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Interspecific and integroup interactions of mantled howling monkeys (*Alouatta palliata*) in primary versus secondary forest at El Zota Biological Field Station, Costa Rica

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Interspecific and intergroup interactions of mantled howling monkeys (*Alouatta palliata*)
in primary versus secondary forest at El Zota Biological Field Station, Costa Rica

by

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A thesis submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of

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2009

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ABSTRACT

Four groups of mantled howling monkeys (*Alouatta palliata*) were observed at El Zota Biological Field Station in northeastern Costa Rica to assess whether resource scarcity caused by anthropogenic disturbance and hypothesized increased competition for limited resources would result in more frequent and more aggressive interactions between neighboring howling monkey groups and between howling monkeys and other, sympatric primate species, namely white-faced capuchins (*Cebus capucinus*) and black-handed spider monkeys (*Ateles geoffroyi*). Using a comparison between the primary forest, as a control, and anthropogenically-altered secondary forest, I examined whether a behavioral difference existed between groups with hypothesized varying degrees of resource competition. Intergroup encounters were broken down into long distance howling bouts, with 46 observed, and close proximity interactions, with 11 observed. Results showed an increased frequency of howling in the primary forest as compared with the secondary forest, but no difference between the frequency, duration, or type of close-proximity intergroup encounters. Forty-five interspecies interactions were observed between howling monkeys and sympatric primate species. These interactions showed no difference between forest type for frequency, duration, or type of interaction. These results suggest that the composition and resource availability of the secondary forest at this site that does not align with current assumptions of habitat degradation. Alternatively results may be a reflection of social pressures such as infanticide, intragroup competition, and genetic relatedness as factors shaping howling monkey behaviors in both primary and secondary forests.

CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW

This study explores the effect of deforestation as a result of anthropogenic-alteration of primate habitat in areas of wet forest and swamp forest in Northeast Costa Rica. Comparing the interactions between conspecific groups of mantled howling monkeys (*Alouatta palliata*) and between primate species living in direct sympatry with these howling monkeys (*Ateles geoffroyi* and *Cebus capucinus*) areas of primary and anthropogenically-altered secondary forests, this study attempts to determine whether forest disturbance is also causing disturbance between the primate species these areas. In times of decreased resource availability and increased dietary overlap, it is assumed that primate competition will be greater than in times, or habitats, where more resources are available for primate consumption.

Costa Rican primates and deforestation

In the Sarapiquí region of Northeastern Costa Rica, the rate of deforestation in unprotected areas increased from 2.8% during the period from 1986-1991 to 3.2% per year between 1991-1995. During this same time period, the number of forest fragments in the region increased from 537 fragments in 1976 to 1231 fragments in 1996, while the average size of the fragments decreased from 0.95 to 0.25 km² [Sanchez-Aofeifa et al., 1999]. The rate of deforestation in Costa Rica has been growing despite government efforts to protect the land [Sanchez-Azofeifa et al., 2003]. With so little undisturbed forest left in Central America, native species are forced to adjust to habitat changes or face extinction. Primates that once inhabited areas that are now cities or farms have faced population declines

[Fedigan & Jack, 2001] and, like the tropical forests they inhabit, these primates have become a conservation concern [Zaldivar et al., 2004].

Though all four species of primates extant in Costa Rica (*Alouatta palliata*, *Ateles geoffroyi*, *Cebus capucinus*, and *Saimiri oerstedii*) are negatively affected by deforestation, fragmentation, agriculture, hunting, and extraction of individuals for the pet trade, they are not equally affected [Zaldivar et al., 2004]. The species within Costa Rica that has declined in population the most is the black-handed spider monkey (*Ateles geoffroyi*), which is listed as endangered, with the subspecies *A. g. geoffroyi* [Cuaron et al., 2008] listed as critically endangered and the subspecies *A. g. ornatus*, the subspecies found in northeast Costa Rica, listed as endangered [Cuaron et al., 2008; IUCN, 2008]. Squirrel monkeys (*Saimiri oerstedii*) in Costa Rica are considered vulnerable according to the IUCN, and their numbers are declining [IUCN, 2008; Wong et al., 2008]. *Alouatta palliata* and *Cebus capucinus* are faring better than the other two species, though populations are declining throughout their range [Zaldivar et al., 2004; Zucker & Clarke, 2003]. The major reason for the decline of these primate species is generally believed to be the loss of resources and suitable habitat resulting from deforestation and fragmentation of remaining forests. Reduction of suitable habitat and available food resources presumably increases competition for available food among primates living sympatrically, making survival difficult for these remaining primate species.

Several New World monkey species live in sympatry throughout Central and South America. Often these species show significant overlap not only in geographical range, but also in resource exploitation. The three primate species that coexist in Northeastern Costa Rica are mantled howling monkeys, white-faced capuchins, and black-handed spider

monkeys. Mantled howling monkeys are the most folivorous of the three species while fruit makes up 12.5% of their diet [Neville et al., 1988]. White-faced capuchins are the most omnivorous of the species with up to 65% of their diet consisting of fruit and including more vertebrate and invertebrate prey than either of the other species [Freese & Oppenheimer, 1981]. Black-handed spider monkeys are the most frugivorous of the three sympatric species, with fruit composing 75-93% of their diet [Kinzey, 1997].

In areas where the three species occur sympatrically, the search for available fruit sources often draws them to the same trees. Moynihan [1976] observed that howling monkeys were often in the same tree as capuchins or spider monkeys, each species being drawn by the same fruits or other features of the environment. At Santa Rosa, a dry forest in northwestern Costa Rica, Rose and colleagues [2003] found that the average dietary overlap between howling monkeys and capuchins was 5%. However in times of food scarcity, overlap between the two species can reach up to 30% [Rose et al., 2003]. Likewise, spider monkeys and capuchins have an average dietary overlap of 24%, but, in times when fruit is scarce, overlap can reach up to 43%. Food sources for these primate species are limited, especially during the season when fruit is less plentiful, and it is during these times when interspecific competition is the greatest and all three species are more likely to revert to fallback food sources [Chapman, 1987]. Although studies have focused on primate competition during times of purported resource scarcity [Terborgh & van Schaik, 1987], less information is known regarding sympatric primates' interactions at other times of the year. Additionally, most study of primate dietary overlap among the Costa Rican primate species has been done within the highly seasonal dry forests of northeast Costa Rica [for example: Chapman, 1987; Rose et al., 2003].

Primate competition

The factors affecting intergroup interactions between conspecifics are complex and reflect competition for food resources, mates, and survival. Though similar to the factors governing the interactions between species, the interactions among opposing members of the same species are further complicated by a lack of differentiation in ecological niche as well as reproductive pressures. So, while sympatric primate species are able to rely on different fall-back foods, members of the same species are competing for access to the same resources to ensure their survival.

In general, competition among sympatric primate species is assumed to exist, even in populations living in undisturbed forest. What happens, however, when the amount and types of available resources are further limited by anthropogenic or human-induced ecological degradation? What behavioral effects does such resource limitation have on primate species in these areas, and how are interspecies and intergroup interactions affected?

Objectives

The main objectives in this study were to explore the interactions between neighboring groups of howling monkeys as well as the interactions between howling monkeys and other sympatric, nonhuman primate species. Additionally, the possibility that differences exist between the interactive behaviors exhibited by those groups living in primary, undisturbed forest and those living in anthropogenically disturbed habitat was examined. In sum, the objectives of this study were to compare interspecific interactions between mantled howling monkeys with white-faced capuchins, and black-handed spider

monkeys inhabiting secondary growth forest with the interactions between these species living in primary growth tropical forest, focusing on frequency and intensity of interactions between primate species. In addition, this study attempted to compare intergroup interactions, both physical and vocal, between howling monkey groups living in secondary and primary growth tropical forest. These objectives and how they were accomplished will be explored in greater detail in the methods section of this paper.

Hypotheses

The objectives of this study led to two major hypotheses; the first examines the frequency of interaction or amount of aggression in interactions between howling monkeys and other species of nonhuman primates in primary and secondary forest habitats. Due to the hypothesized extra limitations on food resources and increased competition for existing resources in anthropogenically disturbed, secondary forest [Arroyo-Rodriguez & Mandujano, 2006; Onderdonk & Chapman, 2000], interspecific interactions between howling monkeys and other nonhuman primate species in this habitat will be (1) more frequent and (2) more aggressive than interactions occurring in primary forest.

The second hypothesis tests the frequency of howling bouts and close proximity interactions between howling monkey groups in primary and secondary forest habitats. Based on a review of the available literature, intergroup interactions between howling monkey groups in the secondary forest were expected to be more frequent regarding both howling bouts and close proximity interactions due to reduced resource availability in this habitat type [Serio-Silva & Rico-Gray, 2002; Clarke et al., 2002].

Previous studies have explored the interactions that take place between howling monkeys in neighboring groups and interactions with other species of nonhuman primates as well as the reaction of howling monkeys to anthropogenic changes to their environment [e.g. Arroyo-Rodriguez & Mandujano, 2006; Arroyo-Rodriguez et al., 2007; Chapman, 1987; Chapman, 1988a; Clarke et al., 2002; da Cunha & Byrne, 2006; Fedigan & Jack, 2001; Knopff & Pavelka, 2006; Pozo-Montuy & Serio-Silva' 2007; Rose et al., 2003; Serio-Silva & Rico-Gray, 2002; Stevenson et al., 2000; Stoner, 1996; Zaldivar et al., 2004]. Yet, there is little information on how these two factors interact. Additionally, the information available on the three focal species in the Caribbean wet and swamp forests of Costa Rica is limited, with most long-term studies stemming from the dry forests of the Guanacaste region of Costa Rica. As a result, this study represents a unique perspective on how primates are coping with anthropogenic disturbance and landscape alteration in wet forests and swamp forests in northeastern Costa Rica.

Literature Review

New World primates are believed to have diverged from the Old World primate lineage around 33-35 million years ago [Schrago & Russo, 2003]. Since that time, Platyrrhines and Catarrhines have existed on separate continents with different sets of ecological pressures shaping their evolution. Platyrrhines are less studied due to their temporal separation from the Catarrhines and subsequently, their phylogenetic distance from the hominid lineage [Kinzey, 1986; Strier, 1990]. Yet within the New World monkey infraorder, every previously described primate social structure has been identified, from monogamy to cohesive and fluid multi-male polygyny to polyandry [Strier, 1990].

Platyrrhines also show great variation in diet, body size, and locomotion patterns [Rosenberger 1993].

As a highly diverse group, Platyrrhines offer insight into many behavioral and ecological questions. As forests throughout the world disappear, primatologists try to gain baseline information on understudied New World and their interactions with sympatric species, with conspecifics both within and between groups, and with the environment around them. With pristine primate habitat vanishing through anthropogenic alteration, it is crucial to gain an understanding of the behaviors of New World monkey species both in primary and secondary forest systems.

Sympatry among living primates

Throughout much of the world where primates are found, several species live sympatrically. Direct sympatry refers to the co-occurrence of primate species in the same habitat at the same time, whereas broad sympatry refers to co-existence of species over a wide geographic region [Stanford, 2006]. Because in direct sympatry different species live in the same immediate habitat, it follows that each species must rely on different resources for survival, or at least diverge slightly in their use of available resources. Each species must occupy a different niche to be able to coexist in the same habitat. If two species occupy the same niche in the same habitat, it may lead to the local extinction of one of the competing species according to “Gause’s principle,” or the principle of competitive exclusion [Gause, 1934; Hardin, 1960; Summers & Neville, 1978; Stanford, 2006; Rose et al., 2003]. It is, however, possible for competing species to live in sympatry if each occupies a different realized niche and some resource partitioning occurs between the

competing species. Within the principle of competitive exclusion, there is some room for co-existence as long as neither species is reduced below some critical dimension [Summers & Neville, 1978].

Four different categories have been described to characterize the relationships that exist between species living in direct sympatry based on each species' niche [Rose et al., 2003]. The first two relationships entail that sympatric species deal with predation. A species may be viewed as a potential predator or as a potential prey item. Though not all primates hunt for food, all primates are susceptible to predation to a certain degree. Primate species may also view sympatric species as either feeding competitors or neutral species. Competitors include those species that rely on overlapping food resources, whether invertebrate prey or fruit and foliage from the same trees [Rose et al., 2003]. Neutral species are those species that are neither prey nor competitors. Though the two neutral species share the same space, they do not use the same resources. The type of relationship (predator, prey, competitor, or neutral) that exists between species determines the expected behavior of each species.

In addition to living in competition with other primate species, primates as part of a larger ecological system may compete with other mammalian orders, reptiles, amphibians, or even insects for food [Sushma & Singh, 2006]. The sustainability of the ecosystem relies on an intricate system of niche divergence. Sushma and Singh [2006] examined the niche divergence of four arboreal mammalian species in Western Ghats, in southern India: the lion-tailed macaque (*Macaca silenus*) the bonnet macaque (*Macaca radiata*), the Nilgiri langur (*Semnopithecus johnii*), and the Indian giant squirrel (*Ratufa indica*). All four species lived in direct sympatry for at least part of the year and exhibited resource

partitioning through differential resource use, differential habitat use, and vertical stratification. The bonnet macaque did not live in direct sympatry with the other species throughout the year, but migrated into the evergreen forest during times of fruit abundance. The authors maintain that the overlap between the bonnet macaque and the lion-tailed macaque is too great to sustain both these species throughout the year [Sushma & Singh, 2006]. Those species that do live in direct sympatry throughout the year show instance of cooperative interaction such as alarm calls, though this was not seen as often with the bonnet macaque. Agonistic interactions between sympatric species were not shown to be related to niche overlap [Sushma & Singh, 2006]. As is seen in this example, niches of various sympatric species may overlap, yet, as in the case with the two macaque species, too great an overlap especially during times when food is not superabundant can make living in direct sympatry throughout the year impossible [Sushma & Singh, 2006].

A similar situation was observed between the putty-nosed monkeys (*Cercopithecus nictitans stampflii*) and Diana monkeys (*Cercopithecus diana diana*) at Tai National Park, Ivory Coast [Eckardt & Zuberbuhler, 2004]. Though the two species fill an almost identical ecological niche, they live in direct sympatry and form nearly permanent mixed-species associations. The authors hypothesized that the larger Diana monkeys tolerated putty-nosed monkeys because of benefits related to increased predator defense [Eckardt & Zuberbuhler, 2004]. In return for the increased predator defense that the Diana monkeys received, the putty-nosed monkeys were given access to feeding trees [Eckardt & Zuberbuhler, 2004]. Though the species held ecological niches that greatly overlapped, they were able to coexist and benefit from the added predator protection of the other species. In this case, each species receives a benefit and a cost associated with the interspecific relationship. In other

cases of closely related species, or species with similar niches living in direct sympatry mechanisms such as vertical stratification, resource partitioning, temporal shifts in resource use, and differences in habitat use [Sushma & Singh, 2006; Vasey, 2000; Porter, 2001].

Interspecific interactions among New World primates

New World primates show a diverse array of social systems, behaviors, body sizes, and diet. They therefore exhibit a wide variety of interspecific interactions with other primates. In some areas of the New World, up to 14 species of primates live sympatrically [Puertas & Bodmer, 1993; Bourliere, 1985]. According to a review of primate study sites in the New World by Peres and Janson [1999], the average number of sympatric species of primates in the Neotropics is 6.0 +/- 3.6, with 42% of areas containing between one and four species. Though the majority of the areas sampled within this study held low levels of sympatric primate species, areas with 10-14 different primate species composed around 13% of the sites studied in the Neotropics. However, forthcoming molecular technologies and evidences may result in the future recognition of even higher numbers of species found in sympatry. Historically, many of the field studies on New World primates have been conducted at just a few sites, such as Santa Rosa National Park, Costa Rica (a tropical dry forest) and Barro Colorado Island, Panama (a tropical moist forest) [Holdridge, 1947]. At both sites there are relatively few sympatric primate species (up to five species including *A. palliata*, *A. geoffroyi*, and *C. capucinus* at both locations and *Saguinus geoffroyi* and *Aotus trivirgatus* on Barro Colorado Island) [Chapman, 1987; Wright et al., 1994]. The three largest species found at these locations (capuchin, howling and spider monkeys) are the best studied regarding behavior and interspecific niche overlap. However, there is little

information available about the interactions of these species in other locations (particularly the Caribbean side of Central America) and other ecosystems (such as tropical swamp forest and wet forest).

Interspecific interactions are usually classified as agonistic or affiliative. Affiliative interactions include those behaviors that involve passive and active affiliation, such as resting in contact, grooming, playing, or alliance formation, whereas agonistic interactions include aggressive and submissive interactions. Aggressive interactions often involve displacements, threats, chasing, and physical fighting [Sussman et al., 2005; Rose et al., 2003]. In some cases, the reasons for these reactions seem, on the surface, to be evident, such as direct competition over resources. However, for interactions such as grooming, the reasons are not always clear [Perry & Manson., 2003].

Rose and colleagues [2003] compiled data on interspecific interactions observed in 11 groups of *C. capucinus* at three sites in a formerly continuous tropical dry forest in the Guanacaste Province in Costa Rica. They found that the amount of agonism and affiliation varied both between the species encountered and the 11 groups. When examining sympatric primate species, the authors found that capuchins most often reacted aggressively toward mantled howling monkeys. According to their data, 54-80% of the interactions between howling monkeys and capuchins were aggressive, with 93-95% of the aggression directed by the capuchins toward the howling monkeys. The aggression was not always centered at feeding trees and did not have any visible cause other than the presence of the howling monkeys. Capuchin interactions with *A. Geoffroyi* were far less aggressive, with about 24% being affiliative or mixed affiliative and aggressive interactions [Rose et al. 2003]. When capuchin and spider monkey interactions were aggressive, they were generally reciprocally

aggressive, involving only threats and chases with no bodily contact. These aggressive interactions also commonly involved large feeding sources, in contrast to those with howling monkeys. In most cases, Rose et al. [2003] found that spider monkeys were socially dominant to the smaller capuchins. Though considered direct competitors for food sources, spider monkeys and capuchins were occasionally observed feeding together in fig trees with minimal aggression. Though these sympatric species compete for limited food resources, the competition does not appear to extend into interspecies interactions, bringing into question the assumption that direct or contest competition between these species will often result in behavioral aggression.

In their study of capuchin interspecific interactions, Rose and colleagues [2003] found that the rate of interactions between howling monkeys and capuchins varied between sites. At Lomas Barbudal interactions between the two species occurred once every 1.5 days. The rate at Santa Rosa was one interaction per 4.5 days, and at Pale Verde, the rate of interaction was one per week [Rose et al., 2003]. At Santa Rosa, the study sites themselves vary from 0.79 to 4.17 interactions every 100 hours [Rose et al., 2003]. Lomas Barbudal, the site with the highest rate of interactions was also the site at which interactions were most likely to be aggressive, with 95% of aggression directed from the capuchins to the howlers. The sites used in this study were chosen due to their close geographical and ecological proximity to one another, indicating that the differences in interaction rate and aggression may not be easily linked to ecology.

The behavior of wild primates is not always predicted according to ecological variables alone. Factors such as social learning and species-specific temperaments, which may themselves be adaptive, may cause variation in observed interactions between species

that are closely related and even within the same species [Rose et al., 2003]. Thus, interspecific interactions are influenced by ecological factors and ecological niches, but also vary between species and site, based on tradition and temperament [Perry & Manson, 2003; Rose et al., 2003].

Competition between Neotropical primates

Though primates in the New World show great diversity of diet, there is usually some degree of dietary overlap between sympatric species. Keystone resources, such as large fig trees and palms, are important food resources for Neotropical primates and can attract all the primate species in the area [Kinzey, 1986]. Though the amount of resource overlap varies seasonally and with geographical location, resource overlap to some degree occurs between all New World monkeys. As a result, it is difficult to classify sympatric primate species as being completely neutral.

Even though competition is present to a degree in all Neotropical primate species, the degree to which that competition affects interspecific interactions differs from species to species and place to place. As discussed earlier, competition between sympatric species can lead to the local extinction of one of those species if the two rely on the same limited resources for survival. Food resource availability is seen as one of the major limiting factors for primate populations in a given area [Cant, 1980; Glander, 1981; Kinzey, 1986]. Dietary niche divergence is generally seen as the reason that primate species, or any group of species, can live sympatrically in an ecosystem that has a limited abundance of food resources.

Fruit comprises a large portion of many primate diets. In certain seasons, however, not enough fruit is available to sustain primate populations. At times of limited fruit availability, fallback food sources become more important [Kinzey, 1986; Eisenberg, 1979; van Schaik et al, 1993]. These foods are often harder to find or abundant yet less nutritious, and are available regardless of season. It is regarding fallback foods that niche differentiation between sympatric primates becomes obvious.

The timing of fruit scarcity varies greatly between forest type. Additionally, primate species that rely more heavily on new leaf flush or flowers may not be negatively affected during the same months as those species that rely more heavily on fruit. A study by Frankie, Baker and Opler [1974], compared the plant phenology of a tropical dry forest on the Pacific side of Costa Rica to a tropical wet forest on the Caribbean side of Costa Rica. The authors found a significant peak in fruiting in the dry forest during April, a month poised at the end of the long dry season (approximately six months in length), with a peak in the amount of trees with leaf flush following immediately (from late April to June). Though some fruiting and leaf flush occurs during other months, the levels drop significantly, conceivably causing primates to rely more heavily on fallback food sources. The wet forest, however, showed phenological patterns that contrast heavily with those in the dry forest. According to this study, the wet forest showed a more consistent pattern of leaf production throughout the year, with only 17% of the species in this study showing a seasonal leaf flushing behavior. Fruiting patterns in the wet forest also showed less variation throughout the year with a spike in the shorter dry season (August through October); yet at any time throughout the year at least 37 species were producing fruit. Such phenology patterns in the wet forest may

result in fewer times of fruit scarcity. However, not all fruits are easily accessible to all primates, nor are all primates going to exploit all available fruits.

Fallback foods differ according to primate species but can include foliage, invertebrates, vertebrate prey, and vegetative parts of plants [Stevenson et al., 2000; Rose et al., 2003]. In some sympatric species, there is partitioning between fruit species. According to a study conducted by Stevenson and colleagues [2000], *Cebus apella* and *Lagothrix lagothricha* showed fruit partitioning when fruit was scarce. In the other species involved in the same study, there was no observed change in fruit partitioning in times of scarcity [Stevenson et al., 2000]. They did, however, find that *Ateles belzebuth* ate the fruit of a palm species (*Oenocarpus bataua*) both during periods of fruit scarcity and abundance, while the ecologically similar species *L. lagothricha* never ate *O. bataua* fruit. They attributed this difference, not to fruit partitioning or niche divergence, but rather to fruit preference [Stevenson et al., 2000]. However, gaining a true measure of fruit preference is difficult as preference may be attributed to individual tastes, health, or ability exploit a food resource, and it is difficult to rule out ecological or evolutionary reasons. Other studies with *Ateles spp.* also emphasize the importance of fruit characteristics, and intraspecific and interspecific competition in fruit partitioning for spider monkeys. For example, on Barro Colorado Island, Panama, because intraspecific and interspecific competition is reduced for spider monkeys, they are able to range over the entire island choosing preferred fruit rather than being limited by fruit availability [Russo et al., 2005]. Therefore, while ecological niche divergence allows primates to live in sympatry, there are other factors, such as food preference, that may contribute to evolutionary divergence between niches. Not all primate species have the same nutritional requirements or expend the same amount of energy in

obtaining preferred foods. This is due to the different energetic constraints and foraging strategies of the species, which is often determined by anatomical and physiological differences between them [Pavelka & Knopff, 2004]. Since the genus *Alouatta* is generally folivorous with food not traditionally believed to be found in monopolizable patches, contest competition for a food source is not predicted to characterize the genus' feeding ecology [van Schaik, 1989; Zucker & Clarke, 1998b]. However, other authors have questioned whether this is an oversimplification based on a lack of understanding of folivore ecology [Snaith & Chapman, 2007]. Evidence exists for selective use of clumped food resources by howlers [Chapman, 1988b]. In fact the distribution of food resources for howling monkeys did not differ significantly from the food distribution of capuchins or spider monkeys [Chapman, 1988b]. Chapman [1988b] did find, however, that howling monkeys were less selective than capuchins or spider monkeys in choosing which food resources to exploit. Species within the genus *Alouatta* expend less energy in an apparent compensation for reduced nutrient intake [Milton, 1980]. In addition, they possess an enlarged gut to better process the foliage in their diet [Milton, 1980]. As a result of this reliance on diminished energy expenditure, any factor that increases energy output for resource exploitation should greatly increase competition for those foods [Pavelka & Knopff, 2004]. Conversely, spider monkeys and capuchins expend more energy in obtaining higher energy food sources and stand to lose more when they do not find preferred food sources [Chapman 1987].

Although fruit composes a relatively small portion of the diet, for some primates such as howling monkeys, fruiting trees are often the site of agonistic interspecific interactions [Rose et al., 2003; Stevenson et al., 2003]. However, not all interactions involving food resources are negative. Large fruiting trees, such as *Ficus*, *Brosimum*, and

palms are often the site of affiliative or seemingly neutral interspecific interactions, as the species are drawn together by the food source [Rose et al., 2003; Kinzey, 1986]. In the case of introducing mantled howling monkeys to a small island already inhabited by Panamanian tamarins (*Saguinus geoffroyi*), the two species were drawn together by common resources. No aggression was noted during interactions between the two groups while using the same resources [Rasmussen and Broekma, 2003]. Spider monkeys and capuchins have also been observed feeding simultaneously from the same tree with little aggression [Rose et al., 2003]. Though competition does exist over limited resources, primate species do not always interact with aggression toward competing species.

Three primate species coexist in northern Costa Rica: mantled howling monkeys, white-faced capuchins, and black-handed spider monkeys. Competition, though present between the three primate species, does not always seem to account for the agonistic or aggressive interspecific interactions that take place. In such cases, one must look at the relative dominance of the species involved [Rose et al., 2003]. In studies involving howling monkeys and capuchins, *Cebus* is invariably dominant, usually causing howling monkeys to leave feeding trees or the area in which the capuchins are traveling. This is surprising due to the relatively low level of dietary overlap (5% at Santa Rosa) between the species as well as the larger body size of the howling monkeys [Rose et al., 2003; Moynihan, 1976]. Though *Ateles* are generally considered dominant to *Cebus* due to their size, capuchins will occasionally use numbers to their advantage to chase away the larger spider monkeys [Rose et al., 2003]. *Cebus*, as a genus, tends to be ecologically dominant to other primate species. Even when traveling in polyspecific groups with *Saimiri*, *Cebus* was observed to take the lead in deciding where and how long to forage [Terborgh, 1983]. Capuchins are smaller

than several other New World primate species, yet they tend to assert social and ecological dominance over other species. This may be due to a species-specific temperament or a socially learned behavior, which may be adaptive for the capuchins' highly opportunistic foraging strategy, active hunting, and predator defense [Rose et al., 2003].

Arboreal, fruit-eating, New World primates are often in competition for the same resources needed to survive. Seasonality of the forest, and the fruit scarcity that results, increases dietary overlap, which then increases competition for the limited fruit supply. It is in these times, when the competition is greatest, that niche divergence and fallback foods become most visible and most important. Though these ecological factors shape the behaviors that we see in different primate species, they also shape the interspecific interactions that occur during times of fruit scarcity and throughout the year. Other adaptive strategies, such as ecological dominance, species-specific temperaments, and dietary preferences may also contribute to the types of interactions observed between Platyrrhines.

Intraspecific intergroup interactions

Intraspecific intergroup interactions vary greatly based on species, with some species defending set territories and others defending resources (as is hypothesized for howling monkeys) [Sekulic, 1982; Sugiura et al., 2000]. Brown [1964] used the idea of economic defendability to explain the variation seen between species and groups in intergroup interactions. This economy refers to the relative profitability of defending a resource [Brown, 1964]. If the profit that is to be gained through an agonistic intergroup interaction is greater than the costs that may be incurred through injury, energy expenditure, or resource loss, then it is economical to act agonistically toward neighboring groups. This means that

for each group, the economic defendability will vary based on how much they have to gain or lose by an agonistic interaction [Sugiura et al., 2000]

In a study of two Japanese macaque (*Macaca fuscata*) Sugiura and colleagues [2000], found that groups in different areas reacted variously in intergroup encounters. In one population, those in Yakushima, intergroup interactions were more likely to result in group displacement, agonism, and a clear intergroup dominance. In the Kinkazan group, intergroup interactions did not often result in group displacement, agonism was likewise rare, and no clear dominance hierarchy was visible [Sugiura et al., 2000]. According to the authors, the observed differences between the groups were results of a higher population density and traveling speed for those groups in Yakushima, which the authors then link to differences in ecology between the areas [Sugiura et al., 2000]. Those macaques that lived in Yakushima were reliant on more clumped resources than the macaques in Kinkazan. Resource defense, regarding clumped food sources may lead to greater levels of competition for those resources. Mate defense may also play a part in the more aggressive interactions at Yakushima due to the instance of intergroup mating on this island, whereas it is not observed on Kinkazan. Though those macaque groups that live on Yakushima did not hold or defend territories, they did defend vital resources through agonistic interactions with neighboring groups.

Certain primate species exhibit very low rates of intergroup encounters and have been shown to take much effort to avoid neighboring groups, even in cases of nearly complete home range overlap [Cashner, 1972; Waser, 1976]. During more than 14 months of studying grey-cheeked mangabeys (*Cercocebus albigena*), whose home ranges overlapped in many cases by approximately 70%, Waser [1976] observed only three close-

proximity intergroup interactions. He attributed this to purposeful avoidance on the part of the mangabey groups, hypothesizing that the benefits of agonistic interaction over any single area of resource would not be outweighed by the costs incurred [Waser, 1976].

Resource availability and distribution greatly affect the carrying capacity of a location and amount and type of competition exhibited by dependent species. In a study of banded mongoose (*Mungos mungo*) in Uganda the authors found that those groups that were dependent on refuse piles as a major food source had more concentrated home ranges and had larger and denser group sizes [Gilchrist & Otali, 2002]. In one case, two groups had home ranges that included the same refuse pile, these two groups interacted with a significantly greater frequency, always at the refuse pile, and often with high levels of aggression [Gilchrist & Otali, 2002]. For the mongooses, the cost of highly aggressive intergroup interactions was outweighed by the guarantee of abundant food that was offered by the refuse pile.

Intraspecific intergroup interactions are a balance of costs and benefits. For some groups, the benefit that may be gained through an agonistic interaction is greater than the possible losses. However, in some cases these losses may be great, resulting in loss of food sources, mates, individual health or fitness, and in some cases intergroup interactions may lead to a loss of life.

Intraspecific intergroup interactions in howling monkeys

Group size and group dynamics among primates are determined by equilibrium between selective pressures. Predation risk must be balanced with the ability to obtain and cooperatively defend resources, such as food and mates [Knopff & Pavelka, 2006]. Group

size is associated with both costs and benefits. For example, a large group size could help defend against predators by adding more eyes to spot an approaching predator or by increasing the chance that each individual will survive a predator attack [Hart & Sussman, 2005, Isbell, 2004]. At the same time, large group size can result in increased intragroup feeding competition [Knopff & Pavelka, 2006]. The factors that are commonly believed to limit group size in *Alouatta* include the quantity and quality of food available in a given habitat, species-specific energy requirements, reproductive success, and social factors such as infanticide by males [Ryan et al., 2008; Treves, 2001]. The ecological constraints that limit group size, as well as the number of sympatric primate species in an area, also limit the number of conspecific groups that are able to exist in a given area.

Competition for food resources within the group exists both directly (contest competition) and indirectly (scramble competition). The same is true between groups of the same species as well as groups of different species [Janson & van Schaik, 1986]. Direct or contest competition occurs when food resources can be monopolized and usually results in the formation of social hierarchies. Indirect competition between groups refers to the common use of a food resource by all the groups in a specific area, and does not result in direct social competition [Janson & van Schaik, 1986]. It is generally assumed that more frugivorous species will more often display behavior consistent with contest competition, while folivorous species, such as howling monkeys will more often experience scramble competition [Janson & van Schaik, 1986]. However, in *A. palliata*, females show a linear dominance within each group that is consistent with the model of a contest competition system [Neville et al., 1988; Zucker & Clarke, 1998].

Within the genus *Alouatta*, the impact of the ecological constraints of limited resource availability can interface with social factors, which may account for the variation from the expected scramble competition in this mostly folivorous genus. Knopff and Pavelka [2006] explored the importance of ecological constraints on *Alouatta pigra* (Belizean black howling monkeys) at Monkey River in Belize using group size as the variable of interest. Black howling monkeys have relatively small group sizes of about 10 individuals, usually including only one adult male. To explain the small group size in *A. pigra*, the researchers looked to feeding competition as a possible limitation. However, they did not find evidence to support this hypothesis [Knopff & Pavelka, 2006]. Because *Alouatta* is considered an energy-conserving genus, food availability is not seen as a limiting factor for the group size in *A. pigra*. This was substantiated through analyses on the daily path length and activity budget of the focal groups. Knopff and Pavelka [2006] then turn to other explanations for group size in howling monkeys, such as competition for mates, and risk of infanticide. Chapman and Pavelka [2005] used the apparently reduced risk of infanticide in *A. palliata* to explain the difference in group size between *A. palliata* and *A. pigra*. Yet instances of infanticide are not unheard of in *A. palliata*, though they are rarer than in other species of howling monkeys [Clarke, 1983]. As a result of the apparent rarity of infanticide in *A. palliata*, ecological constraints may be a better predictor of group size than social factors for the species.

The genus *Alouatta* is characterized by loud vocalizations called howling. Since *Alouatta* species show specialized anatomical adaptations for calling, such as an enlarged hyoid bone that acts as a resonating chamber [Kelemen & Sade, 1960], and expend energy on this activity, when much of their actions are consistent with energy-minimization [Milton

et al., 1979], howling is hypothesized to play an important role in intergroup relations [Palacios, 2000; Crockett & Janson 1993: *A. seniculus*; Kitchen, 2006: *A. pigra*; Clarke, 1983: *A. palliata*]. Within *A. palliata*, howling has been hypothesized to allow mutual avoidance between neighboring troops and to allow for defense of heavily used resources [Whitehead, 1989; da Cunha & Byrne, 2006]. Because howling is an easily observed interaction between howling monkey groups, it has often been used as a tool for analyzing relations between neighboring groups of howlers.

da Cunha and Byrne [2006] tested the function of howling in black and gold howling monkeys (*Alouatta caraya*) by playing back howls of stranger groups at different points within the home range of a study group. According to this study, close proximity encounters always elicited a howling response from the study group. When the playback of the howl was at the edge of the study group's home range, the focal group did not always respond to the stranger group's howl. However, in heavily used areas of the home range or more central locations within the home range, the intruders' howls more commonly resulted in a counter-howl. The results of this study were consistent with howling as a tool for advertising occupancy of an area by a group, as well as reinforcing occupancy and demonstrating the troop's ability to defend resources during an intergroup encounter. In this way, the howling monkey groups were able to settle disputes without physical fights. This conclusion has also been supported in *Alouatta seniculus* [Sekulic & Chivers, 1986] in an earlier study and in *Alouatta palliata* located in an anthropogenically altered landscape in the Guanacaste province of Costa Rica [Whitehead, 1989]. However, other factors elicit howling monkey long calls. Monkeys howl in the morning in what is termed the dawn

chorus at times of inclement weather, and at times of disturbance [da Cunha & Byrne, 2006; Sekulic & Chivers, 1986].

The results in the study by da Cunha and Byrne [2006], suggest that howling monkeys use howling vocalizations to compete with other groups at a distance. Howling is hypothesized to advertise a willingness to defend resources, such as females, that are not spatially fixed. This raises questions about the function of howling in *A. palliata*. In both *A. caraya* and *A. seniculus*, data suggest that howling is in part an exercise that protects access to females [Sekulic & Chivers, 1986; da Cunha & Byrne, 2006]. *A. palliata* troops, however, contain more males than the aforementioned species, resulting in intra-group competition for females being more important than intergroup competition. According to a comparison of *A. seniculus* and *A. palliata* by Sekulic and Chivers [1986], *A. palliata* groups howl less frequently than *A. seniculus* because males are able to assess the strength of their main competition (the other males in the group) through means other than howling.

Forest fragmentation in Costa Rica

Fragmentation and deforestation define many of the landscapes throughout the world. With only 3.7% of the world's land preserved in national forests and reserves, anthropogenic alteration affects the great majority of primate habitat throughout the world [Onderdonk & Chapman, 2000]. Deforestation, fragmentation of remaining forest, and resulting habitat loss for wildlife have become of great concern for conservationists. The rising human population and increased need for cleared land for food production and living space have further encouraged the growing trend toward deforestation and fragmentation [Onderdonk & Chapman, 2000; Sanchez-Azofeifa et al., 2001].

Costa Rica has gained a reputation as one of the world's leaders in conservation. The government has set aside nearly a quarter of the land for preservation, and much of the nation's revenue comes through ecotourism. Yet, forest fragmentation, logging, and deforestation have claimed much of the land that was once suitable habitat for primate and other species in Costa Rica. During the period from 1976-1980, deforestation occurred in Costa Rica at a rate of 3.2% per year, and in 1986-1991 deforestation increased to a rate of 4.2% per year [Sanchez-Azofeifa et al., 2001]. According to an aerial study conducted by Sanchez-Azofeifa and colleagues [2001] deforestation continues at a rate of approximately 4.2% per year with around 70% of the remaining forest occurring in unprotected areas. Not only did this study find a continuing high rate of deforestation in Costa Rica, but the authors also determined that up to 5.5% of the remaining forest is composed of tiny fragments of forest of 0.03-0.05 km², which is an area too small to preserve most vertebrate species.

As a nation that contains 4-5% of the world's plant and bird species and one of the world's hotspots of biodiversity, Costa Rica is a crucial site for conservation [Sanchez-Azofeifa et al., 2001]. Because Costa Rica contains four species of primates, two of which are listed by the IUCN red list as endangered (*Saimri oerstedii* and *Ateles geoffroyi*), it is important for primatologists and conservationists to gain a greater grasp of how to preserve biodiversity within this Central American nation. Much of the remaining forest is broken into fragments through agricultural practices causing unique patterns of native and introduced agricultural plants. Onderdonk and Chapman [2000] predict that this pattern is likely to increase with continuing population growth. They state that researchers should focus their attention on distinguishing which species are most at risk of extinction due to forest fragmentation and what types of fragments can best support continued biodiversity.

Effect of deforestation on primate communities

Deforestation and fragmentation change the composition of remaining forest. In Central America, a once-continuous swathe of forest has become a patchwork of primary forest, secondary and regenerating forest, cropland, pastureland, and land set aside for human habitation. Anthropogenically disturbed forest differs in composition from the undisturbed forest in the amount of secondary growth plants and in the increase in edge effects. Many factors decide the suitability of the fragmented landscape for primate species, so it is difficult to generalize on the necessary composition of a fragment or the ability of certain species to exist within these altered landscapes [Onderdonk & Chapman, 2000; Fleagle & Reed, 1996].

Over the last few decades, the myth of the primary, undisturbed forest has been debunked through paleoecological studies of so-called pristine forests [Whitmore, 1991; Chazdon, 2003; Bush & Colinvaux, 1994]. This means that nearly all forests are in some stage of regeneration due to human disturbance, even those forests that are traditionally referred to as primary forests [Chazdon, 2003]. Though in some cases human disturbance can result in a loss of species diversity and slower forest regeneration, certain types of human or natural disturbance may result in only short-lived effects or these areas may be able to sustain wildlife population in spite of the disturbance [Daily et al., 2003; Chazdon, 2003]. The impact of the disturbance depends on the extent of soil degradation and remaining vegetation [Chazdon, 2003]. Human disturbance to a landscape can take many forms and impact the environment and the wildlife to varying degrees. Selective logging has been shown to be a sustainable practice that does not seem to have as much negative

impact on the forest [Webb and Peralta, 1998; Webb, 1997; Webb 1998]. Agricultural matrices can in some cases allow for high species diversity, particularly when situated next to a patch of remnant forest [Daily et al., 2003, Muñoz et al. 2006]. In other cases, human disturbance for agricultural purposes results in loss of all native species and degradation of the soil [Chazdon, 2003]. In situations where soil has been severely degraded, human assistance may be required for forest regeneration to begin [Chazdon, 2003]. Areas of clear-cut logging and human habitation may favor edge species but would be unsuitable for arboreal mammals that require large areas of land [McIntyre & Hobbs, 1999]. So, though not all areas of human disturbance preclude wildlife habitation, the matrix between forest patches cannot sustain or provide suitable habitat for primate populations.

Within altered landscapes, food availability is dependent on the size of the fragment, the composition of the remaining trees and other plants, and the seasonality of the region [Kay et al., 1997; Cristobal-Azkarate et al., 2004]. Some fragments are too small or isolated in an agricultural matrix to sustain populations of primates, yet not all larger fragments are able to sustain primates [Onderdonk & Chapman, 2000]. The ability to sustain primates is often dependent on the available food resources within the forest fragment. Studies have also shown a positive correlation between the size of the fragment and the primate abundance within that fragment, showing that larger fragments generally have greater carrying capacities [Arroyo-Rodriguez & Mandujano, 2006].

Forest composition and structure in fragments is often altered, with fewer large trees and, as a result, fewer available food resources for primates dependent on those species [Arroyo-Rodriguez & Mandujano, 2006; Onderdonk & Chapman, 2000].

Anthropogenically-altered forest is composed of a greater percentage of secondary growth

trees, whose leaves can contain high concentrations of toxic compounds. However, the new leaves of these same plants are highly nutritional and can provide increased protein and digestibility for primates dependent on these resources [Arroyo-Rodriguez & Mandujano, 2006]. In addition, some of these secondary growth trees compose an important part of primate diets even within primary forests. For example *Cecropia obtusifolia* is considered a secondary growth plant; however parts of this plant compose part *A. palliata*'s diet in studies conducted in continuous and primary forest [Arroyo-Rodriguez & Mandujano, 2006; pers. obs.]. So generalizations of reduced food availability in altered forest landscapes cannot always explain observed behaviors or demographics.

A study by Kay and colleagues [1997] failed to support the hypotheses that alpha diversity of plants, or the number of species present in an area, represents the most important factor in determining primate species abundance, as other studies had claimed. Instead, the authors found that the historical biogeography and productivity of an area were better indicators of local primate richness in the Neotropics. Citing the importance of seasonality, behavioral flexibility, and reliance on fallback foods, the authors deny that a direct relationship exists between plant and primate species richness in the Neotropics. They do, however, explain the importance of historical biogeography, such as seasonality and continuity of habitat type over a geographical area, as an important part of local primate richness [Kay et al., 1997]. Plant productivity is cited as the most important aspect of primate richness in the study [Kay et al., 1997]. Within their definition of plant productivity is a discussion of fruit production by the plants in that area. Thus, according to the findings of this study, it is not as important that there be a wide variety of plant species

available, but rather the right variety of productive plant species to encourage primate richness.

Effects of deforestation on Costa Rican primate species

The effects of fragmentation and deforestation are not consistent across primate species, nor are they consistent from study to study [Onderdonk & Chapman, 2000; Zaldivar et al., 2004]. Dietary flexibility and home range size are two interrelated factors that may influence the ability of a primate species to live in forest fragments. Species that require large home ranges or have highly frugivorous diets, are commonly thought to suffer declines in forest fragments, but this has not always held true [Onderdonk & Chapman 2000; Tutin et al., 1997]. The ability to travel between fragments, as well as dietary and behavioral plasticity, may allow species with normally large home ranges to thrive in forest fragments [Onderdonk & Chapman, 2000].

Primate life history may be linked to how primate species are influenced by habitat fragmentation. Reproductive rate may affect how well a species is able to thrive in secondary forests and fragmented forests. *A. palliata* and *C. capucinus* have much higher reproductive rates than *A. Geoffroyi*, thus they repopulate disturbed areas more quickly and are at a lower risk for extinction than spider monkeys. *A. Geoffroyi* are present in areas of large continuous forest but seldom present in protected areas of smaller size [Zaldivar et al., 2004; Fedigan & Jack, 2001]. Fedigan and Jack [2001] hypothesized that in Santa Rosa, howling monkey populations grew faster than capuchin populations in regenerating forest due to their faster paced life history.

Dietary flexibility may be a key component of survival within human-altered landscapes. Terborgh and van Schaik [1987] argued that the relatively small body size and limited folivory in New World monkeys is due to the seasonality of the regions they inhabit. This seasonal variation in resource availability has caused primate species living in the Neotropics to display dietary and behavioral flexibility to survive from season to season [Fleagle & Reed, 1996]. Such flexibility may allow these same primate species to survive in altered habitats with limited food resources. Another important factor affecting the persistence of a species in areas of deforestation and fragmentation is geographic distribution of a species. For primate species, adaptability to many habitats and high population sizes in those habitats are correlated with a lower risk of extinction for that species [Zaldivar et al., 2004].

Forest fragmentation is said to limit the amount of genetic diversity in primate populations by allowing less dispersal between populations. In theory, the lower the genetic diversity of a species, the greater the effect of inbreeding depression resulting in a smaller chance of survival for that species. This idea has been shown through numerous captive and wild populations in a wide variety of species, including several primate species [Pusey & Wolf, 1996]. Though this is an accepted idea, genetic diversity and survival rate in these primates do not show a clear correlation in practice. Zaldivar et al. [2004] found that there was no correlation between the risk of extinction and a lack of genetic diversity. They found that *A. palliata* and *C. capucinus* showed very low levels of genetic diversity in Costa Rica compared with *A. geoffroyi*, yet these two species are faring much better than *A. geoffroyi* in numbers throughout Central America [Zaldivar et al., 2004]. Though the authors offer no explanation as to why the lack of genetic diversity has not been deleterious for *A. palliata*

and *C. capucinus*, they say that geographic distribution and life history traits may be more important factors on which to focus for conservation [Zaldivar et al., 2004].

White-faced capuchins and mantled howling monkeys have each been cited as species that are commonly found in fragmented and regenerating forests in Costa Rica [Fedigan & Jack, 2001]. At Santa Rosa National Park in northwestern Costa Rica, Fedigan and Jack [2001] compared the return of howling monkeys to that of capuchins into a regenerating pasture. During a previous study in this area, the authors found that the density of primates was greater in the primary forest. But as the regenerating forest became older, primates repopulated the area in a predictable manner [Sorensen & Fedigan, 2000]. Capuchins were the first to move back into the secondary forest, returning when the forest was 14-25 years old. Once reestablished, capuchin populations continued to grow, increasing the size of existing groups within the area. Fedigan and Jack [2001] believed that capuchins, though increasing in population density with the age of the forest, were limited by their need to drink from waterholes during the dry season in Santa Rosa. Though capuchins were living in the secondary forest, the authors established that the capuchin population, as well as the howling monkey population, were positively associated with forest age, and estimated that the maximum density of monkey population occurs in forests that are 150-180 years or older [Fedigan & Jack, 2001; Sorensen & Fedigan, 2000].

In studies conducted by Sorensen and Fedigan [2000] and Fedigan and Jack [2001], howling monkeys in Santa Rosa returned to regenerating forest when the forest reached an age of 30-60 years. Unlike the capuchins in the area, the increasing howling monkey population did not lead to larger groups, but to more groups. When the howling monkey population reentered the secondary forest, the population grew faster than the capuchin

population. This was attributed to the faster life-history of howling monkeys when compared to capuchins [Also seen in Clarke et al., 2002 and Arroyo-Rodriguez & Mandujano, 2006]. According to the authors of this study, howling monkey populations in regenerating forests were limited by their preference for larger trees [Fedigan & Jack, 2001], yet other studies have shown the resilience and plasticity of the genus *Alouatta* even in highly disturbed and fragmented forests [Clarke et al., 2002; Serio-Silva & Rico-Gray, 2002; Muñoz et al., 2006].

Though *A. palliata* seem to do well in disturbed habitats, a study of mantled howling monkeys at Hacienda La Pacifica in northwest Costa Rica showed that individuals living in severely degraded habitats showed decreased chest circumference compared to those living in more intact forest [Jones, 2003]. The diminished size of these monkeys was attributed to the diminished resource availability in the degraded habitat [Jones 2003]. The author speculated that this may be an energy-minimizing and resource-use maximizing response to the highly degraded habitat [Jones 2003].

Many studies on primates in disturbed habitats emphasize the purported decrease in resource availability between primary forest sites and secondary forest areas [e.g. Fedigan & Jack, 2001; Sorensen & Fedigan, 2000; Onderdonk & Chapman, 2000; Zaldivar et al., 2004]. At El Zota Biological Field Station (EZBFS), Lindshield [2006] found that primate species, and particularly *Ateles geoffroyi* were, on average, just as numerous in the disturbed forest as in the primary forest areas. Lindshield [2006] offers several explanations for why this might be the case including similarity in habitat type between the disturbed and undisturbed forest at EZBFS and the even distribution of keystone species such as *Ficus* and palm species throughout both areas. When comparing the varying habitat types found at

EZBFS, Lindshield [2006] found that both disturbed and undisturbed areas were capable of supporting spider monkey populations due to the similar fruit abundance in the different habitat types. Spider monkeys, being the most frugivorous of the three primate species found at EZBFS are a good indicator of the ability of the other two species to persist in each environment.

Howling monkey behavioral changes due to fragmentation

Through behavioral and dietary flexibility, *Alouatta* seem to be able to cope, better than other genera with the challenges presented by decreased resource availability and increased fragmentation of habitat. Clarke and colleagues [2002] looked at the population of howling monkeys in Hacienda La Pacifica, Costa Rica over a 16 year period. During this time, deforestation occurred for agricultural purposes, fragmenting the landscape and affecting howling monkey populations. Clarke et al. looked at a population of *A. palliata* before (1984-2000), during (1991-1993), and after (1994-2000) deforestation. In their comparison, they focused on daily activity, social interactions, travel patterns, foraging patterns, and group composition. During this time, the authors found that the howling monkeys displayed great behavioral plasticity and were able to conform to the challenges of their new home range.

Following deforestation at Hacienda La Pacifica, Clarke et al. [2002] found that howling monkey group behavior showed significant short-term changes in activity patterns, rate of social interaction, and group dynamics. Immediately after the deforestation, the rate of social interaction decreased, while the length of daily travel was increased. Another study conducted in a human-modified agroecosystem showed similar changes in behavioral

patterns. Howling monkeys in this study, by Muñoz et al. [2006], increased daily distance traveled and at the same time increased dietary diversity, suggesting a decline in dietary quality and an active search for new food sources. This same study by Muñoz et al. [2006] showed a decrease in travel distance, when the howling monkeys were more reliant on mature leaves, a food source with less nutritional value.

Howling monkeys living in fragments are more likely to display atypical behaviors such as traveling and foraging terrestrially and feeding on small plants reachable only by hanging by their tails from low tree branches [Clarke et al. 2002]. In the study by Clarke and colleagues [Clarke et al., 2002], females with infants were less likely to engage in these risky behaviors, although infant mortality increased during this time. Clarke et al.'s [2002] observations of more terrestrial movement by mantled howling monkeys living in forest fragments coincide with those noted in black howling monkeys (*A. pigra*) in Mexico by Pozo-Montuy and Serio-Silva [2007]. Pozo-Montuy and Serio-Silva [2007] also observed increased predation on howling monkeys foraging and traveling on the ground between fragments.

Over the long term, the mantled howling monkeys in Clarke et al.'s [2002] study showed increased path length in finding new resources, though not beyond what could be expected in times of fruit scarcity. Group size decreased over time, with fewer migrations into the group. The authors believe that this is likely a direct result of deforestation, disturbed migration routes, or some other environmental disturbance. These changes indicate diminished resource availability. The behaviors seen in this group of howling monkeys, shows the flexibility of *A. palliata* yet leave questions about the long-term sustainability of populations in such fragmented areas [Clarke et al., 2002].

Serio-Silva and Rico-Gray [2002] observed mantled howling monkeys in disturbed and preserved habitats and found that the groups in each area varied in their behaviors. In the preserved habitat, the howling monkeys had larger home ranges (around 75 ha) and occurred at lower densities. However, the howling monkeys in the disturbed forest had smaller home ranges of around 10 ha. According to these authors, the encounters between the troops in the preserved site were rare, whereas in the disturbed forest, troops exhibited continuous agonistic vocalizations [Serio-Silva & Rico-Gray, 2002]. The increased competition for limited resources within the disturbed forest is believed to have caused a change in the behavior of the individual groups as well as a change in the interaction between those groups.

Fragmentation and deforestation are testing the limits of survival in Neotropical primate species. The behavioral and dietary plasticity of these species have allowed species such as howling monkeys and capuchins to adapt to the reduced availability of resources. However, it is uncertain whether their flexibility can allow populations to exist in habitats that are continually diminishing and fragmenting.

CHAPTER 2: METHODS

Study site

The study was conducted at El Zota Biological Field Station (10°57.6'N, 83°75.9'W) in northeastern Costa Rica from May through August of 2008. El Zota Biological Field Station (EZBFS) is a privately owned field site established in 2001 as a result of collaboration of Hiner Ramirez, the land owner, Dr. Jill Pruetz of Iowa State University, Dr. Thomas LaDuke of East Stroudsburg University and is associated with DANTA: Association for Conservation of the Tropics [Pruetz & LaDuke, 2001]. EZBFS is the site for a primatology field school as well as a tropical ecology, ornithology, and various other field schools arranged through DANTA. Through the field school and the agreement with land owner Hiner Ramirez, DANTA works toward the conservation of Neotropical forests and the wildlife species therein [Pruetz & LaDuke, 2001]. In addition to land set aside for conservation purposes, EZBFS land serves as a source of income for the landowners, as well as a source of food for the researchers and the staff at EZBFS, creating a mosaic of primary and anthropogenically disturbed secondary forest areas.

The field station is located in the lowlands in what is classified as tropical lowland wet forest and swamp forest [Holdridge, 1947]. This region averages 4000 mm of rain annually [Sanford et al., 1994]. This study took place during the transition from the dry season into the wet season. EZBFS covers approximately 1000 ha. Of this area, around 700 ha are primary wet forest; the remaining land includes areas of planted native and non-native trees (approximately 270 ha) and pastures that are planted with food crops or used for horse grazing (~30 ha) [Pruetz and LaDuke, 2001]. Wildlife found in the area include important

keystone species as well as several species that are locally or globally endangered. Wildlife known to exist on the property at EZBFS include: jaguars (*Panthera onca*), South American river otter (*Lutra longicaudus*), Baird's tapirs (*Tapirus bairdii*), jaguarondis (*Puma yaguaroundi*), tayras (*Eira Barbara*), mantled howling monkeys (*Alouatta palliata*), black-handed spider monkeys (*Ateles geoffroyi*), white-faced capuchins (*Cebus capucinus*), agoutis (*Dasyprocta punctata*), great green macaws (*Ara ambiguus*), black-and-green dart frogs (*Dendrobates auratus*), fer-de-lances (*Bothrops asper*), red brocket deer (*Mazama americana*), iguana (*Iguana iguana*), and bushmasters (*Lachesis muta*) [Pruetz & LaDuke, 2001; Lindshield, 2006].

Primary forest

Approximately 700 ha at EZBFS are considered primary forest (see Figure 1), including low-lying areas of swamp forest as well as better-drained areas that are classified as wet forest. Within the primary forest areas are some areas that show evidence of selective logging within the last 50-100 years, including the area which two of the focal groups inhabit [Pruetz, pers.comm; Lindshield, pers. comm.]. This forest is not actively logged and is very rarely visited by people. Evidence still visible includes a logging road, and some cut tree stumps; however, there are few gaps visible in the canopy, so the presence of these remnants of old logging practices did not seem to limit the movement of the nonhuman primate species [pers. obs.]. Guariguata and Dupuy [1997] when studying old logging roads in forests both geographically and floristically similar to EZBFS, showed that the edges of logging roads that had been abandoned 12-17 years prior showed a high level of plant diversity though they estimated plant recovery within the road itself to be 80 years. Other

studies have shown that within swamp forest in the Atlantic lowlands of northeast Costa Rica, conservative and selective logging is consistent with biodiversity conservation and is harmful only to the most rarely found plants within the forest, particularly those found in the subcanopy [Webb and Peralta, 1998; Webb, 1997; Webb 1998]. The primary forest at EZBFS shows a greater percentage of canopy cover than the secondary forest (89.9% and 88.3% canopy cover in transects conducted in the primary forest versus 86.8% and 73.8% in the secondary forest transects) [Lindshield, 2006]. The primary forest is also characterized by an increased relative fruit biomass per hectare than the secondary forest, yet not significantly so [Lindshield, 2006].

Secondary forest

The approximately 300 ha of secondary forest, mostly found in the southern portions of the property (see Figure 1) at EZBFS is composed of a mosaic of naturally occurring swamp forest, wet forest, riverine gallery forest, native and nonnative planted trees, pasture regrowth, cleared land for human habitation, and food plants for the human inhabitants of EZBFS [Luckett et al., 2004; Lindshield, 2006]. The planted trees include the native *Hyeronima sp.* and *Carapa guianensis*. *Hyeronima* is a large forest tree with edible fruit that was eaten by the primates within this study [Luckett et al., 2004; pers. obs]. *Gmelina arborea* is the most common planted tree at EZBFS. It is a non-native, fast-growing tree that is commonly used to create paper products [Luckett et al., 2004; Lindshield, 2006; Pruetz & LaDuke, 2001]. At the time of this study, the planted trees were approximately 13 to 15 years old [Luckett et al., 2004] The two groups within this study ranged within the mosaic of anthropogenic disturbance close to the area of human habitation at the southern

side of the EZBFS property. This area was composed of seasonally inundated swamp forest, planted trees gallery forest and plantation [Lindshield, 2006; Pruetz & LaDuke, 2001]. The secondary forest showed a lower fruit biomass in the gallery forest compared to the primary forest, yet the secondary forest held a greater proportion of important *A. Geoffroyi* feeding tree species [Lindshield, 2006].

Subjects

In a preliminary survey of the primate populations at El Zota, Pruetz and LaDuke [2001] estimated densities of approximately 35 howling monkeys/km², 28 spider monkeys/km², and 30 capuchins/km². A systematic study conducted by Lindshield in 2006 at EZBFS showed much lower densities of each species. Lindshield [2006] estimated the numbers of each species in both the primary and secondary forest. For *A. palliata*, Lindshield found that the average estimate for the disturbed forest was 8.5 individuals/km² and in the undisturbed forest, 8.3 individuals/km². She estimated *A. Geoffroyi* populations at 12.0 individuals/km² on average in the disturbed forest and 12.5 individuals/km² in undisturbed forest [Lindshield, 2006]. The average density of individuals between each habitat did not differ significantly. However, the population in the disturbed forest showed greater variation. These data are inconsistent with the assertion that *A. Geoffroyi* are unable to survive in disturbed forest habitats [Fedigan & Jack, 2001]. When considering *C. capucinus*, population densities were inconsistent. Yet, using the available data, the population density was estimated at 5.9 individuals/km² in disturbed forest and 6.0 individuals/km² in undisturbed habitats.

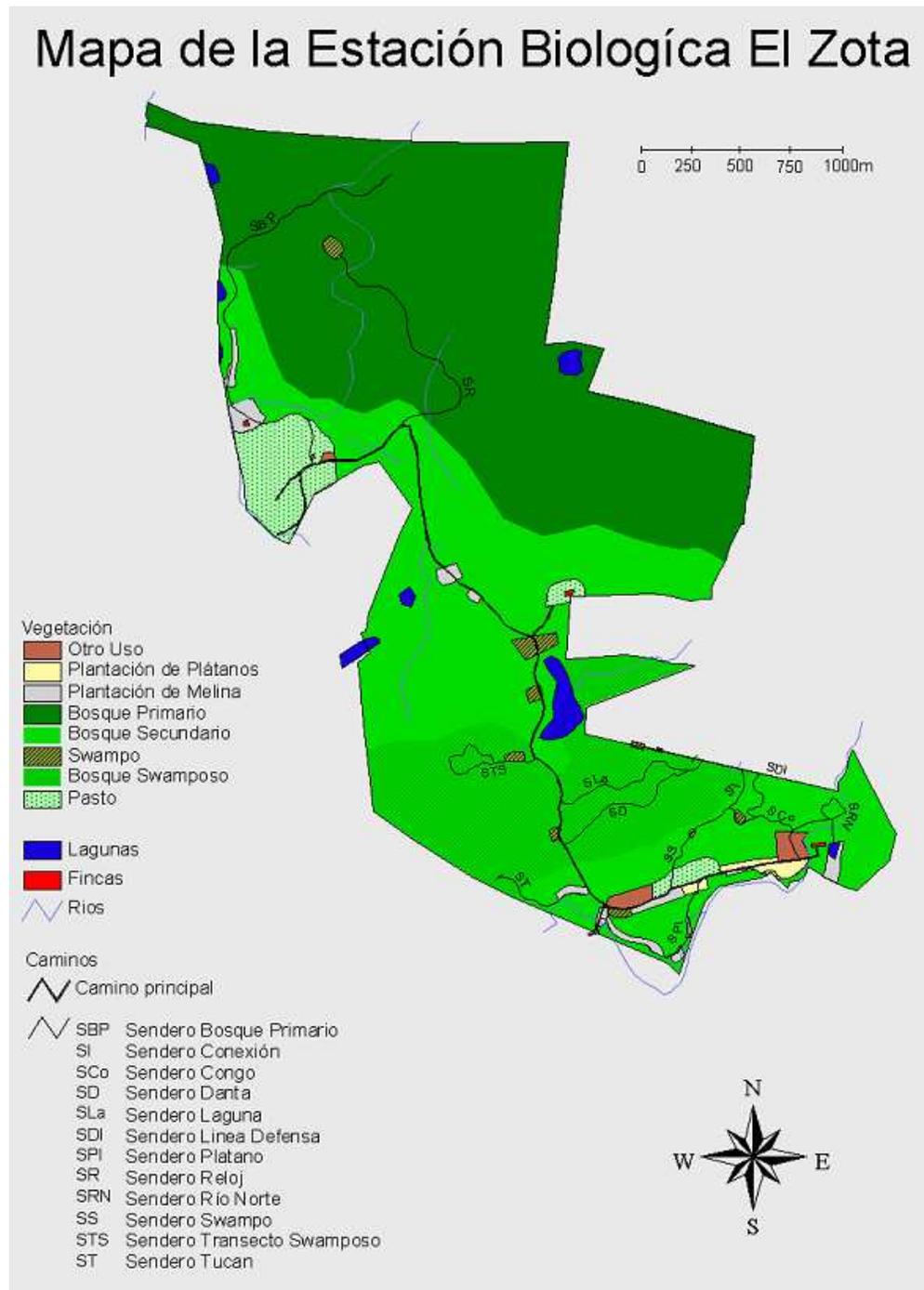


FIGURE 1: Map of EZBFS property taken from Fiebelkorn & Busse, 2005. Vegetation types are outlined by color translated as follows: “Otro uso” = other use, “Plantacion de Platanos” = plantain plantation, “Plantacion de Melina” = Plantation of *Gmelina arborea*, “Bosque Primario” = primary forest, “Bosque Secundario” = secondary forest, “Swampo” = swamp, “Bosque Swamposo” = swamp forest, “Pasto” = pasture, “Lagunas” = lakes, “Fincas” = farms, “Rios” = rivers, “Caminos” = roads, “sendero” = trail. All “senderos” here mentioned refer to the established trail system within the El Zota property, whereas the “camino” refers to a roadway that is used by cars, trucks, and occasionally cattle.

The densities of *A. palliata* for EZBFS, when compared with all the major study sites at which these species are studied, are low. Yet when compared with La Selva, one of the closest research sites to EZBFS both geographically and floristically, the howling monkey densities are consistent between sites (see table 1). La Selva is a site that has been set aside for tropical ecology research since 1956 and since that time has remained relatively undisturbed by humans. Numbers for *A. geoffroyi* and *C. capucinus* at EZBFS fall within the ranges seen at other research sites (see tables 2 and 3).

Species	Study site	Individuals/km ²	Forest type	Source
<i>A. palliata</i>	El Zota Biological Field Station, Costa Rica	8.3-8.5	tropical wet forest	[Lindshield, 2006]
<i>A. palliata</i>	Los Tuxtlas, Mexico	23	tropical wet forest	[Estrada, 1982]
<i>A. palliata</i>	La Pacifica, Costa Rica	77	tropical dry forest	[Glander, 1978]
<i>A. palliata</i>	Barro Colorado Island, Panama	92	tropical moist forest	[Milton, 1980]
<i>A. palliata</i>	La Selva, Costa Rica	7 - 15	tropical wet forest	[Stoner, 1994]
<i>A. palliata</i>	Chiriquia, Panama	1067	premontane wet forest	[Baldwin & Baldwin, 1976]
<i>A. palliata</i>	Santa Rosa, Costa Rica	7.9	tropical dry forest	[Sorenson & Fedigan, 2000]
<i>A. seniculus</i>	Lago Guri, Venezuela	800-1000	tropical dry forest	[Lopez et al. 2005]

Study site	Individuals/km ²	Forest type	Source
El Zota Biological Field Station, Costa Rica	5.9 - 6.0	tropical wet forest	[Lindshield, 2006]
Chiriquia, Panama	68 - 94	premontane wet forest	[Glander, 1978]
Santa Rosa, Costa Rica	7.5	tropical dry forest	[Sorenson & Fedigan, 2000]
Lomas Barbudal, Costa Rica	3.7	tropical dry forest	[Panger et al., 2002]
Palo Verde, Costa Rica	9.4	tropical dry forest	[Panger et al., 2002]

TABLE 3: Density of <i>A. geoffroyi</i> at select research sites			
Study site	Individuals/km²	Forest type	Source
El Zota Biological Field Station, Costa Rica	12 - 12.5	tropical wet forest	[Lindshield, 2006]
La Suerte Biological Field Station, Costa Rica	8-10.6	tropical wet forest	[Pruetz & Leason, 2002]
Hacienda Los Inocentes Reserve, Costa Rica	34.8	tropical wet forest	[McDaniel, 1994]
Santa Rosa, Costa Rica	7.9	tropical dry forest	[Sorenson & Fedigan, 2000]
Los Tuxtlas, Mexico	0.22	tropical wet forest	[Estrada & Coates-Estrada, 1996]

Four troops of howling monkeys were selected for this study: two troops inhabiting secondary forest area and two troops in the primary forest area farther away from human-disturbed areas. Mantled howlers were chosen as the focal species as they usually vocalize or howl prior to both interspecific and intergroup interactions. This behavior increased my ability to anticipate and detect interactions between howling monkey troops. Groups of similar sizes and with similar numbers of males were chosen. However due to subgrouping in one group (Group 1) an inconsistent number of males characterized groups in the secondary forest (see table 4). Within this one particular group, one male appeared to be approaching adulthood. Though he was somewhat smaller than the other two males, he did participate in howling bouts and confronted opposing troops during intergroup encounters. Within this same group, fissioning did occur at times; however, this did not happen with as much regularity as has been reported in studies at other sites [Bezanson et al., 2008]. In a study at Omotepe, Nicaragua, through two years of field study, a community of howling monkeys was only observed together one time. In the course of the current study, Group One did fission at times during the day, especially during periods of resting. When this occurred, three females and one male would often rest or feed around 50 to 100 meters from

the rest of the group. Subgrouping by Group One may be an indication of ecological and resource pressures or of social dyadic and triadic relationships as is suggested by the authors of the study based in the tropical dry forests at Omotepe, Nicaragua [Bezanson et al., 2008].

Group	Habitat	No. males	No. females	No. juveniles	No. infants
1	secondary forest	3	6	1	1
2	secondary forest	2	4		
3	primary forest	2	5	1	3
4	primary forest	2	4	1	1

Though Group One and Group Two had ranges that, in some areas, were cut off from other primate species due to clear-cut forest or swamp land, all of the groups included in this study had vocal or auditory contact with at least five conspecific groups (pers. obs. based on numbers of groups howling). Groups living in the secondary forest in some cases lived near groups that were not able to access one another's home ranges. For example Group One had at least three groups in close vocal range to the west. Yet only one of those three groups overlapped the home range of Group One. Group One and Group Two lived in close proximity to one another but were not seen to overlap home ranges during the time of this study (Figure 2). Group Two lived in an area that became inundated as the wet season began. This swamp area contained some large trees and patches of smaller trees, yet much of the area consisted of long corridors within the swamp leading to larger patches of trees. Because much of the swamp forest was cut off from other groups, most interactions between Group Two and neighboring groups occurred in the eastern and southern borders of their range. Those groups in the primary forest did not have home ranges that were limited by

forest disturbance, thus the home ranges of Groups Three and Four overlapped those of neighboring groups in every direction.



FIGURE 2. Close-up of groups in the secondary forest. The approximate home range for Group One is pictured in orange and Group Two is outlined in violet

Behavioral methods

This study included behavioral follows for four different groups of howling monkeys in two different habitat types. During group follows, I collected behavioral data on the troop throughout the day and conducted an equal number of observation days with each troop. In order to minimize the amount of time spent finding the focal groups during the research period, I stayed with each group for two days (a total of approximately sixteen hours) before moving on to the subsequent group. The order in which I observed the groups was randomized in order to try to control for the effects of the changing season.

After establishing group size and composition, including the age and sex of each member of the troop, I continued to monitor the troop composition each day with the focal group. During the period from May 30 through August 1, I conducted interval or scan samples to monitor the behavior of the focal group at 10-minute intervals throughout the day, using all-occurrence recording taken during interspecific and intraspecific interactions [Altmann, 1974]. I chose interval sampling for behavioral monitoring due to the short duration of the study and the greater time availability for detailed notes during all-occurrence events [Rose, 2000]. In order to establish a rough estimate of home range for each troop, I took note of trail markings whenever possible and marked major fruiting and food trees visited by each troop on a map of the El Zota property.

During times of interspecific and intergroup interactions, I used all-occurrence sampling, focusing on aggressive and affiliative behaviors of each group such as chasing, vocalizations, displacement, or side-by-side feeding (Table 5). I also noted the context in which the interaction occurs, whether it is in a fruiting tree, while traveling, or while one group is resting. In the case of intergroup interactions, I collected data on the number of individuals and the age/sex composition of the interacting troop, whenever possible, focusing on the number of males in the opposing groups.

Within the category of intergroup interactions, I included both long-distance reciprocated howling bouts and close proximity intergroup interactions. For analyses on howling bouts, I used only those instances in which the howling monkeys were 100 meters or more away from the group that was reciprocating the long calls. Close-proximity intergroup interactions were those in which visual and in many cases physical contact was made between members of neighboring groups within 50 meters. For this study, an

interspecific interaction was defined as any time that a sympatric primate species traveled within 50 meters of the focal howler group.

Howling data focused on intergroup interactions consistent with the hypothesis that the purpose of howling is to defend moveable resources [Sekulic & Chivers, 1986]. All instances of howling were recorded in which the troops are in close proximity and are howling in contest. The approximate distance and direction of the howl from the focal troop was recorded as well as the time spent howling and the number of males participating in the howl.

TABLE 5: Interaction behavior catalogue	
aggressive behaviors	affiliative/neutral behaviors
chasing	co-feeding
hitting	resting
grabbing	ignoring
biting	travel through
displacing individuals	play
face-to-face howling	travel together
swinging by tail while howling	
howling advancement	

This is not an exhaustive catalogue, but is a list of the behaviors used to classify interactions within the scope of this study. These classifications are based on the behaviors used in Rose et al. 2003.

In characterizing the type of interactions that took place between neighboring groups of howling monkeys in the secondary forest and those in the primary forest, I classified the interactions as either close-proximity without aggression, close proximity with close contact aggression, or close contact with male display. In using these classifications, each interaction was classified based on the presence or absence of certain close-contact aggressive behaviors such as chasing, hitting, biting, and grabbing (see Table 5 for list of

behaviors). Male display behaviors include close proximity howling, advancing toward the other group's males while howling, swinging by the tail while howling in close proximity to the neighboring males, advancing into the trees closest to the other males. Close proximity interactions without aggression may include howling from a distance without male approach, interactions in which there is no howling, no physical aggression, or interactions that include affiliative behavior. Most of these classifications are based on the behavior of the males due to the more common active interaction and display by males. Often male and female behavior within the group was not cohesive, with males showing a high level of aggressive behavior toward the neighboring group, while females rested, cofed, or played with immatures. At other times females would have some involvement in the interaction, including loud vocalizations, displaying along with males, or would be displaced by males of the neighboring groups. Due to the large number of individuals involved in an intergroup interaction and inability to differentiate between individuals in all groups (particularly females) the data are focused on the actions of the males in the group. When classifying the type of interaction between the howling monkeys and sympatric primates, similar behaviors and methods as were used for intergroup interactions were used to categorize interactions as non-aggressive, aggressive or mixed.

One area of concern as an observer of primates that are not used to seeing people on a regular basis, such as in the primary forest, is that the human presence will change the behavior of the primates under observation. Howling monkeys that do not often see humans will at times vocalize or howl at an observer or move around in a tree [pers. obs.]. Generally, these behavioral changes due to human presence are short-lived, with the howler group returning to resting, foraging, or traveling usually within a few minutes to an hour

after first being observed [pers. obs.]. However, when spider monkeys or capuchins come in contact with a human observer, especially during a short interspecies interaction, they may react more visibly through threats, displays, and vocalizations. In a prior study, Lindshield [2006] found that the spider monkeys in the primary forest at EZBFS reacted to her presence significantly more than those in the secondary forest. Reactions of spider monkeys and capuchins to an observer may be more significant to this study than the reactions of the howling monkeys, due to the much shorter duration of my contact with capuchins and spider monkeys than with the focal howling monkey groups. During occurrences of interspecies interactions in the current study, I took note of the times when my presence caused reactions such as displays, staring, dropping or shaking branches, or vocalizations directed at the observer by the capuchins or spider monkeys interacting with the howler monkeys.

Analyses

A one-way ANOVA was used to analyze the average frequency of howling bouts in the four groups. Each observed frequency was weighted by the number of hours of observation. Using a contrast, the average frequency of howling bouts in primary and secondary forests were compared. In addition to comparing the frequency of howling bouts between the two forests, I compared the duration of the howling bouts between the two forest types. I did this to determine whether significantly more energy was being spent on howling by groups in either forest type, since howling bouts observed within this study varied in length considerably (from 1 minute to 47 minutes in length). The comparative howling duration was analyzed through a one-way ANOVA of the average duration of howling bouts for each group, with the number of interactions used as the weight variable.

In order to determine whether groups in one type of forest had a significantly higher percentage of close-proximity interactions when compared with longer-distance howling bouts, I used a one-way ANOVA of percent of howling interactions for each group, weighted according to the number of hours of observation. This was to determine whether groups in either forest type were more likely to escalate an interaction from a howling bout to a close-proximity interaction.

The same ANOVA analyses as were used to determine frequency and duration of howling bouts were used to determine these results for intergroup interactions between forest types. When focusing on intergroup interactions I used a chi-squared exact test on a 2x3 table, pooling groups from the same forest to compare whether the relative frequency of aggressive, nonaggressive, and mixed reactions were the same between forest types. I also examined the number of times intergroup interactions occurred simultaneously with feeding by one or both groups of howling monkeys to assess if feeding and competition over food sources was a variable differing between groups in different forest types. I used the chi-squared exact test for independence on a 2x2 table of counts, to determine whether evidence existed for increased instance of feeding during interactions

Using the data from the instantaneous scan sampling, which I collected continuously throughout the time spent with each group, I created a time budget of the amount of time spent foraging, resting, moving, or traveling. I defined “moving” as actively changing locations within the same tree without obvious directional intent. I classified “traveling” as any movement between trees with directional intent. All activities that did not fit into the previous four categories were combined into an “other” category, which included such behaviors as play, self grooming, vigilance, vocalizing, and reproductive behaviors. I

analyzed this data using a one-way ANOVA, weighted according to the number of hours of observation and a contrast statement to compare the average amount of time spent by monkeys in each forest type on each activity.

For interspecies interactions, I used a one-way ANOVA weighted by the number of hours of observation to compare the average frequency of interactions with other species by the howling monkey groups in the primary forest and in the secondary forest. A contrast was used to compare the average frequency of interspecies interaction by groups in the primary forest to those in the secondary forest. For the duration of interspecific interaction, when analyzed using a one-way ANOVA to compare the average duration of interaction for each group with a weighted variable of the length of observation and creating a contrast to compare the average duration in the primary versus the secondary,

A chi-squared exact test on a 2x3 table, pooling groups from the same forest, was used to determine whether there was a difference by forest type in the occurrence of aggressive, non-aggressive, and mixed interspecies interactions. Again, I looked at the instance of cofeeding during interaction between primate species. I used a chi-squared exact test on a 2x2 table, pooling groups from the same forest type to see if significantly more feeding during interaction occurred in either forest type. Previous analyses have used outward, physical aggression only. However, as was seen in Rose and colleagues' [2003] study, ecological dominance and species-specific temperaments may play a part in the interactions between these species of sympatric primates. In addition to the aggressive behaviors listed above (Table 4), displacement of an individual or the entire group of howler monkeys by allospecifics is common, and presumably taxing on this energy-minimizing species, so I examined whether monkeys in either forest type showed a statistically larger

instance of individual or group displacement. I used a chi-squared exact test on a 2x2 table, pooling groups from the same forest type.

To check for the strength of my analyses due to small sample sizes, I completed post-hoc power analyses on all non-significant results using a two-sample mean power test for all ANOVA tests which used a contrast statement to determine the sample size needed to gain a power level of 0.80. For post-hoc analysis of chi-squared statistical analyses I used a two-sample proportion test to determine the sample size needed to gain a power level of 0.80. To complete the power analyses I used the program JMP 7.0.

CHAPTER 3: RESULTS

During the period from May 31 to August 1, 2008, 196.9 hours of observation were conducted between the four groups of howling monkeys. The mean amount of time spent with each group was 49.22 hours with the range of 48.01 hours with group 2 to 51.01 hours with group 3. Throughout the time of observation, 46 bouts of reciprocal howling, 11 intergroup interactions, and 39 interspecies interactions were recorded, with instances of each observed within every group.

Intergroup interactions

During the 196.9 hours spent with the 4 groups, I observed 46 instances of long-distance howling: 11 in the secondary forest and 35 in the primary forest. In cases where groups advanced within 100 meters of the focal group, or the reverse, I classified such interactions as close-proximity intergroup interactions. Eleven instances of close-proximity intergroup interactions were observed over the course of this study.

Groups in the primary forest engaged in significantly more howling bouts more than those in the secondary forest (Table 6). One outlier of 12 howling bouts in a single day (9.844 hours of observation) by group 3 occurred in the primary forest. When the outlier was removed from the data, the results remained significant ($t = -2.69$, $p = 0.0128$).

Forest type	Group	Hours of observation	Total number howling bouts	Mean number howling bouts per hour
secondary	1	49.34	7	0.8107
secondary	2	48.01	4	0.4200
primary	3	51.01	24	2.2510
primary	4	48.53	11	1.7596

There was no significant difference in the length of the howling bout between groups in different forest types ($p = 0.1847$). The data were log transformed, after which the results of the one-way ANOVA still showed a result that was not significant for a difference between the log length of howling bout between howling monkey groups living in the two forest types ($p = 0.4191$)

There was not a significant difference in the percentage of howling interactions when compared with close-proximity interactions between groups in different forest types ($p = 0.4339$, one-way ANOVA). The power analysis for this result showed that in order to reach a significant result with a power level of 0.8, a sample size of 511, or 205 for each forest type is required.

Forest type	Group	Hours of observation	Total number interactions	Mean number interactions per hour
secondary	1	49.34	1	0.0203
secondary	2	48.01	3	0.0625
primary	3	51.01	6	0.1176
primary	4	48.53	1	0.0206

Although four intergroup interactions were observed in the secondary forest as opposed to seven interactions witnessed in the primary forest, the frequency of close-proximity interactions did not differ significantly by forest type ($p = 0.3534$, table 7). The power analysis for this intergroup interaction frequency showed a sample size of 1730 would be required to reach a significant result with a power level of 0.8. Duration of the interactions did not differ by forest type either ($p = 0.2458$). The power analysis for this result showed a required sample size of 19 interactions to reach a significant result with a power level of 0.8. There was no significant difference in the number of aggressive interactions, with two interactions classified as aggressive in each forest type ($p > 0.999$, chi-squared exact test on a 2x3 table, pooling groups from the same forest). The number of non-aggressive or mixed aggressive and non-aggressive interactions did not differ significantly by forest type (see TABLE 8). In order to receive a statistically significant result for interaction type the sample size would need to be 191 interactions according to the post-hoc powers analysis.

TABLE 8: Intergroup aggressive, non-aggressive and mixed interactions					
Forest type	Group	No. of aggressive interactions	No. non-aggressive interactions	No. mixed interactions	total number interactions
secondary	1	0	0	1	1
secondary	2	2	1	0	3
primary	3	2	3	1	6
primary	4	0	0	1	1
Total		4	4	3	11

Based on instance of neighboring groups advancing within 50 meters of each other

According to a chi-squared exact test for independence on a 2x2 table of counts, there was no evidence of increased instance of feeding during or preceding encounters in one forest type when compared with another ($p = 0.5455$). The power analysis for this result showed that in order to reach a significant result with a power level of 0.8, these results would require a sample size of 74.42, or 37.21 for each forest type. Thus according to the data collected in this study, there did not appear to be any evidence of a change in the overall behavioral pattern during close proximity intergroup interactions of howling monkeys living in primary forests when compared with those living in the secondary forest.

A comparison of the amount of time spent by groups exhibiting the behaviors of resting, foraging, traveling, moving, or other was determined by a one-way ANOVA weighted by the number of hours of observation. A contrast statement was used to determine whether significant differences existed between forest types for the percentage of time spent engaging in each behavior. For foraging, groups in the secondary forest spent 17.6% of the time in this activity whereas those groups in the primary forest spent 11.9% of the time foraging. This difference was statistically significant ($p = 0.0036$). The time spent resting by monkeys in the secondary forest was also significantly higher ($p = 0.0083$), 46.2% in the secondary forest versus 35.7% in the primary forest. Moving within the same tree accounted for 13.6% of the time in the secondary forest and 16.8% of the time in the primary, which was not a statistically significant difference ($p = 0.0731$). Travelling between trees accounted for 15.7% of the time budget for the monkeys in the primary forest and 7.4% in the secondary forest. The monkeys in the primary forest spent significantly more of their time travelling than in the secondary forest ($p = 0.0019$). The monkeys in the

primary forest spent significantly more of their time engaged in “other” activities than did the monkeys in the secondary forest ($p = 0.0496$).

Interspecific interactions

Interspecies interactions were divided into those with *C. capucinus* (which only accounted for eight of the total interspecies interactions) and those with *A. geoffroyi* (which made up the remaining 37 interactions). These interactions varied greatly in length and behavioral response. In many cases, members of sympatric species just traveled through the area which the howling monkeys were occupying. However, in some cases, spider monkeys would rest in the same trees as the howler monkeys or the howling monkeys and capuchins would travel together for a distance.

In the 45 interactions, I witnessed aggressive displays toward the observer by spider monkeys or capuchins during 13 interactions (28.9%). Six, of the 13 were in the primary forest. A chi-square test of independence between forest type and presence of aggressive displays gives an exact p-value ($p = 0.4935$), indicating no evidence of association between the two variables. In these cases, interaction still took place between the howling monkeys and the other species; however, it cannot be discounted completely that the presence of a human observer may have altered the behavior of these primates. The power analysis for this result showed that in order to reach a significant result with a power level of 0.8, these results would require a sample size of 412.13 instances in which the primate behavior was visibly affected by observer behavior.

There was no significant difference in the frequency of interspecies interactions between forest types ($p = 0.1404$, see Table 9). The power analysis for this result showed

that in order to reach a significant result with a power level of 0.8, these results would require a sample size of 667.99. Though there were noticeably fewer interactions with other species by group four in the primary forest, this variation from the other groups did not create a significant difference in the frequency of interaction between the two forest types when interactions with both spider monkeys and capuchins were combined. I was not able to analyze the capuchin interactions separately from the spider monkey interactions due to the occurrence of only one interaction with capuchins in the primary forest.

The mean duration of interaction in the secondary forest for both *C. capucinus* and *A. geoffroyi* was 18.2 with the range of one to 110 minutes. In the primary forest, the mean length of interspecific interaction was 16.3 minutes (SD = 60.517) and the range was one to 118 minutes in length. There was no significant difference between the two forest types in the duration of interaction ($p = 0.7411$). The power analysis for this result showed that in order to reach a significant result with a power level of 0.8, these results would require a sample size of 1979.55.

Forest type	Group	Hours of observation	Total number interactions	Mean number interactions per hour
secondary	1	49.34	12	0.2432
secondary	2	48.01	17	0.3541
primary	3	51.01	12	0.2352
primary	4	48.53	4	0.0824

Includes information from interactions with both *A. geoffroyi* and *C. capucinus*

The majority of the interactions with capuchins (seven of eight interactions or 87.5% of the interactions) took place within the secondary forest (see Table 10). Interactions with spider monkeys are more evenly distributed with 59.5% of the interactions taking place in the secondary forest.

Forest type	Group	No. interactions with <i>C. capucinus</i>	No. interactions with <i>A. geoffroyi</i>	Total no. interactions
secondary	1	4	8	12
secondary	2	3	14	17
primary	3	1	11	12
primary	4	0	4	4
Total		8	37	45

Forest type	Group	No. of aggressive interactions	No. non-aggressive interactions	No. mixed interactions	Total no. interactions
secondary	1	0	11	1	12
secondary	2	2	11	4	17
primary	3	0	11	1	12
primary	4	0	4	0	4
Total		2	37	6	45

Includes information from interactions with both *A. geoffroyi* and *C. capucinus*

The majority of the interspecific interactions were classified as non-aggressive. Most of these interactions consisted of one or more allospecific primates traveling through the area in which the howling monkeys were resting, foraging, or traveling. There was no

significant difference between the number of aggressive, non-aggressive or mixed reactions by forest types ($p = 0.3549$, see Table 11). When a post-hoc power analysis was completed, a sample size of 178 interactions would be necessary for a statistically significant result given the observed difference between forest types. Because of the small number of interactions with capuchins in the primary forest, the types of interaction could not be broken down on a species basis. In 26 of 45 interactions (55.6%), the allospecifics foraged at some point during the period of interaction with the howling monkeys. Of these instances 20 of 26 times (76.9%) were in the secondary forest. Though the percentage of times foraging by the allospecifics took place during an interaction with howlers in the secondary forest was higher, there was not a statistically significant relationship. However, a trend did exist between forest type and the frequency of foraging during an interaction ($p = 0.0602$). A sample size of 74.32 would be required for a significant result with a power level of 0.8 according to the post-hoc power analysis.

In 18 of 45 (40%) interspecies interactions at least one howler monkey was displaced (13 of 18, or 72.2%, of the times in the secondary forest groups). There was no statistical evidence for association between the forest type and the occurrence of individual displacement ($p = 0.5271$). The power analysis for this result showed that in order to reach a significant result with a power level of 0.8, these results would require a sample size of 365.86. At times displacement was due to chasing or another form of visible aggression, but often it seemed to be a result of allospecifics passing in close-proximity. In seven of 45 interactions, the entire focal group was displaced by the arrival of the other species (two times by the arrival of capuchins, five times by the arrival of spider monkeys). Three of these instances occurred with groups in the secondary forest which does not support an

association between the forest type and group displacement ($p = 0.1310$ chi-squared exact test). The power analysis for this result showed that in order to reach a significant result with a power level of 0.8, these results would require a sample size of 130.93.

These results carry implications for the relations between neighboring groups of howling monkeys as well as the interrelations of both capuchins and spider monkeys with sympatric howling monkeys. Though these results do not follow those predictions made at the start of the research, they may reflect an unexpected state of both the forest and the primate community at EZBFS.

CHAPTER 4: DISCUSSION AND CONCLUSION

The focus of this study was to determine whether anthropogenic influences on primate habitat influence the ways in which these primates interact with one another. Deforestation, forest fragmentation, and environmental degradation, largely due to human influence, have been cited as the main factors leading to the local extirpation and endangerment of primate species within Costa Rica, and throughout the world [IUCN, 2008; Fedigan & Jack, 2001; Zaldivar et al., 2004]. Negative impacts by humans have led to a reduction in the suitable habitat for primate species, with not all species being equally affected. In Costa Rica, howling monkeys and capuchins are faring better within the disturbance mosaic than spider monkeys or squirrel monkeys [IUCN, 2008; Fedigan & Jack, 2001; Zaldivar et al., 2004], yet all primate species' populations seem to be facing a downward trend [IUCN, 2008]. With the increased pressures of human encroachment and supposed loss of resources for both food and suitable habitats, are intergroup and interspecies interactions more frequent and/or more agonistic? Does human disturbance equate with increased primate competition? This study addressed these issues by examining the intra and interspecific interactions of howling monkeys with other nonhuman primate species at El Zota Biological Field Station.

Two major assumptions made by primatologists about the dietary and habitat resource needs of wild primate species are challenged by the results of this study. The first is that the primary forest at EZBFS has not been changed through human alteration and therefore functions as a control condition, and the second assumption is that the secondary forest, as a human degraded habitat, cannot support primates as well as the primary forest.

The primary forest at EZBFS has been altered by humans in the past, yet there is no real evidence that the human alteration has negatively affected the primates living in this habitat. Similarly, the natural condition of this forest does not necessarily reflect the definition of primary forest as seen in most Costa Rican primate studies, such as those in the dry forests of the Guanacaste region [Frankie et al., 1974; Chapman 1987; Fedigan & Jack 2001]. Though it contains many large emergent trees and a fairly continuous canopy, the primary forest area at EZBFS also contains areas of seasonal inundation replete with understory and canopy-level palms (family *Palmaceae*), as well as large light gaps created through both human and natural means [Lieberman et al., 1996]. The second assumption is more relevant to the study at hand and is directly pertinent to the hypotheses being tested within this study. In the secondary forest, the degree of human alteration varies greatly, and the area consists of small patches of primary forest among fallow pasture land, swamp forest, and plantations of planted trees. The secondary forest has been altered from a pristine state by human disturbance; yet it does not follow that it is unable to adequately fill the habitat requirements for the non human primates living therein.

The hypotheses tested within this study are based on the belief that human disturbance will ultimately result in decreased resources for primate species and increased social pressure. These assumptions are challenged by the results of this study. The situation at EZBFS suggests that primates may be able to thrive in the secondary forest areas, and that the mosaic of human disturbance may, in some ways, support the primate population here.

Intergroup interactions

The intergroup interactions recorded in this study included both long-distance reciprocal bouts of calling by neighboring howling monkey groups as well as close proximity interactions where monkeys from neighboring groups approached within less than a meter from one another. Howling bouts ranged from instances when a group from 500 to 600 meters away howled and elicited a single howl as a response to times when all males in the group were howling from 200 meters distance for 42 minutes. The close-proximity interactions ranged from a more vigorous and closer howling bout, with little aggression or contact, to a 115 minute interaction involving all group members and resulting in an aggressive chase that caused a subadult male to fall out of the tree. Each interaction varied in time, energy expenditure, and level of aggression; yet all interactions may help maintain or challenge the social and ecological stability of each group. Each interaction has the potential to result in an overthrow of social hierarchy or a loss of important resources if the group does not present a united front [Sekulic & Chivers, 1986; Chiarello, 1995; Kitchen, 2004; Whitehead, 1989; da Cunha & Byrne, 2006].

Forest type

Howling monkey groups in the secondary forest did not show any significant difference in the frequency of interaction when compared with those groups that live in the primary forest. In fact, those in the secondary forest howled significantly less often than those groups in the primary forest. Additionally, no significant difference existed in the frequency or type of intergroup interaction between the two forests. The post-hoc power analyses show that with the given amount of variation observed between the forest types, the

sample sizes were too small, in most cases, to give statistically significant results. This is true to varying degrees for each test. For example, the results for the frequency of intergroup close-proximity interactions would require a much larger sample size of up to 1730 days of observation to achieve a significant result given the observed variation in frequency between forest types. However, for the duration of close proximity interactions, only 8 more interactions would be required to achieve a significant result at the observed variation. This suggests that the variation seen between the forest types is greater for the duration of interaction than for the frequency of interaction. Given larger sample sizes, a difference may have been observed for howling and intergroup close-proximity interactions. The duration of interaction was the only test for which the power statistics gave a result that was close to the observed sample size, indicating that the other results are not merely a product of the small sample size. These results raise several questions about the focal groups and the forests in which these groups live. Why do we see more howling in the primary forest than in the secondary forest? Why do we see a lack of difference in the way groups react to neighboring groups when they are presumably living in such different habitats with different ecological pressures shaping their behavioral responses? These questions involve multiple factors that could be further explored.

The primary reason that the frequency of interaction between howling monkey troops was expected to be greater in the secondary forest was the assumption that anthropogenically disturbed forest offers fewer resources for primates living therein. This assumption is prevalent among conservationists [for example: Arroyo-Rodriguez et al., 2007; Daily et al., 2003; Pozo-Montuy & Serio-Silva, 2007; Onderdonk & Chapman, 2000]. Additionally, forest disturbance in the form of deforestation, habitat loss, and forest

fragmentation is cited as the most influential reason for the endangered classification of *A. geoffroyi* and the declining populations of *A. palliata* and *C. capucinus* [IUCN, 2009]. Due to the pervasive idea that disturbed forest automatically means reduced resource availability, it is assumed that competition, especially among conspecifics living in the same disturbed area would increase when compared with those living in an undisturbed habitat, and that competition for resources used by sympatric primate species would also increase. However, the result of this study this does not support this assumption.

One possible explanation for the unexpected results of this study may be found within the influence of humans on the forest itself. At EZBFS the forest in the southern portion of the property has been greatly altered by humans. In addition to mature trees being cut down for logging, causing a decrease in available resources for primates, trees have been planted that provide food and corridors between more mature forest areas for the primate species. One example of a planted tree that has added greatly to the available resources for all primate species are the *Hyeronima sp.* These trees were in fruit during the time of this study, and all primate species were observed eating from trees of this species. In addition, banana and plantain plants (*Musa spp.*), which cover several hectares of the area near the clearing for human habitation provide food for the capuchins and occasionally spider monkeys that range in this area of disturbed forest, though howler monkeys have not been observed to feed from these plants [Lindshield, 2006; M. Rodrigues pers. com.; pers. obs.]. The addition of these human-added food resources for primate species in the disturbed forest at EZBFS may result in a higher than expected resource availability in the secondary forest. This is supported by Lindshield's [2006] work which found that spider monkeys, a highly frugivorous species dependent on the availability of fruit and usually believed to be limited

to less disturbed forest [Chapman 1987; Chapman 1988], were evenly distributed throughout the primary and secondary forest at EZBFS. This has implications for the types of interactions observed both between neighboring groups of howling monkeys and sympatric primate species.

The anthropogenically altered landscape of the secondary forest at EZBFS does not seem to increase the frequency or the type of interaction between neighboring groups of howling monkeys; yet it does appear to have changed the resources on which these primates are relying for food (pers. obs.). Future studies should focus on the differences in resource use between the primary and secondary forest as well as on the relative distribution of these sources. Due to the large, nearly monoculture stands of planted trees in areas of the secondary forest, howling monkey groups were able to easily find food sources when those trees were in fruit. Though traditionally tree species, and consequently, food sources are said to be more evenly spread throughout a group's home range within primary forest habitat [Brandani et al., 1988; Loiselle et al., 1996], clumped configurations of some fruiting trees did exist in the primary forest. Yet within the secondary forest, stands of planted trees are not found throughout the home ranges of all the howling monkeys and should therefore result in an uneven distribution of these resources for howling monkey groups. Further study of the diet of those howlers living in the secondary forest and those living in the primary forest would help to inform the owner of the land as well as those groups interested in the conservation efforts at EZBFS, such as DANTA, of the importance of these planted trees. It would also be of interest to compare the diets of the groups within the secondary forest to assess whether there are differences in diet between groups whose home ranges overlap the sections of planted trees and those who do not. The current study did not

provide an accurate view of the extent of home ranges for groups either in the primary forest or the secondary forest, nor can any statements be made about the seasonality of home range use or whether certain home range limits were guarded more closely at certain times of year. However, in the season and time range of this study, howling monkey interactions did not seem to include more agonism due to large abundant patches and introduced resources.

Seasonality should also be taken into account to determine the importance of the planted species on the intergroup interactions within the howling monkey populations in this disturbance mosaic. The timing of this study from May through August, overlapped the end of the dry season and continued through most of the wet season [Frankie et al., 1974]. This study should also be repeated at a different time of year to determine whether results would be different in a time when planted trees such as *Hyeronima sp.* were not fruiting, and other food sources would need to be substituted for *Hyeronima*. According to a study of home ranges of *Cebus apella* by Di Bitetti [2001] neighboring groups of capuchins interacted agonistically every time they came into close proximity, yet these interactions took place with greater frequency in seasons with less fruit availability. Whether the same pattern exists for howling monkeys is unknown. In the study by Di Bitetti, the climate of the site showed great seasonal variation. According to research on the fruiting phenology of wet forests on the Caribbean side of Costa Rica by Frankie et al. [1974], the time period in which the current study took place was during a season with lower fruit availability, yet the markedness of seasons within the lowland wet tropical forest is far less than that of other forest types, such as tropical dry forests where most studies of dietary overlap in Neotropical primate species have been conducted. The reduced variation in fruit and new leaf availability in the lowland wet forest of EZBFS may allow for reduced seasonal fluctuation

in competition, making the results of the current study more applicable to the entire annual cycle, yet it does not necessarily mean reduced competition overall for primates in less seasonal forests.

In addition to additional resources provided by planted trees in the area of anthropogenically disturbed forest, the presence of stands of undisturbed gallery forest and many emergent trees in the midst of the disturbance mosaic at EZBFS may have contributed to the similarity in behavior between groups in the primary and secondary forest. According to a study by Arroyo-Rodriguez and colleagues [2007], the difference between forest fragments in the Los Tuxtlas region in Mexico that can or cannot support a population of *A. palliata* is the number of large trees (with a DBH of greater than 60 cm). Even relatively small forest fragments (smaller than 10 ha²) were able to support howling monkey populations due to the presence of large trees and a diversity of species that provided food for howlers in those fragments. In areas that were formerly logged and clear-cut for pasture at EZBFS, selective emergent trees have been left. These large emergent trees were found more commonly in areas that experience significant seasonal inundation. Between these large trees or swathes of primary forest are smaller planted or secondary growth trees serving as corridors [Luckett et al., 2004; Lindshield, 2006]. The survival of these emergent trees may allow howling monkeys to find sufficient food sources at EZBFS, even in areas that have considerable anthropogenic disturbance.

Howling

In this study, the groups located in the primary forest were observed to exchange howls at a significantly higher frequency than did groups in the secondary forest. Though

this finding does not correspond to predictions, this in itself may be the result of the anthropogenic disturbance mosaic present within the secondary forest. On the southern half of the property, EZBFS is divided into areas cleared for human habitation, pasture regrowth, planted trees, crops plants such as bananas, plantains, and pineapples, and selectively logged forest. Much of these areas, such as the planted *Gmelina* trees [Luckett et al., 2004], serve as arboreal passageways for nonhuman primates but do not provide sufficient food or cover to serve as habitat for the primates (though this is not true for all planted trees, such as *Hyeronima*). In some areas of the southern half of the EZBFS property, large tracts of land are impassable by primates due to a clear cutting of the forest for logging or pasture purposes. It is within this mosaic of habitable and impassable land that the groups living within the secondary forest exist. Thus, though surrounded by other groups of howling monkeys and within audible range, these groups may not be viewed as threats by conspecific groups due to reduced overlap of home range.

For example, within this study, Group One inhabited the area closest to the clearing for human habitation (see appendix for map of location). Within their range they had several tracts of gallery forest with large emergent trees, seasonally inundated forest with signs of logging but continued presence of large trees, and planted *Hyeronima*. Yet, various areas of their home range were cut off from adjacent forest due to clearings for banana plantations, human dwellings, pasture land, and logging. Though at times howling was heard nearby from at least five groups within 500 m of their home range, Group One was less likely to respond to that howling than groups within the primary forest. Group One was surrounded by several groups, yet these groups may not have been able to access group one's home range because of fragmentation. A small tract of gallery forest connected the

majority of Group One's home range to another area where two other howling monkey groups lived. Though both groups ranged within 400-500 m of Group One, only one of the two groups had a range that overlapped that of Group One.

Group Two, the other group living in the secondary forest, had fewer disruptions to the forest in their home range, yet much of the area in which they lived had sparse tree growth due in part to pasture regrowth, but mostly due to swamp and high levels of seasonal inundation. Natural corridors allowed for movement around some of the larger swathes of swamp, yet like Group One, Group Two was cut off from other howling monkey groups due to both natural and human-induced disturbance of the forest cover in part of their range. This reduction in overlap of their ranges may allow for reduced time and as a result, less energy spent in howling for those groups living in the secondary forest at EZBFS. Additionally, there was no significant difference in the average length of a howling bout for groups in both forest types. This implies that in each bout of long-distance reciprocal howling, groups in each forest type are expending approximately the same amount of energy.

In other studies of howling monkeys, groups living in secondary forest, disturbed forest, and highly degraded forests generally have smaller home ranges, yet spend more time actively searching for food [Clarke et al., 2002; Serio-Silva & Rico-Gray, 2002; Muñoz et al., 2006]. Though the extent of home-range size was not measured for the focal groups in this study, qualitatively, the home ranges of those groups in the primary forest appeared to be larger than those groups in the secondary forest. However, if the trend seen in other locations holds true for the groups at EZBFS, it may be that the groups in the primary forest hold larger home ranges and are likely to overlap ranges with more groups. Howling has

been described as an energetically economical assessment of the strength of a neighboring group. Instead of relying solely on energetically costly and physically hazardous interactions, a group of howling monkeys can display both their strength and their willingness to defend their home range [Sekulic & Chivers, 1986; Chiarello, 1995; Kitchen, 2004; Whitehead, 1989; da Cunha & Byrne, 2006]. In large home ranges with multiple overlapping groups, howling as a long distance display of strength may be of greater importance than in areas with fewer overlapping groups and restricted access to a group's home range.

There is a slight but not statistically significant trend for groups within the secondary forest to elevate the type of interaction with a neighboring group from howling to a close-proximity interaction. Howling monkeys are energy-minimizers and howling and close-proximity interactions are presumably energetically expensive behaviors [Milton, 1979; Milton, 1980]. Yet howling monkeys engage in these behaviors frequently. It follows that long-distance howling episodes and close-proximity interactions must be important to promoting the survival and reproductive success of the members of the group to make them energetically economical acts. Howling monkeys must stand to gain more than they lose through energy costs and potential losses of mates or other resources [Brown, 1964].

Social pressures

Though a primate species may persist in an area with significant human influence, monkeys living in that area may display behavior atypical of those living in less disturbed areas [see Pozo-Montuy & Serio-Silva, 2007; Muñoz et al., 2006; Clarke et al., 2002; Serio-Silva and Rico-Gray, 2002]. The human disturbance of the secondary forest at EZBFS does

not appear to correlate with significant differences in intergroup interactions, which may be an indication that food sources are not sufficiently limited in this location or that other pressures believed to influence behavior are greater in this case [Chapman & Pavelka, 2005; Chapman & Balcomb, 1998]. For example, social pressures such as the risk of infanticide or male takeover, the genetic relatedness of neighboring males and females, the presence or absence of infants within the group, group size and dominance hierarchy all may influence the ways in which neighboring groups interact [Chapman & Pavelka, 2005]. If these social pressures are more influential regarding intergroup agonistic encounters than food resource availability, there would exist little or no difference between groups living in anthropogenically altered landscapes and those living in primary forest.

Recent studies with species of *Alouatta* have put great focus on infanticide as an organizing feature of this genus' social structure (for example: Palacios, 2000 and Crockett & Janson 1993; for *A. seniculus*; Kitchen, 2006 for *A. pigra*; Clarke, 1983 for *A. palliata*). The risk of infanticide may be a significant social pressure for both males and female howling monkeys trying to protect their reproductive success, but it is a particularly great pressure for those females that are pregnant or have a young infant. Studies on *A. pigra* in Belize have shown that females who are pregnant or have a dependent offspring are more likely to participate in intergroup encounters [Kitchen, 2006]. Within *A. palliata*, the possibility of infanticide appears less than in other *Alouatta* species, with little evidence to support infanticide as a significant pressure within this species [Méndez-Carvajal et al., 2005; Chapman & Pavelka, 2005]. Within the current study, due to the limitations of time and visibility, the focus of observation during intergroup interactions was on the males of the groups, which does not allow for conclusions to be drawn on the behavior of females in

the group and their interactions with neighboring troops. However, visible female behavior was observed and recorded during intergroup interactions. During intergroup interactions, females were rarely observed at the forefront of the activity and generally stayed behind the males. Though females were usually within 30 m of the male activity, three females in at least one instance formed a subgroup that stayed approximately 150 m behind the rest of the group. Females would occasionally vocalize along with the males or stay in close proximity to the males during interactions or howling bouts. Other times, the females would rest or forage while males howled and displayed toward the neighboring group. Females from the focal group were seen to mix with the females of the other group, sitting nearby or foraging in the same tree. In future studies, it would be informative to be able to distinguish individual female behavior during intergroup interaction. However, the observations in this study support the general belief that for *A. palliata* infanticide is not a significant social pressure, resulting in less agonistic behavior by female howling monkeys toward neighboring groups [Méndez-Carvajal et al., 2005; Chapman & Pavelka, 2005].

The socioecological model holds that for females, the greatest limiting factor for reproductive success is access to food. For males, however, the greatest factor necessary for reproductive success is access to receptive females [van Schaik, 1983]. For female and male howling monkeys, such different pressures result in conflicting pressures on group size and composition by male and female howling monkeys [Treves, 2001; Ryan et al., 2008]. This may explain some of the behavioral differences seen in male and female howling monkeys during intergroup interactions. For females, if the risk of infanticide is not great, the next most important resource to guard is food resource availability, making them less likely to participate in intergroup encounters at times when sufficient food is available. Within adult

female *A. palliata*, intragroup competition and positioning within the female dominance hierarchy may be given more energy than intergroup competition [Zucker & Clarke, 1998]. Males, however, would be more likely to participate and to invest more energy in howling and in intergroup encounters that are important for guarding their access to females or when the alpha male who is challenging or being challenged is a close relation [Sekulic & Chivers, 1986; da Cunha & Byrne, 2006; Kitchen 2004]. This would prove especially important for times when dispersing male howling monkeys enter an area and try to gain entry into an established howling monkey group or when an already established male tries to take over the alpha position [Clarke, 1983]. The factors associated with intragroup competition may affect the way that intergroup interactions are handled within a howling monkey society.

Relatedness of individuals within the groups and the resulting amount of intragroup competition may influence the way in which neighboring groups interact. In a study of *A. pigra* by Kitchen [2004] the likelihood of adult male howling monkeys to respond together to neighboring males was in part determined by the degree of relatedness of the males. For instance, those males who were brothers or fathers and sons were more likely to act aggressively together toward another group. In support of these findings a study of red howling monkeys (*A. seniculus*) shows that competition within the group between rival males may make howling in concert less common [Sekulic, 1982]. The greater the competition between males within the howling monkey group, the less likely they are to support one another during intergroup interactions. Genetic relatedness among howling monkeys of both sexes may account for part of the variation between the types of interactions seen between howling monkey groups at EZBFS. In the secondary forest

groups of howling monkeys at EZBFS there appears to be a high incidence of individuals with blond markings especially on their tails and hind limbs (pers. obs., J. Pruetz pers. comm.). In an area where anthropogenic-disturbances may limit the distance an individual may disperse, it may be an indication that several individuals are genetically linked. Because relatedness is unknown in these groups, no conclusions can be drawn; however, individual relatedness may be another factor explaining some of the inconsistencies seen in the type of interactions observed between groups, though not between forest types. The current study groups are not known well enough and have not been followed long enough to get a true sense of either relatedness or competition between males in each area, so no conclusions can be drawn as to how these factors may have affected the observed results. Yet intergroup interactions showed marked inconsistencies, varying greatly in the amount of visible aggression and apparent energy expenditure.

Intergroup and intragroup aggression is clearly present in howling monkeys. However, the rarity of observing close-contact aggressive interactions between groups has made it difficult to determine exactly when and with what results these interactions are occurring. A study of intergroup aggression in *A. palliata* by Cristobal-Azkarate and colleagues [2004] was conducted by indirect observation through the study of scars and injuries on individual howling monkeys. The authors attributed most of the injuries to immigration events as individuals dispersed from their natal groups. However, the actual circumstances surrounding the injuries were unknown. The results of the study showed no significant relationship between the number of howling monkeys in a forest fragment and the number of injuries visible on individuals. Additionally, the authors did not find any correlation between the amount of visible injury and food availability (measured according

to the population density and the vegetation parameters within an area). Cristobal-Azkarate et al. [2004], however, did find a correlation between injury and a measure of food availability. In this case, a higher diameter at breast height (DBH) of trees in the fragment being studied correlated with a higher instance of injury. The authors explained this correlation as a function of resource concentration. In areas where the DBH was greater, resources were assumed to be more concentrated leading to greater competition for access to those key feeding sites. However, the Cristobal-Azkarate et al. [2004] study was not able to rule out an increased instance of interaction or aggressive interaction that did not result in visible injury.

These findings by Cristobal-Azkarate and others [2004] support the findings at EZBFS, in that there did not appear to be a correlation between howler population aggression in intergroup interactions and a supposed resource scarcity within the anthropogenically altered forest. At EZBFS, the presence of emergent trees with large DBH throughout the secondary forest, when combined with the findings by Cristobal-Azkarate et al. [2004] and Rodriguez and colleagues [2007] would support the lack of significant difference in interactions and aggression between forest types. This study is an example of the interface between social and ecological pressures. To attribute the presence or absence of aggression among howling monkeys solely to one or to the other does not take into account the importance of each factor on the other and weakens our understanding of howling monkey interactions.

The focus in this study was to explore the affects of anthropogenic disturbance and hypothesized resource scarcity on the interactions of neighboring groups of howling monkeys, yet those predicted differences were not seen in the groups observed at EZBFS.

This may indicate that the differences in habitat in this location did not result in the predicted resource scarcity. It may also indicate that, for these groups of howling monkeys, social factors, rather than ecological pressures held greater influence on the interactions between neighboring howling monkey groups. If indeed social factors were more important in determining the type and frequency of interactions between neighboring groups, one would not expect to see significant differences between howling monkeys groups living in primary forest and those living in secondary forest. Most likely, however, it is a combination of social and ecological factors that bring forth the results of this study and affect the interactions between neighboring groups that were observed over the course of this study.

Interspecific interactions

Interspecies interactions at EZBFS occurred in both the secondary and primary forest, between howling monkeys and sympatric primate species at various times during the day and in diverse contexts. These interactions, at times, consisted of individual spider monkeys passing within 50 meters of a resting howling monkey group. Another interaction with a female spider monkey and her juvenile male offspring lasted 110 minutes and included resting, eating, and playing by the juvenile male and his mother in the same tree as the howling monkey group. Interactions with capuchins usually included larger groups of interacting individuals and, at times, included points when the capuchin group and howling monkey group traveled together in the same direction. These interactions are difficult at times to quantify through a classification system of aggressive, nonaggressive, or mixed due to the complexity of the interactions. Yet within these classifications, there did not appear to be a difference between the interactions in the primary and secondary forests.

The results of the power analyses for these results suggest that for the observed amount of variation between the forest types, the sample size would have to be much larger to yield a significant result. Co-feeding by species during interspecific interactions was the only result that showed a trend toward significance and it was likewise, the result that showed the smallest required sample size in the power analyses. All other results would require a sample size of at least three times that of those observed during the timeline of this study in order to be significant, indicating that the variation between the observed results is small and unlikely to become significant unless given a much larger sample size.

Forest type

Howling monkeys' interactions with sympatric species did not significantly vary between the forest types examined in this study. Likewise, between forests, there was no significant difference between the lengths of interactions, showing minimal differentiation between the energy expenditure by groups in each forest type. This also supports that at EZBFS, there exists less difference between forest types than is generally assumed in studies with a conservation focus [for example: Arroyo-Rodriguez et al., 2007; Daily et al., 2003; Pozo-Montuy & Serio-Silva, 2007; Onderdonk & Chapman, 2000]. Howling monkeys and capuchins are generally found to thrive in degraded habitats [Fedigan & Jack, 2001], so the presence of these two species in the anthropogenic disturbance mosaic of the southern half of the EZBFS property does not discount a significant decrease in high quality food resources. Spider monkeys, however, as large-bodied ripe fruit specialists, are generally reported to require large areas of forest with year round fruit availability for continued habitation in an area [Chapman, 1987]. They are also believed to favor primary forest areas,

which are usually the habitat in which the preceding requirements are met. Yet *A. Geoffroyi* inhabits almost every portion of the anthropogenically disturbed forest at EZBFS, suggesting a high level of fruit availability even in the anthropogenically altered secondary forest [Lindshield, 2006].

Lindshield [2006] conducted research on how the ecology of EZBFS allows spider monkeys to exist both within the primary forest, which is believed to be the preferred habitat of the species, and the secondary forest, a rare environment for spider monkey habitation. Comparing fruit availability at three different sites, one in the primary forest, the second in the secondary, and a third in a more swampy location at the edge of the property, Lindshield [2006] found that, though the primary forest did have the largest fruit biomass estimates per hectare, the differences seen between the primary and secondary forest were not significant. In fact, though the fruit biomass was lower in the gallery forest in the secondary forest than in the primary, this disturbed forest held a greater proportion of important *A. Geoffroyi* feeding tree species [Lindshield, 2006]. These findings, though most pertinent to the diet and habits of *A. Geoffroyi*, have implications for the other primate species living in the disturbed forest as all primate species rely to some degree on fruit.

Lindshield [2006] found significant differences in the proportion of time spent resting and feeding by spider monkeys in the primary forest at EZBFS when compared with those in more disturbed areas of the site. Those spider monkeys in the primary forest spent significantly more time resting (41% versus 21%), while those in the disturbed habitat spent significantly more time feeding (48% compared to 24%). A similar behavioral pattern was observed within the current study. Those howling monkeys living in the secondary forest spent more time foraging. This is a behavioral pattern that has been seen in howling

monkeys living in degraded habitats [Muñoz et al., 2006; Clarke et al., 2002]. Authors have suggested that howling monkeys exhibiting this behavioral pattern are more actively searching for food as a result of reduced food availability. The findings by Lindshield [2006], though preliminary in nature, suggest that spider monkeys living in the secondary forest are more actively search for food than those in the primary forest or that those food sources that are of lower quality. *Ateles* continued existence in the areas of anthropogenic disturbance mosaic would support a more primary forest-like pattern of food availability. However, the howling monkeys in the secondary forest in this study engaged in more resting and less travel which differs from what Lindshield observed for spider monkeys. This may be a result of abundant patches of food like the planted *Hyeronima* in the secondary forest or of smaller home ranges as has been observed in other locations. Muñoz et al. [2006] in their study of behavioral patterns of howling monkeys in a cacao (*Theobroma cacao*) plantation noticed an initial increase in daily path length after habitat destruction, but over time, the howling monkeys decreased their travel to a lower level than expected. The authors attributed this change to an energetic compensation for the difficult to digest mature leaves the monkeys were reliant upon for food in the disturbed ecosystem [Muñoz et al., 2006]. The increased time foraging, the decreased time traveling, and the increased time spent resting by howling monkeys in the secondary forest may indicate that the resources available to the groups in the secondary forest at EZBFS are of a lower quality than those in the primary forest, causing the monkeys to behaviorally compensate for the decrease in available energy.

Feeding trees have been cited as one of the most common sites at which sympatric primate species interact, each species coming to feed from a particular tree [Rose et al.,

2004; Janson & van Schaik, 1986]. There was no significant difference seen between instances of feeding during interspecies interactions. Yet the frequency of feeding during interspecies interactions was nearly statistically significant ($p = 0.0602$), showing that there were more instances in which one or both species foraged during an interspecies interaction in the secondary forest. This finding within the current study supports the behavior seen in the previous study by Lindshield [2006]. Additionally, this trend suggests that there may be more dietary overlap in the secondary forest than in the primary forest. According to long-term studies at Santa Rosa during times of relative fruit scarcity, the dietary overlap of howling monkeys, capuchins and spider monkeys greatly increased [Chapman, 1987; Chapman, 1988a]. The increased occurrence of cofeeding in the secondary forest may suggest a greater reliance on the same foods by different species in the secondary forest, when compared with the primary forest. However, there was no evidence of increased aggression in the secondary forest to show that this tendency to feed in close proximity was a cause for greater competition between the primate species in the secondary forest.

Trees within the secondary forest at EZBFS show a tendency toward a clumped distribution due to large tracts of planted trees as well as the selective removal of certain trees for logging. This distribution of food sources in large, abundant patches would make interaction by sympatric species around certain fruiting trees likely in the secondary forest. Primary forest is generally believed to exhibit less clumped distribution of tree species, but this does not always appear to be the case [Brandani et al., 1988; Loiselle et al., 1996]. Dispersal of seeds may not always be evenly distributed. Seed rain and disperser habits may cause more offspring to be centered at mature emergent trees than in the surrounding forest [Loiselle et al., 1996]. In the primary forest at EZBFS, a fruiting event by many trees in a

clumped formation found at the top of one hill became the site of one interspecies interactions, two howling bouts, and two intergroup interactions in just over 6 hours with the focal group (July 13). The focal group interfaced with other groups while each group tried to gain access to the fruiting trees; yet all the howling monkey groups seemed to be held off by the spider monkeys when they entered the area. Within each forest type, clumped distribution of food trees as well as a seasonal change in fruit availability would affect how often and in what manner the species interact with one another.

Like the current study, Lindshield's [2006] data were concentrated during the months of May through August. This means that little seasonal variability exists in either of these studies to reflect seasonal changes in primate behavior or fruit availability. Previous studies have shown that primate diets can vary greatly month to month. Chapman and Chapman [1990] reviewed 46 studies of dietary variability and flexibility in primate species and found that in 82.6% of the primate species reviewed, including all three species in the current study, the diet changed so drastically that the dietary category into which the species fit changed at least one time over the course of a year (for example *A. geoffroyi* changed from being classified as frugivores to folivores to omnivores with 30% of their diet being composed of invertebrates) [Chapman & Chapman, 1990; Chapman 1988]. This evidence of dietary flexibility and variability in one community throughout the course of one year may mean that the interspecies relations change from month to month as each species' diet changes to reflect food availability. However, the study referenced in Chapman & Chapman [1990] was conducted at Santa Rosa in northwest Costa Rica, a dry forest with much higher degree of seasonality and thus greater variability in fruit and new leaf flush availability. In a forest such as at EZBFS with reduced seasonality and a more consistent availability of fruit

and leaf flush one would expect the variability in diet to be likewise reduced, though still present to a degree [Frankie et al., 1974].

In determining the amount of competition that the sympatric primate species at EZBFS experience in the secondary forest, the presence and types of planted trees are relevant. Agroecosystems of certain types, especially those contiguous with larger areas of forest, have been shown to support large numbers of mammal species in other areas of Costa Rica [Daily et al., 2003]. *Hyeronima* trees provided food for all three species, at times bringing together howlers and capuchins or howlers and spider monkeys for feeding events. Also relevant are the banana and plantain plantations that border the home range of focal group number one. Bananas and plantains do not appear to be an important food source for either the spider monkeys or the howling monkeys. They do make up what seems to be a small portion of the diet of some spider monkeys based on rare sightings of spider monkeys within the plantations [M. Rodrigues, pers. comm.]. However, for some capuchins, bananas and plantains seem to provide a stable part of their diet. Feces found under a group of capuchins, a tendency to range alongside the plantations, as well as many sightings therein provide evidence for the use of bananas and plantains in the diet of the capuchins in whose range the plantations exist. Crop raiding by capuchins in other locations may be cause for concern as crop raiding in other primate species has often been cause for negative human-nonhuman primate interactions [Fedigan & Jack, 2001]. However, the small number of humans at EZBFS that are reliant on these crops for food, as well as a strong emphasis on conservation allows the humans and nonhuman primates to coexist without direct negative effects.

Interactions with capuchins occurred more in the secondary forest, with only one interaction occurring in the primary forest. This may be at least in part a reflection of the structure of the human disturbance within the secondary forest. As previously mentioned, capuchins in the area of human disturbance seem to rely on planted foods such as plantains, bananas, and *Hyeronima*. Due to the pattern of disturbance, the majority of the forested area is connected to the plantation area by a small strip of gallery forest, which serves as a small portion of the home range of focal Group One. One group of capuchins was seen travelling along this corridor almost daily, resulting in multiple interactions between capuchins and Group One. Group Two, whose home range did not border plantation area, interacted with capuchins with similar frequency, showing that it was not solely the presence of the plantation land that accounted for the higher number of capuchin interactions in the secondary forest. According to Fedigan and Jack [2001] capuchins tend to be able to exploit regenerating pasture land earlier and better than howling monkeys. This is in part due to the tendency of howling monkey groups to live preferentially in areas with larger trees as well as the ability of capuchins to immigrate into a regenerating area before howling monkeys [Fedigan & Jack, 2001; Arroyo-Rodriguez et al., 2007].

Social and behavioral factors

Along with dietary and resource-related explanations for the results of this study, sociality and species temperament contribute to the interactions observed between these three sympatric primate species. Individual temperament as well as the age-sex class of the interacting individuals may also contribute to the observed results. For example, juvenile male spider monkeys were observed chasing, grabbing, and displaying at adult male, adult

female and subadult howling monkeys in more than one interaction. Though the juvenile spider monkey appeared to be attempting play, the howling monkeys often ran, vocalized, and at times acted aggressively toward the young spider monkey. Varying perspectives on the same behavior could result in different reactions: what for the spider monkey was play, for the howling monkeys appeared to be aggression. Perspective when paired with social dominance seems to affect how these interactions occur.

According to the study on capuchin interspecies interactions by Rose et al. [2003], capuchins are socially dominant to howling monkeys. Spider monkeys, according to the authors of that same study, were ecologically dominant to capuchins, unless enough capuchins worked together to expel a spider monkey from a capuchin-occupied area [Rose et al., 2003]. Howling monkeys, then, are submissive to both capuchins and spider monkeys. This results in a large number of individual and group level displacements of the howling monkeys. Such displacements, which may vary from moving over a few branches to moving over 100 meters, may be energetically taxing for the energy-minimizing howling monkeys. In this study, both spider monkeys and capuchins were observed to cause howling monkey displacement. Yet the results did not show that the greater percentage of individual howling monkey displacements was significant in the secondary forest, nor was there a significant difference between forest types for entire group displacements, making the extra energy exerted in efforts to evade sympatric primate species negligible.

Rose and colleagues [2003] suggested that competition between howling monkeys and capuchins could not account for the amount of aggression seen between the two species at Guanacaste National Park in northwest Costa Rica. Instead the authors spoke of a species-specific temperament that may be responsible for the aggression seen in some cases.

Spider monkeys and capuchins are ecologically dominant to howling monkeys and are easily able to expel howlers from a tree where they are resting or feeding (pers. obs.). Each species has a specific temperament, and certain sex and age classes may react differently to the howling monkey groups. These social factors would not differ significantly between forests. Yet if resources were reduced to a certain threshold in either forest type to the point that survival or reproduction was negatively affected, social factors may also be affected.

The situation at EZBFS is unique in that *A. palliata*, *C. capucinus*, and *A. Geoffroyi* are living sympatrically and have active and viable populations throughout most of the property. Efforts have been made at EZBFS to leave much of the forest intact, to allow regrowth in areas that were formerly pasture, and to plant trees that help support the primate population. Because of these efforts, areas of human disturbance, which are usually considered to be areas of reduced resources, are supporting three species of nonhuman primates. Only indirect behavioral inferences are made here about the level of competition existing between the species and the neighboring conspecific groups. To truly gain evidence of increased competition or increased dietary overlap by the species and groups within this study would take an in depth analysis of the diet of each species throughout the entirety of the year to account for seasonal availability of food sources and would include groups from various points within the disturbance mosaic. These data would allow for a more informed view of the state of the interactions between howling monkey groups and sympatric primate species, yet this is beyond the scope of this study. Instead, this study called into question the purportedly reduced resource availability in secondary forests, which is believed to cause sympatric primates to rely more heavily on fallback foods, increasing competition for limited resources.

Spider monkeys at EZBFS compose two neighboring communities: one found more in the secondary forest and one found in the primary. Capuchins and howling monkeys also have reproducing populations within both the primary and secondary forests. These primates are able to persist in human occupied areas due to absence of hunting on the EZBFS property and continued presence of food and habitat resources needed to sustain these populations. This study supports the conclusion that the nonhuman primate populations living at EZBFS are maintained in both the primary and the secondary forest and do not show behavioral signs of increased resource competition in areas of anthropogenic alteration.

Recommendations for primate conservation at EZBFS

The Caribbean side of Costa Rica has become the site of many large-scale pineapple plantations. Though the land that has been set aside by the Costa Rican government has remained largely protected, land outside of that protection zone has been developed to house a growing population and a growing demand for pineapple and bananas [Sanchez-Azofeifa et al., 2003]. The community of El Zota has been impacted by the financial pressure to sell land to the large fruit companies. EZBFS is a source of income for the owners of the property with a certain amount of the land planted with quick-growing trees (*Hyeronima sp.*, *Carapa guianensis*, and *Gmelina arborea*) that are logged periodically to make paper and cardboard products. Though logging can be done sustainably with little negative effect for the wildlife species dependent on these resources [Webb, 1997], clear-cutting large areas of land or removing arboreal bridges that connect remaining secondary and primary forest areas can isolate primate groups or remove access to important food sources.

In this study, I observed a heavy use of *Hyeronima sp.* by all three sympatric nonhuman primate species. For the primates living in this area, loss of these trees would take away a seemingly important food source, as well as limiting access to other important fruiting trees such as *Ficus* through the loss of travel corridors. During the course of this study areas of the secondary forest that were formerly *Gmelina arborea* were removed for financial reasons. As a result of the clear-cutting, some forest fragments containing howling monkeys became isolated, removing corridors for dispersing individuals and likely limiting available food sources. In the future, I would recommend that corridors of trees be left in areas of logging to allow howling monkeys and other arboreal species a safer passage to other forested areas. Lockett and colleagues [2004] found that all primate species at EZBFS used the plantations of planted trees as corridors to remaining forest patches. The authors proposed the sustainable harvest of the planted trees and the replacement of harvested non-native trees with fast-growing native species such as *Hyeronima sp.* [Lockett et al., 2004]. The enactment of these recommendations would allow for safe arboreal passage by primates between forest fragments. When howling monkeys are forced to travel terrestrially as is the case when corridors between forest fragments are absent, they are at far greater risk of predation, with confirmed cases of predation by domestic dogs in El Zota, specifically [Pruetz, pers. comm.]. In addition, I would recommend planting more trees that have fruit or leaves that could act as food sources for the primates living at EZBFS. *Hyeronima* is a native forest species in Costa Rica and provides both food and passage for the primate species of EZBFS. I would recommend that the *Hyeronima* that is currently found in the secondary forest be left in place and that more *Hyeronima* or other native plants should be planted in areas of future logging. To log planted trees selectively within the forest or to

leave corridors between forested areas would help ensure that EZBFS is promoting conservation of all of the primate species that live within its borders.

Conclusion

Through 132 national parks, biological preserves, national wildlife refuges, forestry reserves, protection zones, wetlands, and other preserved sites, Costa Rica has placed approximately one-fourth of its land under protection. Land put under protection in this way and the land surrounding these preserved sites show negligible deforestation and, in some cases, even a net forest gain [Sanchez-Azofeifa et al., 2003]. Yet, one of the greatest concerns for conservationists and primatologists today remains the high rate of deforestation world-wide. Loss of habitat and food resources has put greater pressure on primate groups living in areas where deforestation and forest fragmentation pervade their habitats. El Zota Biological Field Station is a location where a human disturbance mosaic exists in concert with a diverse, specious wildlife population. It is not uncommon to see the footprints of an endangered tapir (*Tapirus bairdii*) in the midst of the banana and plantain plantations, and jaguarundis (*Puma yaguaroundi*) have been seen within a few hundred meters of the areas of human habitation. This site clearly shows the human-wildlife interface that exists within Costa Rica and is a perfect setting to explore the ways that human alteration of the landscape can affect the behavior of primate species.

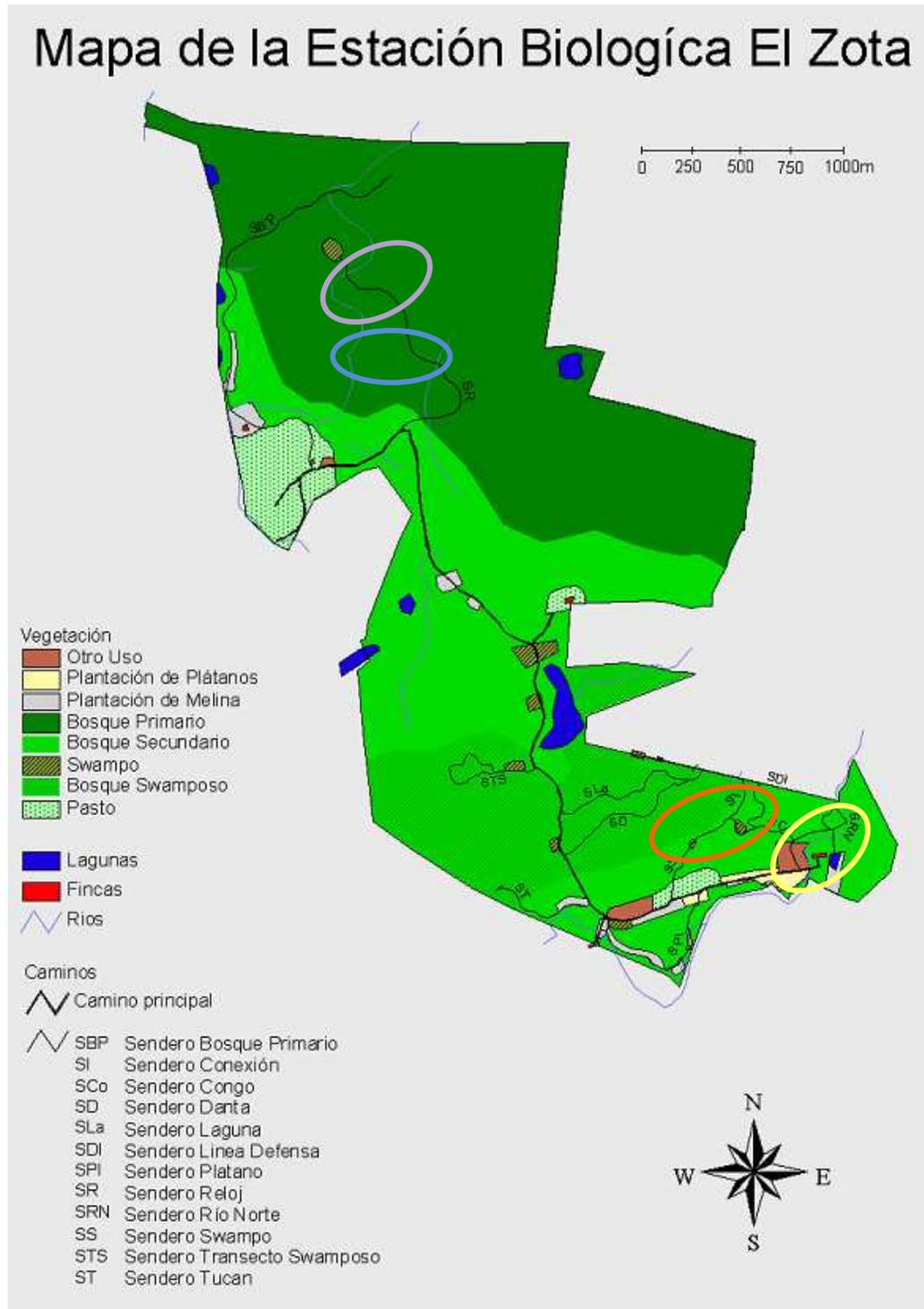
The most common assumption made about human influence within tropical forests is that anthropogenic disturbance always equals habitat degradation. Howling monkeys and their relationships with neighboring groups and sympatric species at EZBFS challenge these assumptions. Though our knowledge of this unique habitat and situation for primates could

benefit from more information and observation, especially during different seasons throughout the year, the implications of this study are that few behavioral differences exist between those howling monkeys living in primary forest and those living in anthropogenically-altered secondary forest habitats. These results call into question whether increased food scarcity and resulting increase in competition are present in this anthropogenic disturbance mosaic. Though humans have altered this environment, the habitat has not necessarily been degraded.

Human alteration of the habitat at EZBFS may not have caused a difference in the way that howling monkey groups interacted at close proximity with their surrounding groups, but it did seem to make a difference in the amount of long-distance howling interactions. This may be a product of the way in which humans have altered the habitat, limiting the number of groups whose home-ranges overlap. Howling monkey interactions with allospecifics also did not appear to alter with the human modification to the habitat, yet there was a trend that suggested that more of the interactions that occur within the secondary forest occur around food sources. This implies that food may be more sparsely located or of lower quality in the secondary forest compared to the primary forest. Supporting this conclusion is the increased time spent foraging and resting by those howling monkeys in the secondary forest. This may be an indication that those monkeys in the secondary forest are searching for food and receiving less energy from lower quality food sources. Also, monkeys in the primary forest traveled more and foraged less, indicating that the foods they are consuming are of higher quality but may be patchier in distribution. All the same, communities of spider monkeys, howling monkeys, and capuchins appear to be persisting and reproducing within the mosaic of human disturbance at EZBFS.

Human disturbance, deforestation, and forest fragmentation continue to be problems for primate species all over the world, including within Costa Rica. In some areas the degree of disturbance can cause extirpation or extinction for affected primate species. However, human disturbance does not automatically mean that a habitat can no longer support primate populations. At EZBFS, the degree of anthropogenic alteration of the primate habitat in certain areas is great. However, the nature of the disturbance still allows for the survival and seemingly unaltered social interaction of the primate species that inhabit these areas.

APPENDIX A. APPROXIMATION OF GROUP HOME RANGE



Map of EZBFS with the approximate positions of each group marked. Group 1 is indicated by the yellow oval, Group 2 is orange, group 3 blue, group 4 violet. The home-ranges marked on this map are not to scale.

APPENDIX B. BEHAVIORAL CATALOGUE

Most common behaviors

1. Rest (re): An inactive state characterized by sitting or laying without accompanying visual vigilance
2. Move (mo): actively changing locations within the same tree without obvious directional intent
3. Travel (tr): moving from tree to tree with directional intent
4. Forage (fo): searching, reaching for, and bringing food to mouth
5. Howl (ho): long, loud, often repetitive vocalization by males in troop, often accompanied by higher pitched female vocalizations, used for intergroup communication
6. Vocalize (vo): softer vocalizations used for intragroup communication
7. Vigilance (vi): either standing or sitting and looking at attention for predators, or rival groups or species
8. Self groom (sg): scratching, biting, or picking at own fur or skin
9. Not visible (nv): activity blocked from the observers view
10. On mother (om): infant clinging to the mother while the mother engages in some activity such as resting or traveling
11. Observer observation (oo): subject is being vigilant of the observer

Less common behaviors

1. Play (pl): usually infants or juveniles playing with other subadults or with an adult
2. Urinate (ur)
3. Defecate (de)
4. Inactive hang (ih): hanging by the tail without any other obvious activity such as foraging or traveling
5. Copulate (co): male and female engaged in reproductive behavior
6. Groom (gr): grooming a conspecific

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