ more than 2 units from one another, nor differed in the number of parameters, providing a range of density estimates. The two top models were uniform key function with a cosine adjustment and the half-normal key function with a cosine adjustment. Population density estimates varied greatly and ranged from 34.5 to 144.9 individuals per km^2. Maximum perpendicular distance provided the lowest estimate and the King method provided the highest estimate. The Kelker method deviated the least from the actual density estimate, followed by CDS. Maximum perpendicular distance underestimates population density by almost 50%, whereas the King method overestimates population density by more than 100%.

Table 3.2: Estimates of population density (individuals/km^2) based on the perpendicular distance of each encountered individual calculated using 4 methods.

Method	ESW (km)	Population density estimate	Confidence intervals	Percent deviation from actual density
Kelker method	0.024	57.8		-11.6
King method	0.011	144.8		121.4
Max PD	0.059	34.5		-47.3
CDS	0.015	92.9 - 93.8	70.8 - 122.2	42 - 43.4

The number of monkeys differs between analyses due to differing truncation distances between methods.

Population density estimates calculated using the CDS and the Kelker method for transects walked slowly (i.e. between 1.0 and 1.49 km/h; 206 sighted individuals) and fast (i.e. between 1.5 and 1.9 km/h; 72 sighted individuals) are presented in Table 3.3. The AIC values of several models run in the software Distance did not differ more than 2 units from one another, nor in the number of parameters, providing a range of density estimates. When transects were walked slowly, the uniform key function with a cosine adjustment and the half-normal key function with a cosine adjustment were ranked as the top models. When transects were walked fast, the half-normal key function with cosine adjustment was the top ranked model.

Table 3.3: Estimates of population density (individuals/km^2) based on the perpendicular distance of each encountered individual when transects were walked slowly and fast, and their percent deviation from the actual density estimate.

Method	**Walking speed**	**ESW**	**Population density estimate**	**Confidence intervals**	**Percent deviation from actual density**
Kelker method	Slow	0.024	62.5		-4.4
	Fast	0.010	79.9		22.2
CDS	Slow	0.015	98.4 - 100.4	70.9 - 138.2	50.5 - 53.5
	Fast	0.010	111.4	66.4 – 186.8	70.3

The number of monkeys differs between analyses due to differing truncation distances between methods.

When transects were walked slowly, population density calculated using the Kelker method deviated the least from the actual density estimate (<5% underestimation), whereas CDS overestimated population density by at least 50%. When transects were walked fast, the Kelker method deviated from the actual density estimate by about 20%, whereas CDS overestimated population density by about 70% (Table 3.3). The population density estimates did not differ within methods in relation to walking speed.

3.4 Discussion

3.4.1 Study design

Individual and subgroup spider monkey counts were not affected by walking speed, and the number of observers, failing to support Predictions 3.1a, 3.1b and 3.1c. Although there are peaks in the activity of spider monkeys in the early morning and late afternoon (Green, 1978, Wallace, 2001), corresponding to peaks in encounter rate (Green, 1978), I found no effect of time of day on spider monkey counts (prediction 3.1a). Similarly, spider monkey (*A. hybridus*) surveys done in forest fragments found no effect of time of day on encounter rate (Marsh et al., 2016). Previous studies on Atelines (*Ateles chamek* and *Lagothrix cana*) support my findings as walking speed did not affect encounter rate (Iwanaga & Ferrari, 2002).

The spider monkeys inhabiting the forest near Punta Laguna are highly habituated to human presence with ecotourism being the major source of income in the village and guides often enter the forest with groups of up to 10 tourists. It is therefore likely that aspects of study design that related to observer behavior, such as the number of observers, would not affect spider monkeys' behavior and therefore the number of monkeys sighted. The high levels of habitation may have confounded my results, as the monkeys' responses to walking speed and the number of observers may not be comparable to populations of unhabituated monkeys. However, studying a habituated group was necessary in order to examine the likelihood of recounting and missing individuals, as well as to compare estimated population densities with known density.

I hypothesized that the fast movement of spider monkeys would result in a high number of recounts (Prediction 3.2a). However, the number of recounted individuals was very low, suggesting that the fast movement of spider monkeys (1.6 ± 0.88 km/hour; Ramos-Fernández unpublished data) does not affect recounting when the observer also walks fast, as all instances of recounting occurred when transects were walked slower than 1.5 km/hour. The low number of recounted individuals is in line with the observation made by Chiarello (2000) who noted that recounting was unlikely as the same species was rarely observed twice on the same transect during mammal surveys in the Brazilian Amazon.

As predicted (Prediction 3.2b), the high degree of fission-fusion dynamics can explain why recounted spider monkey subgroups changed in size and/or composition between first and second encounters and may therefore affect survey results, if it is not taken into account in survey design. During surveys of species that form cohesive groups, surveyors may avoid recounting by excluding groups that have the same size and composition as previously encountered. My results show that for species with high degrees of fission-fusion dynamics this approach may not work as subgroup size and composition can change quickly and over short distances. My results, however, suggest that this potential problem is minimal as only 2.1% of the encountered monkeys were recounted. All occurrences of recounting occurred when transects were walked at a speed of <1.5 km/hour, suggesting that walking slow can increase the chance of recounting spider monkeys. To my knowledge this is the first study in which the recounting of individuals and subgroups was examined. It would be beneficial if similar studies are performed on other habituated populations of primates with lower levels of fission-fusion dynamics to understand the effect on population surveys.

As predicted (Prediction 3.2c), more young went undetected during surveys than adult females. The proportion of adult females that went undetected during surveys was low (1.7%). As male spider monkeys move faster than females (Shimooka, 2005), it cannot be assumed that the number of undetected adult males is similar to adult females, despite the lack of sexual dimorphism in spider monkeys (Rosenberger et al., 2007). I estimate that >10% of individuals over the age of 1 went undetected during surveys, thereby potentially violating the assumption that groups are counted accurately as all the missed young were independently-moving individuals and thus normally included in survey counts.

The proportion of young that were missed equaled 13.1%. This may be problematic when population surveys are aimed at collecting data on group composition, as is often the case in unexplored areas. The young:adult female ratio is an important indicator of population health (Fedigan and Jack, 2001), but missing young individuals disproportionally can bias this ratio. The ratio obtained from the survey data (0.81) was lower than the ratio when missed individuals were included (0.91), suggesting that the population is less healthy than it is. Distinguishing nulliparous subadult females from adult females during population surveys may be problematic due to their similar size (Struhsaker, 1981; Fedigan et al., 1985; Treves 2001) and several studies have therefore grouped subadult and adult females together (Fedigan and Jack, 2001; Treves, 2001). However, as subadult females have yet to contribute reproductively to the population, their inclusion in the adult female age class biases the young:adult female ratio. Like in the case of missing individuals, the young:adult female ratio obtained from the survey data (0.81), in which subadult females were likely included as adult females, is lower than the ratio based on only the actual number of adult females in the group during the study period (1.17).

Interestingly, when I added the number of subadult females to the actual number of adult females in the group the ratio was 0.82, showing a high accuracy of estimates based on survey data. All ratios I calculated to evaluate the issue of missing individuals or misclassifying subadult females during surveys fell within the young:adult female ratios of other spider monkey populations (0.36-1.31; Shimooka et al., 2008). Still, survey data indicate that the study population is less healthy than it actually is. I therefore suggest that young:adult female ratios based on survey data be interpreted as conservative indicators as they likely bias against population health.

3.4.2. Population density

Despite *Ateles* widely ranging from southern Mexico to Bolivia, this is one of few population density studies of the genus. High levels of spider monkey hunting for consumption and the primate pet trade (Freese et al., 1982; Mittermeier, 1991; Peres, 1990; Duarte-Quiroga and Estrada, 2003) often result in low encounter rates during population surveys, which restrict the calculation of population density to the Kelker, King and maximum perpendicular distance methods (Aquino et al., 2012). I therefore aimed to compare densities obtained from commonly used methods to the actual density based on the home range size and the number of individuals inhabiting it during the study period to investigate which method gave the most accurate density estimate.

In contrast to Prediction 3.3a, population density estimates obtained using the Kelker method were more accurate than CDS. The Kelker method with a 50% fall off distance deviated the least from the actual density, underestimating actual density by 11.6% (Table 3.1). Population density estimates obtained using CDS overestimated the actual density estimate by 42-43.4%. Similarly, population density estimates of spider monkeys

(*A. hybridus*) living in a forest fragment estimated by the Kelker method and CDS deviated from the actual density by at least 40% (Link et al., 2010). All estimates fall outside of the <10% deviation from the actual density considered to provide reliable estimates (Whitesides et al., 1988; Hassel-Finnegan et al., 2008).

Following Prediction 3.3b, the King method dramatically overestimated population density (121.4% deviation) in the present study. By contrast, Link et al. (2010) found the King method provided the estimate most similar to the actual density. Although the King method may be applicable to situations where populations occur at high densities (e.g. as a result of forest fragmentation; Link et al. 2010), it has often overestimated primate (Meyler et al., 2012; Kun-Rodrigues et al., 2013) and other mammalian (Beck-King et al., 1999) population densities. Problematically, spider monkey surveys often use the King method to estimate population density (Aquino, 2006; Aldana et al., 2008; Link et al., 2010; Aquino et al., 2012), thereby potentially providing highly inflated density estimates. As all spider monkey species are classed as either Endangered or Critically Endangered on the IUCN red list (Cuarón et al., 2008), inflated density estimates could provide false hope for the well being of surveyed populations.

Line transect surveys for spider monkeys have been carried out by walking at speeds between 1.0 and 2.0 km/hour (Cant, 1978; Pruetz and Leasor, 2002; Iwanga and Ferrari, 2002; Weghorst, 2007; Ravetta and Ferrari, 2009; Link et al., 2010; Aquino et al., 2012), but the effect of walking speed on population density estimates has not been addressed. In contrast to prediction 3.4a, population density estimates deviated less from the actual density when I walked transects slowly (1.0–1.49 km/hour) than when I walked them fast (1.5–1.9 km/hour) for CDS (50.5% – 53.5% vs. 70.3%) and the Kelker method

(-4.4% vs. 22.2%). However, population density estimates were similar between walking speeds for the Kelker method (62.5 vs 79.9 individuals/km^2) and CDS (98.4-100.4 vs. 111.4 individuals/km^2), suggesting that walking speed may not affect population density. Additionally, the confidence intervals of the population density estimates obtained using CDS overlap (70.9-138.2 vs. 66.4-186.8 individuals/km^2). These results support the lack of relationship between walking speed and spider monkey counts (section 3.4.2). I thus found no evidence to suggest that walking transects slowly creates an upward bias in population density estimates (Buckland et al. 2010). Importantly, it must be noted that the spider monkeys in the southern section of the OMYK have been studied for over 20 years and are highly habituated to human presence (Ramos-Fernández et al. 2003). These monkeys therefore do not flee when observers come near, as is expected for unhabituated groups. The high degree of habituation of the study monkeys may have resulted in a slow walking speed not affecting population density estimates.

Population density estimates differed between the Kelker method and CDS for the same walking speed (i.e. either fast or slow). For example, when transects were walked rapidly (1.5–2.0 km/hour), which was comparable or faster than the average speed of the monkeys at the study site (about 1.6 km/hour: G. Ramos-Fernández unpublished data), the Kelker method deviated around 20% and CDS deviated around 70% from the actual density estimate. However, this difference can be attributed to the methods used as the size of the difference between the population density estimates is similar to that obtained from the comparison between methods where walking speed was not taken into account.

My approach of using the home range relative to the study period only to calculate actual population density is different from previous investigations aimed at testing line transect methodology in primatology. For instance, Brugiere and Fleury (2000) compared the home range of several radio collared black colobus monkey (*Colobus satanas*) groups calculated from data collected between May 1995-October 1996, to line transects surveyed between September 1994-November 1995. Likewise, Hassel-Finnegan et al. (2008) compared white-handed gibbon (*Hylobates lar*) home range data collected between November 2003-October 2004 to line transects surveyed between December 2000-September 2001 and February 2002-September 2003. In both examples home ranges were calculated for time periods that only partially overlapped with the survey period. Like my study, black colobus population density was underestimated using the maximum perpendicular distance (-22.2 – -33.3%), but it deviated the least from the actual density estimates (Brugiere and Fleury, 2000). In my study, the Kelker method deviated the least from the actual density estimate (-11.6), yet population density estimates of white-handed gibbons and black colobus were overestimated using the Kelker method (41.3% and 77.7% - 107.4%, respectively). Similar to my study, Hassel-Finnegan et al. (2008) found that estimates obtained with the CDS deviated largely from the actual population density (52.5%). Discrepancies between my study and previously published work suggests that comparisons of population density estimates to actual densities calculated for different periods may not be suitable for the purpose of methods testing due to differences in home range size and/or group size and composition between the two periods. In fact, my study group size and composition, and its home range, have changed over the years and between seasons (Ramos-Fernández et al., 2013b, Smith-Aguilar et al., 2016).

Methods used to estimate home ranges differ across studies, which in turn can affect actual density estimates. The block method (also called the quadrat method or the grid cell method) counts the number of quadrats in which the monkeys are observed at least once (Chapman et al., 1988; Brugiere and Fleury, 2000; Fashing and Cord, 2000; Glessner and Brit, 2005). Unlike the LoCoH (see section 3.2.3), the block method may include empty quadrats surrounded by occupied quadrats in the home range analysis (Brugiere and Fleury, 2000), thereby increasing the area used to calculate actual density. Additionally, differences in quadrat size between studies (e.g., 50 m x 50 m in Fashing and Cord, 2000 and 200 m x200 m in Chapman et al., 1988) may cause inconsistencies in home range estimates. If an animal crosses from one quadrat to the next, irrespective of the amount of time spent or the amount of quadrat area used, the whole quadrat is considered for the analysis. With a large quadrat size, this may inflate home range size if the individual or the group used only a small proportion of the quadrat (Glessner and Brit, 2005). The method of the minimum convex polygon (MCP) creates a polygon by connecting sightings using straight lines (Chapman et al., 1988; Glessner and Brit, 2005). Despite its common use, MCP has been heavily criticized as it tends to overestimate home range size (Cumming and Cornélis, 2012) due to its sensitivity to outlying points and includes unused areas (Grueter et al., 2009). Therefore, MPC is no longer advised as a method to calculate home range (Laver and Kelly, 2008). The block method and MCP were the most relevant methods available when previous studies comparing population density estimates to actual densities were carried out (eg. Chapman, 1988; Brugiere and Fleury, 2000; Fashing and Cord, 2000). However, the suggestions regarding line transect surveys presented in these studies may be questionable as findings may differ when using the more sophisticated methods to calculate home range that are now available.

The kernel-density estimation (KDE) uses the probability of encountering an individual at a specific location to estimate home range size (Pebsworth et al., 2012) and has been used to calculate home range (Boyle et al., 2009) and actual density in primates (Hassel Finnegan et al., 2008). Yet KDE often includes areas not used by the study species into the home range (Pebsworth et al., 2012), potentially overestimating home range size and affecting actual density. The LoCoH is particularly applicable in areas that have natural boundaries such as the lake in OMYK. To my knowledge, mine is the first study using LoCoH to estimate actual population density. I strongly suggest that line transect methods testing be performed on other primate species using up-to-date home range estimation methods to estimate actual densities and further improve population monitoring practices.

Population density estimates obtained from subjectively placed transects are only representative of the area being surveyed and cannot be extrapolated to larger areas (Nijman and Menkin, 2005; Marshall et al., 2008). As my study aimed to evaluate methodological aspects and not to extrapolate population density estimates to other areas of the reserve, the assumption of placing transects randomly was irrelevant (Marshall et al., 2008). However, the home range results for my study period show that my two transects were not representative of the home range, sampling only one portion of the home range. In addition, part of the transects fell outside of the estimated home range. In spite of this, I believe that the population density estimates obtained from the various methods are comparable to the actual density and can be used in the context of line transect methods testing. However, the population density estimates presented here are not representative of the population density in OMYK. As spider monkeys change their home range seasonally in response to fruit availability, a representative population density estimate would include surveys done throughout the year on a larger number of transects spread throughout the study area (see Chapter 5).

3.4.3. Conclusions

My results have shown that aspects of survey design do not affect spider monkey counts and surveys can thus be adapted to the logistical constraints of the survey site. To my knowledge this is the first study to demonstrate that recounting individuals on the same transect walk was rare, but occurred only when transects were walked slowly. My research demonstrated that young:adult female ratios obtained from subgroup composition during population surveys may bias against population health estimates.

Population density estimates obtained using the Kelker method were closest to the actual density followed by CDS. The King method highly overestimated population density and should not be used to calculate spider monkey encounter rate. I found no evidence that walking speed affects spider monkey population density, but recommend that surveys be performed at a speed of >1.5 km/hour to minimize the recounting of individuals.

Chapter 4: The effects of habitat disturbance on Geoffroy's spider monkey populations in the Yucatan Peninsula

4.1 Introduction

Tropical forests have experienced wide-scale changes since the end of the 20th century (Malhi et al., 2014). Large tracts of forest have been lost, fragmented, and degraded as a result of anthropogenic and natural causes. Extreme climate-related events such as forest fires and severe droughts are increasingly common phenomena (Lewis et al., 2015). Human population continues to increase, with 1.5 billion people currently relying on tropical forest products (Lewis et al., 2015), causing overlap with wildlife and competition for resources. As a result, large-scale defaunation has taken place across tropical habitats (Harrison et al., 2013; Dirzo et al., 2014). Primates have not been the exception, as local extinctions have been reported in all primate-inhabited regions: Neotropics, Africa, Madagascar and Asia (Meijaard and Nijman, 2000; Michalski and Peres, 2005; Parker et al., 2008; Benchimol and Peres, 2014; LaFleur et al., 2016). The abundance and distribution of primates are determined by an interplay of ecological factors (Linder and Lawler, 2012; Barelli et al., 2015; Serckx et al., 2016), but increasing evidence exists that as habitats are changing in response to human influences, such as infrastructure expansion and deforestation, so are the factors determining primate distribution (Imong et al., 2013).

From an ecological perspective, primate abundance can be explained by ecological variables such as forest maturity (Reinartz et al., 2006; Pyritz et al., 2010), canopy cover, tree height (Hamard et al., 2010; Morrogh-Bernard et al., 2013), tree width (Marsh et al., 2016), mean and total basal area of large trees (Rovero et al., 2012), forest composition (Morgan et al., 2006) and tree species diversity (Rovero and Struhsaker, 2007, Carvalho et al., 2014). Interestingly, the relationship between primate abundance and ecological variables differ between taxa. For instance, mean and total basal area of large trees are positively related to red colobus (*Procolobus gordonorum*), Angolan colobus (*Colobus angolensis palliatus*) in the Udzungwa Mountains (Rovero and Struhsaker, 2007), but negatively related to baboon abundance (*Papio cynocephalus*; Rovero and Struhsaker, 2007) and chimpanzee nest abundance (Carvalho et al., 2014). Additionally, the relationship between forest structure and primate abundance may change across sites. For instance, Angolan colobus and sykes monkey (*Cercopithecus mitis*) abundance was positively related to the proportion of trees with liana coverage (Rovero and Struhsaker, 2007). However, in an area experiencing greater human impact, the relationship was negative (Rovero et al., 2012).

Spider monkeys are generally found in mature forest but have been observed to inhabit a range of different habitats including those experiencing anthropogenic pressures such as fragmented landscapes, secondary, and logged forests (van Roosmalen and Klein, 1988; Morelos-Juárez et al, 2015; Marsh et al., 2016). Their preference for mature forests may be related to the high abundance of tall trees as spending large amounts of time spent in tree canopies (Campbell et al., 2005) or a higher number of sleeping trees, which tend to be large (varying from DBH ≥ 35.18cm in fragmented forest to DBH ≥ 62.4 – 75.8 in continuous forest; Chapman, 1989; Gonzalez-Zamora et al., 2012; Velázquez-Vázquez et al., 2015). Additionally, mature forest may contain a larger number of important feeding trees (Chapman, 1989; Gonzalez-Zamora et al., 2012; Velázquez-Vázquez et al., 2015).

For instance, the high number of spider monkeys on and near archeological sites in the mature forests of the Yucatan Peninsula was attributed to the high density of important feeding trees such as *Brosimum alicastrum* at those sites (Estrada et al., 2004).

Food abundance is a key factor influencing primate abundance (Hanya and Chapman, 2013). For instance, primate abundance and encounter rate correlate with food availability and food tree density (Stevenson, 2001; Worman and Chapman, 2006, *Hylobates albibarbis*, Hamard et al., 2010; *Ateles belzebuth*, Mourthé, 2014), food tree basal area (*Procolobus rufomitratus*: Mbora and Meikle, 2004; *Cercocebus galerticus*, Wieczkowski, 2004; *Colobus angelensis palliatus*; Anderson et al., 2007) and food tree species richness (*Procolobus gordonorum*; Rovero and Struhsaker, 2007). Frugivorous primate biomass is correlated with fruit production (Stevenson, 2001). However, specific studies evaluating the relationship between food abundance and monkey encounter rates are limited (Mourthé, 2014). Additionally, the aforementioned correlations often show large variation that may reflect the importance of other ecological or human-induced factors on primate abundance and encounter rate.

Forest loss is the main cause of primate population declines and it has been estimated to have negative effects on 76% of primate species (Estrada et al., 2017). Not only does forest loss result in loss of habitat, it is often coupled with expansion of agriculture, urban centers and roads, increasing access to previously undisturbed neighboring areas. For example, chimpanzee abundance is positively correlated with the distance to human settlements and roads (Carvalho et al., 2013), which is in line with the prediction that species with low rates of reproduction, large home ranges and low densities will respond negatively to roads (Fahrig and Rytwinski, 2009). Even though chimpanzees have been observed to cross roads at other sites (Hockings et al., 2006; 2015), this does not mean that they are not negatively affected. For instance, although spider monkeys in Costa Rica regularly cross roads that are located within their home range using canopy bridges, they changed their use of habitat and movement patterns in relation to roads (Asensio et al., 2017). Several primate species live in or near human settlements: marmosets live within cities in Brazil (Duarte et al., 2011), chacma baboons (*Papio ursinus*) live around urban areas on South Africa's Cape Coast (Hoffman and O'Riain, 2012), macaques often live in temples in Indonesia (Riley and Fuentes, 2010), chimpanzees raid fields close to rural villages for crops in Guinea Bissau (Hockings et al., 2015), and black howler monkeys (*Aloutta pigra*) in Mexico can live in forest fragments close to human settlements Mexico (Pozo-Muntoy et al., 2008). These examples illustrate that there is a large amount of variability in how primates respond to anthropogenic disturbance and that studies are needed examining individual species' responses (Irwin et al., 2010).

4.1.1 Spatial scales

The spatial scale refers to the size of the area in which data are collected and the analysis is performed. Most primate studies examine the effects of habitat disturbance at small spatial scales, such as the fragment or habitat patch scale (e.g. Onderdonk and Chapman, 2000; Rovero et al., 2007; Rovero et al., 2012). At this scale, primate presence is related to measures of patch size, tree species composition, and/or tree density (Onderdonk and Chapman, 2000). These factors may be related to local environmental changes (Rovero et al., 2007), and the analysis is performed at a local scale. However, an increasing number of researchers are calling for study designs to account for spatial or landscape scales (Chapman and Peres, 2001; Arroyo-Rodríguez and Fahrig, 2014;

Ordóñez-Gómez et al., 2015). Conversely, landscape-scale studies focus on factors affecting primate responses to habitat changes related to the study fragment and to the matrix surrounding the fragment (Anzures-Dadda and Manson, 2006; Pyritz et al., 2010; Arroyo-Rodríguez and Fahrig, 2014). Landscape scale studies thereby integrate the overall landscape into the analysis, incorporating data such as the isolation distance of forest fragments (distance between fragments) and distance to human settlements (Anzures-Dadda and Manson, 2006; Pyritz et al., 2010; Ordóñez-Gómez et al, 2015). Landscape scale studies often cover large areas, incorporating multiple fragments or sites into the analysis. Factors may also affect abundance at a range of spatial scales. For instance, studies on nest site selection of bonobos revealed that forest structure was important at 750 m, whereas food availability was most important at distance of less than 600 m (Serckx et al., 2016).

Anthropogenic disturbance affects the habitat on a range of spatial scales. Studies on the effects of habitat disturbance should therefore combine factors from both local and landscape scales into their designs (Pyritz et al., 2010; Ordóñez-Gómez et al, 2015). Combining local and landscape scales would involve merging the detailed small-scale variables obtained from changes occurring at the individual patch or fragment level (e.g., microhabitat changes, species composition changes), with larger-scale variables obtained from the matrix of habitat surrounding these patches or fragments (e.g., presence and/or distance to roads in the surrounding area). Such an approach allows the effects of anthropogenic disturbance on primates to not only be understood at multiple spatial scales, but also allows for investigation of how these effects interact. As primates may respond to anthropogenic habitat disturbance at different spatial scales, research into primate adaptation to disturbance should focus on integrating spatial scales to help understand how primates are coping with changes in their environment (Magurran et al., 2010; Arroyo-Rodríguez and Fahrig, 2014). Such information is especially valuable from a conservation perspective for the development of effective species action and management plans (Magurran et al., 2010).

The combination of ecological factors and anthropogenic habitat disturbance factors into primate population studies is becoming more common, given that solid conclusions about the effects of habitat disturbance on primate abundance cannot be drawn when vegetation parameters are not controlled for (Wieczkowski, 2004; Anderson et al., 2007; Pyritz et al., 2010; Rovero et al., 2012; Imong et al., 2013; Ray et al., 2015). Additionally, studying the effects of disturbance at the inappropriate spatial scale may make gaining biologically viable conclusions difficult. For example, the categories of forest types were too coarse as an ecological predictor of great ape abundance, explaining little of the variance in the data (Stokes et al., 2010). In this case, no local-scale data on vegetation structure (e.g. tree basal area) were collected in the field (Stokes et al., 2010).

Anthropogenic and natural habitat disturbance must be estimated with the same diversity of measures as used for ecological factors (see section 4.1) and at multiple spatial scales to ensure that their effects on primate abundance can be properly evaluated. I therefore studied the effect of anthropogenic and natural habitat disturbance on spider monkey encounter rate at multiple spatial scales. The Yucatan Peninsula is a very dynamic area undergoing a range of anthropogenic habitat disturbances. This interplay of factors creates a unique study location to test the effects of different types and degrees of habitat disturbance on spider monkeys, a primate species often referred to as vulnerable to the effects of habitat disturbance (Ramos-Fernández and Wallace, 2008).

4.1.2 Aims and objectives

The aim of this chapter was to determine how different types of habitat disturbance and ecological factors affect spider monkeys in the Yucatan Peninsula.

4.1.2 Hypotheses and predictions

H 4.1: Type of anthropogenic and natural habitat disturbance affect spider monkey encounter rates.

P 4.1a: Spider monkey encounter rate is positively correlated to the distance from regularly used roads and human settlements.

P 4.1b: Spider monkey encounter rate is negatively correlated with the amount of forest loss and the number of forest fires in the vicinity.

H 4.2: Forest maturity and fruit availability affect spider monkey encounter rate.

P 4.2a: Spider monkey encounter rate is positively correlated with the basal area of feeding trees, fruit tree species richness and the basal area of *Brosimum alicastrum*.

P 4.2b: Spider monkey encounter rate is positively correlated with canopy height and the basal area of large trees.

4.2 Methods

4.2.1 Study sites

Data were collected using 18 transects distributed among 5 study sites in the three states of the Yucatan Peninsula: Yucatan, Quintana Roo and Campeche (see section 2.1). Transects differed in length, canopy height, tree species composition, and type of habitat disturbance (Table 4.1). Four transects were opened in the southern part of the Otoch Ma’ax yetel Kooh (OMYK) reserve around the lake of OMYK (Figure 2.2). Due to restrictions set by the reserve management, no new transects were cut in Calakmul Biosphere Reserve and I used 6 pre-existing transects between kilometers 20 and 27 of the road connecting the reserve entrance to the ancient Mayan city of Calakmul (Figure 2.3). Given the size of Los Arboles, I placed two transects in the area, which passed through several plots on which houses had been built, were under construction, or where construction was planned for the near future. Four transects were opened in the protected area of Bala’an K’aax (Figure 2.5).

Table 4.1: Transects used for spider monkey surveys and their characteristics.

Site	Transect ID	Transect length (km)	Main vegetation types
OMYK	Laguna	5	Mature forest, regenerating forest, savannah
	Cirilo	4	Regenerating forest
	Yodzonot-Laguna	4	Regenerating forest, mature forest
	Nuevo Yodzonot	3.2	Regenerating forest, mature forest
Calakmul	Parking	2	Medium forest, mature forest
	Careterra	2	Mature forest and low forest
	Archeo	2	Low forest, mature forest
	Ateles	2	Mature forest, low forest
	Hurtado	2	Mature forest, low forest
	Reina	2	Mature forest, low forest
Los Arboles	LA-A	1.8	Mature forest
	LA-B	1.9	Mature forest
Bala'an K'aax	A	3.2	Mature forest
	B	3.25	Mature forest
	C	3	Regenerating forest, mature forest
	D	3.4	Mature forest

4.2.2 Study design

To generate detailed maps of all study areas and randomly select transect start points (when possible), prior to site visits I overlaid a grid onto the study area (White and Edwards, 2000) using geographic information software (ArcView 10.2.2). The number of transects per site depended on the size and logistical constraints of the site; the minimum number of transects was 2 (in Los Arboles) and the maximum number of transects was 6 (in Calakmul). When possible the distance between transects was set at a minimum of 1 km; however, the shape and size of the study area affect the orientation and distance between transects. The lengths of transects in the four study sites varied between 1.8-5 km. Transect length depended largely on constraints of the different study sites. In areas where several habitat or disturbance types existed in the same area I placed transects so that they passed through several habitat types. To ensure that all transects could be surveyed starting at roughly the same time of the day, the transect length did not exceed 3.5 km in sites where the start and end points of the transects were difficult to access.

In each site, I performed 6 replicates of each transect walk. To avoid an effect of seasonality on spider monkey habitat use, and therefore potential sightings and encounter rate, I distributed survey walks throughout a full year (May 2015-June 2016), at least one month apart to increase independence between repeated walks. Transects were walked at least twice in morning (07:00-11:00) and twice in the afternoon (14:00-18:00).

In order to reduce the probability that the monkeys flee from observers before the observers have seen them, and reduce the chance of recounting the same individuals (see section 3.3.2), transects were walked at a speed of 1.0-2.6 km/hour (average = 1.6 km/hour) which is slightly faster than previously recommended (eg. 1.2 km/hour Peres, 1999). Transects walked around 1 km/hour were located on difficult terrain, such as at Los Arboles where we were not allowed to cut vegetation which prevented us from walking fast. Transects walked faster than 2.0 km/hour were cleared and generally located on flat terrain with few obstables. To investigate the effects of anthropogenic disturbance on spider monkey encounter rate, I used access ways such as roads, trails and paths used by tourists as transects on a few occasions. For instance, in Calakmul one transect was an unpaved road with low vehicle traffic.

4.2.3 Data collection

Data on individual spider monkey counts (number of individuals) were collected from May 2015-June 2016 during 6 surveys per transect. The location on the transect where each independently-moving spider monkey and each subgroup were encountered was recorded on a GPS unit. Additionally, data on the sex and age of the individual spider monkeys were recorded. Data on anthropogenic and natural disturbance variables were collected at a landscape scale, whereas data on ecological variables were collected at a local scale.

4.2.3.1 Anthropogenic and natural habitat disturbance

To determine the distance from transect segments to roads and villages, I used shapefiles depicting roads (INEGI) and villages (CONABIO 2010; Table 4.2) Villages that were no longer inhabited were removed for the analyses. Villages were considered for the analyses when they contained at least 25 inhabitants. Raster files of forest loss and forest gain from 2000 to 2015 were obtained from Hansen et al. (2013). Shapefiles with the number and location of yearly forest fires (2005-2015) taken by the MODIS satellite were obtained from USDA Forest Service (2017). Tracks of all hurricanes and tropical storms that passed through the Yucatan Peninsula between 1980 and 2015 were obtained from the National Oceanic and Atmospheric Administration (NOAA, 2017; Figure 4.1).

Table 4.2: Anthropogenic and natural habitat disturbance and vegetation structure variables used in general linear mixed models.

	Variables	**Units**	**Variable type**	**Source**
Anthropogenic disturbance	Distance to roads	M	Continuous	INEGI
	Distance to villages	M	Continuous	CONABIO
	Forest loss	km^2	Continuous	Hansen et al., 2013
Natural habitat disturbance	Hurricanes	presence/absence	Categorical	NOAA
	Forest fires	presence/absence	Categorical	USDA
		Number of forest fires	Continuous	USDA
Vegetation structure	Basal area of *Brosimum alicastrum*	m^2/ha	Continuous	This study
	Basal area of large trees	m^2/ha	Continuous	This study
	Basal area of feeding trees	m^2/ha	Continuous	This study
	Richness of feeding trees	Number of species	Continuous	This study
	Canopy height	M	Continuous	This study

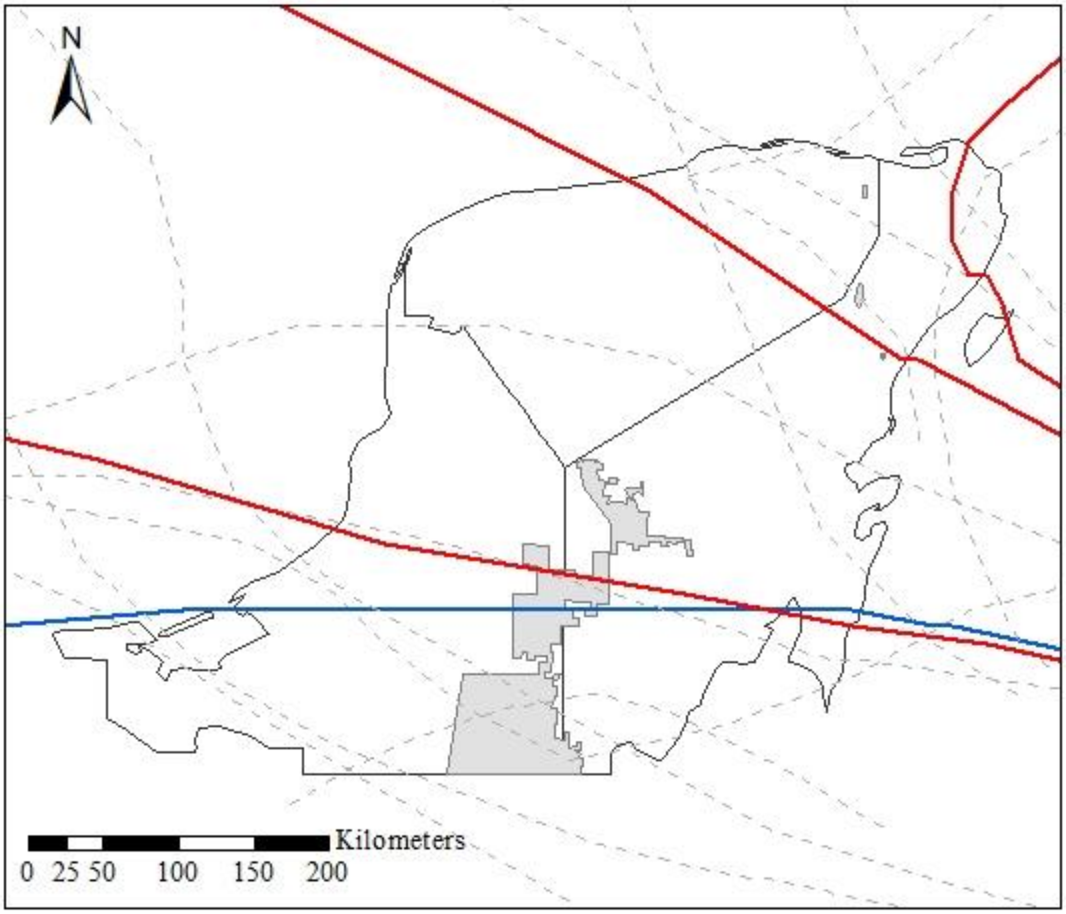

Figure 4.1. Example of the tracks of tropical storms and hurricanes that passed through the Yucatan Peninsula from 2005-2015. Dotted grey lines: tropical storms and hurricanes of category 1. Blue line: hurricane category 2. Red lines: hurricanes category 4 and 5.

4.2.3.2 Vegetation structure

Vegetation transects (also known as “strip,” “belt” or “Gentry” transects: Gentry, 1982) with a strip width of 2 m were placed along the entire length of all transects used for monkey surveys. Variations of this method have been used to relate vegetation measures to primate abundance (Worman and Chapman, 2006) and to survey vegetation in areas where single transects cross through several vegetation types (Wieczkowski, 2004; Rovero and Struhsaker, 2007). All trees of a diameter at breast height (DBH) over 5 cm were measured using a measuring tape at 1.30 m and its species identified with the help of a botanist. A 5 cm cutoff is smaller than the DBH ≥ 10 cm commonly used in primatological studies (Ganzhorn, 1995), and provides more information regarding forest regeneration, as younger regenerating forest contains more trees of smaller size. Lianas were not recorded. Lianas were detached from tree trunks at 1.30 m before performing measurements. If tightly attached, the component belonging to the liana was deducted from the DBH measurement. When trees had buttress roots at 1.30 m, we measured DBH above the buttress; if this was too high in the tree, we had to estimate DBH visually. DBH was measured below 1.30 m for trees that forked lower than 1.30 m (White & Edwards, 2000). When trees had multiple stems, each stem of DBH ≥5 cm was measured separately (Worman & Chapman, 2006), and thus considered as an individual tree for subsequent analyses. Canopy height was determined at 50 m intervals along the transects using a Suunto clinometer.

4.2.4 Data Analysis

Transects were divided into 500 m segments and the spider monkey count was calculated for each individual segment (Rovero & Struhsaker, 2007; Serckx et al., 2016). Data on spider monkey sightings were pooled for the six surveys. This was done for each segment instead of examining the effect of seasonality, as surveys were distributed throughout the year. A transect segment length of 500 m was selected to avoid a high number of segments with no sightings and few segments with many sightings (which can occur if transect segments are very short), while at the same time allowing predictor variables to be tested at a local scale (Serckx et al., 2016). Transect segmenting was performed from the start of the transect using the COGO toolbox in ArcGIS 10.0. As the transects differed in length, the final transect segments of each transect varied in length.

4.2.4.1 Landscape scale analysis

To determine the shortest straight-line distance from any point on each transect segment to roads and villages I used the "Near" tool in the Proximity toolbox of ArcGIS 10.22. I calculated total area of forest loss between 2000 and 2015 per km^2 within a 1 km buffer around the transect segment. I determined presence and calculated the number of forest fires between 2005 and 2015 within a 1 km buffer around the transect segment (Figure 4.2). The impact of hurricanes and tropical storms on the forest vegetation were determined following the buffer sizes proposed by Mascorro and colleagues (2016) for the Yucatan Peninsula. I used buffers of 5 km around tropical storms and hurricanes category 1, 10 km for hurricanes category 2 and 3, and 15 km for hurricanes category 4 and 5 (Figure 4.3). These buffer sizes are most likely conservative indicators of hurricane impact as the nearest distance from the track of category 4 hurricane Emily to the village of Punta Laguna was 17.6 km and hurricane Emily greatly impacted the village and surrounding forest (Bonilla-Moheno, 2012). Likewise, hurricane Wilma, a category 5 hurricane that also greatly affected Punta Laguna was too far to be included in analyses of segments in OMYK, based on the buffer sizes used by Mascorro et al. (2016). I created all buffers using the buffer tool in ArcGIS 10.22.

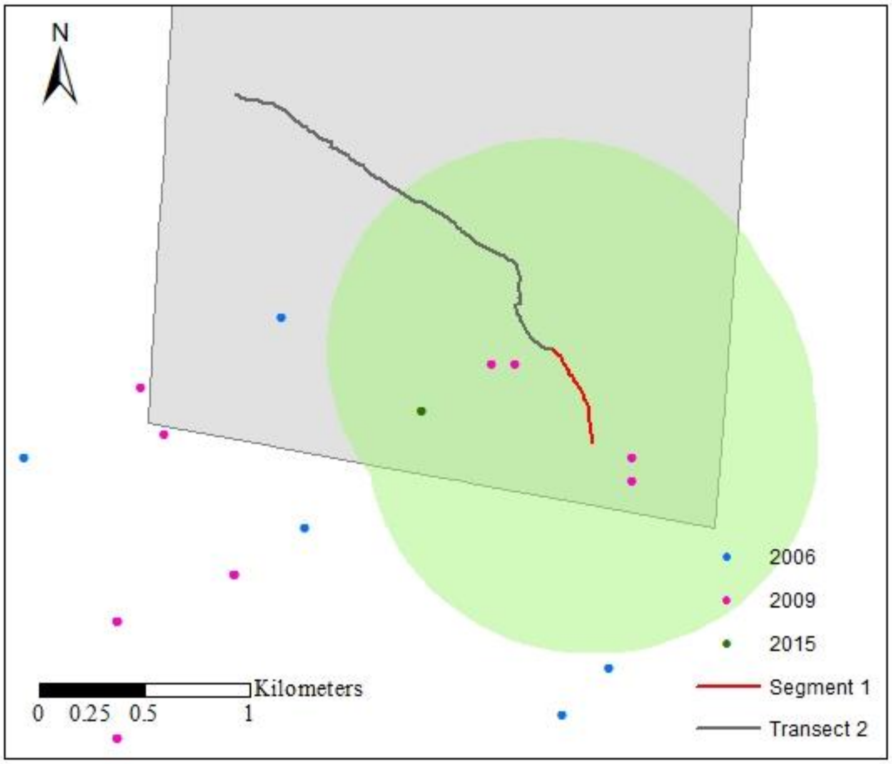

Figure 4.2. Example of a 1 km buffer (green area) around the transect segment to determine the presence or absence of forest fires (points) between 2005-2015 based on MODIS data. The grey area represents the study site Santa Clara.

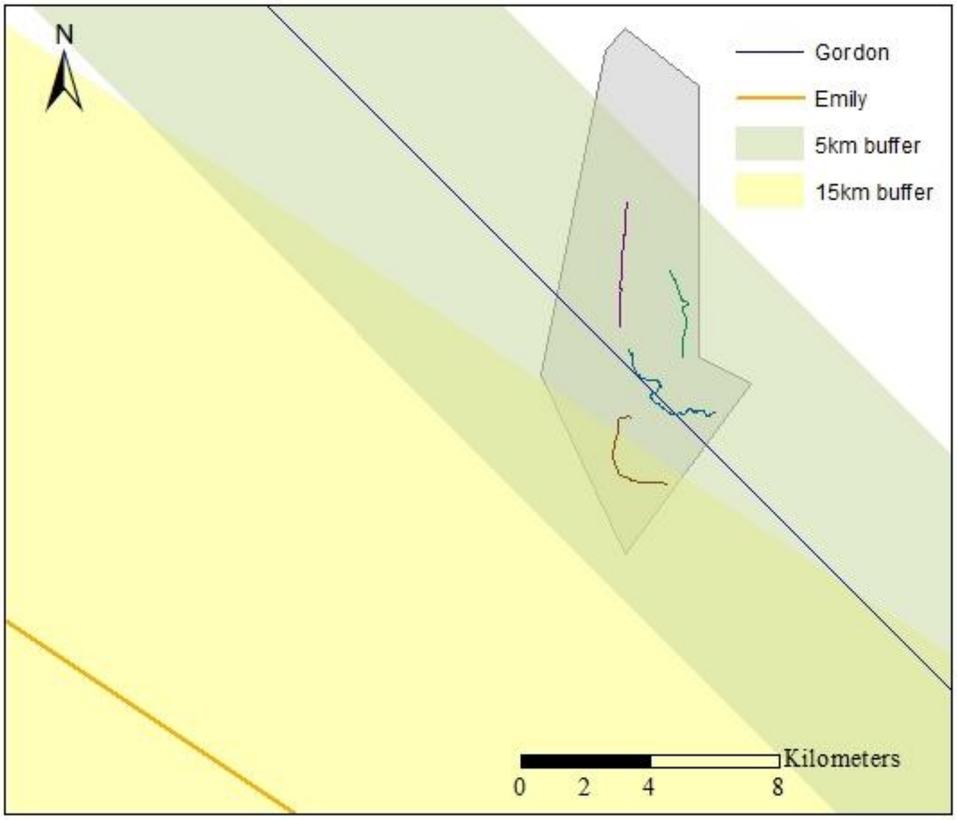

Figure 4.3. Otoch Ma'ax yetel Kooh protected area with 4 study transects and hurricane buffers. The light green-grey buffer represents a 5 km buffer around tropical storm Gordon which passed the area in the year 2000. The yellow buffer represents a 15 km buffer around category 4 hurricane Emily, which passed the area in 2005. Some segments of the southern-most transect were affected by both storms (the green area of overlap between the buffers) whereas the majority were only affected by Gordon.

Variables obtained from the vegetation transects included: tree basal area, species richness, and canopy height. Three categories of tree basal area were considered: basal area of large trees based on the minimum sleeping tree size (DBH ≥ 35.18 cm; Chapman, 1989; Gonzalez-Zamora et al., 2012; Velázquez-Vázquez et al., 2015), basal area of an important feeding tree (*Brosimum alicastrum*), and basal area of potential spider monkeys feeding trees based on records of tree species on which spider monkeys feed. Only feeding trees with a DBH>30 cm were considered as spider monkeys generally do not feed on trees smaller than this. Species were classified as feeding trees according to data obtained from studies of spider monkey feeding behavior in OMYK (Ramos-Fernández and Ayala-Orozco, 2003). For tree species present at other study sites, which do not occur in OMYK, their potential as a feeding tree was established by their presence in published lists of spider monkey feeding trees (González-Zamora et al., 2009).

Basal area is a measurement that takes tree size into account, thereby providing information on the importance of different trees in the habitat (White & Edwards, 2000). Basal area (*BA*) for a single tree was calculated as:

$$\boldsymbol{BA = \pi * \left(\frac{DBH}{2}\right)^2}$$

Single tree basal areas were summed to calculate the total basal area (White & Edwards, 2000) per transect segment in m^2/ha.

Species richness refers to the number of species that are present in an area. However, results can be influenced by survey design and it is recommended to either sample large areas or survey a large number of small quadrants, ensuring that rare species are recorded (Hernández-Stefanoni and Dupuy, 2008). Each 500 m segment had a sampled area of 1000 m^2. Species richness of feeding tree species was calculated by summing the number of feeding tree species in the transect segment. The canopy height measurements that were taken every 50 m along transects were averaged per transect segment.

I determined the effect of measures of anthropogenic and natural habitat disturbance and vegetation structure on spider monkey counts (Linder and Lawler, 2012; Rovero et al., 2012; Imong et al., 2013; Barelli et al., 2015) using general linear mixed models (GLMMs). Spider monkey count was entered as the dependent variable in the model. To control for differences in transect segment length, the final transect segments that varied in length were excluded from analyses. Variables related to anthropogenic and natural habitat disturbance and vegetation structure were calculated per transect segment (Table 4.2). Before entering predictor variables into the GLMM, all continuous variables were z-transformed to a mean of 0 and a standard deviation of 1 (Schielzeth, 2010) so that estimates could be compared irrespective of the scale they were on (Kirkpatrick et al., 2017).

I used a Variance Inflation Factor (VIF) to assess the collinearity between predictor variables (Sikkink et al., 2007). The variables presence/absence of forest fires, presence/absence of hurricanes, the basal area of large trees, and feeding tree species richness were excluded from further analysis due to high VIF values (see section 2.3). Hypotheses regarding these variables could thus not be tested. Table 4.3 shows the variables entered into the GLMM model. Although my data had a large number of zeros (Figure 4.4), I found no evidence of overdispersion or spatial autocorrelation (Moran's Index = -0.024, p = 0.92).

Table 4.3: Variables entered into the GLMM of individual spider monkey counts.

Variables	**VIF value**
Road	1.471
Village	1.161
Forest loss	1.286
Number of forest fires	1
Basal area of feeding trees	1.423
Basal area of *Brosimum alicastrum*	1.417
Canopy height	1.391

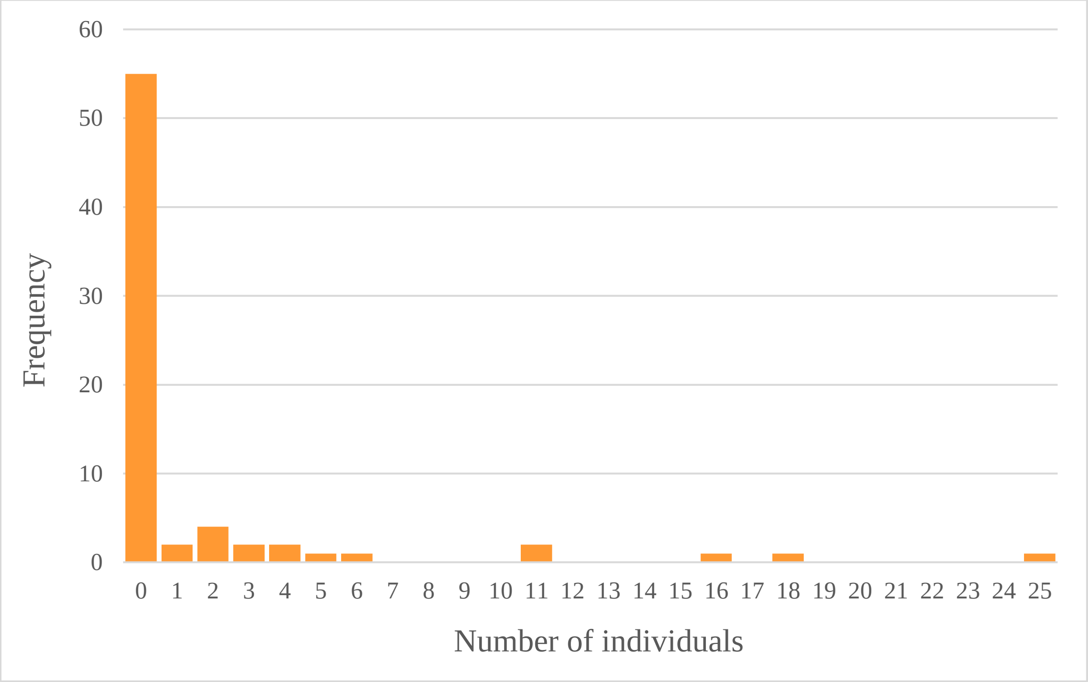

Figure 4.4. The frequency distribution of individual spider monkey sightings in transect segments (all walks combined) for four study sites.

To control for multiple transects in the same site, I entered transect ID as a random factor in the GLMM (Bolker et al., 2009). Although transects were located in sites and there were four study sites, site ID was entered as a fixed factor in the model as there were not enough levels within the variable (<8 levels) to enter the variable as a random factor

(Bolker, 2015). I compared the full model to a null model using a likelihood ratio test (Forstmeier and Schielzeth, 2011; Barelli et al., 2015). The null model contained only the random factor transect ID and site ID as a fixed variable. Additionally, a second null model was run without site ID as a fixed variable.

4.2.4.2 Ecological differences among sites

To investigate how sites differed in vegetation structure (i.e. the basal area of all trees DBH >5 cm, tree species richness, basal area of *Brosimum alicastrum* DBH >5 cm, basal area feeding trees DBH >30 cm, feeding trees species richness), I ran analyses of variance (ANOVA) for normally distributed data with Tukey post hoc tests and Kruskall Wallace analyses with Mann-Whitney U post hoc tests for non-normally distributed data.

To compare species composition between sites, I calculated the Importance Value Index (IVI) to determine the five dominant tree species (DBH >5 cm) and the five dominant feeding tree species (DBH >5 cm) per study site (Krebs, 1994). The IVI of each species was calculated based on the equation:

$$\text{IVI} = \text{relative density} + \text{relative frequency} + \text{relative dominance}$$

Where

$$Relative\ density = \frac{\text{number of individuals of species } x}{\text{total number of individuals of all species}} \times 100$$

$$Relative\ frequency$$

$$= \frac{\text{number of transects where species } x \text{ was present}}{\text{total number of transects in which any species was present}} \times 100$$

$$Relative\ dominance = \frac{\text{total basal area of species } x}{\text{total basal area of all species}} \times 100$$

The maximum IVI is 300, which indicates that only one species is present in that area. High IVI values reflect greater species dominance within a site.

4.2.4.3 Site specific analyses

To analyze the effect of site specific variables on spider monkey counts I ran generalized linear models (GLM). Spider monkey count was entered as the dependent variable. I modeled one to two predictor variables per study site, so as not to saturate the models. I selected the predictor variables for each site based on which anthropogenic or natural habitat disturbance variable and vegetation structure variable seemed most relevant to the site. Distance to village and basal area of *Brosimum alicastrum*, and the distance to roads were selected as the predictor variables for OMYK and Los Arboles, respectively. I was not able to run models for the sites Calakmul and Bala'an K'aax due to the low number of spider monkey sightings and high aggregation of these sightings. To control for repeated measures within the same transect, Transect ID was entered into the GLM as a control variable as Transect ID had fewer than 8 levels at all sites and could not therefore be entered as a random factor (Bolker, 2015). GLMs were run with Poisson error structure and log link, and over-dispersed models were run with a negative binomial error structure. Outliers were removed when necessary. Full models were compared to null models using likelihood ratio tests with the anova function in R. Null models contained Transect ID as a control variable.

4.3 Results

4.3.1 Landscape scale analyses

On transect segments of 500 m length I recorded a total of 116 individual monkeys in 4 sites across the Yucatan Peninsula for an overall encounter rate of 0.54 individuals per km walked. Sites ranged from 8-64 individuals and 4-16 subgroups observed during surveys (Table 4.4)

Table 4.4: Survey effort and spider monkey encounter rates in all sites for 500 meter transect segments.

Site	**Number of transects**	**500 m segments**	**Survey effort (km)**	**Number of individuals**	**Individual encounter rate**	**Number of subgroups**	**Subgroup encounter rate**
OMYK	4	26	78	64	0.82	16	0.21
Los Arboles	2	6	18	8	0.44	4	0.22
Bala'an K'aax	4	22	66	29	0.44	6	0.09
Calakmul	6	18	54	15	0.28	4	0.07
Total	16	72	216	116	0.54	30	0.14

The 16 transects that were surveyed were divided into 72 500 m segments. These data were used in the following analyses. Spider monkeys were sighted on 17 of the 72 transect segments (23.6%). The total number of individuals and subgroups sighted per segment during 6 transect walks ranged from 1 to 25 and 1 to 6, respectively.

Transect segments were located between 0 and 11,567 m (mean ± SE = 3,484.06 ± 402.41 m) away from roads and between 341 and 26,917 m (10,174.33 ± 969.66 m) from the nearest village. From 2000 to 2015, transect segments lost between 0 and 0.3 (0.052 ± 0.009) km^2 of forest. Over the past 10 years, forest fires passed through 6 of the 72 transect segments (8.33%). The number of forest fires per transect segment ranged from 0 to 2 fires.

Ecological variables were calculated using data from a total of 17,075 live trees with a DBH >5 cm measured along transect segments. The number of tree species per transect segments ranged from 16 to 52 (39 ± 1) species. The number of feeding tree species per transect segment ranged from 6 to 21 (13 ± 0.4) species. The average height of transect segments' canopy ranged between 7.7 and 19.2 m (15.4 ± 0.3 m). Tree basal area varied greatly between transect segments. Basal area of large trees (DBH >35.18 cm) ranged from 0 to 91.6 (10.8 ± 1.5) m^2/ha. Basal area of feeding trees (DBH >5 cm) ranged from 2.5 to 208.5 (31.8 ± 5.5) m^2/ha. Basal area of *Brosimum alicastrum* (DBH >5 cm) ranged from 0 to 22.9 (1.6 ± 0.5) m^2/ha.

Table 4.5: GLMM results of the effect of anthropogenic and natural habitat disturbance and ecological variables on spider monkey counts at 4 sites across the Yucatan Peninsula.

Variable	**Estimate**	**SE**	**Z**	**p value**
Distance to road	-0.024	0.29	-0.08	0.934
Distance to village	1.405	0.68	2.07	**0.038**
Forest loss	-0.273	0.14	-1.97	**0.049**
Forest fires (number)	-0.166	0.14	-1.22	0.224
Basal area of feeding trees	0.357	0.13	2.75	**0.006**
Basal area of *Brosimum alicastrum*	0.3	0.13	2.30	**0.021**
Canopy height	0.099	0.14	0.72	0.471
Site *	-	-	-	**0.026**

p values <0.05 are in bold

* Site is a control variable

The GLMM results reveal that the predictor variables affected individual spider monkey counts (likelihood ratio test comparing the full and null models with Site as a control variable in the null model: $X^2 = 185.23$, df = 8, p<0.001; and without Site the null model: $X^2 = 189.56$, df = 11, p<0.001). Distance to villages was positively correlated and forest loss negatively correlated with spider monkey counts (Table 4.5). Furthermore, distance to villages had the strongest effect on spider monkey counts. Basal area of food trees and basal area of *Brosimum alicastrum* were positively correlated with spider monkey counts. There was no effect of distance to road, number of forest fires, and canopy height on spider monkey counts.

4.3.2 Ecological differences among sites

The median basal area of trees with DBH >5 cm differed significantly between study sites ($X^2 = 7.82$, df = 3, p = 0.049; Figure 4.5). The median basal area of trees in Bala'an K'aax was significantly larger than Calakmul (U = 279, $n_1 = 22$, $n_2 = 18$, p = 0.027) and OMYK (U = 403, $n_1 = 22$, $n_2 = 26$, p = 0.015). There were no other differences between sites.

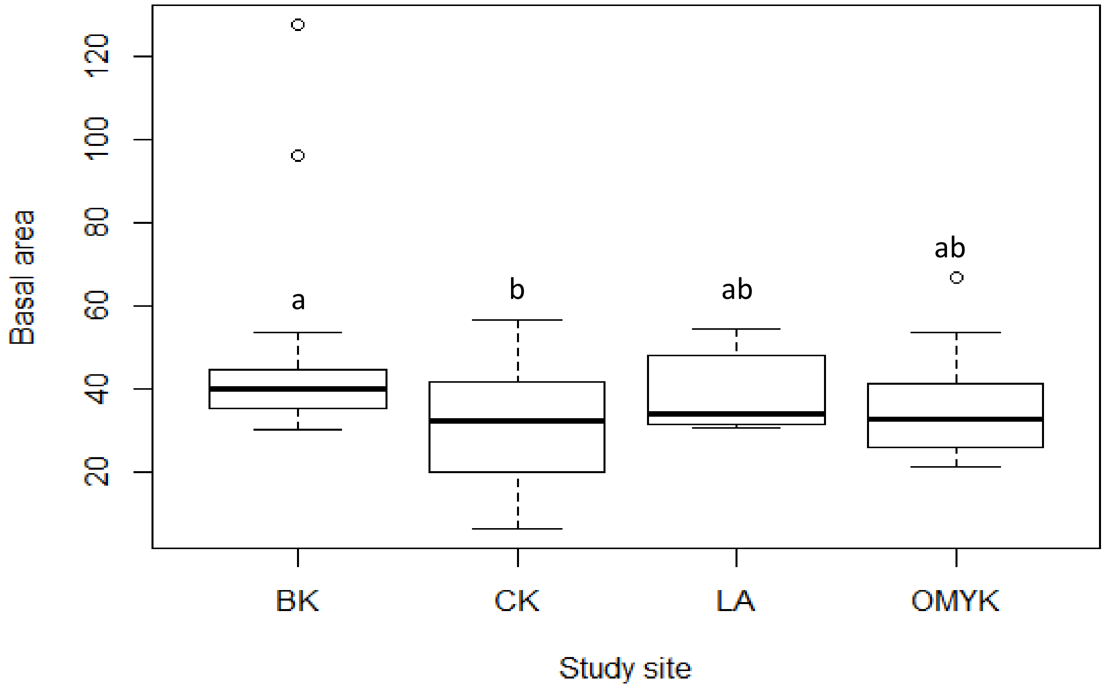

Figure 4.5. Median (and first and third quartiles) basal area (m^2/ha) of all trees with DBH >5 cm at each study site: Bala'an K'aax (BK), Calakmul (CK), Los Arboles (LA), and OMYK (Otoch Ma'ax yetel Kooh). The circles represent outliers and different letters represent significant differences between sites.

Study sites differed in the mean number of tree species ($F_{3,68} = 40.175$, $p<0.001$; Figure 4.6). Calakmul had fewer tree species in the surveyed vegetation plots than Bala'an

K’aax (Tukey, $p<0.001$), Los Arboles ($p<0.001$) and OMYK ($p<0.001$). There were no other differences between sites.

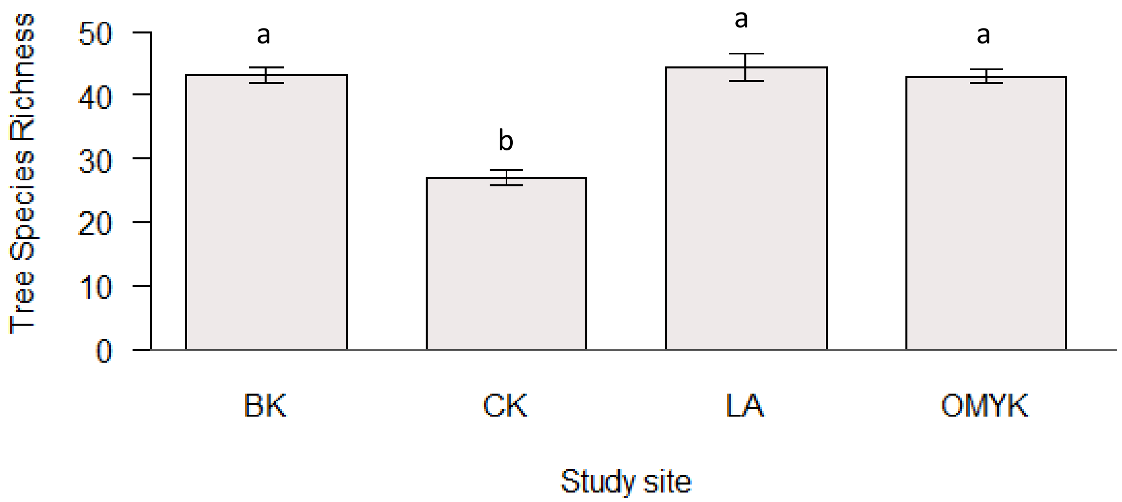

Figure 4.6. Mean (± SE) tree species richness along the 500 m transect segments at each study site: Bala’an K’aax (BK), Calakmul (CK), Los Arboles (LA), and OMYK (Otoch Ma’ax yetel Kooh). Different letters represent significant differences between sites.

The study sites did not differ in the basal area of *Brosimum alicastrum* (Ramon; $X^2 = 4.62$, df = 3, $p = 0.202$) nor in the basal area of feeding trees with a DBH>30 cm ($X^2 = 2.01$, df = 3, $p = 0.571$). However, study sites did differ in feeding tree species richness ($F_{3,68} = 23.97$, $p<0.01$; Figure 4.7). Bala’an K’aax had significantly fewer species than Los Arboles (Tukey, $p<0.001$) and OMYK ($p<0.001$). Calakmul had significantly fewer species than Los Arboles ($p<0.001$) and OMYK ($p<0.001$).

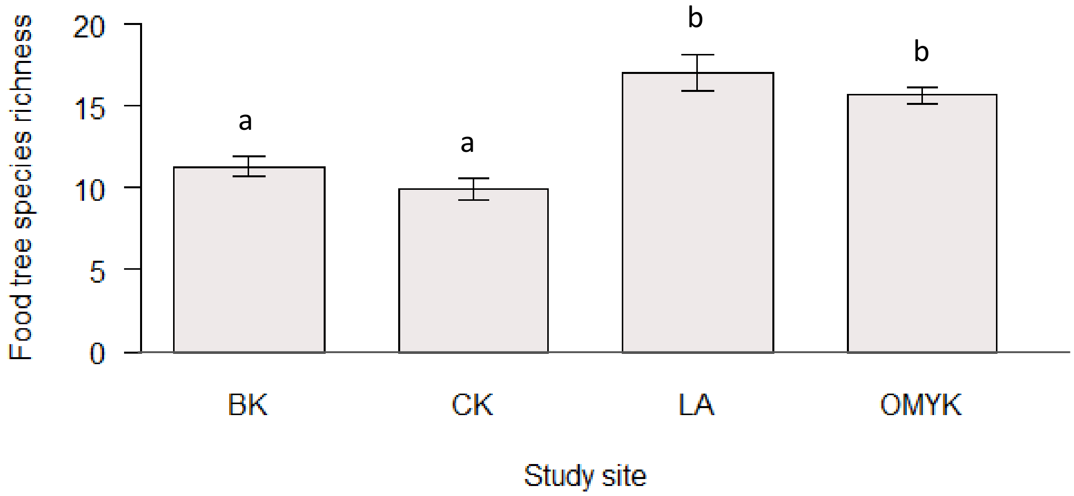

Figure 4.7. Mean (± SE) number of feeding tree species per study site: Bala'an K'aax (BK), Calakmul (CK), Los Arboles (LA), and OMYK (Otoch Ma'ax yetel Kooh). Different letters represent significant differences between sites.

The composition of the five dominant tree species varied across sites (Figure 4.8), but in each site at least three of them were feeding tree species (Appendix 5). In Bala'an K'aax, the five dominant tree species made up almost one third of the tree species present at the site. OMYK and Los Arboles showed the greatest similarity in composition, sharing two of the five dominant species (*Metopium brownei* and *Lysiloma latisiliquum*). In Bala'an K'aax one species has a higher IVI value than the than the other four species (*Gymnantes lucida*), whereas in Calakmul, all five dominant species have similar IVI values.

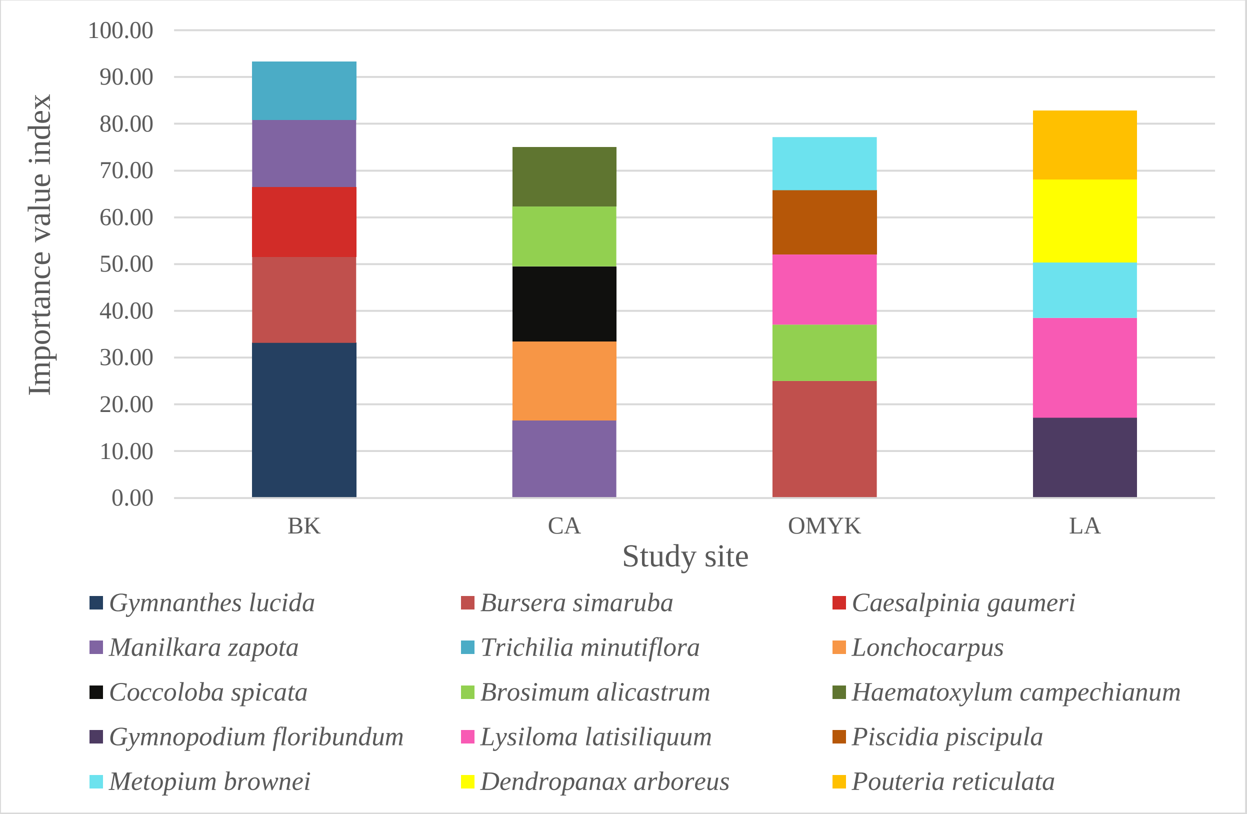

Figure 4.8. IVI of the five dominant tree species at each study site: Bala'an K'aax (BK), Calakmul (CK), Los Arboles (LA), and OMYK (Otoch Ma'ax yetel Kooh).

The five dominant spider monkey feeding tree species varied among the study sites (Figure 4.9, Appendix 6). In all sites, the five dominant feeding tree species make up around a fifth of the tree species in a site. No species were among the five dominant species in all four sites but *Bursera simaruba* was dominant in three sites. OMYK and Los Arboles showed the greatest similarity in feeding tree species composition, sharing three species. Interestingly, *Vitex gaumeri* and *Metopium brownei* have similar IVIs in both sites, but *Bursera simaruba* is more dominant in OMYK than Los Arboles.

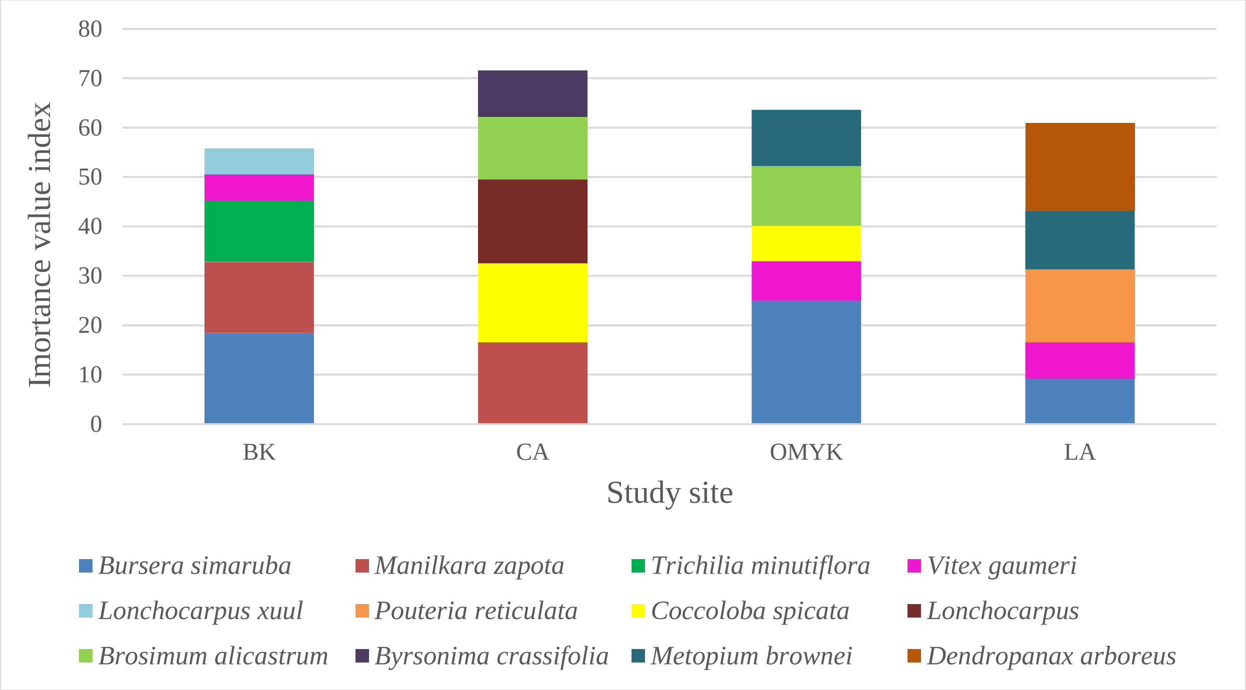

Figure 4.9. IVI of the 5 dominant feeding tree species at each study site: Bala'an K'aax (BK), Calakmul (CK), Los Arboles (LA), and OMYK (Otoch Ma'ax yetel Kooh).

4.3.3 Site specific analyses

The predictor variables affected individual spider monkey counts in Otoch Ma'ax yetel Kooh (X^2 = 11.15, df = 18, p = 0.003). Distance to village and the basal area of *Brosimum alicastrum* were positively correlated with spider monkey counts (Table 4.6). There was no effect of the predictor variable on spider monkey counts in Los Arboles (X^2 = -0.002, df = -1, p = 0.96).

Table 4.6. GLM results of the effect of anthropogenic habitat disturbance and ecological variables on spider monkey counts for Otoch Ma'ax yetel Kooh.

Predictor variable	Estimate	SE	X^2	df	p-value
Distance to village	4.81	2.5	3.87	1	**0.049**
BA of *Brosimum alicastrum*	1.99	0.78	7.86	1	**0.005**
Transect *	-	-	9.29	3	**0.026**

* Transect is a control variable

4.4 Discussion

Detailed information on the ecology and factors affecting population declines are lacking for most species of spider monkeys. Such information is critical for the development of effective conservation strategies, especially as all species are listed as endangered (Cuaron et al., 2008), and *Ateles geoffroyi* was recently named one of the World's 25 most endangered primates (Schwitzer et al. in prep), highlighting the need for conservation-based research.

The main finding of my study was that at the landscape scale spider monkey counts were affected by anthropogenic and natural habitat disturbance, as well as ecological factors. Human presence and activities are therefore directly affecting spider monkey populations. Human activities can constrain primate distribution. This is the case of cross river gorillas (*Gorilla gorilla diehli*), which restricted themselves to areas with lower hunting pressure without using potentially suitable habitat (Imong et al., 2014). I found spider monkeys in higher numbers in areas with lower impact of anthropogenic disturbance and greater food availability. If areas with high food availability start to disappear due to anthropogenic pressures, spider monkey populations may decline.

The effect of human infrastructure on spider monkeys is related to the type of infrastructure. Spider monkey counts were positively correlated with distance to human settlements (Prediction 4.1a), but I found no effect of distance to roads. As the roads closest to transect segments generally had low to medium levels of vehicle traffic, they probably did not create a physical barrier for the monkeys' movements. Spider monkeys can use branches as aerial pathways to cross over roads (Asensio et al., 2017), and I observed spider monkeys in OMYK to cross roads using both aerial crossing points and walking on the road. It can therefore be assumed that if roads are not very wide (e.g. single car width) and vehicle traffic is low, they do not affect the number of spider monkeys living in the vicinity. Villages, on the other hand, may have more direct negative impact on spider monkeys. Villages may present predation pressure from domestic dogs, and in some regions hunting for the primate pet trade is still prominent (Lizarralde, 2002; Shepard, 2002; Duarte-Quiroga and Estrada, 2003; Naranjo et al., 2004). I personally, observed a spider monkey pet in one of the villages bordering Bala'ax K'aax protected area, presumably taken from forests near the village, and was told of an injured infant spider monkey kept in Conhuas, Calakmul that was later released back into the forest. Distance to villages had the greatest effect of all variables tested on spider monkey counts. This clearly shows that spider monkeys prefer to be farther away from villages, and forest must thus be preserved in areas with very little or no human contact.

Forest loss has recently been named one of the main drivers of primate population declines (Boyle, 2017; Estrada et al., 2017), including spider monkeys (Ramos-Fernández and Wallace, 2008). Forest loss causes a reduction of habitat for many forest-dependent species and changes the quality of the remaining habitat through increasing edge effects

(Murcia, 1995). Changes in tree species composition and reduction of overall area may decrease food availability, which in turn, may negatively affect individual fitness and eventually reproductivity of the population. Therefore, the time it takes to observe changes resulting from forest loss on a population will depend on the life-history of the species. Population declines will be evident more quickly for species that have multiple offspring per year than for species that have on offspring every few years. As predicted, forest loss was negatively correlated with individual spider monkey counts (Prediction 4.1b). Species with large home range requirements, such as spider monkeys, need large tracts of connected forest (Benchimol and Peres, 2014). Forest loss through either natural or anthropogenic causes thus directly threatens spider monkeys as it causes reduction in available habitat. For instance, forest fires can clear away large swathes of forest and are common during the dry season in the Yucatan Peninsula (Ellis et al., 2017). However, I found no effect of the number of forest fires on spider monkey counts. These results together suggest that it is the overall amount of lost forest, due to various causes including fires, which affects spider monkeys. Problematically, population numbers will decline with decreasing forest availability, as exemplified by spider monkeys not occupying forest fragments smaller than 28.6ha (Michalski and Peres, 2005). It is therefore imperative to protect well-connected forest patches from future forest loss to ensure the continued presence of spider monkeys in the Yucatan Peninsula.

It is important to consider the role of time in the effects of anthropogenic or natural habitat disturbance on spider monkey counts. Changes in population size caused by changes in the environment may not be immediately apparent. Time lags between environmental changes and population declines are related to the life-history of the species.

The effects of changes in the environment on populations of species with long life-histories may be apparent only years after the event occurred. For instance, howler monkey populations in Belize declined directly after a hurricane occurred but continued to decline for three years after the event, due to decreased infant survival (Pavelka and Chapman 2005; Pavelka et al., 2007). Spider monkeys are long-lived primates that take longer to reach sexual maturity, and have longer interbirth intervals and gestation periods than howler monkeys (McFarland Symington, 1988; Ramos-Fernández et al., 2003; Vick, 2008). Therefore, the effect of a disturbance event on the population or on spider monkey counts may take at least 3 years (the interbirth interval; Ramos-Fernández et al., 2003), and potentially longer to become apparent. Therefore, it is possible that the effects of roads and the number of forest fires on spider monkey counts can become apparent in the future. It is therefore important to perform regular population surveys to determine the long-term effects of anthropogenic or natural habitat disturbance on primate populations.

Spider monkey counts were positively correlated with the abundance of feeding trees, but were not affected by structural components of mature forests (Hypothesis 2). Spider monkey counts increased with increasing basal area of feeding trees and *B. alicastrum* (Prediction 4.2a). This finding is in line with previous studies in which *A. belzebuth* density was positively correlated with fruit supply in the dry season (Mourthé, 2014) and home range use was concentrated in areas with large fruit trees (Schimooka, 2005). The fruits and leaves of *B. alicastrum* are consumed throughout the year and account for 27-40% of spider monkey feeding time (Ramos-Fernández and Ayala-Orozco, 2003). Additionally, *B. alicastrum* is often found at very high densities in medium forest. For instance, *B. alicastrum* occurs at a density of 288 trees/ha around the lake of OMYK, compared to less than 1 tree/ha in regenerating forest in the same protected area (Ramos-Fernández and Ayala-Orozco, 2003). Unlike many other tree species in the Yucatan Peninsula, *B. alicastrum* does not shed its leaves during the dry season, thereby potentially providing shelter from predation and shade from the sun. Interestingly, I found that *B. alicastrum* is among the 5 dominant feeding tree species only in OMYK and Calakmul. This finding, along with the lack of difference between the basal area of *B. alicastrum* among sites, suggests that although *B. alicastrum* may not be one of the dominant species at a site, the monkeys prefer areas with a large amount of *B. alicastrum*.

Canopy height is a measure of forest maturity in the Yucatan Peninsula, where forests are in differing stages of regeneration and older forests are taller than younger forests (Dupuy et al., 2012). The lack of a relationship between canopy height and monkey counts (prediction 4.2b) indicates that spider monkeys use regenerating forest. Overall, my results suggest that although spider monkeys are found in forests with a range of successional stages, and thus highly flexible in their use of different forest types, they may prefer mature forest due to the high availability of food (van Roosmalen and Klein, 1988). Conservation efforts should therefore be focussed on maintaining mature forest and promoting forest regeneration.

Structural composition of the forests differed between the sites. The IVI values of the 5 most dominant species in Calakmul were all relatively similar, suggesting that no species is more dominant than another. In the other sites one species was more dominant than the rest, suggesting that the habitat may be more heterogeneous. Importantly, in all sites at least 3 of the 5 dominant species were also spider monkey feeding tree species meaning that there is an abundance of potential feeding trees at all sites, and that differences in spider monkey numbers between sites may be related to anthropogenic pressures.

Sites differed in feeding species richness and they showed great diversity in the 5 dominant feeding tree species. Los Arboles and OMYK had significantly more feeding trees species than Calakmul and Bala’an K’aax. This may be partially due to the wealth of information on spider monkey diet in OMYK (Ramos-Fernández and Ayala-Orozco, 2003), which is in Yucatan. Although I used a list of tree species consumed by spider monkeys throughout Mesoamerica (González-Zamora et al., 2009), there were no accounts of spider monkey diet from Campeche and Quintana Roo, where Calakmul and Bala’an K’aax are located. This lack of information may have influenced the results. Dietary information from more sites is therefore needed to assess the availability of feeding trees in different sites, and to determine their importance for spider monkey conservation.

4.4.1 Conclusions

Both ecological and habitat-disturbance factors influence the distribution of spider monkeys. In particular, the distance to villages and amount of forest loss were identified as the anthropogenic (and natural) disturbance factors affecting spider monkey counts, with spider monkeys being farther away from villages and in lower numbers where forest loss is greater. Spider monkey counts were higher in areas with greater basal area of feeding trees, especially *B. alicastrum*. My results therefore suggest that forests with a high abundance of feeding trees, located far away from villages must be protected from forest loss to conserve spider monkey populations in the Yucatan Peninsula.

Chapter 5: Comparing spider monkey population size over time in Otoch Ma'ax yetel Kooh Protected Area: the effect of forest fires, small-scale ecotourism and the termination of slash-and-burn agriculture

5.1 Introduction

Slash-and-burn agriculture is practiced by millions of people worldwide (Karthik et al., 2009) and has been a common practice in the Yucatan Peninsula (milpa agriculture) for centuries (Chazdon, 2014). A patch of land is cleared of all or most large trees, burnt, and crops are planted. The land is generally used for 2-3 years until the soil loses fertility, after which it is left to rest and regenerate naturally (fallow period) while the next patch is cleared. The original plot is traditionally cleared again after a period of around 30-50 years (Karthik et al., 2009; García-Frapolli et al., 2007). Although slash-and-burn agriculture has caused wide-scale deforestation, mature forest is not necessarily lost if communities decide to only use regenerating forests for their milpas (García-Frapolli et al., 2007).

Contradicting evidence exists on the effect of forest regeneration on biodiversity. Bird species richness takes around 20 years, and ant species richness 39 years to recover after forest clearance (Dunn, 2004). While large herbivores and small-bodied primates may benefit from the abundance of young leaves and insects, species with specialized diets are less abundant in young regenerating forests (Parry et al., 2007). For instance, ripe-fruit specialists such as spider monkeys (*Ateles paniscus*) were absent from regenerating forests in Brazil (Parry et al., 2007). Regenerating forests have lower tree species richness and differ in tree composition from mature forests (Aide et al., 2000), potentially affecting the diversity of available fruits (Parry et al., 2007). The distance to mature forest also negatively affects the abundance of species with specialized diets in regenerating forests (Dent and Wright, 2009; Chazdon et al., 2009). Additionally, younger stages of forest regeneration have smaller trees both in height and DBH and a more open canopy (Parry et al., 2007; Omeja et al., 2016), potentially limiting the movement and activities of canopy-dwelling species.

In 2002, Otoch Ma'ax yetel Kooh (OMYK) was decreed a Federal Protected Area, which prohibited the use fire for clearing milpas. Traditional slash-and-burn agricultural practices were thus stopped, and the forest was left to regenerate naturally, increasing available habitats for canopy dwelling species as forest ages. Despite a ban on the use of fire within the Protected Area in 2011 around 1,000ha were lost in the north of OMYK due to a forest fire, started by neighboring villagers living outside OMYK.

How animals use regenerating forest is often affected by hunting levels in the area. For instance, the level of hunting is more important in determining the biomass of medium-large mammals (>2kg) in agricultural fields left to regenerate than age of the regenerating forest (Naughton-Treves et al., 2003). The banning of hunting within OMYK provides a unique situation to test the effect of forest regeneration in the absence of hunting.

Tourism is a major source of income in the Yucatan Peninsula and is often portrayed as a conservation activity supporting local income, but its effects on the primates in the area remains largely unstudied. Tourism may affect primates negatively, leading to stress in spider monkeys both in captivity and in the wild (Davis et al., 2009; Rangel-Negrín et al., 2009; Behie et al., 2010). Howler monkeys avoid visitors by using lower-quality habitats when visitor numbers were higher (Aguilar-Melo et al., 2013). In 2002, around 900 tourists visited the eco-tourism area of OMYK near the village of Punta Laguna each month (García-Frapolli et al., 2014). Although numbers fluctuated depending on environmental and socio-economic circumstances (e.g. hurricanes and economic crises), the area received a maximum of around 2,300 visitors per month between 2006 and 2008 (García-Frapolli et al., 2014). In 2011, after a major tourism company stopped sending tourists to the area, tourism became much more small-scale (5-7 visitor per day; García-Frapolli et al., 2014). In 2015 tourism was most likely higher, possibly similar to 2002.

5.1.1 Long-term monitoring of populations

Monitoring wildlife allows researchers to track populations over time, documenting their welfare and extinction risk (Kühl et al. 2008). Long-term monitoring is necessary to understand how changes in the environment or its management affect primate populations (Chapman and Lambert, 2000; Magurran et al., 2010). Variations in population abundance and population dynamics as a result of anthropogenic or natural habitat disturbance may take time to become apparent. For instance, populations may be forced into smaller areas as habitats become fragmented, causing short-term increments in population density (Link et al. 2010). Over time, the constraints of this smaller area likely cause a decrease in the number of individuals due to limited resources. Problematically, constraints imposed by time and funds lead to a larger number of short-term monitoring programs (Struhsaker, 2008), often only a few months in length. Additionally, the long life-history of many primate species make long-term monitoring challenging (Chapman and Lambert, 2000), and long-term monitoring of primate populations only occurs at a few field sites (e.g.

Chapman et al., 2010; 2017). Moreover, it is important to understand the role of natural change (unrelated to human or natural disturbance events) on populations (Struhsaker, 2008) in order to determine the role of human activity in shaping the population abundance and dynamics. For instance, the decline of vervet monkey (*Chlorocebus aethiops*) population densities in Amboseli, Kenya resulted from an interplay of factors including the rise of the water table and subsequent food tree mortality (Struhsaker, 2008). Observing natural change in populations requires that these populations are monitored at regular intervals over a long period of time. Although spider monkeys have been surveyed at different sites across their range, long-term monitoring and publication of changes in populations over time are lacking.

5.1.2 Aims and objectives

The aim of this investigation was to determine whether slash-and-burn agriculture, small-scale ecotourism and a forest fire affected the spider monkey population in the south of the Otoch Ma'ax yetel Kooh protected area. Specifically, I compared spider monkey population densities and encounter rates obtained per forest type (mature forest, regenerating forest, savannah and farmland) in 1997-98 and 2015. I compared the behaviour of spider monkeys sighted during surveys between forest types. Additionally, I compared population density estimates obtained with different methods to estimate ESW to examine whether changes in population density over time are observed using all methods.

5.2 Hypotheses and predictions

H 5.1 Spider monkey population density changes in response to changes in land use management

P 5.1a. Population density is higher in mature forest compared to regenerating forest and savannah.

P 5.1b. Population density in mature forest remains stable between 1997-98 and 2015.

P 5.1c. Population density in regenerating forest is lower in 2015 than in 1997-98 as forest has been left to regenerate, a greater area of suitable forest is available, but the slow life history of spider monkeys would not necessarily cause the same increase in population size.

H 5.2 Habitat use by spider monkeys differs in relation to vegetation type.

P 5.2a. Spider monkeys show a wider range of behaviours in mature forest than regenerating forest or savannah.

P 5.2b. Spider monkeys spend more time travelling and foraging than resting in regenerating forest.

H 5.3 The method used to calculate effective strip width affects population density estimates.

P 5.3a. The King method provides the highest population density estimates.

P 5.3b. The Kelker method gives lower population density estimates than CDS.

P 5.3c. The population density estimates obtained using the maximum perpendicular distance are around half that of the King method.

5.3 Methods

5.3.1 Study design

Otoch Ma'ax yetel Kooh (OMYK) is a protected area in the Mexican state of Yucatan where spider monkey populations were surveyed in 1997-98 (see section 2.1.1 for a detailed description of the study site). Surveys carried out in 1997-98 were conducted on seven transects in the southern section of the protected area (Ramos-Fernández, 2000a). In 2015, I established three transects of varying length in areas where the 1997-98 surveys took place with the help of local assistants. A member of the local community of Punta Laguna who originally opened the 1997-98 transects and has continued working in the area, located the approximate locations of some of these transects. Together, we opened two transects: transect "Laguna" and transect "Cirilo", and used an existing trail: transect

"Yodzonot." The "Yodzonot" transect was used in the 1997 survey. The transects measured 5.04 km, 4.98 km and 2.485 km in length, respectively.

Transects were selected to cover the main vegetation types present in OMYK, which were used in the previous survey: mature forest, regenerating forest, savannah, and milpa (see section 2.1.1). Savannahs are areas with tall grasses that grow along the edge of the lake. As the report of the 1997-98 survey did not provide a definition of savannah I decided to label any section of the transect that was within 10 m of the edge of a lake where savannah vegetation was visible as savannah. Slash-and-burn agriculture (milpa agriculture) is no longer practiced in the southern sector of the reserve and thus was not present on any of the transects in 2015 (Table 5.1). Areas that were classified as milpa in 1997-98 were classified as regenerating forest in the current survey as the forest has started to regenerate. Transects "Laguna" and "Yodzonot" contained mature forest, regenerating forest and savannah, while transect "Cirilo" contained mostly regenerating forest with small patches of mature forest. In 1997-98, the total length of all transects equaled 19.6 km compared to 12.5 km in 2015. Regenerating forest constituted the majority of transect length: 13.2 km in 1997-98 and 7.9 km in 2015. Table 5.1 presents percentages of the total transect length consisting of each vegetation type in the two periods.

Table 5.1: Percentage of total transect length (km) for each vegetation type in the two study periods.

Survey	Regenerating forest	Mature forest	Savannah	Milpa
1997-98	67.0	21.2	6.8	5.0
2015	63.0	30.0	7.0	0.0

5.3.2 Data collection

The different vegetation types present along the transects were determined with the help of a member of the local community of Punta Laguna who was knowledgeable in the history of the area and helped to identify the different vegetation types along transects in 1997-98. Changes of vegetation type were marked using a GPS.

To allow comparison between data from surveys carried out in 1997-98 and 2015, methods were kept as similar as possible. Transects were walked between 7:00-11:00 and 13:00-18:00 at a speed of 1.25-2.0 km per hour. Transect walks were distributed evenly between the morning and afternoon (Table 5.2). Transects were walked at least once and maximum four times (twice per month) every two months for the entire year of 2015. For information collected during transect walks see section 2.2.3. Transect walks were terminated early on two occasions, once due to heavy rain (transect “Laguna”) and once due to a large swarm of bees blocking the path (transect “Yodzonot). On both occasions I took a GPS point at the location where the transect walk was terminated to determine the actual distance walked.

Table 5.2: Encounter rate and survey effort per transect for the 2015 survey.

	Number of surveys		**Kilometers walked**				
Transect	**AM**	**PM**	**AM**	**PM**	**Total km surveyed**	**Number of sighted monkeys**	**Encounter rate**
Laguna	5	5	20.14	21.74	41.88	66	1.58
Cirilo	5	5	24.89	24.89	49.77	11	0.22
Yodzonot	8	7	19.46	17.4	36.85	6	0.16
Total	18	17	64.48	64.02	128.5	83	0.65

I recorded the activity of each individual upon sighting, before the individual changed it in response to the observers, according to the definitions in Schaffner et al. (2012). Travelling was recorded when the individuals were moving within or between trees; foraging was recorded when individuals were observed ingesting or manipulating fruits or leaves; resting was recorded when the individuals were sitting or lying down in the trees. I marked the location on the transect where the individual was sighted using a GPS unit to determine the vegetation type the individual was sighted in.

5.3.3 Data analysis

I calculated the individual encounter rate (individuals per km) and subgroup encounter rate for each transect and vegetation type in 2015, and for regenerating and mature forest in 1997-98. In 1997-98, population density (D) was calculated per vegetation type (i.e. regenerating forest, mature forest and savannah) using Haynes estimator (i.e. the King method):

$$D = \frac{n}{2L}\left(\frac{1}{n}\sum r_i\right)$$

Where n refers to the total number of individual spider monkeys sighted, L refers to the total transect length (total survey effort) and r_i refers to the perpendicular distance (PD) to each individual (Ramos-Fernández, 2000a; Pierce et al., 2012). Following this formula, transect width is thus calculated as the mean perpendicular distance. For the 1997-98 results, one PD value per sighted subgroup was used, instead of the PD to each sighted individual (Ramos-Fernández, 2000b). Therefore, transect width was calculated as the mean perpendicular distance of subgroups in 1997-98. In order to compare population densities between 1997-98 and 2015, I recalculated the 1997-98 results using the mean PD of each sighted individual for mature forest. I also recalculated the population density of regenerating forest but I was not able to perform this calculation for savannah as the raw data were not available.

I corrected individual density for the potential error in estimating distances to monkeys encountered during surveys (see section 2.2.3 for calculations of distance estimation error) for the 2015 data. I calculated population density using the corrected perpendicular distances (hereafter perpendicular distances).

To compare population density estimates between methods I also calculated population density of mature and regenerating forest for both study periods using the Kelker method and maximum perpendicular distance (see section 2.3.2). I could only estimate population density using conventional distance sampling (CDS) for the 2015 data as the number of surveys in which no spider monkeys were observed in 1997-98 was not available, which is essential to run the analyses with the software Distance (Thomas et al., 2010). I could only estimate population density using CDS for mature forest as the number of sighted individuals in regenerating forest was less than 40, the minimum to perform CDS (Peres, 1999). I had to discard one monkey sighting in which the perpendicular distance was not recorded in 2015. I limited the comparison of methods to data collected from mature and regenerating forest, as the number of sighted monkeys was very low in savannah in 2015, and no raw data were available for and savannah for 1997-98.

The methods to estimate population density differ in how the ESW is estimated and therefore the number of individuals and the area included in the calculation of population density varied. All 102 and 61 individuals sighted in mature forest and 26 and 7 individuals in regenerating forest were included in the population density estimates for 1997-98 and

2015, respectively. With the Kelker method I grouped perpendicular distances into bins of 4, 5, 6, and 7 m for mature forest, and chose the histogram with the 4 m and 6 m bins for 1997-8 and 2015, respectively (see section 2.3.2). For regenerating forest, I grouped perpendicular distances into bins of 3, 4, 5 and 7 m, and chose the histogram with the 5 m and 7 m bins for 1997-8 and 2015, respectively. These histograms included 89 and 61 sighted individuals in mature forest and 25 and 7 individuals in regenerating forest for 1997-98 and 2015, respectively. After right truncation, 59 individual sightings were included in the CDS analyses for mature forest for 2015.

5.4 Results

During the 2015 survey, distance measurements were recorded for 83 spider monkeys in all vegetation types for a total survey effort of 128.5 km (Table 5.2). Encounter rate was much higher on the Laguna transect than the other two transects (Table 5.2).

Encounter rates per vegetation type for 1997-98 and 2015 are presented in Table 5.3. Encounter rate of spider monkeys in mature forest was 1.76 individuals per km in 2015, whereas it was 1.52 individuals per km in 1997-98. Encounter rate of spider monkeys in regenerating forest was lower in 2015 than 1997-98 (Table 5.3).

Table 5.3: Encounter rate (individual per km) per vegetation type for the 1997-98 and 2015 surveys.

Year	Vegetation type	Kms walked	Number of sighted monkeys	Encounter rate
1997	Mature forest	72.9	111	1.52
	Regenerating forest	146.8	26	0.177
2015	Mature forest	34.605	61	1.763
	Regenerating forest	85.724	7	0.082
	Savannah	8.175	15	1.835

Data on the activity of spider monkeys at first sighting were recorded for 77 spider monkeys in 2015. In regenerating forest, spider monkeys were observed travelling (4 individuals) or foraging on figs (3 individuals), supporting Prediction 5.2b. In mature forest, spider monkeys were observed to be travelling (24 individuals), resting (21 individuals), foraging (12 individuals). In savannah, spider monkeys were seen travelling (6 individuals), resting (4 individuals) and foraging (3 individuals), partially supporting Prediction 5.2a.

Population density of individual spider monkeys in savannah calculated with the King method for 2015 was 96.6 individuals/km^2. Population density estimates for regenerating forest are much lower than for savannah and mature forest in 2015 (Table 5.4).

Table 5.4: Population density estimates (individual per km^2) for mature and regenerating forest in 1997 and 2015 using different methods.

Vegetation type	Year	Method	ESW (km)	Length (km)	N	Population Density	CI
Mature forest	1997-98	King method	0.008	72.9	102	77.3	
		Kelker method	0.016	72.9	89	38.2	
		Maximum PD	0.029	72.9	102	24.1	
	2015	King method	0.011	34.6	61	78.6	
		Kelker method	0.030	34.6	61	29.4	
		Maximum PD	0.028	34.6	61	31.5	
		CDS	0.018-0.019	34.6	59	44.9 - 47.6	24.4 - 87.4
Regenerating forest	1997-98	King method	0.012	146.8	26	7.6	
		Kelker method	0.015	146.8	25	5.7	
		Maximum PD	0.037	146.8	26	2.4	
	2015	King method	0.008	85.72	7	4.9	
		Kelker method	0.014	85.72	7	2.9	
		Maximum PD	0.013	85.72	7	3.2	

CI = confidence intervals
ESW = effective strip width
Length = total kilometres walked
N = number of sighted monkeys considered in the calculation

Population density estimates with the Kelker method and maximum PD were much lower than those calculated using King's method in both vegetation types for both 1997-98 and 2015 (Table 5.4). Population density estimates with the Kelker method and maximum PD for 2015 in both vegetation types were extremely similar, whereas in 1997-

98 the population density estimate in both vegetation types obtained using the Kelker method was higher than the maximum PD. Population density estimates of both vegetation types obtained using the Kelker method were slightly higher in 1997 compared to 2015, whereas estimates obtained for mature forest using the maximum PD were slightly lower in 1997 than 2015. Estimates obtained using the maximum PD for regenerating forest were very similar between 1997 and 2015. The three models (the one with the uniform key function with a cosine adjustment, the one with the half-normal key function with a hermite polynomial adjustment, and the one with the half-normal key function with a cosine adjustment) run with the software Distance for the conventional distance sampling method did not differ from one another either in the AIC values (less than 2 units) or in the number of parameters. Thus, I considered the conventional distance sampling method as providing a range of density estimates (Table 5.4) for mature forest.

5.5 Discussion

In line with prediction 5.1a spider monkey population density was higher in mature forest than regenerating forest in 2015, confirming what was found in 1997-98. The same trend has been observed for red colobus (*Procolobus rufomitratus*), which were twice as abundant in mature forest compared to regenerating forest (Omeja et al., 2016). In my calculations I did not differentiate young regenerating forest (short period since the start of regeneration) from older regenerating forests. Species with specialized diets are often absent from young regenerating forest (Chazdon, 2014). My results support this claim as all spider monkeys were observed in regenerating forest of 40 or more years old. As slash-and-burn agriculture is no longer practiced within the southern section of the protected area, forest has been left to regenerate and with time more forest will enter the older age classes of regenerating forest, thereby increasing spider monkey habitat. One of the main determinants of the composition and abundance of biodiversity in regenerating forest is the distance between regenerating forest and mature forest (Chazdon, 2014). Regenerating forest that is closer to mature forest has an abundance of fauna more similar to mature forest than regenerating forest that is at greater distances (Chazdon, 2014). The low density of spider monkeys in regenerating forest may also be a function of its distance to mature forest.

Surprisingly, population density was very high in savannahs. However, savannahs were found along the edge of the lake of OMYK and often contained high density of the tree *Manilkara zapota*, an important spider monkey food source (Ramos-Fernández and Ayala-Orozco, 2003). Surveying spider monkeys for a full year, meant that surveys were also performed during the fruiting season of *M. zapota*, which attracts spider monkeys to the lake edges. In addition, savannahs are often found in close proximity to mature forest, potentially explaining the high population density in this habitat type, which constituted only about 6% of the surveyed vegetation types. It must be noted that the areas that I classified as savannah should have been considered as mature forest, as these areas contained mature forest tree species.

In line with prediction 5.1b population density and encounter rate of individual spider monkeys in mature forest remained relatively stable between 1997-98 and 2015. My results suggest that in the absence of hunting, spider monkey populations may not be negatively affected by small-scale ecotourism and forest fires that occurred at a distance of at least 8 kms. At this site no spider monkey surveys were conducted between 1997-98 and

2015. Yet, the fact the population did not change over a 17-year period suggests that although small fluctuations in population size could have occurred during this period, the population has remained stable in the long run. Likewise, the initial population density of spider monkeys in Tikal, Guatemala was estimated at 45 individuals/km^2 (Coelho et al., 1976), at 26 individuals/km^2 a few years after (Cant, 1978), and 56.5 individuals/km^2 around 30 years later (Estrada et al., 2004). The population of spider monkeys thus remained relatively stable. However, these results should be interpreted with caution as the authors of these studies used different methods to calculate population densities. In my study, I used a method as similar as possible to the 1997-98 survey to more reliably compare population density estimates for mature forest between the two periods.

In line with prediction 5.1c population density in regenerating forest was slightly lower in 2015 than in 1997-98. Since slash-and-burn agriculture stopped within the protected area in 2002, milpas have started to regenerate naturally and regenerating forests have not been cut and continued to age. More forest in older stages of regeneration, which are regularly used by spider monkeys, may thus be present in the southern section of the protected area than in 1997-98. As the population density of spider monkeys in regenerating forests remained relatively stable, the overall population of spider monkeys in the southern section of the protected area may have increased.

Spider monkeys do not use each forest type for the same purposes. In contrast to prediction 5.2a, spider monkeys were not only observed to rest, forage and travel in mature forest but also in savannah, potentially due to the close proximity of savannahs to mature forest. Moreover, in line with prediction 5.2b, spider monkeys were foraging and travelling in regenerating forest but not resting. Tree species such as *Metopium brownei* and *Bursera* *simaruba* are important spider monkey feeding sources and very abundant in regenerating forest (Ramos-Fernández and Ayala-Orozco, 2003). The lack of observations of resting spider monkeys suggests that they do not spend large amounts of time in regenerating forest, potentially only using regenerating forest to move between patches of mature forest. However, these results must be interpreted with caution as line transect surveys only provide a snap-shot of habitat use. Unlike detailed behavioral studies, line transect surveys provide no information on the amount of time that species spend in different habitat types and may create a false picture of habitat use when sightings are low. For instance, I only observed 7 individuals in regenerating forest, none of which were observed to be resting, but this may be an artefact of small sample size. Detailed studies of regenerating forest use are needed to quantify how important this habitat type is for spider monkeys and their conservation as regenerating forests and degraded forests are becoming more common (Arroyo-Rodríguez et al., 2015; 2017).

5.5.1 Estimating spider monkey population density

Population density estimates for mature forest using the King method were similar between the two periods and there was only a small difference in the estimates using the maximum perpendicular distance and the Kelker method. Estimates for regenerating forest using maximum perpendicular distance were similar between the two periods and there was a small difference in the estimates using the King method and the Kelker method. Although the estimates differed greatly among methods (see also Chapter 3), the estimates from each method suggest that the spider monkey population in the southern section of OMYK has been relatively stable between 1997 and 2015. The fact that the same tendency was found using all three methods suggests that all methods can be used to monitor populations over time, if population density was calculated using the same method for each period.

Following Prediction 5.3a, the King method gave population density estimates much higher than the Kelker method and maximum PD for both periods. However, the estimate fell within the confidence intervals of CDS for mature forest in 2015. The comparison of population density estimates in Chapter 3 also found that the King method provided much higher estimates than the other methods and overestimated the actual density by 121%. Therefore, it is likely that the King method is overestimating the population density of spider monkeys in mature and regenerating forest in both 1997-98 and 2015.

In contrast to prediction 5.3b, although the CDS provided higher population density estimates for 2015 than the Kelker method, the population density estimates from the Kelker method fell within the confidence intervals of CDS, suggesting that the estimates do not differ. Previous studies of spider monkeys and lemurs found no difference in population density estimates obtained using Kelker and CDS (Link et al., 2010; Meyler et al., 2012; Kun-Rodrigues et al., 2014). In contrast, in Chapter 3, CDS provided higher population density estimates than the Kelker method, and the estimate provided by the Kelker method was much closer to the actual density.

I found that in general the maximum perpendicular distance gave population density estimates that were less than half the King method, supporting prediction 5.3c. Similarly, in Chapter 3 the population density obtained by the maximum perpendicular distance was much lower than the estimate of the King method. In 1997, the estimate obtained using the maximum perpendicular distance was slightly lower than the Kelker and in 2015 they were almost equal. These similarities can be explained by the fact that the 50% fall off distance of the Kelker method for 2015 almost equaled the maximum perpendicular distance. Greater differences between the methods are expected if the maximum perpendicular distance is much larger than the 50% fall off distance (see Chapter 3). The maximum perpendicular distance may be especially unreliable when surveying areas with differences in visibility, as the maximum perpendicular distance will reflect greater visibility in some areas.

5.5.2 Conclusions

Regular population monitoring is critical to understand the response of primates to changes in their environment. The population density estimates from each method indicate that the spider monkey population in the southern section of OMYK has been relatively stable between 1997 and 2015, suggesting that all methods can be used to monitor populations over time. Yet, differences between the methods used to estimate population density indicate that the King method provides much higher population density estimates than the other methods and should not be used to calculate spider monkey population density.

Spider monkey population densities were much higher in mature forest than in regenerating forest, suggesting that although spider monkeys use regenerating forest, they prefer mature forest. This is supported by the observation that spider monkeys were observed to forage and travel in regenerating forest, but not rest. Spider monkeys were only sighted in 40 year-old regenerating forest. As slash-and-burn-agriculture has stopped within the protected area, forests are regenerating and more regenerating forest in the older age classes may be available in 2015 than in 1997-98. Therefore, as population density remained relatively stable in regenerating forest between 1997-98 and 2015, the overall number of spider monkeys in the southern section of OMYK may be higher in 2015.

Chapter 6: General Discussion

For a long time, spider monkeys have been considered to be vulnerable to the effects of anthropogenic and natural habitat disturbance (van Roosmalen, 1985; Ramos-Fernández and Wallace, 2008). In recent years, budding evidence suggests that spider monkeys may be able to cope with some levels of habitat disturbance. For instance, spider monkeys occur in a range of human-modified habitats including forest fragments (Link et al., 2010; Ordóñez-Gómez et al., 2015), forests regenerating from cattle ranching (Sorenson and Fedigan, 2000), selectively logged forest (Morelos-Juarez et al., 2016), and areas undergoing seismic oil exploration (Kolowski and Alonso, 2012). Yet our understanding of how spider monkeys cope with changes in their environment has been largely limited to studies carried out at one site, which investigate one type of disturbance (see Estrada and Coates-Estrada 1996 for a multiple site study). However, a single site may experience a range of anthropogenic and natural habitat disturbances that either simultaneously or successively affect spider monkeys. For instance, selective logging increases the susceptibility of forests to fire during droughts (Siegert et al., 2001), and opening of roads increases hunting (Laurence et al., 2009). Furthermore, the results of single site studies often have only very local conservation implications, as conditions between sites vary. By using a landscape scale, my study addressed the need for information from multiple sites as well as on different types of habitat disturbance from the same site, aiding conservation of spider monkeys throughout the Yucatan Peninsula, and not just in the individual sites where surveys took place.

My research has demonstrated that spider monkeys are not affected by a single type of disturbance; instead they respond to specific types of disturbance differently.

Additionally, my research suggests that a habitat disturbance tolerance threshold may exist, beyond which the population will sharply decline (van Schaik, 2013). For instance, when a more forest is lost than the threshold amount for an area, no monkeys are found there, suggesting that there is a minimum quantity of habitat that monkeys need and beyond this amount of loss they cease to use that area. The loss of substantial forest could therefore cause population declines. It is therefore vital that sufficient forest is conserved to ensure the survival of spider monkey populations in the Yucatan Peninsula. My research also suggests that different tolerance thresholds may exists for different types of disturbance. For instance, although spider monkeys were found in larger numbers farther away from villages, they were also observed in villages. The villages in which spider monkeys were observed (Otoch Ma'ax yetel Kooh (OMYK) and Los Arboles) in my study were small villages, with relatively few inhabitants, and were rich in spider monkey feeding trees. Spider monkeys may start to disappear completely from villages once the villages reach a certain size. This is likely as Mungía et al. (2016) found a negative correlation between spider monkeys and a human settlement index. Higher human population density will likely lead to greater construction to accommodate more people, thererby increasing the size of villages and reducing suitable monkey habitat. This theory remains to be tested as all the nearest villages to transect segments were small villages. Future studies should focus on the effect of towns and cities on nearby spider monkey populations.

Spider monkeys are often characterized as mature forest specialists and in some studies have been found exclusively in mature forest (Parry et al., 2007). However, my study has shown that spider monkeys use a range of different habitat types including mature forest, savannahs and regenerating forest (Chapter 4 and Chapter 5), raising the question as to whether spider monkeys are mature forest specialists or whether they prefer mature forest, but can use other types of vegetation for extended periods (van Roosmalen, 1985; Chapman et al., 1989). As shown in Chapter 5, spider monkeys were not only observed travelling through regenerating forest, but also used regenerating forest to forage. Studies of forest regeneration have shown that species richness in regenerating forest increases with decreasing distance from mature forest (Dent and Wright, 2009; Chazdon et al., 2009). It is therefore plausible that spider monkeys use habitat types other than mature forest especially when they are within close proximity of mature forest. For example, the savannah patches in OMYK where spider monkeys were observed in my research were all located at the edge of mature forest (Chapter 5). Overall, my results suggest that management should focus on conserving regenerating forest and promoting natural forest regeneration, as forests in later stages of regeneration are useful for spider monkeys, and regenerating forests are the most common vegetation type in human-modified environments (Arroyo-Rodríguez et al., 2015).

My research has strong conservation management implications. The number of spider monkeys increased with increasing distance from villages, greater feeding tree availability and less forest loss (Chapter 4). This information can be used by conservation practitioners to identify and update priority areas for the conservation of spider monkeys in the Yucatan Peninsula. Previous priority areas were identified based on the availability of primary or secondary forest and their value in the Mexbio index, which combined various anthropogenic variables, including land-use, infrastructure, climate change and habitat fragmentation (Tobón et al., 2012). The Mexbio index is based on some coarse scale variables, as some of variables used in the index grouped different types of information into a single variable; for instance, infrastructure was made up of the distance to roads and the distance to villages. My research has shown that coarse scale variables such as infrastructure may mask or wrongly assume an impact on spider monkeys, as spider monkeys were affected by distance to villages but not by distance to roads (Chapter 4). Based on the information from my research, priority areas for the conservation of spider monkeys in Mexico can be updated.

A particularly important result of my reseach, is that basal area of *Brosimum alicastrum* was highly correlated with the number of spider monkeys sighted in an area (Chapter 4). This knowledge is invaluable in the development of future spider monkey surveys in the Yucatan Peninsula. Unmanned aerial vehicles (conservation drones) are increasingly being used to survey wildlife, including great apes (van Andel et al., 2015; Wich et al., 2015). Conservation drones have also been used to identify fruit trees important in the chimpanzee diet (van Andel et al., 2015). As *B. alicastrum* often occurs at high densities and in clumped patches, identifying areas rich in *B. alicastrum* would enable more focused line transect surveys in areas where spider monkeys are likely to occur. Thereby, larger areas can be surveyed for spider monkeys with less effort on the ground, efficiently enhancing our knowledge on the location and size of spider monkey populations in the Yucatan Peninsula.

Despite spider monkeys having a large distribution across Meso and South America, surveys to determine the size of their populations across their range have been limited and are lacking from many regions (Weghorst, 2007; Link et al., 2010; Aquino et al., 2012, Marsh et al., 2016). Such information is critical to develop species or site specific management plans (Plumptre and Cox, 2006; Kühl et al., 2008; Peck et al., 2011). One of the possible reasons for the lack of such information is the difficulty of surveying spider monkeys due to their fast, arboreal movement and high degrees of fission-fusion dynamics (Fedigan and Jack, 2001). My research has contributed new information and recommendations on how spider monkeys can be surveyed to promote and facilitate population monitoring (Chapter 3).

My research is the first to use the identity of habituated individuals to verify whether assumptions of line transect surveys were violated (Chapter 3). Such research is vital to ensure that population estimates are reliable. I found that recounting individuals and missing adult females on the same transect walk was rare. Problematically, enough young were missed during surveys due to their small size that it biased against population health. My research shows that young:adult female ratios based on survey data may not be reliable and should not be used to inform management decisions.

The comparison of population density estimates obtained with different methods to the actual density showed that some methods highly over- or under-estimate population density (Chapter 3). As population density estimates form the base of many management decisions, over- or under-estimating population density may lead to very distinct management decisions and potential inefficient use of available resources. The King method has commonly been employed to provide population density estimates due to its ease of use when sightings are few (Aquino et al., 2012). However, both Chapters 3 and 5 clearly demonstrate that this method highly overestimates population density, potentially providing a false sense of hope for the population being studied. Estimates obtained with the Kelker method differed the least from the actual density, suggesting that this method should be used to calculate population density of spider monkeys.

Conventional distance sampling (CDS) is increasingly advocated as the method to estimate population density (Buckland et al., 2010a, 2010b). However, the need for 40-60 independent sightings (Peres, 1999) limits the applicability of this method to survey data on elusive species. Previous studies found no differences between CDS and the Kelker method (Link et al., 2010; Meyler et al., 2012; Kun-Rodrigues et al., 2014), suggesting that the Kelker method can be employed as this method has no minimum sighting requirement and can therefore be used when sightings are low, an advantage for spider monkey surveys as sighting numbers are often very low even after intensive survey effort (Chapter 4). In my study population density estimates obtained with the Kelker method were lower than CDS in Chapter 3 but they were more similar in Chapter 5. These contrasting results may be explained by differences in the survey design. In Chapter 5, I performed line transect surveys on more transects of greater length than Chapter 3. The transects of Chapter 3 fell entirely within the home range of a habituated spider monkey group (Ramos-Fernández et al., 2013) whereas the transects of Chapter 5 extended beyond the home range of the habituated spider monkey group. Additionally, surveys in Chapter 5 were performed over a full year, whereas surveys in Chapter 3 were restricted to the rainy season. As such, the results of Chapter 5 are more reliable as it is less likely that habituation or seasonality may have affected the results. Therefore, population density estimates based on spider monkey surveys can be calculated using CDS when more than 40 individuals have been sighted or using the Kelker method when few individuals were sighted.

An important aspect of my research has focused on creating new methods to solve current problems in survey methods. In dense forest habitats, especially the regenerating forests which dominate the Yucatan Peninsula, the use of laser rangefinders or measuring tapes to accurately measure distances is difficult to regularly implement. Due to high tree density obtaining the measurement between the transect centerline and the monkey sighting is challenging and requires making several measurements. Although this may be possible when measuring the distance to the group center (as it requires only a single measure of distance), measuring distances to each individual spider monkey before they flee from observers is impractical and time consuming (Marshall et al., 2008). I therefore estimated distances by eye and applied an error correction to my distance estimates in order to account for erroneous distance estimates (Chapter 2). Regular distance estimate exercises combined with the actual measurement obtained with a measuring tape enabled me to calculate the distance estimation error for a range of distances on a monthly basis and incorporate such an error to obtain the corrected perpendicular distances, i.e. reliable estimates in conditions where the use of distance measuring instruments is restricted. Buckland et al. (2010b) stressed that it is important to take the correct distance measurement (i.e. perpendicular distance to the group center or to every individual) regardless of using measuring tapes, rangefinders or estimating distance by eye. By applying an error correction to perpendicular distances, minimal bias is introduced into the population density estimates. This error correction approach is simple and efficient, and can be applied to a range of survey settings where researchers resort to estimating distances. I therefore recommend the use of distance correction in situations where instruments to measure distance cannot be used.

I estimated the perpendicular distance to each individual spider monkey thereby avoiding the use of a mean subgroup size to calculate population density which may cause biased population density estimates as mean subgroup size, unlike mean group size, is not a relevant measure of the population (see section 3.1.2). Furthermore, estimating the distance to every sighted individual monkey prevents incorporating bias resulting from using the distance to the first sighted individual, which is a common practice in studies aimed at comparing methods to estimate population density (Chapman et al., 1998; Brugiere and Fleury, 2000; Fashing and Cords, 2000) and in spider monkey surveys (Iwana and Ferrari, 2002; Aquino et al., 2012; Kolowski and Alonso, 2012). Using the distance to the first sighted individual rather than the distance to group center or to each sighted individual can increase population density estimates as the first sighted individual is often located closer to the transect than the group center (Buckland et al., 2010a). Using the perpendicular distance to each sighted individual monkey allowed me therefore to obtain reliable population density estimates.

Spider monkeys are quite unique among the primates due to their high degrees of fission-fusion dynamics and fast, arboreal movement. The recommendations presented in this thesis regarding survey methods may therefore not be applicable to species with other forms of locomotion or lower levels of fission-fusion dynamics. Future research should focus on testing similar methods on other individually recognized primate groups to aid in the development of species specific survey methods, which is necessary to draw regional or between-site comparisons. Policy makers and conservation practictioners often require data on larger scales than a single site. Currently, surveys are not often comparible between sites or species of the genera due to differences in methods (Shanee and Shanee, 2001; Wich et al., 2016). My research has provided recommendations to help standardize spider monkey surveys, but similar research is needed for other primate species to understand and combat the global decline in primate populations (Estrada et al., 2017).

In conclusion, my research has shed new light into the resilience of spider monkeys to habitat disturbance. My research has thereby brought new insights into the theory of how primates are affected by habitat disturbance, as well as practical applications on how to investigate the effect of disturbances on primates. My research can help to identify and prioritize areas in the Yucatan Peninsula where conservation action is urgently needed and is not limited to individual sites. The new developments presented in survey methods should promote spider monkey population surveys across their range.

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Appendices

Appendix 1: Tree species list Otoch Ma'ax yetel Kooh

Family	Species	Common name	Feeding tree
Anacardiaceae	*Astronium graveolens*	K'ulin che'	
	Metopium brownei	Chechen	✓
	Spondias purpurea	Abal ak', Ciruelito, Ciruela de monte	✓
Annonaceae	*Mosanonna depressa*	E'elemuy	
	Oxandra lanceolata	Botox	✓
Apocynaceae	*Cascabela gaumeri*	Akits	
	Plumeria obtusa	Nicte ch'oom, Flor de mayo silvestra	
Araliaceae	*Dendropanax arboreus*	Sak chechen	✓
Bombacaceae	*Ceiba pentandra*	Ceiba	✓
	Ceiba schottii	Pi im	
Boraginaceae	*Bourreria mollis*	Sak bay éek	
	Cordia gerascanthus	Bojom	✓
Burseraceae	*Bursera simaruba*	Chakah	✓
	Protium copal	Pom	✓
Capparidaceae	*Capparis pachaca oxysepala*	K'ooch, X-chooch kitam	
Cecropiaceae	*Cecropia pelata*	Guarumbo, X-k'ooch le'	
Celastraceae	*Semialarium mexicanum*	Sak boob	
Cochilospermaceae	*Cochlospermum vitifolium*	Ch'oy chu'um, Chu'um	✓
Commelinaceae	*Calea urticifolia, C. jamaicensis*	Xikin	
Ebenaceae	*Diospyros tetrasperma*	Silil	✓
	Diospyros yucatanensis	U chul che'	
Erythroxylaceae; Euphorbiaceae	*Erythroxylum rotundifolium, Croton icche*	Ikilché	
Euphorbiaceae	*Cnidoscolus aconitifolius, Cnidoscolus souzae*	Chaya silvestre	
	Croton yucatanensis, Croton reflexifolius	Chin kuts	
	Drypetes lateriflora	Eek k'ulu'	

	Jatropha gaumeri	Pomolché	
Fabaceae	*Haematoxylon campechianum*	Tinta	
Lauraceae	*Nectandra coriacea*	Jochok ché, Jok che	✓
Leguminosae	*Acacia spp.*	Subín	
	Albizia tomentosa	Sak pich	
	Apoplanesia paniculata	Cholul, Chuulul che	
	Bauhinia divaricata	Ts'uru'tok, Pata de vaca	
	Caesalpinia gaumeri	Kitanche	
	Caesalpinia yucatanensis	Tak'inché	
	Chloroleucon mangense leucospermum	X'ya'ax eek'	
	Cojoba arborea arborea	Jujub	✓
	Diphysa carthagenensis	Ts'u'ts'uk	
	Enterolobium cyclocarpum	Pich	✓
	Erythrina standleyana	Chak ch'obenche, Chak mo'ol che	
	Harpalyce rupicola	Sak jabin	
	Havardia albicans	Chukum	
	Lonchocarpus punctatus	Balche	✓
	Lonchocarpus rugosus	K'anasin	✓
	Lonchocarpus xuul	Xu'ul, K'an xu'ul	✓
	Lysiloma latisiliquum	Tsalam	
	Piscidia piscipula	Ja'abin	
	Platymiscium yucatanum	Subin ché, Granadillo, Chak subinche	
	Senegalia gaumeri	Boxkatsim, Katsin	
	Swartzia cubensis cubensis	K'atal oox	
	Caesalpinia mollis	Chakté	
	Caesalpinia vesicaria	Chak ché	
Malpighiaceae	*Bunchosia swartziana*	Sipche, Manzanillo	
	Malpighia glabra, M. lundellii, M. emarginata	Waya'te'	
Malvaceae	*Ceiba pentandra*	Ya'ax che	
	Hampea trilobata	Jool	
	Helicteres mexicana	Joolol	
Meliaceae	*Cedrela odorata*	Cedro	✓
	Trichilla glabra	Ch'obenche, X-k'an lool	✓
Moraceae	*Brosimum alicastrum alicastrum*	Ramón	✓

	Chlorophora tinctoria	Moras	✓
	Ficus cotinifolia	Koopo	✓
	Ficus crocata	Alamo	✓
	Ficus pertusa	Ju'um ch'iich'	✓
	Ficus spp.	Akum	✓
	Ficus spp.	Sak awa	✓
Myrtaceae	*Eugenia foetida*	Sak loob	
	Eugenia spp.	Xjirmich	
	Psidium sartorianum	Pichi che’	
Nyctagynaceae	*Neea choriophylla*	Ta'tsi	
Palmae	*Sabal mexicana, S. yapa*	Huano	✓
Phyllantheae	*Astrocasia tremula*	Pay juul	
Piperaceae	*Piper amalago*	X ma'jas ché	
Polygonaceae	*Coccoloba acapulcensis*	X-tojyub	✓
	Coccoloba spicata	Boob	
	Gymnopodium floribundum	Ts'I'ts'ilche	
	Neomillspaughia emarginata	Sak iitsa’	
Rhamnaceae	*Colubrina greggi; Colubrina arborescens*	Pimienta che	
	Krugiodendron ferreum	Chintok	
Rubiaceae	*Antirhea lucida*	Palo de Rosa	
	Guettarda combsii	Tasta'ab	✓
	Randia longiloba	K´aax	
	Randia spp.	X-peech kitam, Kajal k'aax	
Rutaceae	*Amyris elemifera, A. sylvatica*	Gas che, Palo de gas	
	Casimiroa tetrameria	Yuy	
	Zanthoxylum caribaeum, Z. fagara, Z. juniperinum	Si na'an che	
Salicaceae	*Zuelania guidonia*	X Ta'amay	
Salicaceae; Olacaceae; Rutaceae	*Casearia emarginata, Ximena americana, Esenbeckia pentaphylla*	Naranja che	
Salicaceae; Putranjivaceae; Phyllanthaceae	*Casearia corymbosa, Laetia thamnia, Drypetes lateriflora, Margaritaria nobilis*	Ts´inché, Ts'iuche, Ixiimche	
Sapindaceae	*Exothea paniculata*	Wayuum koox	
	Melicoccus oliviformis	Wayam	
	Thouinia paucidentata	K'anchunuup	
Sapotaceae	*Chrysophyllum mexicanum*	Chi keej	
	Manilkara zapota	Zapote	✓

	Pouteria campechiana	K'anisté	
	Pouteria reticulata reticulata	Zapotillo	✓
	Sideroxylon foetidissimum gaumeri	Caracolillo	✓
Simaroubaceae	*Alvaradoa amorphoides amorphoides*	X'bel sinikché	
	Simarouba amara	Pa'sak	
Sterculiaceae	*Guazuma ulmifolia*	Pixoy, Sak pixoy	✓
Theophrastaceae	*Bonellia sp.*	Chak sik'in	
Tiliceae	*Luehea speciosa*	X k'ascaat, Peres kuts	✓
Verbenaceae	*Callicarpa acuminata*	Pukin	
	Vitex gaumeri	Yaxnik	✓
Violaceae	*Hybanthus yucatanensis*	Saakbakekam	
	Unidentified	Ahbach	
	Unidentified	Chacnich	
	Unidentified	Chechema	
	Unidentified	Chin che	
	Unidentified	Chirichohom	
	Unidentified	Chulul chakte	
	Unidentified	Chulul jabin	
	Unidentified	Chulul tsu	
	Unidentified	Grasiliana che	
	Unidentified	Ob che	
	Unidentified	Po ol	
	Unidentified	Tan che	
	Unidentified	Titsya	

Appendix 2: Tree species list Calakmul

Family	**Species**	**Common name**	**Feeding tree**
Anacardiaceae	*Metopium brownei*	Chechen	✓
	Spondias purpurea	Ciruella	✓
	Spondias radlkoferi	Jobo	✓
Annonaceae	*Oxandra lanceolata*	Xirutan, Botox	✓
Apocynaceae	*Aspidosperma megalocarpon*	Pelmax	
Boraginaceae	*Cordia dodecandra*	Ciricote	
	Cordia gerascanthus	Bojom	✓
	Ehretia tinifolia	Roble	✓
Burseraceae	*Bursera simaruba*	Chakah	✓
Cecropiaceae	*Cecropia peltata*	Guarumbo	
Combretaceae	*Bucida buceras*	Pukte'	
Euphorbiaceae	*Croton glabellus*	Cascarillo	
	Croton spp.	Achotillo	
	Jatropha curcas	Piñon	
Euphorbiaceae: Apocynaceae	*Sebastiania adenophora, Cameraria latifolia*	Sak chechen	
Fabaceae	*Crotalaria longirostrata*	Chipilin	
	Dialium guianense	Fierillo	✓
	Gliricidia sepium	Cocoite	
Iridaceae	*Cipura campanulata*	Tela de cebolla	
Lauraceae	*Nectandra coriaceae*	Laurel, Palo de gas	✓
	Nectandra salicifolia	Laurelillo, Lecherillo	✓
Leguminosae	*Acacia globulifera*	Carnisuelo, Sak subin che', Subin che'	
Leguminosae	*Acacia riparia*	Katsin	
	Acacia spp.	Acacia	
	Apoplanesia paniculata	Palo de sangre, Chulúul, K'i'ik' che'	
	Caesalpinia gaumeri	Kitinche	
	Caesalpinia mollis	Chakte viga	
	Haematoxylum campechianum	Tinto Negro, Tinta roja	
	Harvadia albicans	Chukum	
	Lonchocarpus	Xuul	✓
	Lonchocarpus castilloi	Machiche	✓
	Lysiloma latisiliquum	Tsalam	

	Mimosa bahamensis	Sak katsin	
	Piscidia piscipula	Jabin	
	Pitchecellobium tortum	Verde lucero	✓
	Platymiscium yucatanum	Granadillo	
	Senegalia gaumeri	Box katsin	
	Senna racemosa		
	Vatairea lundellii	Amargoso	
Malpighiaceae	*Byrsonima crassifolia*	Nance	✓
Malvaceae	*Ceiba schotii*	Lomo de lagarto	
	Hampea trilobata	Majagua	
	Pseudobombax ellipticum	Amapola	
Meliacaea	*Cedrela odorata*	Cedro rojo	✓
	Swietenia macrophylla	Caoba	
Moraceae	*Brosimum alicastrum*	Ramón	✓
	Ficus spp.	Alamo	✓
	Maclura tinctoria	Mora	
	Trophis racemosa	Campanillo	✓
Muntingiaceae	*Muntingia calabura*	Capulín	
Myrtaceae	*Psidium sartorianum o Eugenia sp*	Guayabillo	
Opiliaceae	*Agonandra macrocarpa*	Canta rana, Pak'aalché, Naap che'	
Polygonaceae	*Coccoloba spicata*	Uvero, Boob	✓
	Gymnopodium floribundum	Tsitsilche	
Rhamnaceae	*Karwinskia humboltiana*	Bag-sog	
	Krugiodendron ferreum	Chintok, Rompe hacha, Quiebra hacha	
Rubiaceae	*Alseis yucatanensis*	Papelillo, Pichiche	
Rubiaceae; Malpighiaceae	*Guettarda combsii, Bunchosia swartziana*	Manzanillo, Manzanita, Manzanito	
Rutaceae	*Amyris elemifera, A. sylvatica*	Palo de gas	
	Esembeckia pentaphylla	Naranjillo	
Salicaceae	*Casearia arborea*	Yaya	
Sapindaceae	*Talisia oliviformis*	Guaya	✓
	Thouinia paucidentata	Kanchunub	
Sapindaceae; Mimosoideae	*Matayba oppositifolia, Albizia niopoides*	Cedrillo	
Sapotaceae	*Manilkara zapota*	Zapote	✓
	Pouteria campechiana, P. reticulata	Zapotillo	✓
	Sideroxylon floribundum belizense	Tempesquite	
Simaroubaceae	*Alvaradoa amorphoides*	Ruda	

	Simarouba glauca	Pasac	✓
Verbenaceae	*Lippia umbelata*	Gusanillo	
	Vitex guameri	Yaxnik	✓
Zygophyllaceae	*Guaiacum sanctum*	Guayacan	
	Unidentified	Falso tamarindo	
	Unidentified	Frijolillo	
	Unidentified	Jobillo	

Appendix 3: Tree species list Bala’an K’aax

Family	**Species**	**Common names**	**Feeding tree**
Anacardiaceae	*Astronium graveolens*	K'ulinche	
	Metopium brownei	Chechem	✓
	Spondias mombin, Spondias radlkoferi	Jobo	✓
	Spondias radlkoferi	Abal ak', Ciruella de monte, Ciruelito	✓
Annonaceae	*Mosanonna depressa*	E'elemuy	
	Sapranthus campechianus	Sak elemuy	
Apocynaceae	*Cascabela gaumeri*	Akits	
	Plumeria obtusa	Nikte ch'oom, Flor de mayo silvestre, Sak nikte	
Arecaceae	*Acrocomia aculeata*	Tuk', Cocoyol	
Asteraceae	*Koanophyllon albicaulis*	T'oom tzu, Tóom tsu', Tomtsu'	
Bixaceae	*Cochlospermum vitifolium*	Chu'um, Ch'oy chu'um	
Boraginaceae	*Bourreria pulchra*	Bakal che, Bakche, Sak boj	
	Cordia dodecandra	Siricote, K'opte	
	Cordia gerascanthus	Bojom	✓
Burseraceae	*Bursera simaruba*	Chaka	✓
Capparaceae	*Forchhammeria trifoliata*	Tres marías, Yuy, X-pak'al che	
Capparidaceae	*Crataeva tapia*	Kokche, K'olomax	✓
Celastraceae	*Bonellia spp.*	Choch kitam	
	Semialarium mexicanum	Chun tok’	
Ebenaceae	*Diospyros tetrasperma, D. yatesiana, D. verae-crucis*	Silil, Box silil	
Erythroxylaceae	*Erythroxylum rotundifolium*	Ik'il che, ik'iche', iik'il che', Ixiimche, Ixinche	
Euphorbiaceae	*Croton glabellus*	Peres kuts	
	Croton glandulosepalus	Sak peres kuts	
	Gymnanthes lucida	Bak'ayim, Yayté, Yaytik, Ya’ay tiik, Ts’iitil	
	Jatropha gaumeri	Pomol che	

	Sebastiana adenophora	Sak chechem, Chechem blancho	✓
Hippocrateceae	*Hippocratea excelsa*	Sak boob	
Lauraceae	*Nectandra coriacea*	Laurelillo	✓
Lauraceae; Boraginaceae	*Nectandra salicifolia, Bourreria mollis*	Laurel	
Leguminosae	*Apoplanesia paniculata*	Cholul, Chuulul che'	
	Bauhinia divaricata	Ts'uru'tok, Pata de vaca, Sak ts´uro´tok	
	Caesalpinia gaumeri	Kitinche	
	Caesalpinia mollis	Chakte viga	
	Chloroleucon mangense leucospermum	X'ya'ax eek	
	Diphysa carthagenensis	Ts'u'ts'uk, Sak ts'uts'uk	
	Gliricidia maculata	Balche keej	
	Havardia albicans	Chukum	
	Lonchocarpus punctatus, L. hondurensis	Balche	✓
	Lonchocarpus rugosus	K'anasin, Chu'ul	✓
	Lonchocarpus xuul	Xu'ul	✓
	Lysiloma latisiquum	Tsalam, Boox tsalam	
	Mariosousa dolichostachya	Sitt'uul, Subint'uul	
	Mimosa bahamensis	Sak katsin	
	Piscidia piscipula	Ja'abin	
	Platymiscium yucatanum	Subinché, Granadillo	
	Senegalia gaumeri	Boxkatsim, Katsin	
Malpighiaceae	*Bunchosia swartziana*	Sipche, Manzanillo	
	Byrsonima bucidifolia	Sak paj, Nance silvestre	✓
	Malipighia emarginata	Wayate'	
Malvaceae	*Ceiba aesculifolia*	Pochote	
	Hampea trilobata	Majagua, Majaua	
	Helicteres mexicana	Joolol	
	Luehea speciosa	X k'ascaat	
	Pseudobombax ellipticum	Amapola	
Meliaceae	*Cedrela odorata*	Cedro	✓
	Guarea petenensis	Copal	✓
	Trichilia minutiflora	Tsiimin che', Caballito de madera, Tsiminche	✓
Menispermaceae	*Hyperbaena winzerlingii*	Chooch kitanche	

Moraceae	*Ficus crocata, F. cotinifolia, F. maxima*	Alamo	✓
	Brosimum alicastrum	Ramón	✓
	Ficus crassinervia, F. crocata, F. maxima	Higo	✓
Myrtaceae	*Eugenia spp.*	Kisiuc	
	Eugenia spp.	Sak loob	
	Eugenia winzerlingii, Myrcianthes fragans, Psidium sartorianum	Guayabillo	
	Eugenia winzerlingii, Myrcianthes fragans, Psidium sartorianum	Wayam kox	
	Psidium sartorianum	Pichi' che	
Nyctagynaceae	*Neea choriophylla*	Ta'tsi	
Opiliaceae	*Agonandra macrocarpa*	X-napche, Pakalche	
Palmae	*Sabal japa, S. mexicana*	Huano	✓
Phyllanthaceae	*Savia sessiliflora*	Chii'che, Tamarindo de monte	
Polygonaceae	*Coccoloba acapulcensis*	Tojyub	✓
	Coccoloba cozumelensis , C. acapulcensis , C. barbadensis	Bobchiich	✓
	Coccoloba spicata	Boob	✓
	Gymnopodium floribundum	Ts'I'ts'ilche	
	Neomillspaughia emarginata	Sak its'a, Sak tzaitza'	
Rhamnaceae	*Karwinskia humboldtiana*	Lu'um che'	
	Krugiodendron ferreum	Chin tok	
Rubiaceae	*Alseis yucatanensis*	Ja'as che, Tabaquillo	
	Guettarda combsii	Tasta'ab	✓
	Guettarda elliptica	Kibche, X-kibche'	
	Machaonia lindeniana	K'uch'el, Tankanche', Box k'uch'ee, Kuchel	
	Simira salvadorensis	Chaktekoc	
Rutaceae	*Amyris elemifera*	Taray	
	Amyris elemifera, A. sylvatica	Gas che, Palo de gas	
	Esenbeckia pentaphylla	Naranja che, Jo'k'o	
	Esenbeckia pentaphylla	Yuuy	
	Pilocarpus racemosus racemosus	Tamkasche, Cruz che	
Rutaceae	*Zanthoxylum caribaeum, Z. fagara, Z. juniperinum*	Si na'an che, Pakalche	
Salicaceae	*Zuelania guidonia*	Sabakche, X Ta'amay	
Sapindaceae	*Melicoccus oliviformis*	Huaya	
	Talisia floresii	K'oolok	

	Thouinia paucidentata	K'anchunuup	
Sapotaceae	*Chrysophyllum mexicanum*	Chike, Kayumito de monte	✓
	Manilkara zapota	Zapote	✓
	Pouteria campechiana	K'aniste	✓
	Pouteria reticulata reticulata	Zapotillo	✓
	Sideroxylon obtusifolium buxifolium	Puts' mukuy, Káapoch	
	Sideroxylon salicifolium	Chak ya	
Simaroubaceae	*Alvaradoa amorphoides amorphoides*	X'bel sinikché	
	Simarouba amara	Pa'sak', Sak cedro	
Theophrastaceae	*Bonellia flammea*	Chaksikin	
Urticaceae	*Cecropia peltata*	Guarumbo	
Verbenaceea	*Vitex gaumeri*	Yaxnik	✓
	Unidentified	Chamalche	
	Unidentified	Ch'okche	
	Unidentified	Guayanche	
	Unidentified	Jokche	
	Unidentified	Obche	
	Unidentified	Sak silil	
	Unidentified	Toxok	

Appendix 4: Tree species list Santa Clara

Family	**Species**	**Common name**	**Feeding tree**
Anacardiaceae	*Astronium graveolens*	K'ulin ché'	
	Metopium brownei	Chechen	✓
Apocynaceae	*Cascabela gaumeri*	Akits	
Araliaceae	*Dendropanax arboreus*	Sak jab, Sak chakah	✓
Bombacaceae	*Ceiba pentandra*	Ceiba, Ya'axche	✓
	Ceiba schottii	Pi im	
Boraginaceae	*Cordia spp.*	Bojom	✓
Burseraceae	*Bursera simaruba*	Chakah	✓
Cecropiaceae	*Cecropia pelata*	Guarumbo	✓
Celastraceae	*Semialarium mexicanum*	Unknown 2	
Celastraceae, Polygonaceae	*Semialarium mexicanum, Elaeodendron xylocarpum, Coccoloba cozumelensis*	Sak boob	
Cochilospermaceae	*Cochlospermum vitifolium*	Ch'oy chu'um, Chu'um	✓
Ebenaceae	*Diospyros anisandra*	X K'ak'alche	
	Diospyros spp.	Silil	✓
Euphorbiaceae	*Jatropha gaumeri*	Pomolché	
	Sebastiania adenophora	Sak chéchén	✓
Flacourtiaceae; Olacaceae; Rutaceae	*Casearia emarginata, Ximena americana, Esenbeckia pentaphylla*	Naranja ché	
Flacourtiaceae; Salicaceae; Putranjivaceae, Phyllanthaceae	*Casearia corymbosa, Laetia thamnia, Drypetes lateriflora, Margaritaria nobilis*	Ixiimché	
Lauraceae	*Nectandra salicifolia; Licaria campechiana*	Laurelillo	
Leguminoseae	*Acacia pennatula*	Chimai	
	Albizia tomentosa (Micheli) Standl.	Sak pich	
	Caesalpinia gaumeri	Kitanché	
	Caesalpinia mollis	Chakté	
	Caesalpinia yucatanensis	Kanlol, Flor amarillo	
	Chloroleucon mangense leucospermum	X'ya'ax eek'	
	Cojoba arborea arborea	Jujub	✓

	Diphysa carthagenensis	Ts'u'ts'uk	
	Enterolobium cyclocarpum	Pich	✓
	Harpalyce rupicola	Sak jabin	
	Lonchocarpus punctatus	Balché	✓
	Lonchocarpus rugosus	K'anasin	✓
	Lonchocarpus xuul	Xu'ul	✓
	Lysiloma latisiliquum	Tsalam	
	Piscidia piscipula	Ja'abin	
	Platymiscium yucatanum	Subin ché, Granadillo	
	Senegalia gaumeri	Box katsin	
	Swartzia cubensis cubensis	K'atal oox	
Malvaceae	*Hampea trilobata*	Mahawa, Jool	
Meliaceae	*Cedrela odorata*	Cedro	✓
Moraceae	*Brosimum alicastrum alicastrum*	Ramón	✓
	Chlorophora tinctoria	Moras	✓
	Ficus cotinifolia	Koopo	✓
	Ficus spp.	Alamo	✓
	Ficus spp.	Alamo negro	✓
	Ficus spp.	Awa negra	✓
	Ficus spp.	Sak awaj, Alamo blanco	✓
Myrtaceae	*Calyptranthes pallens*	Chaknii	
	Eugenia spp.	Sak loob	
	Psidium sartorianum, Eugenia buxifolia	Pichi ché	
Nyctagynaceae	*Neea spp.*	Ta'tsi	
Olacaceae	*Schoepfia schreberi*	Sak bakché	
Palmae	*Sabal*	Huano	✓
	Thrinax radiate	Palma de chit	
Polygonaceae	*Coccoloba acapulcensis*	X-tojyub	✓
	Coccoloba spicata	Boob	✓
	Gymnopodium floribundum	Ts'I'ts'ilché	
Putranjivaceae	*Drypetes lateriflora*	Box ché	
Rhamnaceae	*Colubrina arborescens*	Pimienta ché, Chak bulunché	
	Karwinskia humboldtiana	Pimientillo	
Rubiaceae	*Cosmocalyx spectabilis*	Palo de rosa	
	Guettarda combsii	Tasta'ab	✓
	Randia longiloba	K'aax	
Rutaceae	*Amyris elemifera, A. sylvatica*	Palo de gas, Gasche	
	Casimiroa tetrameria	Yuy	

Salicaceae	*Zuelania Guidonia*	X Ta'amay	
Sapindaceae	*Melicoccus oliviformis*	Wayam de monte	
	Thouinia paucidentata	K'anchunuup	
Sapotaceae	*Chrysophyllum mexicanum*	Chi keej, Boca de venado	✓
	Manilkara zapota	Zapote	✓
	Pouteria glomerata glomerata	Chochte	✓
	Pouteria spp.	Zapotillo	✓
Simaroubaceae	*Alvaradoa amorphoides amorphoides*	X'bel sinikché	
	Simarouba glauca	Pa'sak	✓
Solanaceae	*Solanum diphyllum; S. nudum*	Chilillo	
Sterculiaceae	*Guazuma ulmifolia*	Pixoy	✓
Tiliaceae	*Heliocarpus donnell-smithii, H. mexicanus*	Joolol	
	Luehea speciosa	X k'ascaat, Caracolillo	✓
Ulmaceae	*Phyllostylon brasiliense*	Unknown 1	
Verbenaceae	*Rehdera trinervis*	Sak wisil che', Sak wisilché	
	Vitex gaumeri	Yaxnik	✓
	Unidentified	Chirichojom	
	Unidentified	Guanché	
	Unidentified	Sak lol	
	Unidentified	Sak ta	
	Unidentified	Subul	
	Unidentified	Titsya	

Appendix 5: IVI values of the 10 most dominant tree species per site.

BK = Bala'ax K'aax, CA = Calakmul, OMYK = Otoch Ma'ax yetel Kooh, LA = Los Arboles. Maximum IVI value is 300.

		SITE			
Family	**Species**	**BK**	**CA**	**OMYK**	**LA**
Euphorbiaceae	*Gymnanthes lucida*	33.18			
Burseraceae	*Bursera simaruba*	18.41		24.98	9.20
Leguminosae	*Caesalpinia gaumeri*	14.89		7.59	
Sapotaceae	*Manilkara zapota*	14.38	16.58		
Tiliceae	*Trichilia minutiflora*	12.42			
Leguminosae	*Piscidia piscipula*	11.94		13.72	11.09
Euphorbiaceae	*Croton glabellus*	7.84	10.84		
Erytroxylaceae	*Erythroxylum rotundifolium*	6.15			
Sapindaceae	*Thouinia paucidentata*	5.72		7.50	7.97
Tiliceae	*Luehea speciosa*	5.37			
Leguminosae	*Lonchocarpus*		16.95		
Polygonaceae	*Coccoloba spicata*		15.98	7.16	
Moraceae	*Brosimum alicastrum*		12.77	12.06	
Leguminosae	*Haematoxylum campechianum*		12.70		
Polygonaceae	*Gymnopodium floribundum*		12.20	7.19	17.12
Salicaceae	*Casearia arborea*		10.19		
Simaroubaceae	*Alvaradoa amorphoides*		9.52		
Malpighiaceae	*Byrsonima crassifolia*		9.27		
Leguminosae	*Lysiloma latisiliquum*			15.01	21.40
Anacardiaceae	*Metopium brownei*			11.41	11.88
Verbenaceae	*Vitex gaumeri*			7.99	
Araliaceae	*Dendropanax arboreus*				17.69
Sapotaceae	*Pouteria reticulate*				14.76
Euphorbiaceae	*Drypetes lateriflora*				8.58
Annonaceae	*Mosanonna depressa*				7.86
Leguminosae	*Cojoba arborea*				
Ebenaceae	*Diospyrus*				
Leguminosae	*Lonchocarpus xuul*				

Appendix 6: IVI values of the 10 most dominant feeding tree species per site.

BK = Bala'ax K'aax, CA = Calakmul, OMYK = Otoch Ma'ax yetel Kooh, LA = Los Arboles. Maximum IVI value is 300.

		SITE			
Family	**Species**	**BK**	**CA**	**OMYK**	**LA**
Burseraceae	*Bursera simaruba*	18.4166		24.9848	9.19575
Sapotaceae	*Manilkara zapota*	14.3846	16.5762	5.51731	6.18587
Meliaceae	*Trichilia minutiflora*	12.4247			
Verbenaceae	*Vitex gaumeri*	5.35514	7.44503	7.99261	7.33728
Leguminosae	*Lonchocarpus xuul*	5.17185		4.8416	
Sapotaceae	*Pouteria reticulate*	4.61675			32.39
Lauraceae	*Nectandra coriacea*	3.90097			14.7601
Polygonaceae	*Coccoloba spicata*	3.50141	15.9795	7.1617	7.08382
Polygonaceae	*Coccoloba*	2.83075			
Rubiaceae	*Guettarda combsii*	2.70015			
Leguminosae	*Lonchocarpus*		16.9499		
Moraceae	*Brosimum alicastrum*		12.7712	12.0574	
Malpighiaceae	*Byrsonima crassifolia*		9.27333		
Sapotaceae	*Pouteria*		8.90952		
Sapindaceae	*Talisia oliviformis*		6.95034		
Anacardiaceae	*Metopium brownei*		6.05052	11.4069	11.8843
Lauraceae	*Nectandra salicifolia*		5.03548		
Moraceae	*Ficus cotinifolia*			5.33609	
Ebenaceae	*Diospyros tetrasperma*			5.22463	
Leguminosae	*Lonchocarpus rugosus*			4.2998	
Araliaceae	*Dendropanax arboreus*				17.6914
Tiliceae	*Luehea speciosa*				6.59361