RESPONSES TO THE AUDIO BROADCASTS OF PREDATOR VOCALIZATIONS BY EIGHT SYMPATRIC PRIMATES IN SURINAME, SOUTH AMERICA

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ABSTRACT

The selective pressures exerted on primate populations from threat of predation have led to numerous behavioral and morphological adaptations that allow for pre-emptive detection and evasion of predators. Predators evolve counterstrategies, and an arms race is born. Anti-predator strategies are costly, in the sense that employing them may divert energy from activities more directly related to fitness, such foraging or mating. Therefore, one would expect higher frequencies of more severe anti-predator behaviors to be expressed by primates who have regular interactions with potential predators, because temporal allocation of those behaviors would be reinforced.

A snapshot of natural primate populations reveals that predation is often a substantial source of mortality. Here I investigate the anti-predator strategies of eight sympatric primates in Suriname, South America, to examine how astute wild primates are at detecting predators by only audio cues, how strategies vary by taxa, and whether these strategies vary depending on level or perception of risk within a location. The results suggest that neotropical primates can identify predators as such by vocalizations alone, that anti-predator strategies are highly variable, and that some degree of experience and reinforcement is required for an appropriate level of response behavior. Further, primates in the neotropics appear to evaluate the relative safety of their surroundings and make decisions based on them when confronted with the perceived presence of predators.

CHAPTER ONE
INTRODUCTION

"During any given day, an animal may fail to obtain a meal and go hungry, or it may fail to obtain matings and thus realize no reproductive success, but in the long term, the day's shortcomings may have minimal influence on lifetime fitness. Few failures, however, are as unforgiving as the failure to avoid a predator: being killed greatly decreases future fitness."

-Lima and
Dill, 1990

Threat of predation has been shown to substantially impact the behavior of primates in a variety of ways. Primates employ a wide variety of adaptive anti-predator behaviors and characteristics, including sociality (Hamilton, 1971), group size (Stanford, 2002), body size (Dunbar, 1988), social structure (Hill and Lee, 1998), habitat use and activity patterns (Enstam, 2007; Hill and Weingrill, 2007; Cowlishaw, 1997), sleeping site selection and activity (Franklin et al., 2007), alarm vocalizations (Zuberbühler, 2007), ingestion of toxic materials (Hagey et al., 2007), mode of locomotion (Crompton and Sellers, 2007), vigilance (Treves, 1999; Cords, 1990), mobbing (Gursky, 2005; Stanford, 2002), interspecific associations (Treves, 1999), feeding behavior (Buzzard, 2006), and myriad others (see Isbell, 1994 for a comprehensive review).

Anti-predator strategies can be classified as dichotomous, including behaviors that are related to avoidance (including pre-emptive detection) and those that are related to active defense. Variation in anti-predator response may be related to body size, with smaller primates (< 1kg) tending to adopt avoidance strategies rather than active defense strategies (Cheney and Wrangham, 1987), though this view has been increasingly challenged by documented reports of small-bodied primates engaging in active mobbing behavior (Bezerra and Souto, 2008; Gursky, 2005). In general, avoidance strategies are expected to be front-line defenses against predators employed by primates of all body sizes, as relaxed attention to detection would be decidedly maladaptive and would limit the effectiveness of coordinated defense strategies.

Perception of risk is also an important factor in shaping the anti-predator behaviors of animals. Primates have been demonstrated to alter their feeding, resting, and grooming patterns in risky habitats, range near refugial areas of escape or concealment, and differentially select sleeping sites, all in terms of minimization of perceived risk (Enstam, 2007; Hill and Weingrill, 2007; Cowlishaw, 1997). It is expected that primates will err on the side of caution under perceived presence of predators, as failure to act appropriately could have dire consequences. Active defense behavior, such as mobbing, is then expected to supplement avoidance behaviors (flight, concealment, crypsis) as necessary. Presumably, anti-predator responses are directly linked to the presence of predators in a given area, in that frequency or severity of responses by primate groups should correspond with the severity or regularity of the threat of predation. This has been demonstrated in some recent literature (Gil-da-Costa, 2007; Gil-da-Costa et al., 2003). Response to the perceived presence of predators is also thought to be predator species specific, because different predator species employ different strategies that may inflict different selective pressures on different species (Cheney and Seyfarth, 1981).

1.2 – Predation risk in the neotropics

Neotropical primates are mostly frugivorous, mostly diurnal, and strictly arboreal, and they cohabitate with a high diversity of predators. Because of these factors and others, overall predation risk is known to be high in the neotropics, and risk of avian predation is markedly higher than in other biogeographical regions (Hart, 2007). If risk of raptor predation in the neotropics is higher than Madagascar, where Karpanty (2006) demonstrated that raptor predation accounted for anywhere between 2 and 100% of diurnal primate mortality, then it is expected that neotropical primates face substantial risk. Avian predator guilds are represented by a number of large falconiform raptors, including hawk eagles, crested eagles, and the most powerful raptor in the world, *Harpia harpyja*, all of which prey upon primates (Miranda et al., 2006; Gilbert, 2000; Julliot, 1994; Heymann, 1990; Eason, 1989; Rettig, 1978). Several mammalian predators pose risks to primate populations, including most felids, some canids, and one mustelid. Various reptilian predators are also present in the neotropics, including terrestrial and semi-arboreal vipers and constricting snakes. Most of the predators in the neotropics could be considered sit-and-wait or ambush predators.

Although hawk eagles are smaller than the harpy or crested eagles, they are also known to prey upon primates. Black hawk eagles (*Spizaetus tyrannus*) and ornate hawk eagles (*S. ornatus*) forage in the emergent canopy and dive into the understory with precision and agility to capture prey in their talons (Miranda et al., 2006). These raptors are capable of capturing juvenile and infant howler monkeys, but possibly not adults

(Miranda et al., 2006), suggesting that they are probably also capable of capturing most or all of the callitrichids, and at least infant and juvenile small- and medium-sized cebids wherever these raptors and primates are sympatric.

Crested eagles (*Morphnus guianensis*) and harpy eagles (*Harpia harpyja*) are large, powerful understory ambush raptors that are nearly indistinguishable from one another in size and ornamentation, and as such are often confused with one another when seen in the wild (Hilty, 2003; Frechette, pers. comm.; pers. obs.). Both eagles are capable of capturing and killing a wide range of neotropical primates, from infant tamarins (Vasquez and Heymann, 2001) and adult squirrel monkeys (pers. obs.) to juvenile atelines (Julliot, 1994), adult male bearded sakis (Martins et al., 2005), and adult male howler monkeys (Sherman, 1991; Peres, 1990; Boinski, unpub. data), reflecting a preferred prey weight dispersion of 1-8 kg (Ford and Boinski, 2007). Even terrestrial animals as large as immature brocket deer are potential prey items for adult *H. harpyja* (Rettig, 1978). This prey weight range encompasses a wide variety of neotropical primate species, suggesting that predation pressure from *M. guianensis* and *H. harpyja* ought to exist wherever these raptors and primates coexist. Ford and Boinski (2007) report that pitheciines and members of the genus *Cebus* were the most represented primate taxa in the discarded faunal assemblages found underneath a single *H. harpyja* nest site over four years, and these data are consistent with those reported by Fowler and Cope (1964) and Rettig (1978).

Smaller raptors and forest falcons are also considered potential predators of small-bodied primates (Mendes Pontes and Soares, 2005). These smaller birds include

Micrastur semitorquatus and *Polyborus plancus* (the collared forest falcon and crested caracara, respectively). If both are capable of capturing common marmosets (Mendes Pontes and Soares, 2005), which weigh 236-256 grams (Ford, 1994), they are probably capable of capturing other species of marmosets, but not adult tamarins or other callitrichids. Although these smaller raptors are probably capable of capturing immature tamarins, their size may make them more susceptible to mobbing behavior, which is a considerable deterrent of raptor species (Frechette, 2007).

Felids can exert substantial predation pressure on primate populations. There are documented instances of primate predation from a variety of neotropical felids, including ocelots (*Leopardus pardalis*: Bianchi and Mendes, 2007; Miranda et al., 2005), jaguars (*Panthera onca*: Olmos, 1994; Peetz et al., 1992), margays (*Leopardus wiedii*: Gleason and Norconk, 2002), puma (*Puma concolor*: Ludwig et al., 2007), and possibly smaller neotropical cats (Gleason and Norconk, 2002). Although arboreal animals may enjoy some cushioning from terrestrial predators by virtue of height, low visibility, and rapid flight ability, predation events are rarely documented or observed and detection of such events is difficult. Therefore, the percentage of successful terrestrial predator attacks targeting arboreal animals (3%: Emmons, 1987) may be skewed toward the low side. Bianchi and Mendes (2007) provide evidence of a much higher rate of primate predation by ocelots in Brazil, where primate matter (mostly *Cebus, Brachyteles,* and *Alouatta*) was found in more than 27% of the ocelot fecal samples analyzed.

Domestic dogs (*Canis lupus familiaris*) can act as predators of neotropical primates, but these events seem to be restricted to fragmented forest areas, presumably associated with higher degrees of human encroachment. In some sections of Brazil, for example, *C.l. familiaris* are semi-frequent predators of common marmosets (Bezerra and Souto, 2008; Mendes Pontes and Soares, 2005), but most commonly when marmosets move to the ground to cross open, deforested patches (Mendes Pontes and Soares, 2005). Dogs have also been known to attack capuchin monkeys (Oliveira et al., 2008).

Some primates are also under predation pressure from tayras (*Eira barbara*). These large, cunning mustelids weigh roughly 7 kg (Bezerra et al., 2008) and are known to attack or prey upon smaller primates, especially tamarins (Bezerra et al., 2008; Moynihan, 1970; B. Grafton, pers. comm.) and squirrel monkeys (Galef et al., 1976). There is also documentation of larger-bodied primates such as *Alouatta* and *Cebus* exhibiting anti-predator behaviors in response to the presence of tayras (Asensio and Gómez-Marín, 2002; Phillips, 1995). However, the Ansensio and Gómez-Marín (2002) case involved active defense or mobbing behavior by adult group members, suggesting that a legitimate threat of predation by tayras may exist, but most likely involves non-adult members of these taxa. Differential response exhibited by *Alouatta* species in the two cases cited above indicate that anti-predator strategies are dynamic and situation-specific, and may vary between and within species.

Snakes can pose significant threats to primates. Actual predation events as well as interactions between primates and predatory vipers and constrictors indicate the level of risk (Gursky, 2005; Boinski, 1988; Heymann, 1987; Chapman, 1986). Primates captured by a variety of snakes in the neotropics range in size from small (*Callithrix jacchus*, 236-256 g; Mendes Pontes and Soares, 2005; Ford, 1994) to medium-sized (*C.*

capucinus, 2.5-4 kg; Chapman, 1986; Ford, 1994). Constrictors (*Boa constrictor* and *Eunectes murinus*) appear to provide most of the serpent predation pressure (Cisneros-Heredia et al., 2005; Heymann, 1987; Chapman, 1986).

1.3 Predation risk vs. predation rate

Predation is rarely observed in the wild and calculated predation rates may be low. These observations have been interpreted in several conflicting ways that range from suggesting that predation plays a minimal role in the evolution of primate behaviors (see review in Boinski et al., 2000), or conversely, that primates have particularly well-evolved anti-predator strategies (Cowlishaw, 1994). As a result, the risk of predation a given species faces must often be studied by proxy measures such as frequency of vigilance activities (e.g. Kirchof and Hammerschmidt, 2006; Gil-da-Costa et al., 2003), patterns of selective habitat use (Enstam, 2007; Cowlishaw, 1997), and frequency of alarm calls (Cowlishaw, 1994). These indirect lines of evidence, along with the mounting body of more direct studies that can estimate prey mortality by examining predator kill residues from nest droppings (Karpanty, 2006; Mitani et al., 2001; Rettig, 1978) and scat (Bianchi and Mendes, 2007), to name a few, offer compelling arguments in favor of the view that predation (particularly raptor predation) can significantly impact primate population densities (Karpanty, 2006) and that actual rates of predation may be higher than expected in some populations (Cowlishaw, 1997).

Clearly, primates in the neotropics are faced with high *risk* of predation, though the *rates* at which primates encounter predators or succumb to them will presumably vary by location. Regardless, the soundest strategy for animals is to react with anti-predator behaviors regardless of whether risk or rates are high, because these calculations are likely to be relatively inconsequential to the perceived risk of predation by the members of the social groups in question (Dunbar, 1988), and relatively infrequent predation attempts can still have dramatic behavioral impacts (Gil-da-Costa et al., 2003; Janson, 1992).

1.3 Primate alarm vocalizations

Alarm vocalizations are anti-predator strategies employed by a wide variety of extant primate taxa to announce threats to conspecifics and polyspecifics, to indicate location of a predator, and to deter predation events. Many animal species possess distinctive vocalizations that are emitted when the presence of a predator is detected or perceived. All primates exhibit some form of vocal communication, and many have co-opted vocal abilities to be utilized as anti-predator strategies in the form of alarm calls. Multiple explanations have been offered for the selective pressures that would promote alarm calling behavior (see review in Wheeler, 2008). Most studies of primate alarm calling behavior have focused on two hypotheses: that alarm vocalizations benefit the caller's kin and therefore the caller by way of inclusive fitness, or that alarm vocalizations benefit the caller more directly by decreasing their susceptibility to predation because of their function as predator deterrents. Alarm calls also carry a potential cost, in that callers may alert predators of their presence. Recent studies (Zuberbühler et al., 1999) have found that alarm vocalizations may be important deterrents, in that prey send signals to stealthy predators that they have been detected, and the likelihood of predator success is decreased. This may be especially important among platyrrhines, whose predators largely employ ambush tactics. One additional possibility is that alarm calls attract conspecifics to the area of the caller and thereby diffuse the probability that the caller will be taken by a predator, by way of the selfish herd effect described by Hamilton (1971). These variable explanations may not be mutually exclusive, and multiple explanations may be valid for variable circumstances or contexts in which alarm vocalizations are elicited.

Although the ultimate explanation for alarm vocalizations remains disputed, the proximate effects seem clearer. Alarm calls function to elicit learned anti-predator responses from conspecifics (Boinski et al., 2000), though the appropriateness of both the call and the reaction to it may vary by the age and sex class of the caller (van Schaik and van Noordwijk, 1989; Seyfarth et al., 1980) and other factors to be discussed herein. Animals have been shown to exhibit anti-predator reactions to intraspecific (Seyfarth et al., 1980), interspecific (Gautier-Hion and Tutin, 1988; Terborgh, 1983), and extrageneric (Zuberbühler, 2000) alarm vocalizations.

Though there is some variability in alarm vocalizations, in that some are predator-specific (referential) and others are urgency-based, many primates have been known to emit some vocal sound in response to predator stimuli. Differences in referential and urgency-based alarm systems have been correlated with number of distinct escape strategies available (Kirchhof and Hammerschmidt, 2006). For example, savanna-dwelling terrestrial primates frequently exhibit urgency-based alarm systems, while arboreal primates that can utilize a wider variety of forest habitats tend to exhibit referential alarm systems. Availability of predation escape avenues has also been correlated with predator-sensitive ranging behavior (Lima, 1992).

Many savannah baboons and some lemurs utilize urgency-based alarm systems, where calls are not necessarily predator-specific, but vary along a continuum of volume and frequency, indicating the urgency of active or passive defensive strategies. A more variable set of escape options (ascend or descend) is available to arboreal primates, which may partially explain why many primarily arboreal species appear to utilize predator-specific vocalizations more often than their terrestrial counterparts.

Alarm calls vary greatly and exist along a continuum, from a single call having multiple functions (*Alouatta*: da Cunha and Jalles-Filho, 2007), to a single call with variable volume and pitch which portray the urgency of the threat (*Papio*: Fischer et al., 2001), to multiple, acoustically distinct calls that are predator specific (*Cebus apella*: Wheeler, 2008; *Cercopithecus aethiops*: Cheney and Seyfarth, 1981). As predicted by the continuous nature of alarm vocalizations, primates in the neotropics vary greatly in their vocal repertoires.

1.4 Vigilance

Vigilance behavior has long been quantified as a baseline indicator of predation risk. Theoretically, animals under less intense risk of predation would devote less energy to exhibiting vigilance behavior at the expense of allocation to other activities (e.g. mating, foraging, territorial enforcement), because doing so reflects a considerable fitness trade-off. Vigilance frequency has therefore been the focus of many behavioral studies (see review in Elgar, 1989), and used as the method of comparison to describe how groups minimize predation risk via behavioral repertoires, such as the formation of interspecific associations (Treves, 1999) or selective use of less risky habitats (Boinski et al., 2003). However, it stands to reason that baseline frequencies will vary with habitat variables, and that animals ranging in dense habitats will, by virtue of lowered visibility, reduce the frequency with which they exhibit vigilance (Boinski et. al, 2003). Therefore, the dense, low-visibility habitats that plague researchers and protect animals in neotropical forests may foster lower rates of vigilance, regardless of risk perception or actual predation rates. For this reason, alarm vocalizations rather than vigilance were chosen as the primary proxy measure of perceived risk in this study, although vigilance behaviors were recorded.

1.5 Habitat use

Several studies have focused on differential habitat use as it pertains to the reduction of risk and enhancement of detection, as well as how habitat variables can structure the anti-predator response of a species. Baboons may selectively engage in resting and grooming behavior on cliff edges that are difficult for predators to traverse (Hill and Weingrill, 2007). Other baboons may more frequently travel in areas with lower risk of leopard encounters and lower quality food resources (Cowlishaw, 1997). Patas monkeys and vervets exhibit differential responses based on availability of tall trees and density of cover (Enstam and Isbell, 2004; Enstam and Isbell, 2002). New world monkeys may also alter their behaviors in select habitats, as evidenced by differential rates of vigilance exhibited by squirrel monkeys in dense liana forests (Boinski et al., 2003) and reports of white-faced sakis taking refuge in dense cover following a perceived threat of predation (Gleason and Norconk, 2002).

1.6 Playback studies

Playback studies have been used extensively in studies of predator-prey interactions to measure the responses of various species to auditory broadcasts of various stimuli. These stimuli have included intraspecific alarm vocalizations (Kirchof and Hammerschmidt, 2006; Cheney and Seyfarth, 1981), terrestrial predator vocalizations (Stephan and Zuberbühler, 2008; Zuberbühler et al., 1999), and aerial predator vocalizations (Stephan and Zuberbühler, 2008; Gil-de-Costa, 2007; Gil-de-Costa et al., 2003; Treves, 1999). These studies attempt to elicit anti-predator responses from primates, either to examine the referential nature of a species' alarm vocalization or the responses to the perceived presence of predators. This study attempts to do the latter in order to measure various habitat variables as potential indicators of anti-predator behavior and to gauge the appropriateness of the response as a potential indicator of the frequency with which prey are encountered by specific predators.

Hypotheses

This study sought to evaluate the anti-predator responses to the broadcasts of avian predator vocalizations by eight sympatric neotropical primates in Suriname, South

America. These primates were naturally occurring at two separate parks with assumed differential predation pressure, and were thus expected to exhibit differential patterns of response to the perceived presence of a predator. A review of the literature suggests that anti-predator responses are not necessarily equal or consistent, and may covary with habitat and predator contexts.

I attempted to elicit anti-predator responses from groups of primates by broadcasting predator vocalizations, which served to simulate the presence of a predator. The four major hypotheses tested in this study are as follows:

> H1) Frequency of alarm vocalizations emitted by primate groups will be higher during broadcasts of predator vocalizations than during non-predator vocalizations,
>
> H2) The audio broadcasts of predator vocalizations will cause primate groups to move into areas with higher overstory density, because canopy cover reduces the risk of predation,
>
> H3) Frequency of alarm vocalizations emitted by primate groups will be higher in populations with suspected greater frequencies of aerial predator interactions than in those with unknown or suspected lower frequencies of contact,
>
> H4) Frequency of alarm vocalizations emitted by free-ranging primate groups will be more stimulus-appropriate than the frequency of alarms emitted by captive-born groups.

The goal of this project was to describe and test hypotheses about anti-predator behavior across eight sympatric neotropical primates, to hopefully elucidate subtle differences in strategies between species, examine how habitat variables may influence responses of monkeys to the broadcasts of predator vocalizations, and explain how predator presence may facilitate and reinforce the learning of appropriate alarm response.

CHAPTER TWO
METHODS

2.1 - Study Area

Behavioral research was conducted from 29 May through 7 August 2008 at two protected natural parks in Suriname, South America: Brownsberg Nature Park (BNP; 5º 01' N, 55º 34' W) and Raleighvallen-Voltzberg Nature Park (RV; 4º 43' N, 56º 12' W) (fig. 2.1). Suriname is located in Northeastern South America, sandwiched between Guyana and French Guiana on the Atlantic coast of the continent. The political boundaries of the country contain over 163 km^2, 75% of which is forested habitat where roughly 5% of the population resides (Baal et al., 1988).

BNP is Suriname's only national park, consisting of over 12,000 ha (Fitzgerald et al., 2002). BNP is characterized by montane forest with a variety of incremental ecozones found along the slopes leading down the mountain. The Mazaroni Plateau forms the highest elevation of the mountain at 530 m, and the majority of research activities occurred within 5 km of this plateau (figs. 2.2 and 2.3). The eastern base of the mountain is formed as the slopes of the plateau cascade down to one of the largest man-made lakes in the world, Lake Brokopondo. The northern and western bases taper off to the sparsely populated and minimally developed Brokopondo district, with a population of roughly 8000 Saramakans Maroons. The faunal diversity on the berg is high because the rapid rise of the slopes supports a wide range of diverse ecozones (Lim et al., 2005; Fitzgerald et al., 2002). Hunting and mining activities are legal outside the borders of the park, and are practiced illegally near the borders and within the park, to an extent not fully known. Therefore, the high density and diversity of wildlife in the park may also reflect the refugial or island nature of BNP's relatively pristine forest structure, in that human activities around the base of the mountain have forced wildlife to colonize areas along the slopes and plateau of the berg.

The study area at RV is part of the 1.6 million ha Central Suriname Nature Reserve (CSNR), and largely consists of lowland riverine habitat supported by the Coppename River. The lowland forest in which the study was centralized is characterized by dense secondary vegetation, as well as swamp and bamboo forests. These bamboo thickets and dense undergrowth are thought to be related to previous Amerindian settlements in the area (Boinski, 2008). RV also supports a wide variety of faunal diversity, and the species represented within the boundaries of the study area (fig. 2.4) are similar to those found at BNP and other locations in Suriname (Lim et al., 2005; Reichart, 1993).

Though there are two Kwinti Maroon villages (Witagron and Kaaimanston) along the Coppename River, north of the study area at RV, there are no current permanent settlements within RV or the CSNR.

2.2 - Study subjects

Eight primate species are found within the borders of both parks: *Alouatta macconnelli*, *Ateles paniscus*, *Cebus apella*, *C. olivaceus*, *Chiropotes sagulatus*, *Pithecia pithecia*, *Saguinus midas*, and *Saimiri sciureus*. These species form a rich primate community, encompassing a wide range of habitats, diet types, group sizes, and social structures (see table 2.1). That said, all primate species at BNP and RV are arboreal and diurnal. Body size of the species represented ranges from 0.4-11 kg (Ford, 1994; Ford and Davis, 1992), which makes them vulnerable to a variety of predators (table 2.2). As a result, primate species represented in Suriname exhibit a wide variety of anti-predator strategies and vocal repertoires.

Alouatta

Guianan howler monkeys (*Alouatta macconnelli*) exhibit vocalizations in response to perceived threat of predation, like other species of howlers (Gil-da-Costa et al., 2002). Long roars are also utilized for territory defense and boundary enforcement (da Cunha and Jalles-Filho, 2007). Although low grunts and barks are also associated with this species, the roaring vocalizations were classified as anti-predator vocalizations in this study (as documented by Eason, 1989), and other studies have demonstrated that singular vocalizations can be used in a variety of contexts, including signaling alarm (Zuberbühler et al., 1997). Other species of *Alouatta* possess as many as 22 distinct calls in their vocal repertoires (Baldwin and Baldwin, 1976).

Ateles

Black spider monkeys (*Ateles paniscus*) are high-canopy dwellers who employ a variety of vocalizations in their anti-predator behavior, including non-referential bark-like alarm vocalizations, as in other species of *Ateles* (Chapman et al., 1990). There is some suggestion that number of kin in the area of a caller directly impacts the intensity, duration and frequency of the alarms (Chapman et al., 1990). Spider monkeys also engage in predator-mobbing behavior, which typically involves breaking and dropping branches from high in the canopy.

Cebus

Brown capuchin monkeys (*Cebus apella*) have distinct, functionally referential alarm vocalizations that identify and are used to distinguish between terrestrial and aerial predators (Wheeler, 2008; pers. obs.). Some of these vocalizations may be signals of stress or general disturbance (Boinski et al., 1999), but the aerial alarm vocalization is thought to be emitted only in response to the presence (or perceived presence) of aerial predators (Wheeler, 2008). Previous studies have asserted that these alarms were given only in response to visual cues of predators (Wheeler, 2008).

Like brown capuchins, wedge-capped capuchins (*Cebus olivaceus*) produce predator-specific alarm vocalizations (Norris, 1990; Freese and Oppenheimer, 1981), including an alarm bark that was only heard during intervals 4 and 5 during this study (see below). Although Robinson (1984) describes a wide variety of vocalizations emitted by wedge-capped capuchins, an alarm vocalization is not described specifically. Alarm vocalizations emitted by this species are referred to as “grrah” calls by Freese and Oppenheimer (1981), and the description provided by the authors is consistent with what I interpreted as an alarm call emitted by wedge-capped capuchins during this study.

Chiropotes

Bearded sakis (*Chiropotes satanas*) have characteristic whip-like vocalizations that potentially serve as contact calls, movement indicators, and indicators of general disturbance. They also emit alarm vocalizations (Silva and Ferrari, 2009), which are likely more intense forms of the whip vocalization (van Roosmalen et al., 1981). Observers were able to distinguish loud whip vocalizations from contact whip vocalizations. As such, all loud whip vocalizations emitted by groups of bearded sakis were tallied as alarm vocalizations.

Pithecia

White-faced sakis (*Pithecia pithecia*) are lower-strata dwellers that have a vocal repertoire of between 12-18 distinct calls, including an "alarm chuck" (Henline, 2007; Buchanan et al., 1981). Henline also reports several vocalizations as being utilized in the context of "heterospecific" interactions, and although Buchanan and colleagues (1981) report an "alarm chuck" vocalization, these vocalizations appear to be used in more contexts than the specific alarm vocalizations emitted by other neotropical species.

The white-faced saki alarm vocalization was never emitted in any of the playback experiments at BNP, although some unhabituated groups emitted chuck vocalizations in apparent response to the presence of observers. Sakis are documented to exhibit multiple anti-predator strategies (including silence and immobility) in response to real or perceived threats (Gleason and Norconk, 2002).

Saguinus

Several species of *Saguinus* (though not *S. midas*, specifically) have been reported as employing referential alarm call systems in response to various predators (Kirchhof and Hammerschmidt, 2006; Sproul et al., 2006). Golden-handed tamarins (*Saguinus midas*) in Suriname emitted a short, high-pitched call that appeared to be in response to playback experiments, and this call was recorded as an alarm vocalization in this study. Day and Elwood (1999) report *S. midas* alarm vocalizations in response to aerial predators and "trill" vocalizations in response to snakes, suggesting functional referentiality in their alarm vocalizations. This is to be expected given the high risk of predation associated with these small-bodied monkeys (Kirchhof and Hammerschmidt, 2006).

Saimiri (2.2-7)

Unlike many other neotropical monkeys, some species of *Saimiri* reportedly lack a dedicated alarm vocalization. Instead, twitters are reportedly given in response to "high emotional arousal," including response to threat of predation (based on *Saimiri oerstedii* data; Boinksi and Newman, 1988). However, common squirrel monkeys (*Saimiri sciureus*) are reported to have a vocal repertoire of 21 distinct calls including a dedicated "alarm peep" (Winter et al., 1966).

2.3 - Predation risk in the study areas

Forests of the Guiana Shield feature diverse predator guilds, comprised of all major primate predators in the neotropics. Anecdotal evidence from the 2008 field season (May through August) indicates a relatively high density (or at least a regular presence) of some of these predators, especially felids, at BNP. On the other hand, primates ranging within the RV study area may face a particularly high threat from harpy eagles (*Harpia harpyja*), due to range proximity to a known harpy nest and documented reports of regular predation events (Boinski and Ford, 2007)(fig. 2.5). A list of the known and potential primate predators at BNP and RV, as gathered from personal observation, animal density surveys, and other published and unpublished accounts, indicates that predator guilds at BNP and RV are intact (Table 2.3).

Although exact density or distribution of potential primate predators at BNP and RV is currently unknown, the predator guilds at both parks are intact (Lim et al., 2005; Reichart, 1993; Trail, 1987), if for no other reason than the ecosystem supports a rich collection of prey species. Because of this predator diversity, and the inference of high density or high frequency of contact of some of the felids (based on frequency of animal or tracks/scat/scratch marks/kills; table 2.4) and/or raptors, it is concluded that the primates of BNP and RV face substantial predation risk.

2.4 - Playback experiments

For the purposes of studying the general responses to the perceived presence of a predator in all eight sympatric species, I conducted playback experiments consisting of both non-predatory (control; screaming piha - *Lipaugus vociferans*) and predatory (experiment; harpy eagle - *Harpia harpyja*) bird vocalizations. Because observation of actual predation is rare (Stanford, 2002), these playback experiments were designed to measure the responses of primate groups to the perceived presence of predators.

Playback vocalizations

Screaming pihas are small, frugivorous, territorial birds, common in high canopy, non-flooded neotropical forests. Males frequently emit signature territorial vocalizations, and these vocalizations are ubiquitous in the forests of Suriname. This vocalization was chosen for the control group because of the commonality of the bird and the vocalization, and because the monkeys of Suriname show no apparent reaction to these vocalizations (pers. obs.). During all but one of the playback experiments at BNP (but none of the experiments at RV), live conspecifics responded to recorded screaming piha vocalizations by producing like vocalizations.

Harpy eagles are one of the most powerful raptors in the world (Fowler and Cope, 1964), and are significant threat to primate species in the neotropics (Ford and Boinski, 2007; Rettig, 1978; Fowler and Cope, 1964). These ambush predators mostly occupy lowland forests (Piana, 2002), can swiftly navigate even dense understory to capture prey (Fowler and Cope, 1964), and are capable of killing and transporting prey that weigh 5-6 kg (Ferrari, 2009). Kill residue analysis from harpy eagle nest sites suggests that typical prey body mass ranges from 1 to 8 kg (Ford and Boinski, 2007), and other studies of below nest kill assemblages have suggested that primates may be important prey items for these raptors (Touchton et al., 2002; Rettig, 1978).

While the high-pitched scream vocalization of harpy eagles is probably a contact call or a threat response (Piana, 2002; Rettig, 1978), the broadcast call during playback experimentation was expected to elicit a response to the presence, if not the intention, of the raptor. There is some evidence to suggest that harpy eagles also emit this scream vocalization during hunting activity (Gil-da-Costa et al., 2003). In addition, adult harpys will frequently emit vocalizations from the nest site or after a kill to signal to juveniles that prey has been captured (Piana, 2002; pers. obs.). As such, the broadcast of these vocalizations may more closely simulate auditory cues of predator proximity rather than that of an actual predation attempt, but should elicit a response in either case.

Though harpy eagles are said to inhabit Brownsberg Nature Park through published reports (De Dijn et al., 2006; Lim et al., 2005; Fitzgerald et al., 2002) as well as localized reports from knowledgeable staff and park researchers, no nest site is known. Therefore, the representation, exact range, density, and distribution of harpy eagles at BNP are unknown. On 6 October, 2008, a predation event on an immature howler monkey was verified by the presence of multiple bones and numerous associated feathers (consistent with predation events; Martins et al., 2005; Piana, 2002). This assemblage was found on the eastern slope of the mountain, roughly 2 km from the top of the plateau. Additional details about the predation event are unknown, though the presence of bones may indicate proximity to a nest site, since harpy eagles typically transport their kills to the nest prior to feeding or discarding bones (pers. obs.; Piana, 2002; Rettig, 1978).

At RV, there was a monitored harpy eagle nest site from 2002 to 2007, containing at least one adult and one juvenile. At least three troops of brown capuchins and several groups of howler monkeys inhabit home ranges well within the expected harpy eagle hunting perimeter (up to 10,000 ha; Thiollay, 1989), and several of these groups spent considerable amounts of time within 1 or 2 km of the nest site (pers. obs.) along with unknown numbers of groups of spider monkeys, bearded sakis, tamarins, squirrel monkeys, and white-faced sakis that have been observed in the area (pers. obs.). From direct anecdotal evidence from previous field seasons, it is concluded that the primates ranging within the central study area at RV have regular, substantial periods of contact with harpy eagles.

Experiment protocol

Experiments lasted 31 min in duration and were conducted not more than once per week per group, to ameliorate the threat of habituation. The experiments themselves consisted of the broadcast of a single, high-quality audio file through a portable, battery-powered SME-AFS field speaker (Saul Mineroff Electronics; Elmont, NY; frequency response: 100 Hz to 12 KHz) using a Zoom H4 digital audio recorder (Samson Technologies Corp.; Hauppauge, NY). The audio file was created from non-compressed wav. files ordered from the Macauley Sound Library at Cornell University (fig. 2.6). Vocalizations that were originally recorded at close range and thereby featured minimal ambient noise were specifically selected from the larger file to maximize the natural ambient effect of the forest in which they would be broadcast. These selected vocalizations were then spliced together, normalized[1] to achieve relatively consistent volume, and recombined into stereo channels using Sound Forge 5.0 (Sonic Foundry, Inc.). The final audio file consisted of five distinct intervals (table 2.4).

During experiments, the volume control on the playback speaker was held constant at maximum volume, and the output volume control on the digital player device was held constant at unity gain.

Due to logistical and temporal constraints in conducting the playbacks spontaneously and quickly to unhabituated groups of monkeys, the original goal of hoisting the playback speaker to a pre-determined and consistent height was abandoned. Instead, the speaker was positioned on the ground, and placed strategically to be out of direct view of the monkey troop, usually concealed by understory vegetation. To direct the audio into the canopy and to obfuscate the exact source of the sound, the speaker was tilted to roughly 45 degrees. The speaker was routinely placed between 20 m and 50 m from the group. Whenever possible, the speaker was positioned along a ridge to broadcast sound to a troop of monkeys along the descending slopes, thereby giving the illusion of height when the speaker was placed at ground level.

On 4 July 2008, the maximum distance at which piha and harpy eagle audio could be heard was measured. At maximum speaker volume with the speaker placed on the ground and facing observers located at 100 m intervals along a straight, cleared trail through medium-density low rainforest, the audio files were broadcast. The highest,

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[1] Audio normalization is the process through which the amplitude of an audio waveform is increased to its maximum possible peak without distorting. This process was conducted on the audio files used here in order to decrease large gain discrepancies between calls.

loudest phrase of the screaming piha vocalization could be heard 300 m away by human observers with no reported hearing deficits, but the harpy eagle vocalization could not be detected by those observers beyond 250 m. Therefore, playbacks were never conducted on any troop located within 250 m of another playback experiment on the same day.

2.5 - Data collection

Two distinct types of behavioral data were harvested during playback experiments: activity data and response data. Some generalized data were also recorded for each set, including estimates of troop population size when such estimates could be made and GPS locations of the speaker during experimentation. Each line of data consisted of an activity code, troop spatial spread in meters, group dispersion, troop height range in meters, overstory density, and understory density. In addition, forest type (table 2.6) was noted at the beginning of each experiment, and again if the monkeys changed forest type within the 31 min interval.

Activity data

All activity measurements were collected via instantaneous group scans taken at 1 min intervals during 31-min playback experiments. General activity codes recorded what the majority of the individuals in the group were doing at the time of the scan. Behaviors addressed included foraging, resting, and traveling. Speed of transport was also considered with activity measurements, and was qualified as “slow,” “medium,” or “fast.” For the purposes of analysis, the modal activity during a given playback interval was coded as the activity for that interval sample. In the event of a tie, preference was given to the activity with the most consecutive observations.

Group spread and dispersion data quantified “intra-group positioning”. Spatial spread was a widthwise-by-lengthwise measurement in meters that quantified the overall distribution of the troop in space. Spatial area of occupation (width x length) was calculated for use in analysis as a measure of group spread in space. Dispersion was a categorical measurement qualifying the distribution of monkeys within the spatial area of occupation of the group. The categories of group spatial dispersion were clumped, uniform, and moderate (figure 2.7).

Height of both the lowest and highest observed monkey was recorded in meters. Height differential was also calculated for use in analysis ($h^{max} - h^{min}$) as a measurement of vertical spatial dispersion.

Overstory density was measured at 1-min intervals during experimentation by using a concave spherical densiometer (Forest Densiometers, Inc.; Arlington, VA). A densiometer is a small box containing a grid-etched mirror (see fig. 2.8). Each square on the etched grid is mentally subdivided by the observer into four smaller squares. Points of light allowed through open areas of the canopy appear on the mirror’s surface, and each point equal to one of the four subdivisions in each square is counted. Densiometer measurements (d) are then converted to percentages of canopy cover (c) by using the following formula:

$$c = 100 - (d \times 1.04)$$

Densiometer readings were taken with every 1-min group scan and were, when possible, comprised of the average of three densiometer readings taken from the vanguard edge, middle, and rear edge of the troop.

Understory density (UD) was qualified by visual estimation on a scale from 0 (clear understory) to 3 (impassable growth) in 0.5 increments, similar to the scale used by Cords (1990). UD was intended to quantify the difficulty with which a skilled understory raptor would have in moving through the area. As such, and because avian ambush predators do not hunt from the ground, the understory in question referred to any forest growth between roughly 5 m and the maximum height at which the monkey troop being followed was ranging. Model habitats of each were found at each study area and used as templates for estimating cover. Extreme values of 0 and 3 were reserved for totally open understory (usually anthropogenically cleared, and found only at BNP) and dense liana tangles or bamboo thickets, respectively. A UD value of 3 was coded in only 10 samples, while a UD of 0 was observed, but never coded during observation. (See fig. 2.9 for examples of UD habitats)

Response data

Response data were collected at 30 s intervals using one/zero continuous group scan sampling through all playback intervals. With each 30 s interval, the presence or absence of any anti-predator responses was recorded (see ethogram; table 2.7). If the behavior was observed to be exhibited by any member of the group during the sample period, it received a “1”. If not, a zero was entered for that time interval. In analysis, these data were totaled for each interval then normalized for duration of the interval to provide a frequency of behaviors per 30 s scan.

Alarm vocalizations are energetically expensive (da Cunha and Jalles-Filho, 2007) and ubiquitous in neotropical primates (Ferrari, 2009), and are appropriate proxy measurements of risk perception (Stanford, 2002). As such, alarm vocalizations are viewed as critically important and were the primary focus of this study. Frequency of alarm vocalizations was used to gauge the impact of the harpy eagle vocalization broadcasts and the appropriateness of the reaction to the perceived presence of a predator. Vocalization data were collected by all occurrences sampling rather than one/zero, to capture the true frequency of the behavior.

Vigilance and surveillance behaviors (aerial, terrestrial, and source scan) were recorded when any individual was observed scanning the sky, the ground, or the source of the avian vocalizations, where the gaze was fixed upon a point beyond the length of that individual's arm. This distinction was used by Treves (1997) and Cords (1990) to distinguish vigilance behavior from foraging behavior. Although a distinction between true vigilance and scanning for competitors, food, or mates cannot be made, it is the contention of this methodological program that scanning for competitors or mates does not preclude an individual from detecting predators, or vice versa. When observation scans were being conducted, vigilance behavior was recorded as presence or absence per scan. Vigilance data were collected when possible, but because of dense forest conditions at BNP and RV, these data were recorded relatively infrequently. Due to the inefficiency with which vigilance was recorded at RV, these data were excluded from analysis.

2.6 - Captive experiments

To supplement the free-ranging behavior data, and to test whether appropriate response to the perceived presence of predators is learned or instinctual, playback experiments were conducted on two populations of captive-born brown capuchins (*C. apella*). One additional playback experiment was conducted with a captive-born group of squirrel monkeys (*S. sciureus*). All captive experiments (7 experiments; 217 observation minutes) were conducted at Hiram College in Hiram, OH. IACUC approval was granted from Hiram College (IACUC reference number: 08-009).

The data collection protocol used during captive playback experiments was similar to that used in the field tests. The same 31-min audio file was used, though, unlike in the field tests, focal animal sampling was possible due to high visibility in the enclosures. One individual was chosen from each age/sex class (adult male, adult female, juvenile [one male, one female]) for focal sampling throughout the experiment on each experiment date (adult male: 11 September; adult female: 18 September; juvenile: 23 October). All three squirrel monkeys were males (data collected on 11 September). Continuous focal scan sampling occurred in 30 sec intervals, and measured only response data (see above and in table 2.7). A total of 7 observations were obtained: six with brown capuchins (two simultaneous observation periods during each of three experiment days) and one with squirrel monkeys.

Each captive colony is housed in a separate enclosure, but the enclosures are on the same floor. These enclosures are separated by concrete walls and doors, but the area is not sound-proof. Therefore, the playback speaker was placed in a central hallway in such a way that the audio broadcasts could be sufficiently heard in each enclosure. With the assistance of two observers, data were simultaneously harvested from multiple groups during single broadcasts.

2.7 Sampling problems

The degree to which forest densiometers accurately report canopy cover has been called into question (Cook et al., 1995). However, the device used in this study served its purpose by providing an estimate of overall overstory density as a mechanism of protection from detection by birds of prey circling overhead. Thus, more precise measurements of canopy cover desired by forest ecologists were not required here.

Some portions of playback experiments have been excluded for analysis due to loss of visual contact with the troop during the experiment. Because of unpredictable range behavior, lack of habituation, and lack of knowledge regarding general ranging area of the troops of squirrel monkeys at BNP, only a single sample was able to be obtained. As such, this sample has been excluded from analysis.

Some unhabituated, skittish groups (particularly tamarins and wedge-capped capuchins) had higher flight risk, so the initial ten minute baseline period was reduced to five or, in some cases, zero minutes. For pairwise analyses, these empty or incomplete lines of data were removed.

2.8 Statistical analysis

All statistical analyses were conducted using SPSS 16.0 and Systat Software (SigmaStat 11.0). All histograms and boxplots were created using SigmaPlot 11.0. Comparisons of canopy density measurements and alarm call frequencies between playback intervals were conducted using paired t-tests. The original canopy density and alarm frequency data were highly kurtotic (kurtosis=12.487 and 12.972, respectively), probably due to the frequency of similar values across all five intervals. A square root transformation ($X' = \sqrt{X + 0.5}$; Zar, 1984) was applied to normalize the data. Subsequent examination revealed that the distribution of the mean differences between pre- and post-harpy eagle playback values approached normality (post-transformation kurtosis: canopy density = 0.428; alarm frequency = 2.057). Therefore, parametric tests of hypothesis were appropriate.

To analyze the differences in alarm call frequency between playback intervals, different locations in Suriname, and captive-born and free-ranging populations, I conducted a two-way repeated measures analysis of variance. To analyze possible species-level, population-level, and treatment-level effects and their interactions, I conducted a three-way ANOVA on data from free-ranging populations of howler monkeys and brown capuchins at BNP and RV. Post-hoc analyses were conducted using Bonferroni t-tests.

Figures and tables

Table 2.1 – Size and composition of monkey groups encountered at BNP and RV. Groups in study area at RV denoted with parentheses. Question marks indicate that individual groups were not recognized. In those cases, group differentiation was based on geographic proximity.

Species	**Relative group size**	**Social structure**	**Stratum occupation**	**Groups in study area**	**Diet**[1]	**Reference**
Alouatta macconelli	Medium	♂-♀♀	High	6 (2)	FO	Julliot, 1996
Ateles paniscus	Variable / large	Fission/fusion; ♀ dispersal	High	?	FR	Mittermeier and van Roosmalen, 1981
Cebus apella	7-30	♂♂-♀♀; ♂ dispersal	Mid	1 (3)	O	Wheeler, 2008; DiBitteti and Janson, 2001; Van Schaik and van Noordwijk, 1989
C. olivaceus	6-30	♂♂-♀♀	Mid	2	FR, I	Freese and Oppenheimer, 1981
Chiropotes satanas	Large	Fission/fusion	High	2?	S	Silva and Ferrari, 2009
Pithecia pithecia	Small	♂-♀♀	Low	3	FR, S	Buchanan et al., 1981
Saguinus midas	Small	♂♂-♀♀	Low	2	I	Mittermeier and van Roosmalen, 1981
Saimiri sciureus	Variable / large	♂♂-♀♀; ♂ dispersal	Low	1	FR, I	Baldwin and Baldwin, 1981

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[1] Fo=folivore; S=seed predator; Fr=frugivore; I=insectivore; O=omnivore

Table 2.2 – The documented and potential predators of primates of South America. Potential predators based on documented cases of predation by exact or similar species in other regions in the neotropics. Domestic dogs were not included as potential prey species because of a lack of significant presence within the boundaries of either park, though they may constitute a higher threat outside the borders of BNP.

Species	**Weight**[1]	**Potential predators**
Alouatta macconnelli	4.2-9.0 kg	Raptors (Sherman, 1991), Tayra (Asensio and Gómez-Marín, 2002) Felids (Peetz et al., 1992)
Ateles paniscus	5.4-11.0 kg	Raptors (Julliot, 1994) Felids
Cebus apella	1.3-4.8 kg	Raptors (Ford and Boinski, 2007) Felids (Bianchi and Mendes, 2007) Tayra (Phillips, 1995) Serpents (Boinski, 1988)
Cebus olivaceus	2.4-3.0 kg	Raptors (Ford and Boinski, 2007) Felids (Bianchi and Mendes, 2007) Tayra (Phillips, 1995) Serpents (Boinski, 1988)
Chiropotes sagulatus	1.9-4.0 kg	Raptors (Martins et al., 2005) Serpents
Pithecia pithecia	0.8-2.5 kg	Raptors (Ford and Boinski, 2007) Felids (Gleason and Norconk, 2002) Serpents (Gleason and Norconk, 2002) Tayra (Gleason and Norconk, 2002)
Saguinus midas	0.4-0.6 kg	Raptors (Vasquez and Heymann, 2001) Tayra (Galef, 1976) Serpents (Heymann, 1987)
Saimiri sciureus	0.5-1.3 kg	Raptors (pers. obs.) Tayra (Asensio and Gómez-Marín, 2002)

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[1] Weight estimates are from Ford and Davis, 1992, except *C. olivaceus* and *S. midas*, from Ford, 1994.

Table 2.3 – Documented predator presence at Brownsberg (Fitzgerald et al., 2002) and Raleighvallen (Reichart, 1993). All species are considered “rare” except *Bothrops* and *Eunectes*. Reports of *Cebus* exhibiting active defense behavior in the presence of *Bothrops* (Boinski, 1988) may warrant this species’ inclusion on the potential predator list. Presence of *Morphnus guianensis* is questionable at Brownsberg.

Group	**Species**	**Common name**
Felids	*Leopardus pardalis*	Ocelot
	L. weidii	Margay
	Panthera onca	Jaguar
	Puma concolor	Puma
Raptors	*Harpia harpyja*	Harpy eagle
	Harpyhaliaetus coronatus	Crowned eagle
	Morphnus guianensis	Crested eagle
	Spizaetus ornatus	Ornate hawk eagle
	S. tyrannus	Black hawk eagle
Mustelids	*Eira barbara*	Tayra
Serpents	*Boa constrictor*	Boa constrictor
	Eunectes murinus	Anaconda
	Bothrops atrox	Fer-de-lance

Table 2.4 – Predator sightings at Brownsberg during the 2008 field season. Locations of the felid sightings suggest more than one animal in the study area. Serpent sightings were frequently observed but not recorded. No predators were observed at Raleighvallen during the study period.

Date	**Predator**	**Observation**	**Observer(s)**[1]
29 May 2008	Jaguar	Tracks	ON
05 June 2008	Jaguar	Sighting (eye shine)	RAP Staff
06 June 2008	Ocelot	Tracks	CT
18 June 2008	Jaguar	Sighting	CT
22 June 2008	Jaguar	Tracks	AR, LTG
22 June 2008	Jaguar	Sighting	AR, LTG
27 June 2008	Tayra	Sighting	ON
28 June 2008	Ocelot	Sighting	ON
29 June 2008	Ocelot	Tracks	ON
30 June 2008	Jaguar	Sighting	Tourists
04 July 2008	Tayra	Sighting	ON
09 July 2008	Ornate hawk eagle	Sighting	MN
15 July 2008	Jaguar	Scratch	ON
16 July 2008	Puma	Tracks	AV, EG
16 July 2008	Ocelot	Tracks	AR, LTG
16 July 2008	Ornate hawk eagle	Sighting	EG
06 October 2008	Harpy eagle	Feathers	LTG

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[1] Observers are: Andrew Ritchie (AR), Arioene Vreedzaam (AV), Cynthia Thompson (CT), Errol Gezius (EG), L. Tremaine Gregory (LTG), Marilyn Norconk (MN), Orin Neal (ON), and Conservation International Rapid Assessment Team members (RAP)

Table 2.5 – Protocol for playback experiments.

Interval	**Duration**	**Description**
1 (Baseline)	10 minutes	Interval 1 consisted of ten minutes of silence
2 (*Lipaugus vociferans* (LV) - control)	5 minutes	Interval 2 consisted of 38 intermittent LV vocalizations with slight variation in frequency, amplitude, and volume to preserve the appearance of normality
3 (Intermission)	1 minute	Interval 3 was designed to allow an adjustment to any behavioral shift due to Interval 2
4 (*Harpia harpyja* (HH) – experiment)	5 minutes	Interval 4 consisted of 29 intermittent HH vocalizations with slight variation in frequency, amplitude, and volume to preserve the appearance of normality
5 (Post-playback)	10 minutes	Interval 5 consisted of ten minutes of silence

Table 2.6 – Descriptions of forest type at Brownsberg and Raleighvallen. Bamboo (*Guadua latifolia*; Family *Poaceae*) and swamp forests were only found at Raleighvallen.

Habitat type	**Description**
LRF	Low rain forest; categorized on the basis of tree height, understory density, and tree dispersion
HRF	High rain forest; categorized on the basis of tree height, understory density, and tree dispersion
LF	Liana forest; categorized by thick liana tangles and low-level canopy
BB	Bamboo forest; categorized by heavy bamboo thickets and minimal vegetation variation
SWF	Swamp forest; categorized by extremely dense understory and low-level secondary vegetation common at Raleighvallen

Table 2.7 – Ethogram of response behavior

Behavior	**Code**	**Description**
Aerial vigilance	AV	Visual scan of the sky
Terrestrial vigilance	TV	Visual scan of the ground
Scan source	SS	Visual scan toward broadcast source
Alarm call	AC	Distinct alarm vocalization (or non-distinct, in the case of species with limited vocal repertoire)
Flight	F	Rapid travel away from the speaker / observer

Fig. 2.1 – Map of Suriname, South America, courtesy of University of Texas at Austin libraries. Brownsberg Nature Park and Raleighvallen are marked by blue and red circles, respectively.

Fig. 2.2 – Satellite image of the main study area at Brownsberg Nature Park (courtesy of Bart de Dijn).

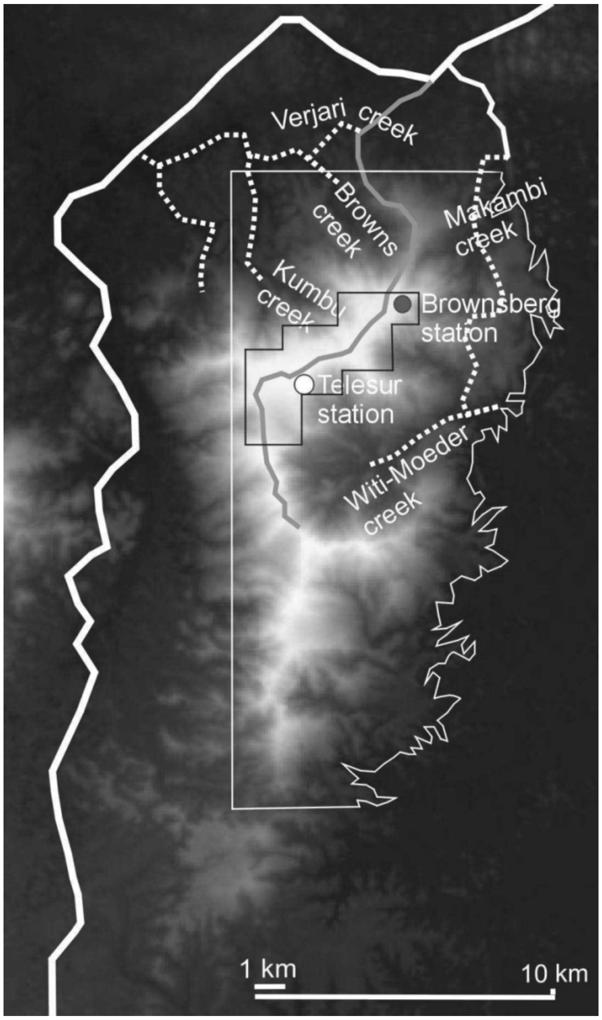

Fig. 2.3 – Map of the main study area (with trails) at Brownsberg (map created by Evan Bailey). Locations of playback experiments are marked by colored stars.

Fig 2.4 – Map of the main study area (with playback experiment locations and other important landmarks) at Raleighvallen. The borders of the main study area were the Coppename River to the north, the Manari Canal to the west, Stream A to the south, and the eastern edge of two large bamboo patches to the east. Map is not to scale. Green triangle indicates camp location. Red and blue stars indicate *C. apella* and *A. macconnelli* playback locations, respectively.

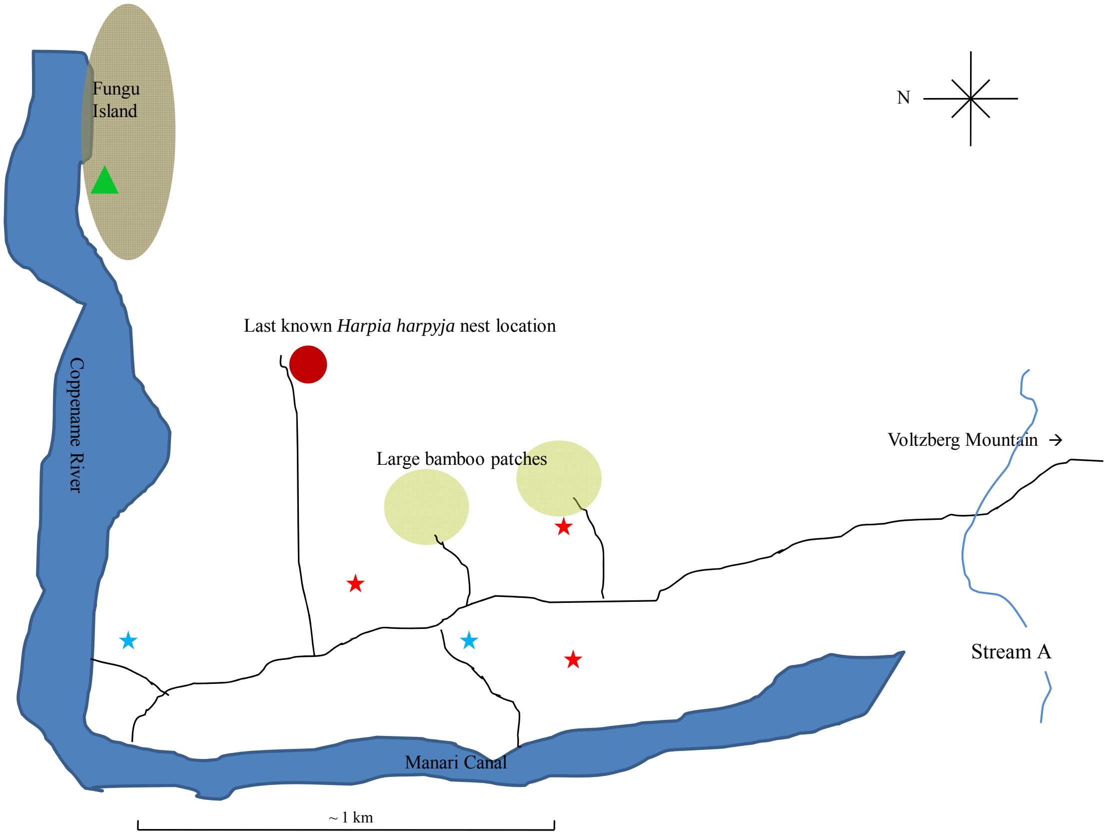

Fig. 2.5 – Harpy eagles exert considerable predation on primates. This photograph shows a documented predation event in which a resident harpy eagle at Raleighvallen captured a squirrel monkey (2003; photograph courtesy of Stacy Neal).

Fig. 2.6 – Spectral display of screaming piha (*Lipaugus vociferans*; top) and harpy eagle (*Harpia harpyja*; bottom) vocalizations (courtesy of Delanie Hurst).

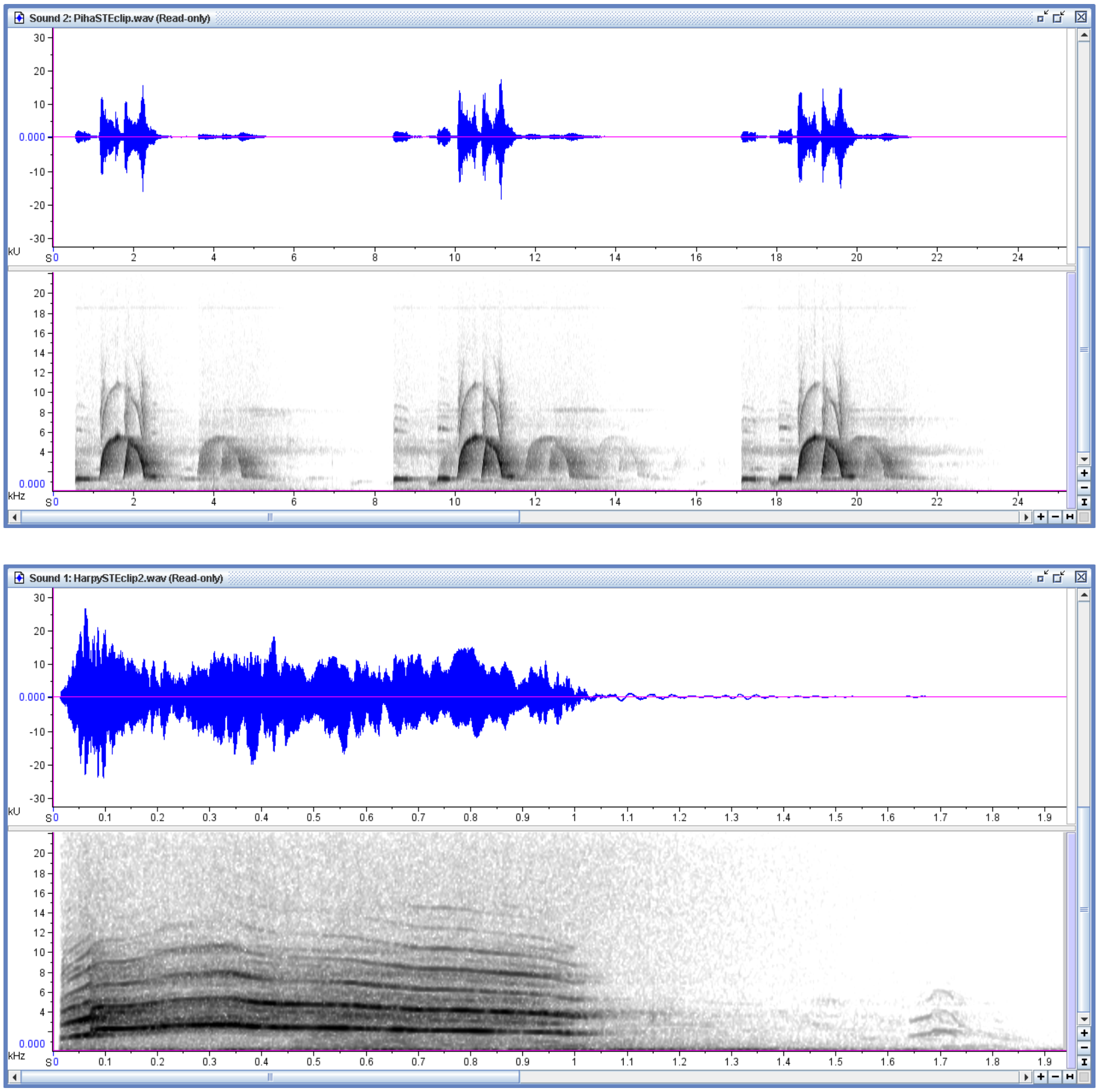

Fig. 2.7 – Degree of dispersion was quantified by neighbor proximity and intragroup positioning.

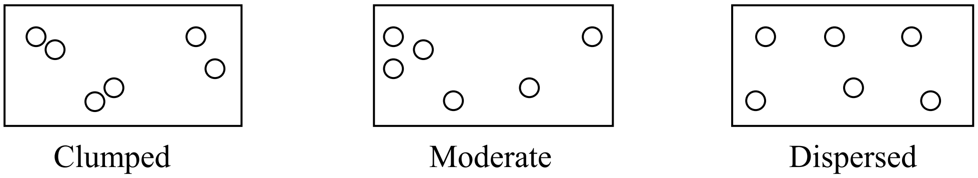

Fig. 2.8 – Concave spherical densiometer. The densiometer consists of a large, concave spherical mirror (center) with grids etched onto its surface. The smaller sphere in the lower right hand corner of the densiometer is a level used in taking densiometer readings. Each square in the grid is mentally subdivided by the user into four smaller squares. Light allowed through the overhead canopy is depicted as points of light on the mirror surface, with four possible points of light for each square of the grid. Visible points are summed, and this sum roughly estimates percentage of unobstructed canopy. The sum multiplied by 1.04 and subtracted from 100 provides the percentage of canopy density.

Fig. 2.9 – Sample of habitats at Brownsberg Nature Park and Raleighvallen used for understory density (UD) estimates. UD = 1 in high rainforest habitat (above); UD = 3 in bamboo forest (below). Bamboo photograph courtesy of Stacy Neal.

CHAPTER THREE
RESULTS

3.1 Total sample sizes

Forty-one field playback experiments were conducted on eight primate species (social groups) totaling 1271 experiment observation minutes over the course of the field season (table 3.1). Seven experimental observations were conducted on the captive groups at Hiram College, for a total of 217 observation minutes. As expected, sampled groups exhibited increases in their anti-predator strategies and shifts in their habitat use patterns with the broadcast predator vocalizations. These responses were found to be often related to habitat variables, and responses were found to vary greatly by location.

3.2 Anti-predator response

While few anti-predator responses were observed during baseline and screaming piha intervals, most species exhibited some response to the perceived presence of a harpy eagle. Several social groups (n=6) rapidly fled the area in response to the initiation of the harpy eagle broadcast. Those samples were excluded from analysis if general data could not be collected due to rapid flight. Howler monkeys, spider monkeys, wedge-capped capuchins, white-faced sakis, and squirrel monkeys all exhibited flight so rapid that visual contact with the focal group was lost at some point during the experiments.

In total, 26 rapid flight responses were recorded in interval 4 (0.28 bouts per minute), and 11 in interval 5 (0.037 bouts per minute). Only 4 flight responses were recorded during screaming piha broadcasts (interval 2; 0.02 bouts per minute). Flight responses during the 10 min baseline interval (2 by brown capuchins and 1 by tamarins; 0.008 bouts per minute) were probably related to the presence of observers or the level of anthropogenic noise disturbance (tourist groups, construction, etc.) in the area. No flight responses were recorded during the 1 min intermission interval.

Although white-faced sakis emitted no alarm vocalizations in response to playback experiments, they did occasionally emit chucks, whistles and z-trills during intervals 4 and 5. During one playback experiment with a group of white-faced sakis, the group became highly agitated, emitting chuck vocalizations and rapidly fleeing the area. During this period, a relatively independent juvenile repeatedly attempted to climb onto a neighboring adult female's dorsum and underbelly. These actions received considerable resistance from the female, who repeatedly tugged at the juvenile and rejected his attempts to be carried. The female emitted frequent chucks and scanned the source of the broadcast while attempting to flee the area.

Spider monkeys also exhibited several interesting anecdotal behaviors. During one experiment in which the observed social group consisted wholly of an adult female and a single independent juvenile, the adult female rapidly ascended to the top of a *Virola sp.* tree immediately following the initiation of interval 4. The juvenile descended to mid-strata while the adult female remained vigilant and emitted alarm vocalizations. At the end of the experiment, the juvenile resumed foraging behavior while the adult female continued to scan the area around the feeding tree.

During a separate spider monkey experiment, several adult individuals responded to the initiation of the harpy eagle broadcast by moving immediately to the area directly above the playback speaker and dropping large branches onto it. Anecdotally, there appeared to be a direct relationship between spider monkey group size and the length of the display period, the number of calls emitted, and the intensity of response. This anecdotal evidence may support the suggestion by Chapman and colleagues (1990) that number of kin in proximity to a caller may impact intensity and duration of alarm calls in other species of *Ateles*. On the other hand, the duration and intensity of response may increase with an increase in population density of a group.

In 4 of 41 experiments (9.76 %), a previously unseen group of howler monkeys vocalized in response to the harpy eagle broadcast. Also, on one occasion, a group of spider monkeys was only noticed by observers once they began emitting alarm vocalizations in response to the initiation of harpy eagle broadcasts. In this situation, the spider monkey group (N=7) emitted 63 alarm vocalizations and exhibited 3 branch-break/mob displays over a 15 minute period.

Vigilance behavior

White-faced sakis exhibited the highest rates of vigilance of all species, followed by brown capuchins, howler monkeys, and spider monkeys (fig. 3.1). Tamarins exhibited relatively low rates of vigilance. Poor sample sizes, visibility issues, and lack of habituation led to absent vigilance scores for bearded sakis and squirrel monkeys. No vigilance data were collected from Ralighvallen due to these visibility issues. Unlike any other species in this study, spider monkeys exhibited higher mean rates of terrestrial vigilance and source-scanning behavior than aerial vigilance. This is potentially a reflection of the strata most frequently occupied by the species. Surprisingly, aerial (ρ= -0.087, p=0.258; n=171) and source-scanning (ρ= -0.0736; p=0.338; n=171) vigilance rates did not correlate with group size, though terrestrial vigilance rates did show a slightly negative relationship (ρ= -0.176; p=0.021; n=171).

Rates of vigilance behavior were affected by playback interval, as expected (fig. 3.2). When corrected for interval duration, mean aerial vigilance and source scanning increased with harpy eagle broadcasts, but the same pattern applied only slightly to terrestrial vigilance. Rates of aerial and terrestrial vigilance returned to baseline levels after cessation of the harpy eagle broadcasts, though source scanning behavior remained at elevated levels when compared to rates exhibited during screaming piha broadcasts.

Alarm vocalizations

A total of 653 total alarm vocalizations were recorded during this study, none of which were recorded during the 1-min intermission interval between screaming piha and harpy eagle playback (table 3.2). As such, that interval was discarded from analysis of alarm frequencies. Thirty alarm vocalizations (4.59% of the total) were recorded during the baseline period, interval 1, by all species save howler monkeys and white-faced sakis. 26 alarms (3.98%) were recorded during the screaming piha broadcast, all of which were emitted by bearded sakis. As expected, the harpy eagle broadcast and post-harpy playback period elicited the highest percentage of alarm vocalizations, with the majority (344; 52.68%) occurring during interval 4 (harpy eagle playback). The remaining 253 alarm vocalizations occurred during the post-playback interval, constituting 38.74% of the total. It should be noted that the baseline and post-playback intervals were each 10 min in duration, while the broadcast intervals (piha and harpy) each lasted 5 min. Data were corrected for interval duration prior to analysis.

Wedge-capped capuchins and spider monkeys emitted the most vocalizations, followed by bearded sakis and brown capuchins (fig. 3.3). Howler monkeys, squirrel monkeys, and tamarins produced alarm vocalizations at low frequencies, while white-faced sakis failed to produce a single vocalization during any experiment. There was a positive relationship found between group size and alarm frequency ($\rho=0.371$; $p<0.0001$; $n=172$). However, among those species that emitted any alarm vocalizations during any interval, frequency was higher in interval 4 than any other (table 3.2).

Analysis of alarm frequency was best conducted by paired samples t-tests, because of repeated measurements of the same groups. Data were paired according to the available data. Missing lines resulted in exclusion of those pairs, which resulted in 29 paired observations. A considerably higher frequency of alarm vocalizations are associated with post-initiation of harpy eagle vocalization broadcast intervals than in intervals before them (intervals B and A, respectively) (see fig. 3.4).

The mean difference between intervals A and B was -1.205 alarm vocalizations, showing that alarm frequencies significantly ($t_{28}= -2.638$; $p=0.013$, 2-tailed) increased with the onset of harpy eagle broadcasts (table 3.3). Therefore, the probability that harpy broadcasts in any given sample will increase baseline alarm call frequency by 0.43 to 1.98 is 95%. The standardized distance is 1.206, indicating that the average frequency of alarm vocalizations in interval A was more than one common standard deviation from the average in interval B. This indicates that the difference in alarm behavior, while significant, is fairly small. However, this analysis included mean differences between species that emitted no vocalizations (white-faced sakis) and those who did so infrequently (tamarins), which may partially explain the results.

In the interest of caution, the non-parametric equivalent to the test of hypothesis employed above (Wilcoxon signed rank test) was also run on non-transformed variables. These results were consistent with those described above, in that frequency of alarm vocalizations was shown to be significantly higher in Interval B than Interval A ($Z = 3.455$; $p=0.001$).

No significant relationship was found between time of day and alarm frequency ($\rho=0.0459$; $p=0.55$). There were no significant correlations found between alarm vocalization behavior and aerial ($\rho=0.0358$; $p=0.641$) or terrestrial ($\rho= -0.0804$; $p=0.296$) vigilance, but there may be a slight relationship between alarm vocalizations and source-scanning behavior ($\rho=0.177$; $p=0.021$).

3.3 General habitat use

Data were collected on spatial occupation, overstory density, understory density, and forest type during experimental observation. Because of the significant anti-predator responses described above, it was concluded that the broadcasts of harpy eagle vocalizations was efficient at simulating the presence of a significant neotropical predator and eliciting responses. Therefore, habitat variables were analyzed by playback interval to investigate changes in habitat use as they pertained to the perceived presence of predators and as general predator avoidance strategies. Overall, many of the patterns of habitat use observed in the sampled social groups can be explained in these terms.

Spatial occupation

Estimated height in the forest was examined in terms of height range (average lowest individual and average highest) and height differential, or h^{max} - h^{min}. The combined mean across species reflected a range of 11-17 m above the ground, with a range of intraspecifc means from 1 m to 28 m (table 3.4). Squirrel monkeys occupied the lowest strata, though the range was based on only one experiment. Four other species (brown capuchins, tamarins, white-faced sakis, and wedge-capped capuchins) were lower than 10 m at the low end of their mean height ranges. This contrasts with bearded sakis and spider monkeys, whose minimum height during playback experiments exceeded 20 m. Height differential reflected the vertical area of space occupied by a group. Brown capuchins and wedge-capped capuchins had the highest mean height differential, while white-faced sakis had the lowest (table 3.4).

During playback experiments, spatial occupation across all species was highly variable, ranging from 2 m x 2 m to 100 m x 150 m (table 3.4). A strongly positive relationship between length and width of spatial dispersion ($\rho=0.7$; $p<0.0001$; $n=173$) indicates simply that an increase in one dimension is associated with a simultaneous increase in the other. The overall interspecific mean spatial occupation (21 m x 32 m) suggests that social groups of many of the species in this study occupy relatively small patches of forest, and spatial positioning data suggest that they are relatively clumped within that space. There is an obvious, expected positive relationship between estimated group size and area of occupation ($\rho=0.559$; $p<0.0001$; $n=172$).

However, intragroup positioning within a spatial area may not be a function of group size. White-faced sakis and wedge-capped capuchins, with mean estimated group sizes of 5 and 25 individuals, respectively, were the least spatially clumped of all species, and were the only species to not exhibit "clumped" as the modal distribution across all scans. Correlation analysis confirmed a lack of relationship between degree of dispersion and group size ($\rho= -0.065$; $p=0.4$; $n=172$).

Mean occupied area (width x length) was also calculated for each species (fig. 3.5), providing measures, along with height differential, of habitat utilization in three dimensional space. Bearded sakis and wedge-capped capuchins occupied the largest total three-dimensional area (width x length x height), while white-faced sakis clearly occupied the smallest. Height differentials exhibited no pattern when examined by playback interval, but did appear to vary by species (fig. 3.6).

Intragroup distribution within a general area may influence alarm calling behavior during playbacks. In this study ($n=171$), the mean alarm frequency emitted by "clumped" groups was nearly three times greater than "moderately dispersed" or "dispersed" groups (fig. 3.7). Spatial area of occupation is positively correlated with alarm frequency ($\rho=0.304$; $p<0.0001$)(fig. 3.8a), as is height differential ($\rho=0.237$, $p=0.0018$)(fig. 3.8b), suggesting that alarm frequency is higher when groups occupy larger three dimensional spaces, and highest when groups within that larger area are clumped.

Understory density

Modal understory density measurements ranged from 1.5 (most open; bearded sakis) to 3 (most closed; golden-handed tamarins), and the across-species modal score was 2 (table 3.4). The remaining species exhibited the modal pattern, save squirrel monkeys, whose modal understory density score was 2.5. Understory density values were similar in groups at both Brownsberg and Raleighvallen. This indicates that at these sites, all species range in areas without clear understory, and most species have moderate visual obstruction to the forest floor. There was no difference in modal understory density measurements between playback intervals.

Although flight responses during playback experiments were rare (occurring in 19.10% of 178 intervals), the occurred more often in less dense understory. In 37.88% of the total 66 flight responses occurred in habitats with understory density scores equal to or greater than 2, while an additional 42.42% occurring in habitats with understory density scores of 1.5.

Forest types were scored on a scale from less dense to more dense, in the following order: high forest, low forest, swamp forest, liana forest, and bamboo thicket. Forest types were found to be positively correlated with understory density (ρ=0.203, p=0.0077), and negatively correlated with maximum height (ρ= -0.608, p<0.0001). Examination of modal forest type across all species indicated that most species were found most often in high-forested habitat. While brown capuchins were found in all five forest types, most species were found in only high and low forests, with the exceptions of black spider monkeys (observed only in high forest habitat) and golden-handed tamarins (observed only in low forest habitat)(fig. 3.9). Bamboo and swamp forest habitats were only found at Raleighvallen.

Understory density appeared to have an inverse effect on rates of vigilance, with mean incidences of aerial vigilance and source-scanning behavior per scan decreasing with an increase in the degree of understory density (fig. 3.10). Paradoxically, forest type also appeared to influence frequency of aerial vigilance, but not terrestrial vigilance or source-scanning behavior. Higher aerial vigilance frequencies were recorded in low forest and liana forest than in high forest habitats (fig. 3.11). This may indicate that although there is generally a positive relationship between forest type and understory density, there is a substantial range of variation in understory density within forest type.

Forest type may also have influenced the frequency of alarm calling behavior (fig. 3.12). The highest frequencies of alarm vocalizations were recorded in bamboo patches, high rainforest, and swamp forest, though alarm vocalizations were recorded in all five habitat types.

Percentages of overstory density from densiometer readings

Canopy cover ranged from relatively open (11.60%) to closed (98.96%) (n=176), with an average densiometer measurement of overstory density of 83.33%. While these data suggest that primates in Suriname range under relatively dense canopy cover, there was some noticeable variation when densiometer readings were considered by playback interval (see below).

The general pattern among all observed species portrays an increase in overhead canopy in post-harpy eagle playback when compared to pre-harpy eagle playback broadcasts (fig. 3.13), suggesting that groups sought refuge in more densely covered habitat when the presence of a predator was simulated. To measure the effect of the harpy eagle broadcast on change in canopy density (i.e. animals moved into areas with denser overstory cover), the data were reorganized into paired groups: interval A and interval B, as described in section 3.2.2, above.

Interval 3 (intermission) measurements were discarded, as densiometer measurements did not significantly differ from other pre-harpy eagle playback measurements. All lines of data containing empty scans from any of the four intervals were discarded. Remaining lines of pre- and post-harpy eagle initiation observations were paired, resulting in 29 paired observations.

Canopy density estimates increased significantly (t_{28}= -2.357; p=0.026, 2-tailed) from interval A to interval B (i.e. from screaming piha playback to harpy eagle playback; table 3.5). Therefore, the mean difference in canopy density within a given population is predicted to be significantly higher after that population is exposed to aerial predator vocalizations in 95% of cases ($1.69\% < \theta < 10.43\%$). The standardized distance was 1.212, indicating that the means between intervals are more than one standard deviation apart from one another. This effect is significant but small, which is to be expected, given the measurements are a percentage and the average baseline levels were already fairly high.

Black spider monkeys and bearded sakis were the only species that did not show clear increase in the degree of canopy obstruction in Interval B. Black spider monkeys exhibited an initial slight decrease in overstory density with the initiation of the harpy eagle broadcast (87.17% and 86.83% in intervals 1 and 2, respectively; 84.75% in interval 4). However, in interval 5, the mean overstory density was 88.91%. Similarly, bearded sakis appeared to have relatively constant overstory density measurements throughout the intervals, with a slight increase during screaming piha playback and subsequent decrease during harpy eagle playback (83.88% and 86.83% in intervals 1 and 2; 85.44% and 83.01% in intervals 4 and 5). These two species had among the highest overstory density averages of all species, though samples sizes for both were small ($n=16$).

Overstory density was found to be inversely correlated with aerial vigilance ($\rho= -0.267$; $p<0.0001$) (fig. 14) and terrestrial vigilance ($\rho= -0.201$; $p=0.0084$), but there was no apparent relationship between overstory density and source-scanning behavior ($\rho=0.092$; $p=0.231$) ($n=171$). Contrary to expectations, degree of overstory density was not correlated with the frequency of alarm vocalizations ($\rho=0.044$; $p=0.57$).

3.4 Activity patterns

Group activity data (described in previous section 2.5) were evaluated on the basis of "feeding" versus "non-feeding" activities that occurred during playback intervals, which were simplified into the dichotomous intervals A (baseline and screaming piha vocalizations) and B (harpy eagle vocalizations and post-playback period) (as above in section 3.2.2) for evaluation. The modal activity for all species throughout both periods was “stationary foraging.”

Overall activity patterning of the intermission period was not found to be aberrant to period A (37.84% stationary feeding, 24.32% stationary non-feeding, 37.84% traveling). Therefore, the intermission interval (1 min) was excluded to temporally equate periods A and B. Two categories were excluded from analysis due to their rarity: stationary resting behavior and medium-rate travel/forage.

When feeding behavior (all intervals containing any combinatorial feeding behavior: feeding while traveling, feeding while resting, feeding while stationary) was compared to non-feeding behavior (exclusively stationary behavior), a dramatic pattern was revealed. Of 137 total activity intervals involving feeding behavior, 103 occurred during period A (75.18 % feeding, 24.82% non-feeding). In period B, activity patterns shifted significantly, with 33 of the 44 (75.00%) total non-feeding bouts occurring during that period. The modal activity budgets during playback intervals show a preference for stationary, non-foraging behavior during period B, where stationary behavior is comparatively rare during period A.

Stationary non-feeding behavior (including resting behavior, which contributed to 11.69% of the activity in interval A, but only 1.49% in interval B) constituted 15 of 77 total counts, or 19.48% of scans within period A (fig. 3.15a). Stationary non-feeding behavior, including rest, constituted 50.75% of all scans within period B (fig. 3.15b). While stationary foraging behavior was fairly prevalent within interval A scans (45.45%), it made up only 14.93% of scans in interval B. Finally, with resting behavior excluded from interval A scan samples, only 7.79% of the scans include stationary non-feeding behavior. When the harpy eagle broadcast interval (interval 4) is isolated (n=35), stationary behavior is the modal pattern, occurring in 20 samples (57.14%).

Traveling behavior constituted 35.06% and 34.33% of the activity scans in intervals A and B, respectively. This suggests that while travel behavior appeared relatively consistent, the modal patterning of stationary non-foraging behavior was highly variable. In addition, it is worth mention that when all feeding vs. non-feeding categories are analyzed (travel and stationary non-feeding vs. travel and stationary feeding), the activity comparison revealed is 71.43% to 20.90% feeding in periods A and B, respectively. Fast-rate travel behavior was only observed during interval B (5.97% of scans), and overall non-feeding travel time was more prevalent in interval B (9.09% in interval A; 28.36% in interval B).

3.5 Differential alarm and vigilance response by location

Brown capuchin response data were isolated and analyzed to compare anti-predator responses between three locations: Raleighvallen, Brownsberg, and Hiram College. Brown capuchin reactions to harpy eagle broadcasts varied by location, but individuals in all three locations emitted alarm vocalizations during playback experiments. However, alarm frequencies and responses by playback interval varied between wild and captive populations (fig. 3.16), suggesting that the more "appropriate" level of alarm response was elicited by wild monkeys. The overall alarm frequency was found to be higher within Raleighvallen populations than in either Brownsberg or Hiram College populations (fig. 3.17).

A repeated measures two-way analysis of variance was conducted to test the effects of playback interval and park on alarm call frequency. There were very highly significant effects of playback interval (F_3=17.32; p<0.001) and location (F_2=12.033; p=0.002), as well as a very highly significant interaction between the two (F_6=13.034; p<0.001) (table 3.6). As expected, subsequent Bonferroni t-test pairwise comparisons (table 3.7) illustrated that the only note-worthy, significant comparison in alarm frequency was “park” by “interval 4” (Brownsberg vs. Raleighvallen vs. Hiram College, during the harpy eagle broadcast). Difference in brown capuchin alarm frequency was significantly expressed when comparing the response of Raleighvallen populations to harpy eagle broadcasts with captive response to the same (t=9.563; p<0.001), and in comparing Raleighvallen response to harpy broadcasts with Brownsberg response to the same (t=8.428; p<0.001). Comparisons of response to harpy broadcasts between brown capuchin groups at Brownsberg and Hiram College were not significant (t=0.503). Similarly, brown capuchin mean alarm frequency was significantly higher in playback interval 4 than in intervals 1, 2 (t=8.46; p<0.001), and 5(t=8.195; p<0.001) at RV (table 3.8), but not significantly different at Brownsberg or Hiram College (table 3.9). The results obtained from running repeated measures ANOVA were not substantially different from those obtained by a standard two-way ANOVA.

A two-way analysis of variance was conducted to measure differences in response behavior between Brownsberg and Raleighvallen populations of brown capuchins and howler monkeys. Results were consistent with two-way analyses described above. Significant differences in mean alarm call frequencies were found in "playback interval" (F_4=14.803; $p<0.001$) and "park" (F_1=8.687; p=0.004), with a highly significant interaction between the two (F_1=11.271; $p<0.001$).

Within the Raleighvallen subset, alarm response to interval 4 (harpy eagle broadcast) was significantly higher than all other intervals, and none of the other intervals were significantly different from any other. Likewise, the bulk of the "park" variation in mean was explained by comparing alarm response within interval 4 between Raleighvallen and Brownsberg, the results of which indicated that alarm response frequency was significantly higher at Raleighvallen (t=7.202; $p<0.001$).

A three-way ANOVA was also conducted, to measure the effect, if any, of species membership on differences between mean alarm frequencies by location. A significant interaction (table 3.10) was found between species, location, and playback interval (F_4=6.875; $p<0.001$). However, the source of this variance appears to be largely attributed to higher species-interval interaction within howlers and brown capuchins at Brownsberg ($p<0.001$) than at Raleighvallen (p=0.734).

Aerial and terrestrial vigilance frequencies did not appear to be significantly different between Brownsberg and Hiram College locations (fig. 3.18), and insufficient data prevented a comparison between Raleighvallen and these two locations. However, the Hiram College population of brown capuchins exhibited a substantially greater frequency of source scanning behavior than those populations at either Brownsberg or Raleighvallen (fig. 3.19).

Figures and tables

Table 3.1 – Total field observation minutes by species (RV experiments in parentheses).

Species	**Common name**	**# of experiments**	**Observation minutes**
Alouatta macconnelli	Red howler	8 (2)	310
Ateles paniscus	Black spider monkey	4	124
Cebus apella	Brown capuchin	4 (3)	217
Cebus olivaceous	Wedge-capped capuchin	2	62
Chiropotes satanas	Bearded saki	5	155
Pithecia pithecia	White-faced Saki	6	186
Saguinas midas	Golden-handed tamarin	5	155
Saimiri sciureus	Squirrel monkey	1	31
TOTALS		**35 (5)**	**1240**

Table 3.2 – Mean alarm vocalizations per minute emitted during five playback intervals. All column refers to overall means across all species. AM: howler monkey; AP: spider monkey; CA: brown capuchin; CO: wedge-capped capuchin; CS: bearded saki; PP: white-faced saki; SM: golden-handed tamarin; SS: squirrel monkey.

	AM	**AP**	**CA**	**CO**	**CS**	**PP**	**SM**	**SS**	**ALL**
Baseline	0.000	0.025	0.057	0.050	0.500	0.000	0.025	0.300	0.081
L. vociferans	0.000	0.000	0.000	0.000	1.733	0.000	0.000	0.000	0.137
Silence	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
H. harpyja	0.275	3.000	2.000	13.000	3.467	0.000	0.680	0.800	1.966
Post-playback	0.513	3.500	0.114	6.400	1.100	0.000	0.040	-	0.843

Table 3.3 - Paired samples t-test output of mean differences of alarm vocalizations in interval A vs. interval B, where A= interval 1 (baseline) + interval 2 (screaming piha playback), and B= interval 4 (harpy eagle playback) + interval 5 (post-playback). Mean equals the mean difference in alarm vocalizations per minute between intervals A and B.

	Paired Differences							
				95% Confidence Interval of the Difference				
	Mean	Std. Deviation	Std. Error Mean	Lower	Upper	t	df	Sig. (2-tailed)
Interval A - Interval B	-1.20	2.46	0.46	-2.14	-0.27	-2.638	28	0.013

Table 3.4 – General habitat utilization and intraspecific spatial organization by all species at Brownsberg and Raleighvallen. Modal values were averaged between two bimodal values in the cases of ties. Width, length, and height range values of group dispersion are in meters. Means are rounded to the nearest whole number. “DD” is degree of intraspecific dispersion. “D%” is the mean percentage of overstory cover, from densiometer readings. “UD” is understory density, qualified as open=0; closed=3. Overall across-species means are shown in the last row.

Species	**$\bar{x}$ width**	**$\bar{x}$ length**	**Modal DD**	**$\bar{x}$ h range**	**$\bar{x}$ D (%)**	**Modal UD**	**Modal forest type**	**$\bar{x}$ est. group size**
AM	14	21	Clumped	16-22	81	2	HRF	6
AP	19	43	Clumped	21-28	87	2	HRF	9
CA	30	53	Clumped	4-15	78	2	LRF	20
CO	69	77	Mod-disp	9-18	88	2	HRF	25
CS	43	42	Clumped	21-28	85	1.5	HRF	25
PP	19	22	Moderate	7-11	84	2	LRF	5
SM	10	17	Clumped	5-10	87	3	LRF	7
SS[1]	50	58	Clumped	1-6	89	2.5	LN	25
ALL SPECIES	**21**	**32**	**Clumped**	**11-17**	**88**	**2**	**HRF**	**15**

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[1] *Saimiri* data come from a single observation period

Table 3.5 - Paired samples t-test of mean differences of overstory densities in interval A versus interval B, where A= interval 1 (baseline) + interval 2 (screaming piha playback), and B= interval 4 (harpy eagle playback) + interval 5 (post-playback). Mean equals the mean difference in overstory density between intervals A and B.

	Paired Differences							
				95% Confidence Interval of the Difference				
	Mean	Std. Deviation	Std. Error Mean	Lower	Upper	t	df	Sig. (2-tailed)
Interval A – Interval B	-6.06	13.85	2.57	-11.33	-0.79	-2.357	28	0.026

Table 3.6 – Two-way repeated measures analysis of variance showing very highly significant differences in alarm frequency by playback interval and park. Additionally, there is a very highly significant interaction between interval and park on alarm frequency.

Source of variation	**DF**	**SS**	**MS**	**F**	**Significance**
Park	2	9.006	4.503	12.033	0.002
Interval	3	19.825	6.608	17.320	<0.001
Park x Interval	6	29.838	4.973	13.034	<0.001

Table 3.7 – Post-hoc pairwise comparisons of park within playback interval (Bonferroni t-tests).

Park within baseline

Comparison	Diff of Means	t	P	P<0.05
BNP vs. RV	0.100	0.212	1.000	No
BNP vs. HC	0.0833	0.210	1.000	No
HC vs. RV	0.0167	0.0383	1.000	No

Park within screaming piha broadcasts

Comparison	Diff of Means	t	P	P<0.05
HC vs. RV	0.233	0.536	1.000	No
HC vs. BNP	0.233	0.587	1.000	No
BNP vs. RV	1.522E-016	3.233E-016	1.000	No

Park within harpy eagle broadcasts

Comparison	Diff of Means	t	P	P<0.05
RV vs. HC	4.167	9.563	<0.001	Yes
RV vs. BNP	3.967	8.428	<0.001	Yes
BNP vs. HC	0.200	0.503	1.000	No

Park within post-playback

Comparison	Diff of Means	t	P	P<0.05
RV vs. HC	0.0667	0.153	1.000	No
RV vs. BNP	0.0333	0.0708	1.000	No
BNP vs. HC	0.0333	0.0838	1.000	No

Table 3.8 – Post-hoc pairwise comparisons of playback interval at RV (Bonferroni t-tests); Intervals 1 and 2 are baseline and screaming piha broadcasts; intervals 4 and 5 are harpy eagle broadcast and post-playback periods.

Interval within RV

Comparison	Diff of Means	t	P	P<0.05
4.000 vs. 1.000	4.267	8.460	<0.001	Yes
4.000 vs. 2.000	4.267	8.460	<0.001	Yes
4.000 vs. 5.000	4.133	8.195	<0.001	Yes
5.000 vs. 1.000	0.133	0.264	1.000	No
5.000 vs. 2.000	0.133	0.264	1.000	No
2.000 vs. 1.000	6.410E-017	1.271E-016	1.000	No

Table 3.9 – Post-hoc pairwise comparisons of playback interval at BNP and Hiram College (Bonferroni t-tests).

Interval within BNP

Comparison	Diff of Means	t	P	P<0.05
4.000 vs. 2.000	0.300	0.687	1.000	No
4.000 vs. 1.000	0.200	0.458	1.000	No
4.000 vs. 5.000	0.200	0.458	1.000	No
5.000 vs. 2.000	0.100	0.229	1.000	No
5.000 vs. 1.000	8.327E-017	1.906E-016	1.000	No
1.000 vs. 2.000	0.1000	0.229	1.000	No

Interval within HC

Comparison	Diff of Means	t	P	P<0.05
2.000 vs. 1.000	0.217	0.608	1.000	No
2.000 vs. 5.000	0.167	0.467	1.000	No
2.000 vs. 4.000	0.133	0.374	1.000	No
4.000 vs. 1.000	0.0833	0.234	1.000	No
4.000 vs. 5.000	0.0333	0.0935	1.000	No
5.000 vs. 1.000	0.0500	0.140	1.000	No

Table 3.10 – Three-way analysis of variance examining differences in howler monkey and brown capuchin alarm frequency at BNP and RV, by species, park and group. All interaction terms are highly significant.

Source of Variation	**DF**	**SS**	**MS**	**F**	**P**
Species	1	2.112	2.112	6.742	0.012
Park	1	1.188	1.188	3.793	0.056
Group	4	10.828	2.707	8.643	<0.001
Species x Park	1	3.041	3.041	9.709	0.003
Species x Group	4	8.942	2.236	7.138	<0.001
Park x Group	4	7.050	1.762	5.628	<0.001
Species x Park x Group	4	8.613	2.153	6.875	<0.001
Residual		60	18.790	0.313	
Total		79	71.210	0.901	

Fig. 3.1 – Mean vigilance frequencies (aerial: AV; terrestrial: TV; source-scanning: SS) by species across all intervals. Data on bearded sakis (CS) and squirrel monkeys (SS) are lacking due to poor visibility. Sample sizes are as follows: Brown capuchins (CA): n=35; CS: n=16; howler monkeys (AM): n=45; spider monkeys (AP): n=15; SS: n=4; tamarins (SM): n=24; wedge-capped capuchins (CO): n=9; white-faced sakis (PP): n=26.

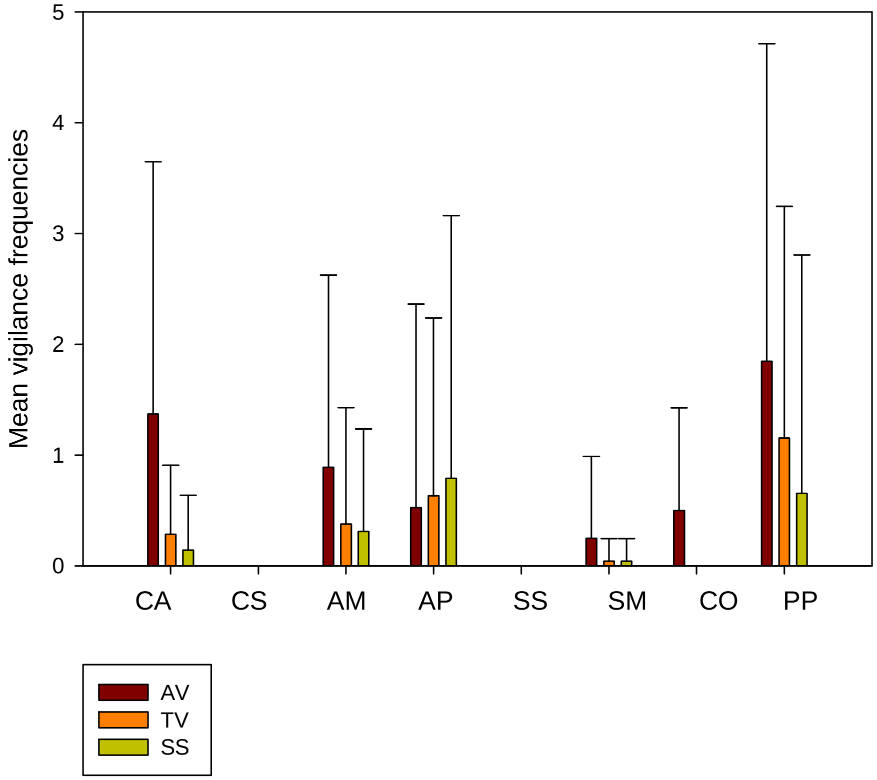


Fig. 3.2 – Mean vigilance frequencies increase when the harpy eagle broadcasts begin. Red bars indicate aerial vigilance, orange bars indicate terrestrial vigilance, and yellow bars indicate source-scanning behavior.

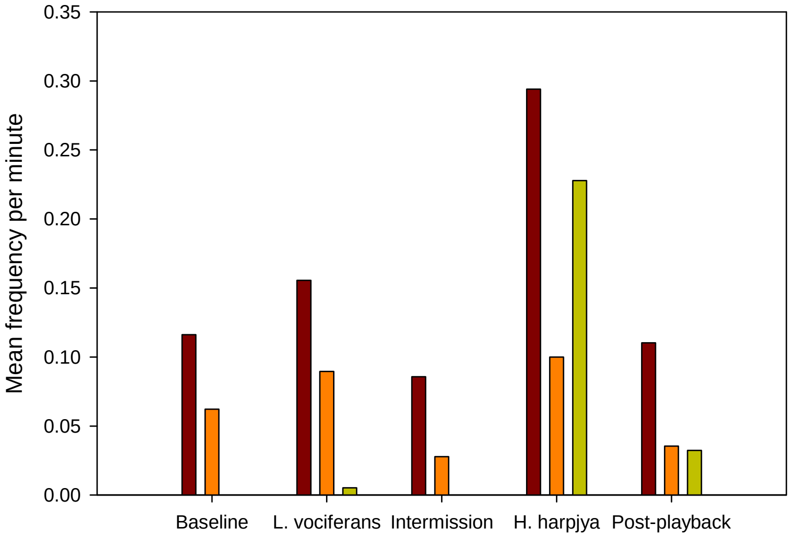


Fig. 3.3 – Frequency of alarm vocalizations in all species averaged across all playback intervals. Wedge-capped capuchins, spider monkeys, bearded sakis, and brown capuchins had the highest alarm frequencies. Species codes (x axis) are the same as described in Fig. 3.1.

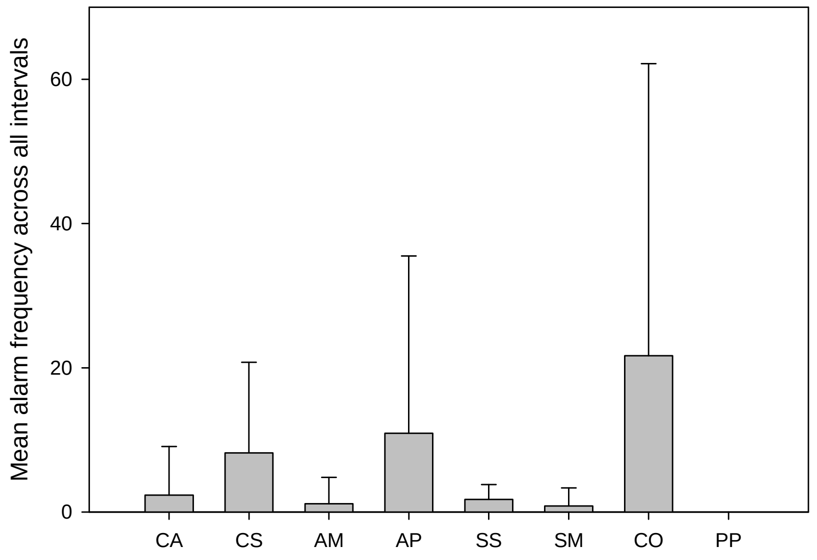


Fig. 3.4 – Dichotomous alarm response data for all species, normalized for duration of playback intervals. Mean alarm frequencies were substantially higher in interval B, which included the harpy eagle broadcasts and post-playback periods, compared to interval A, which included the baseline and screaming piha broadcast periods.

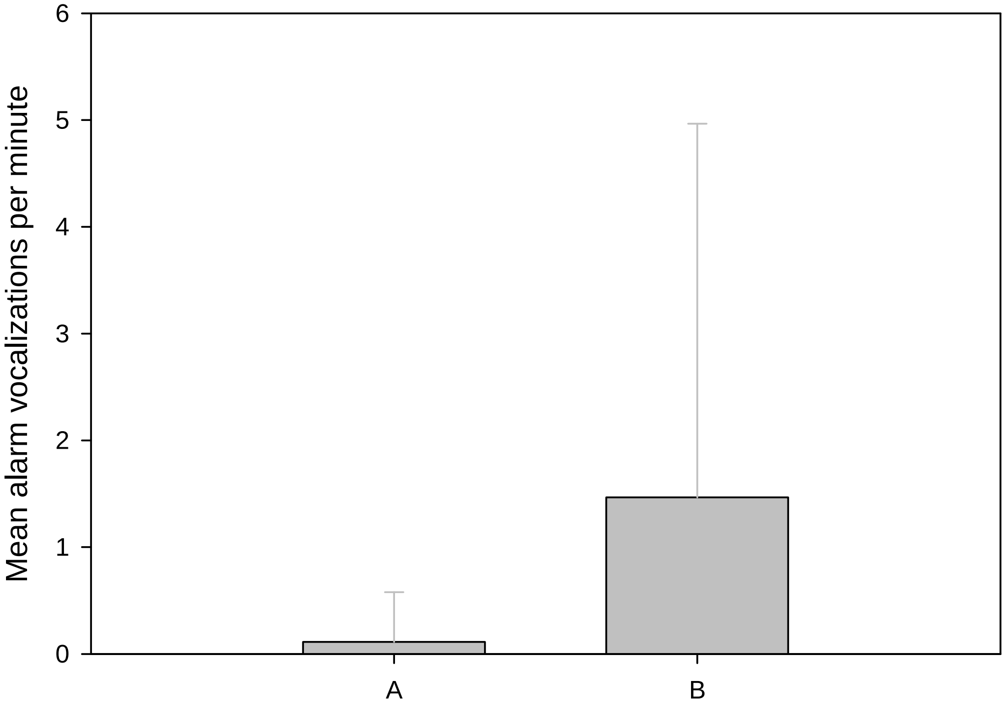


Fig. 3.5 – Length and width of the area occupied by the species during the experiments. Wedge-capped capuchins occupied the largest overall area; golden-handed tamarins occupied the smallest. Spider monkeys and bearded sakis were the most variable in area occupied by social groups at the time of the experiments. This is possibly a reflection of the highly variable nature of their social organizations.

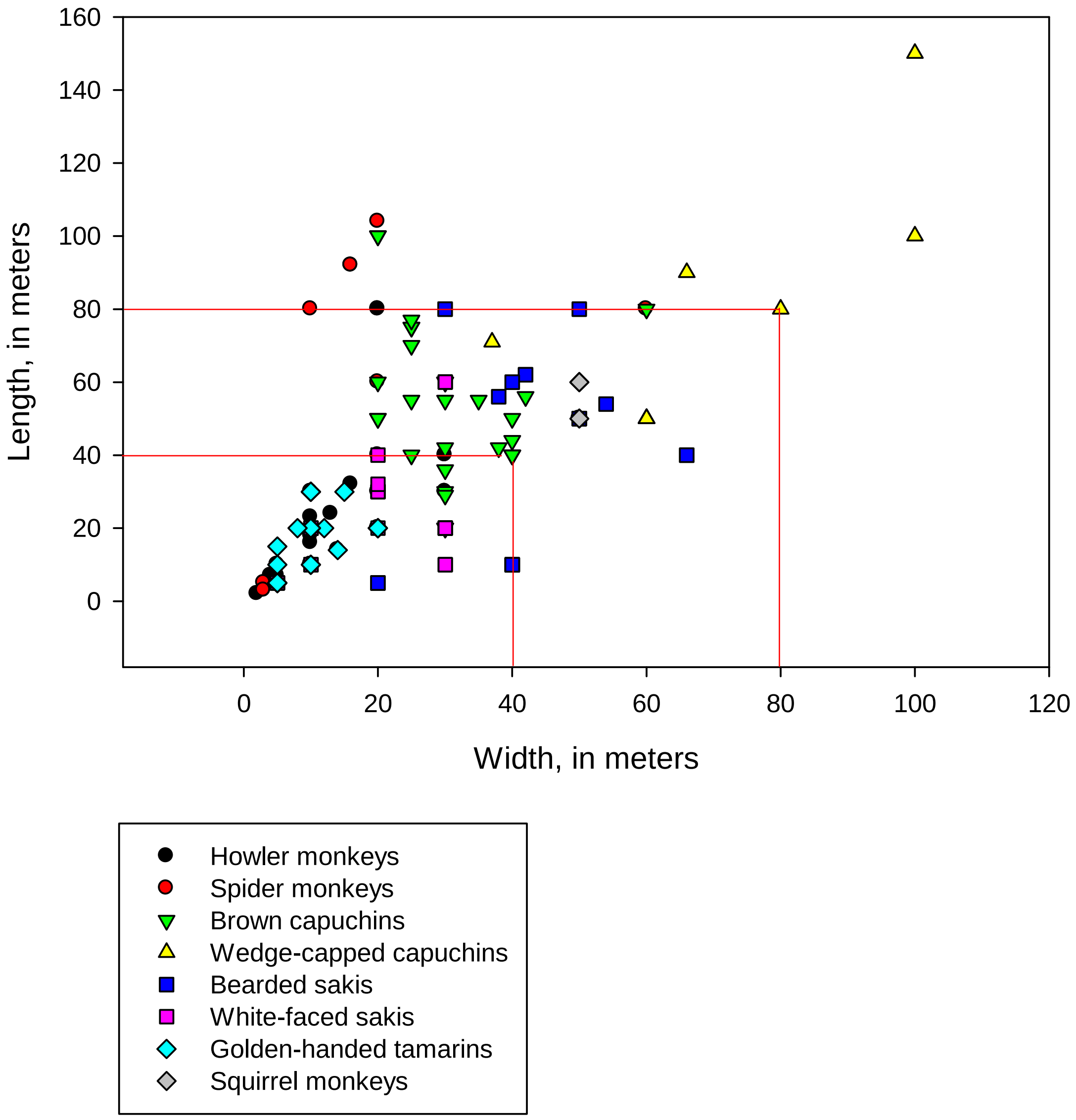


Fig. 3.6 - Maximum and minimum height occupation for each species. Spider monkeys, bearded sakis, and howler monkeys were found in the highest canopy strata, and all were considerably variable in their height distributions; mid- and low-strata species were less diverse in their vertical areas of occupation.

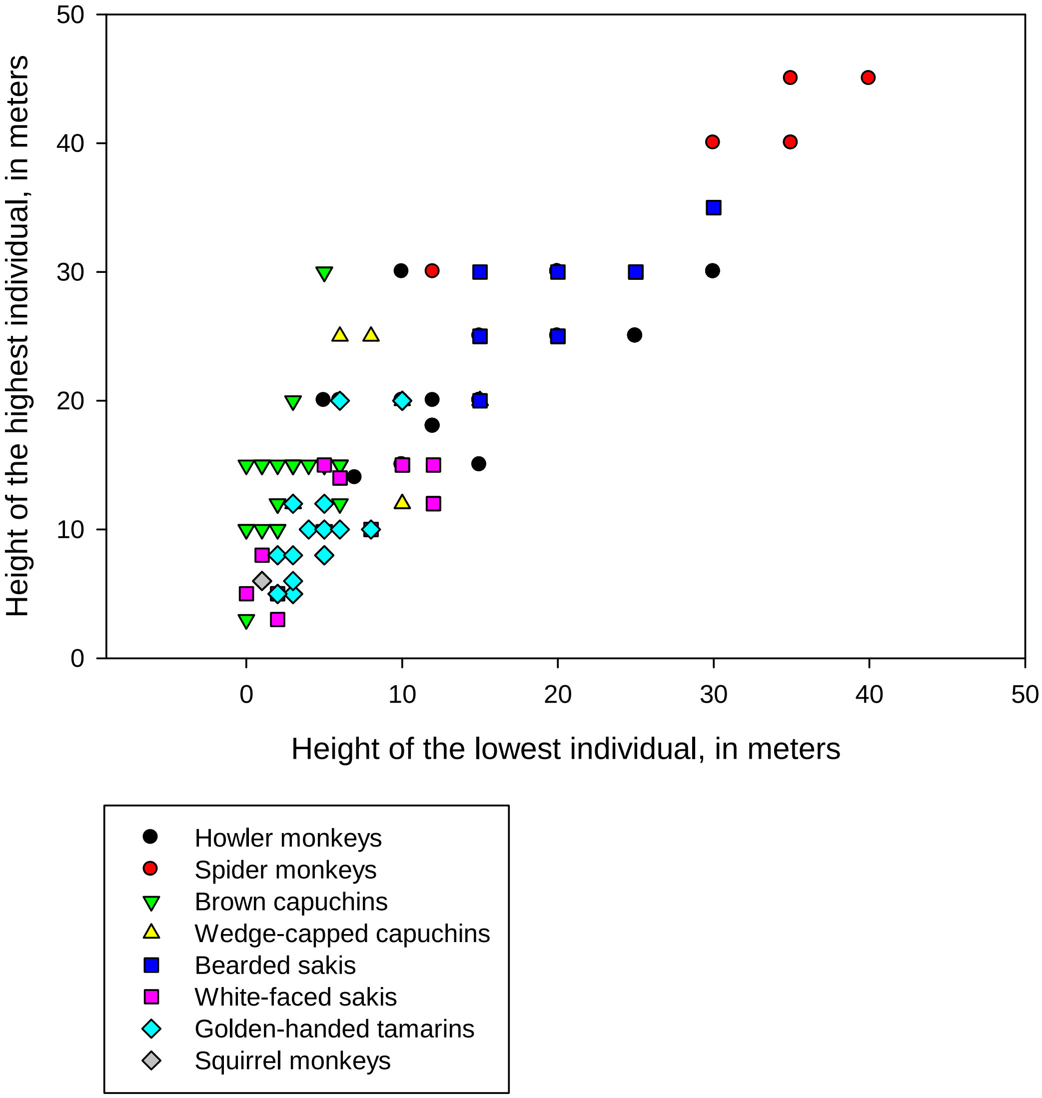


Fig. 3.7 – Relationship between alarm frequency and within group spatial dispersion.

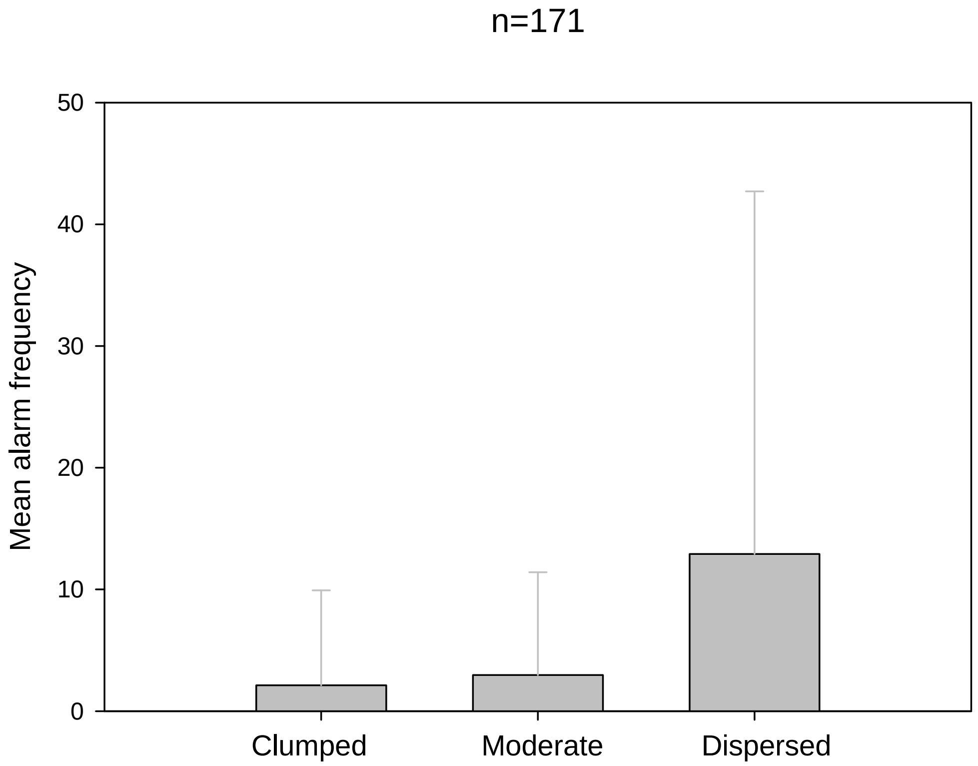
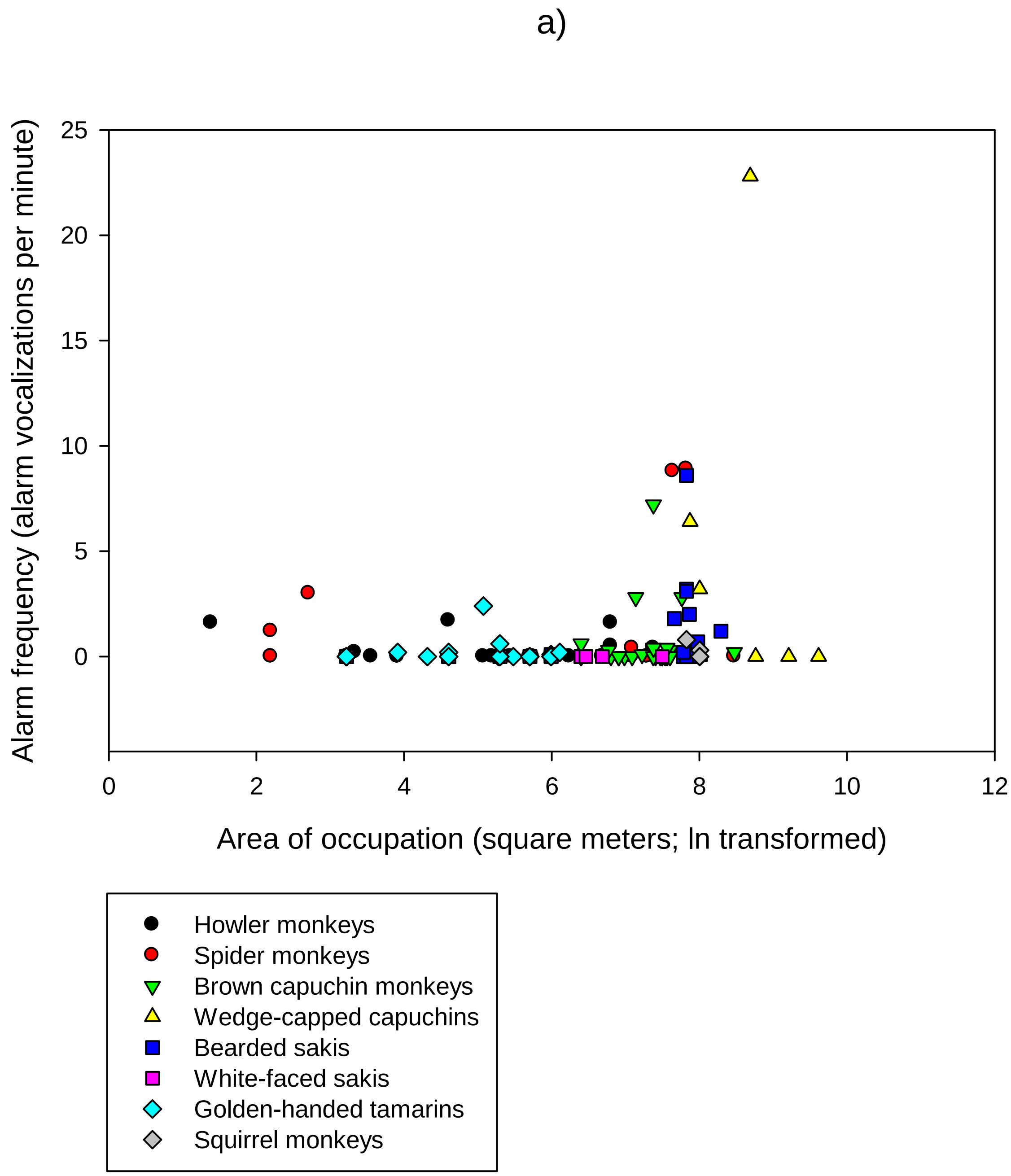


Fig. 3.8 – Area of occupation (a) and height differential (b) may influence alarm frequency.



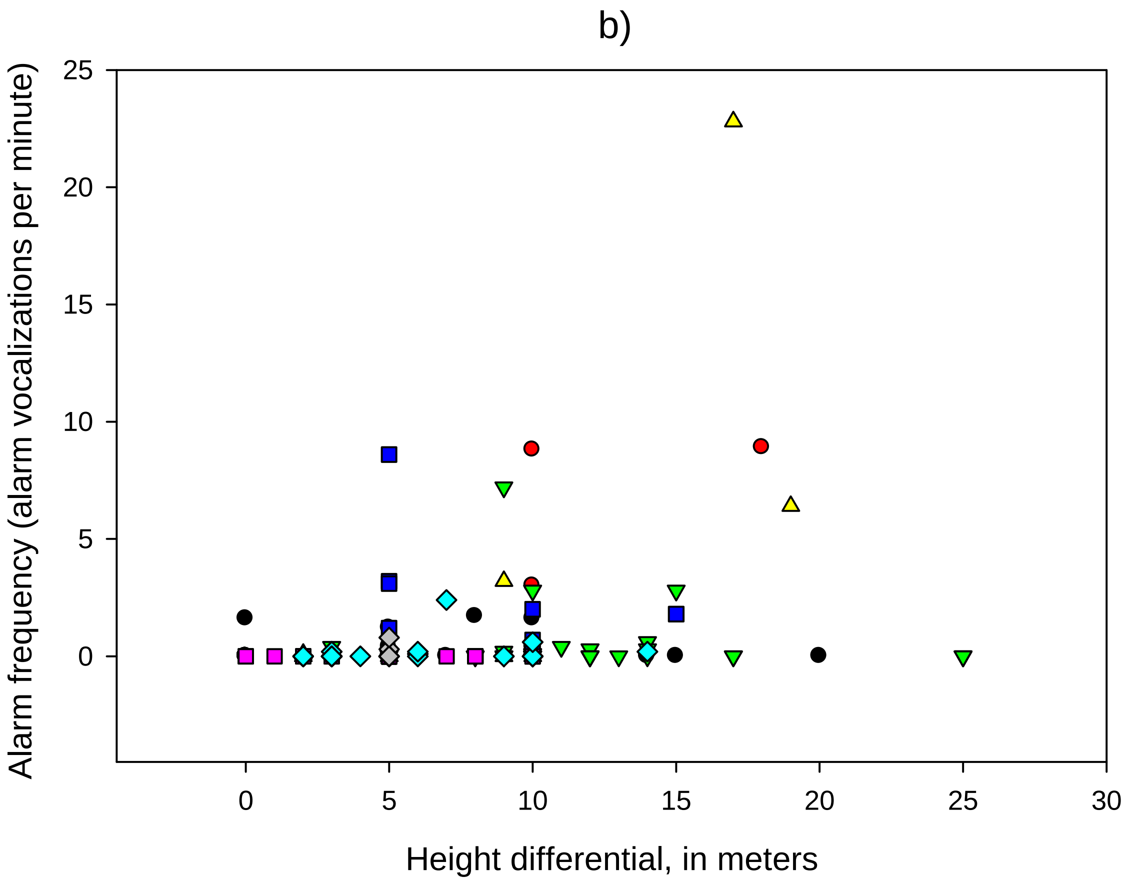

b)
Alarm frequency (alarm vocalizations per minute)
25
20
15
10
5
0
0
5
10
15
20
25
30
Height differential, in meters

Fig. 3.9 – Species comparison of forest types utilized. 1) high rainforest; 2) low rainforest; 3) swamp forest; 4) liana forest; 7) bamboo forest. Brown capuchins (CA) used all five forest types. Squirrel monkeys (SS), tamarins (SM), and spider monkeys (SM) were found in only one habitat each (liana, low, and high forests, respectively). The remaining species were found in both high and low forests.

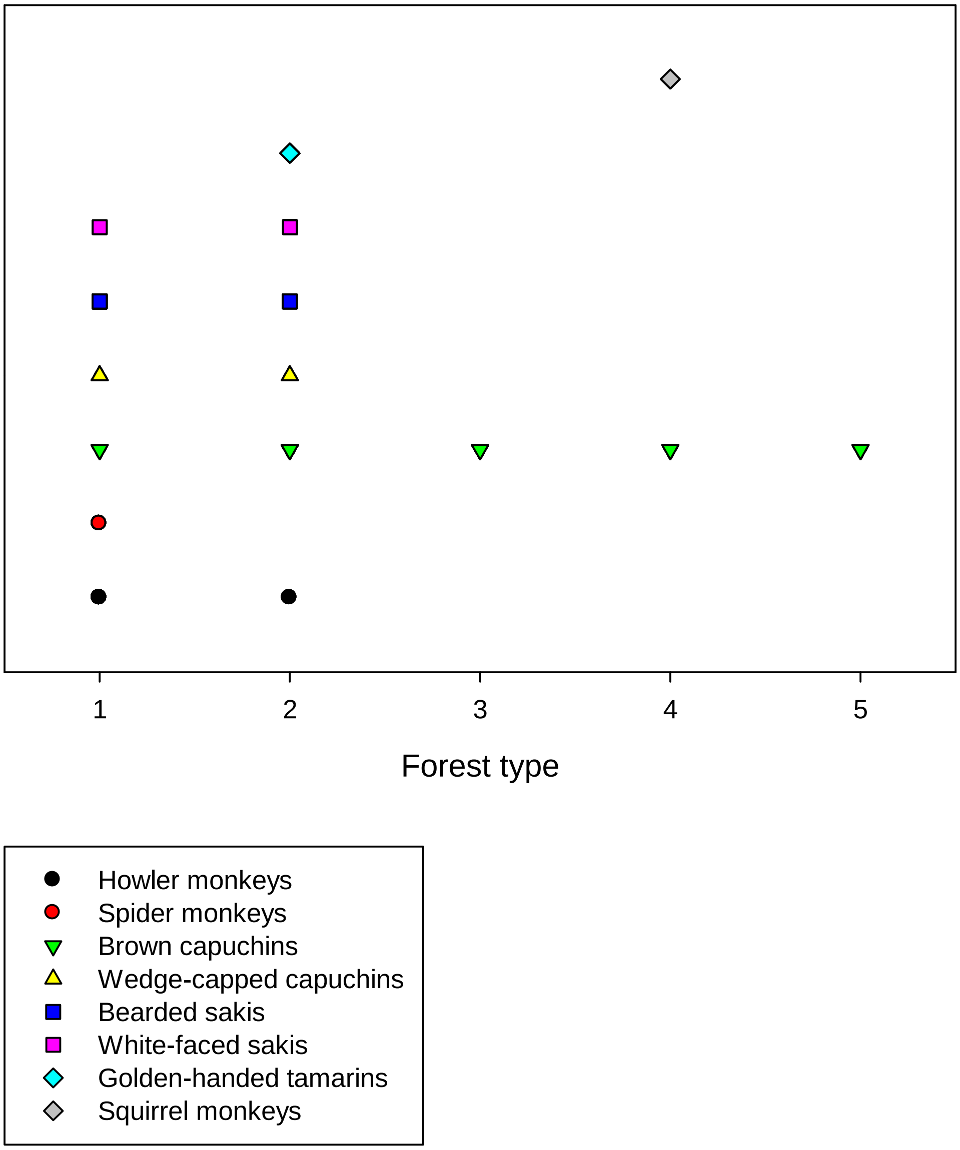


Fig. 3.10 – Mean vigilance rates (aerial vigilance: AV; terrestrial vigilance: TV; source-scanning: SS) decrease with increasing degree of understory density (n=178) where 0.5 is most open and 3.0 is most closed understory.

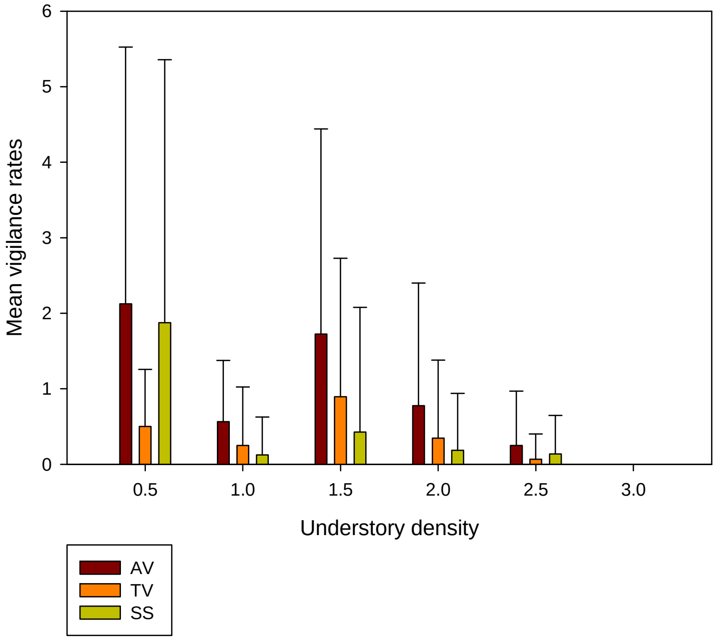


Fig. 3.11 – Frequency of aerial vigilance in high rainforest (HF), low rainforest (LF), bamboo patches (BB), liana forest (LNF), and swamp forest (SF).

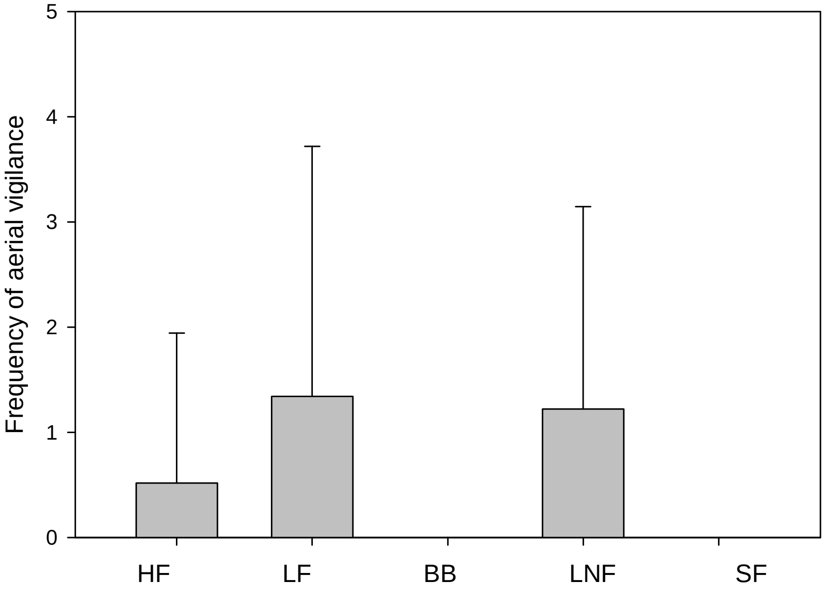


Fig. 3.12 – Frequency of alarm vocalizations in high rainforest (HF), low rainforest (LF), bamboo patches (BB), liana forest (LNF), and swamp forest (SF).

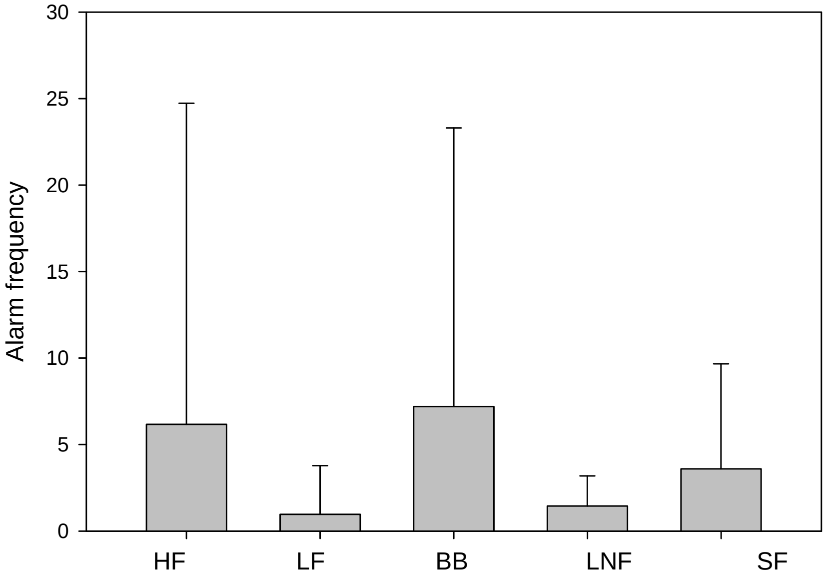


Fig. 3.13 – Overstory density increases with the introduction of HH vocalizations across all species.

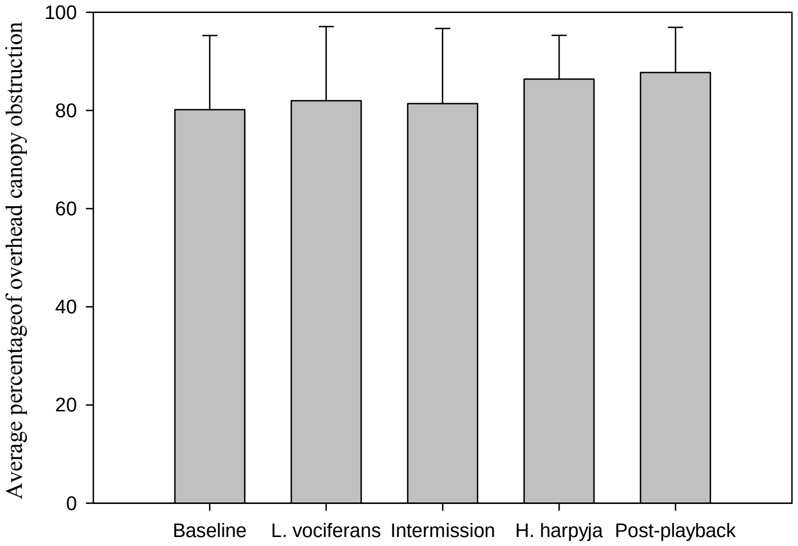


Fig. 3.14 – Mean aerial vigilance rates decrease with an increase of overstory density.

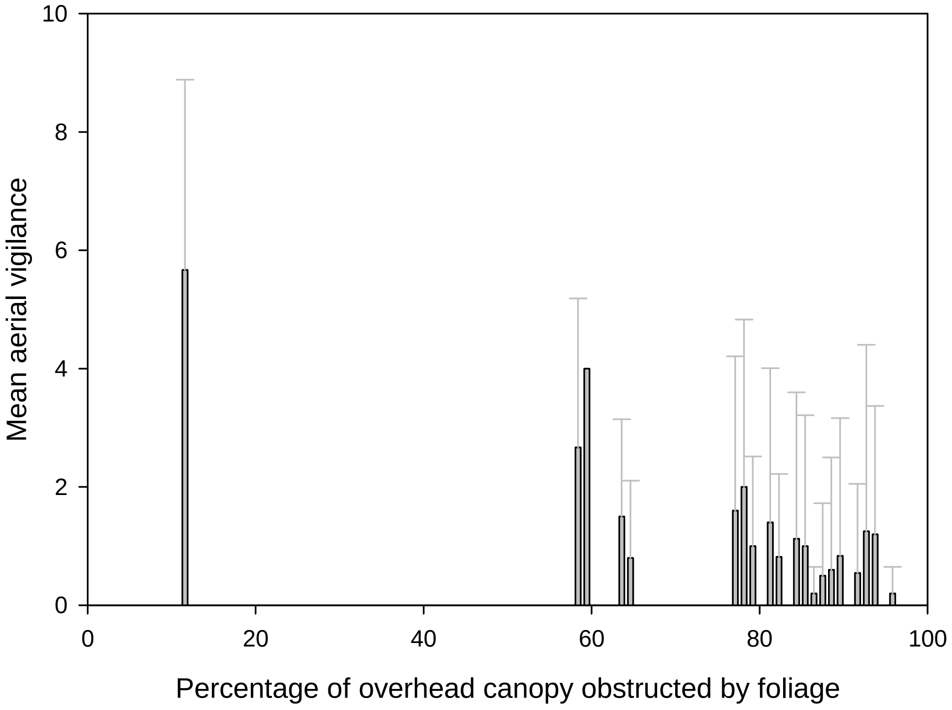


Fig. 3.15 - Activity budget by playback interval across species. Feeding activity is presented in red, while non-feeding activity is presented in gold. (a) reflects activity within baseline and LV intervals. (b) reflects activity within HH and post-playback intervals.

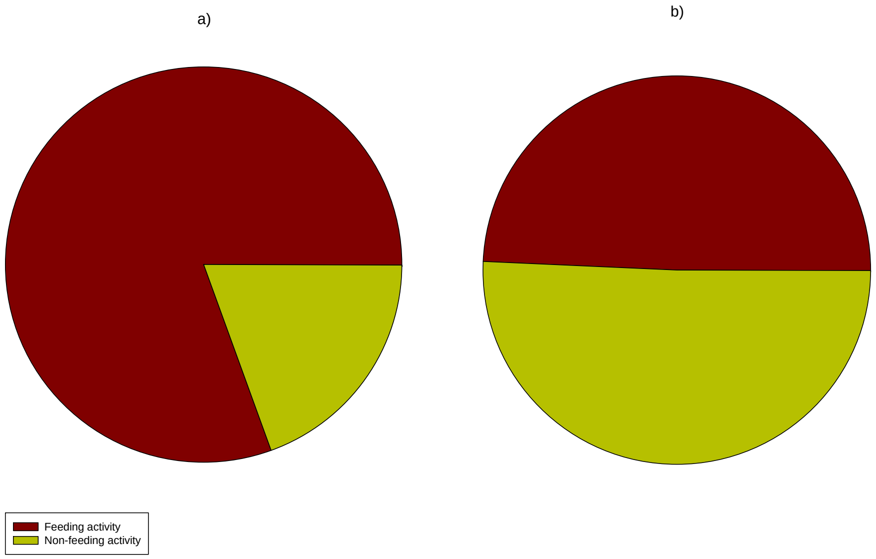


Fig. 3.16 – Mean alarm frequencies per minute by playback interval (corrected for duration). There are significant differences between free-ranging populations a (n=177; all species) and b (n=35; CA and SS).

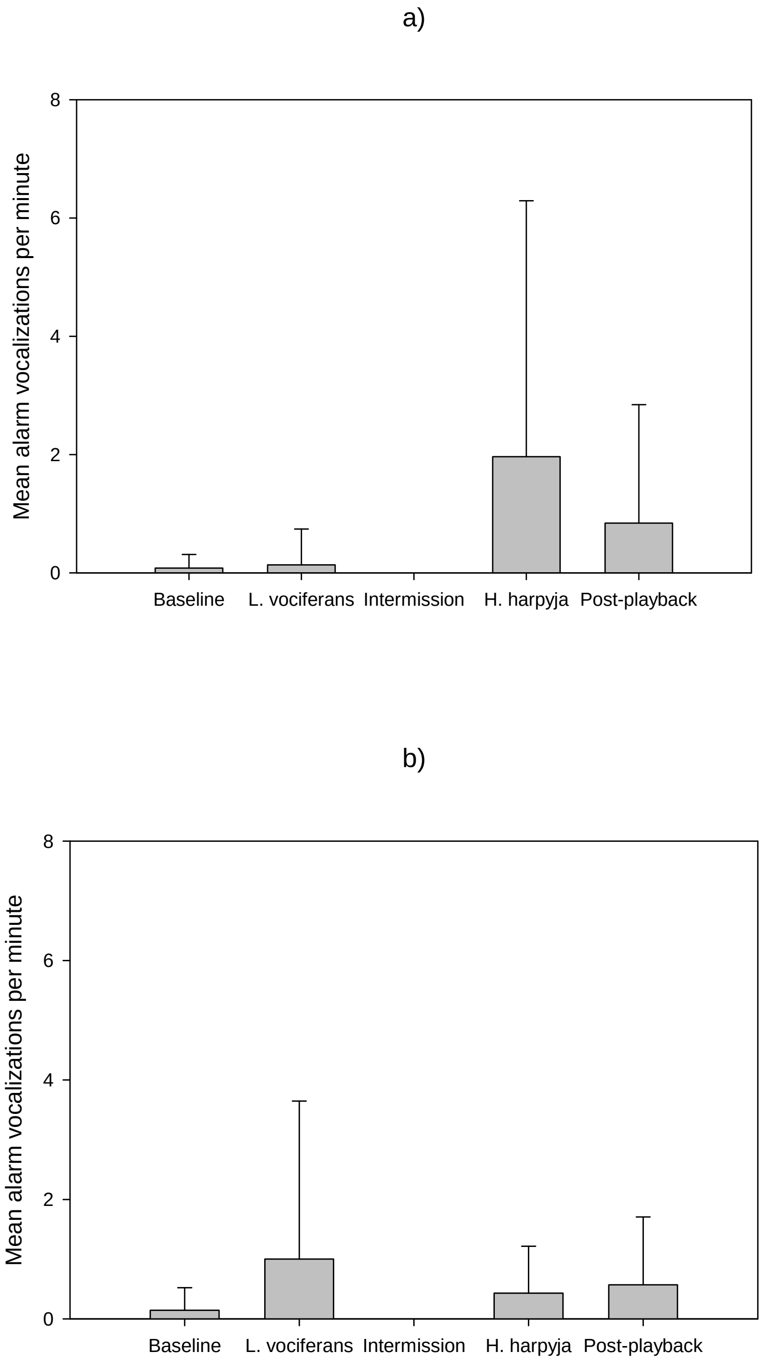


Fig. 3.17 – Overall alarm frequency is higher at RV than at BNP or Hiram College.

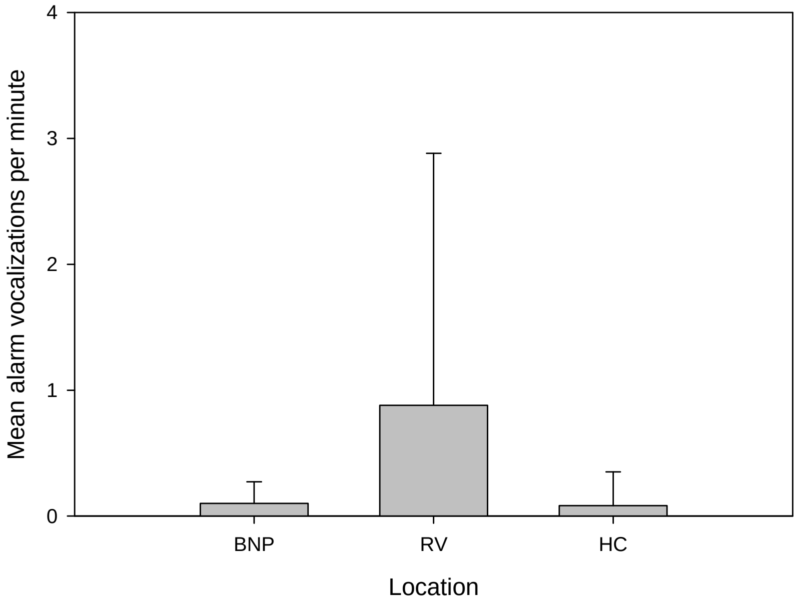


Fig. 3.18 – There is no significant difference in rates of aerial vigilance between populations of *C. apella* at BNP and Hiram College.

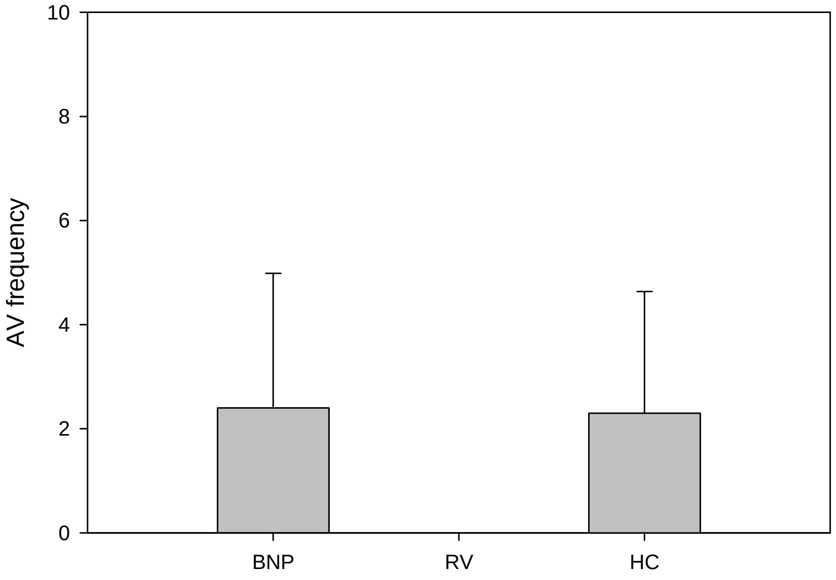
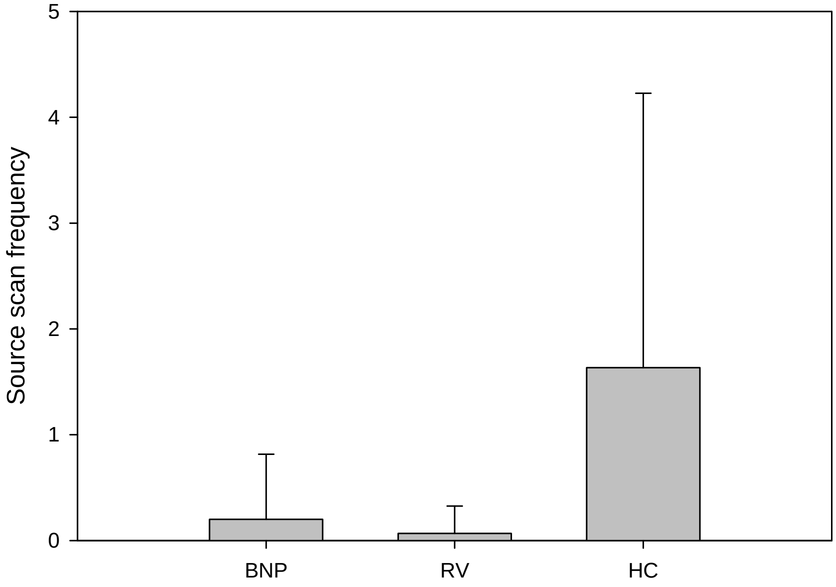


Fig. 3.19 – Source scanning frequency is significantly higher in the Hiram College population of *C. apella* than at either BNP or RV.



CHAPTER FOUR
DISCUSSION

The results clearly indicate that anti-predator behaviors were elicited by primates who were exposed to vocalizations of predator species. Alarm call vocalizations were given in greater frequencies in playback interval 4 (harpy eagle vocalization) than in any other playback interval. Groups at both parks differentially used their habitats dependent on playback interval, and more often sought areas with more densely covered overstory in intervals 4 and 5 (post-playback silence). Once these areas of the forest were attained, the groups were observed to act cryptically and exhibit stationary behavior at higher rates, while vigilance frequencies were increased.

Moreover, they suggest that, in order for primates to most effectively and most appropriately react to predators, some exposure to those predators is required. Alarm vocalizations were emitted with greater frequencies at Raleighvallen than at Brownsberg or Hiram College, and overall response was most severe among Raleighvallen capuchins.

4.1 - General patterns

The striking differences in alarm call frequencies, vigilance rates, and general behavioral response between intervals prior to and after the initiation of harpy eagle vocalizations are important in several ways. First, these results are consistent with other studies that indicate that primates react appropriately to auditory cues of predation (Gil-da-Costa, 2007; Gil-da-Costa et al., 2003; Treves, 1999; Zuberbuhler et al., 1999; Zuberbuhler et al., 1997; Gebo et al., 1994), adding to the mounting body of empirical evidence suggesting that animals can identify potential predators by auditory cues alone, and not only by visual contact.

Second, these results suggest that primates exhibit anti-predator responses to the vocalizations of potential predators (whether or not the primates recognize those audio cues as belonging to predators), and that the severity of response may depend on the degree of familiarity with the predator in question. The extent to which primates at Brownsberg have exposure to harpy eagles is unknown, but the primates there responded to the broadcast vocalizations of the raptor with anti-predator behaviors. The captive-born primates housed at Hiram College have had no known prior exposure to harpy eagles or any other predator (Phillips, pers. comm.), and although their responses were not consistent with those exhibited by their free-ranging counterparts, they did seem to respond to unfamiliar noises with anti-predator response behaviors.

Some free-ranging primate groups at Raleighvallen have regular, substantial contact with harpy eagles, and exhibited the most severe response of all groups sampled. These results suggest that the most appropriate (and likely most effective) responses to threat of predation from specific predators are learned and reinforced by regular antagonistic interactions with them, providing evidence in agreement with Ferrari's (2009) position that the production of alarm calls may be instinctual, but departing from the author's position in the suggestion that any anti-predator responses are "universal".

Third, these results show that vigilance frequencies, while valid and widely used indicators of predation risk (Gil-da-Costa, 2007; Boinski et al., 2003; Treves, 1997; Cords, 1990), are not its only applicable measurements. Components of this study suggest that frequencies of alarm vocalizations are valid measurements of risk perception by primates. As visibility is often constrained by the dense foliage associated with the neotropics, alarm vocalizations provide a reliable estimate of predation risk and risk perception when vigilance cannot be reliably measured.

4.2 - Predator-sensitive habitat use

The perceived presence of a predator appeared to have a major effect on the habitat use patterns of the primates in this study. Analysis of this data set indicates that not only do forest type, spatial occupation, and foliage density appear to influence anti-predator strategies (as in Boinski et al., 2003; Enstam and Isbell, 2002), but also that primates within these habitats evaluate their surroundings and seek refuge in more densely covered areas when faced with threat of predation, as suggested by other studies (Gil-da-Costa, 2007; Gil-da-Costa et al., 2003; Gleason and Norconk, 2002). These results add additional empirical evidence to previous studies documenting that habitats are selected in part to ameliorate the risk of predation, and that habitat use patterns are related to risk perception and risk reduction (Frechette, 2007; Boinski et al., 2003; Cowlishaw, 1997; Lima and Dill, 1990).

Spatial distribution and the selfish herd

Spatial occupation data indicate that an increase in area in one dimension (width, length, and height) is associated with corresponding increases in area in all other dimensions. However, modal spatial distribution patterns indicate that primates preferentially range in clumped distributions, seemingly regardless of spatial occupation variables. This suggests that small areas of occupation in all dimensions allow larger clumps that are more closely spatially packed, but larger areas of occupation demand clumps that consist of fewer individuals who are more widely dispersed throughout space.

Two patterns of spatial organization observed in this study may support the “selfish herd” function of alarm calling behavior, as hypothesized by Owens and Goss-Custard (1976). The authors suggest that alarm calls in shore birds, rather than serving to benefit close kin of the caller, instead serve to congregate more widely dispersed group members around the caller, thus reducing by diffusion the likelihood that the caller would be taken by a predator.

First, roughly three times as many alarm calls were associated with clumped groups in this study than with moderately dispersed or dispersed groups. Some observations support that non-clumped groups had a tendency to become clumped following alarm vocalizations (observed in spider monkeys, brown capuchins, wedge-capped capuchins, and potentially others), though it is difficult to tease apart whether the call or the clumped dispersion came first in the data, as well as whether both alarm frequency and clumped dispersion were both functions of the harpy eagle broadcasts. Additionally, individuals in more clumped groups may emit more frequent alarm vocalizations to diffuse the conspicuity of the alarm vocalizations themselves, limiting the amount to which the caller is faced with additional threat of predation or detection, and serving the same essential purpose as the selfish herd function.

Secondly, the frequency of alarm vocalizations increased with an increase in area (both spatial occupation and height differential). These results support the hypothesis that alarm calling functions to bring conspecifics in closer proximity to the caller. Already clumped groups have the benefit of near neighbors to dilute the effects of predation on any given individual, whereas dispersed individuals may emit alarm calls to bring other individuals closer to them.

As with distribution data above, causes and effects of alarm call behaviors are difficult to distinguish. It is difficult to ascertain whether spatial occupation increases as part of an anti-predator response, or whether the anti-predator response increases due to larger areas of occupation. Therefore, additional study is warranted to determine the causal nature of spatial organization and dispersion data on anti-predator strategies. The predator deterrence function of alarm behavior (Zuberbühler et al., 1999) is presumed to be very important for neotropical primates, as the majority of their predators employ ambush strategies.

Foliage density, visibility, and refugial areas

The modal degree of understory density was relatively high, and there was no difference in modal density between pre- and post-harpy eagle broadcast intervals. Significant increases in the degree of overstory density after the initiation of harpy eagle playback suggests that most of the study species utilize the density of overhead canopy as part of their anti-predator behavioral suite. This is consistent with documented observations by van Schaik and van Noordwijk (1989) that brown capuchins sought cover in dense vegetation in response to conspecific alarm vocalizations.

Further, these results suggest that perceived risk of predation within densely-covered canopy is lower. Theoretically, aerial predators would have a more difficult time capturing prey moving laterally or diving through obstructed canopy than they would through open, less continuous canopy. Boinski and colleagues (2003) have argued that liana forests pose serious risk of injury to understory raptors. Gleason and Norconk (2002) have demonstrated that white-faced sakis may remain motionless in dense understory for several hours after exposure to predator stimuli. As such, the pattern of refuge seeking behavior in neotropical primates is a potentially sound anti-predator strategy.

In addition, the unexpectedly high average overstory density and modal degree of understory density suggest that even when not directly faced with a perceived threat, primates preferentially range in areas more densely covered than not. This is consistent with observations that old world monkeys minimize predation risk by refraining from foraging in risky habitats (Cowlishaw, 1997; Isbell, 1994), that some primates are cognizant of the effect of habitat structure on predator efficacy (Enstam, 2007), and that primates may seek out refugial areas because of a reduced predation risk within them (Ferrari, 2009; Boinski et al., 2003).

Several researchers have proposed that some animals tend to forage in high risk areas despite being conspicuous to prey because the limited cover that led to their conspicuity would also necessarily leave ambush predators without concealment

(Cowlishaw, 1997; Lima, 1992). Theoretically, this strategy would be effective against harpy eagles and other sit and wait raptors in the neotropics, due to the tendency of those raptors to rely on concealment for hunting efficacy (Boinski et al., 2003). However, the pattern of habitat use described above suggests that the study populations do not employ that strategy. This may support raptor efficacy, as predators are suggested to be most attracted to areas that a) support high densities of prey species, and b) support efficient hunting behaviors (Cowlishaw, 1997).

Lima (1992) also describes a pattern of predator-sensitive habitat use in which groups may prefer to range in areas that offer escape or refuge opportunities. This may explain the apparent tendency of monkeys to range in dense understory, and the frequency with which Raleighvallen primates exploit bamboo patches and liana forests (Frechette, 2007; Boinski et al., 2003; pers. obs.)

The patterns of habitat use exhibited by spider monkeys and bearded sakis did not conform to those exhibited by all other species, which can be explained in a variety of ways. First, the overall overstory density means were high for both species, suggesting that species consistently ranging within highly-covered canopy would not further alter their habitat in response to the perceived presence of a predator because the preferred risk-reducing cover had already been achieved.

Alternatively, higher overstory densities may correlate with lower visibility, so that these high canopy dwelling species may move to more open canopy areas in order to more rapidly locate and identify a predator and its position. This may be critically important for groups under high threat of predation from raptors, as detection prior to an attack is thought to substantially reduce predator efficacy (van Schaik and van Noordwijk, 1989).

Finally, sample sizes were relatively small for both spider monkeys and bearded sakis (n=16 lines of observation; n=3 full experiment periods), so sampling error could have contributed to these seemingly abnormal responses.

4.3 – Activity patterns

Though cryptic behavior, in which animals freeze in hopes of escaping detection by predators, is over-used to explain the anti-predator strategies of species whose anti-predator strategies are not well understood (e.g. Stanford, 2002), the modal activity pattern across all primates in this study suggests that crypsis is a dominant and important anti-predator strategy. Stationary, non-foraging behavior was significantly more frequent after the initiation of the harpy eagle vocalizations than in any interval before them, not unlike observations of the reactions in other taxa to predator presence described elsewhere (Ferrari, 2009; see review in Boinski et al., 2000). When combined with patterns of increasing canopy density following harpy eagle broadcasts, these results suggest that neotropical primates evaluate the presence of a predator, seek refuge in dense areas of the forest, and remain there for a period of time.

This pattern, observed across all species observed in this study, may contradict Ferrari's (2009) suggestion that elongated stationary response exhibited by howler monkeys following a predation attempt or event was a consequence (or luxury) of a folivorous lifestyle. Conversely, the reduction of activity budget devoted to feeding across all species in this study may indicate a considerable devotion of more time and energy to predator detection (vigilance) and evasion (alarm calling, mobbing, flight, refuge-seeking) when the presence of a predator is perceived.

What was not expected was the reduction of travel time after the initiation of the harpy eagle broadcast. The emergent activity pattern suggests the following sequence of events: a) detection of a perceived predator, b) movement into a refugial area, c) then modal activity budget expenditure to detection and deterrence, exhibited by lack of movement and feeding behaviors, with an increase in vigilance behaviors and alarm vocalizations. These results are consistent with observations made by Gleason and Norconk (2002) regarding white-faced saki anti-predator strategies.

4.4 - Vigilance

Vigilance behavior was shown to be positively associated with perceived risk, as the frequency of aerial vigilance and source-scanning behavior was substantially higher after the initiation of harpy eagle vocalization broadcasts. This finding suggests that aerial vigilance and source scanning behaviors are important anti-predator responses and that these behaviors are emphasized with greater activity budget allocation (and possibly greater opportunity costs) in the presence of a potential predator stimulus. This is exceptionally important for the prey species of large-bodied raptors that employ ambush tactics, as once they are detected, their hunting efficacy rapidly and significantly decreases (Touchton et al., 2002; van Schaik and van Noordwijk, 1989). Therefore, primates theoretically benefit greatly from devoting time to attempting to detect predators. These findings reflect the prediction of Lima and Bednekoff (1999), which suggests predators are more effectively detected by prey when greater time is allocated toward vigilance behaviors.

Aerial vigilance frequency is lower in both denser understory and overstory, suggesting that primates evaluate the relative safety of their habitats and potentially benefit from allocating time to activities other than vigilance behavior while ranging in areas where perceived risk of predation is low. Findings of relationships between foliage density and vigilance are quite variable (Treves, 1997; Cords, 1990). Because understory raptors are predicted to be less likely to attempt an attack in very dense vegetation due to risk of injury (Boinski et al., 2003), it is presumed that denser patches of forest carry reduced perception of risk. Additionally, several researchers (Hill and Weingrill, 2007; Boinski et al., 2003) have suggested that fewer bouts of preemptive vigilance are required in denser habitats because detection is compromised due to low visibility. Both or either explanation that lower vigilance is a function of lower perception of risk or lower visibility may be supported by these results.

In a curious contrast, low forest and liana forest, which are considered relatively low-risk habitats in terms of their comparatively higher understory density, were associated with increases of aerial vigilance. This may reflect a height differential between high and low forest types: because the most significant avian threats to Surinamese primates are mid-canopy ambush predators, groups found in the emergent regions of high forest habitats are logically less likely to scan the sky for aerial predators because the presence of soaring hawks is low, whereas groups ranging in lower strata may need to increase their vigilance frequency to detect perched raptors.

Unfortunately, vigilance data were not gathered at Raleighvallen due to observer visibility constraints, so a comparison of vigilance rates between Raleighvallen and Brownsberg is not possible at this time. However, because alarm vocalizations and vigilance rates are honest indicators of perceived risk of predation, and because of the results of the comparisons between Raleighvallen and Brownsberg on the basis of alarm vocalizations, it is assumed that vigilance rates at Raleighvallen are higher than those at Brownsberg.

4.5 - Alarm vocalizations

As predicted, mean alarm vocalizations emitted during and after harpy eagle vocalization broadcasts were substantially higher than any other interval, strongly indicating that alarm vocalizations are indicators of perceived risk and proxy measures of predation risk. However, alarm vocalizations were emitted with greater frequencies in denser overstory and understory. This is perhaps contrary to suggestions that actual and perceived risk of avian attack is lower in dense habitats because of predator mobility limitations (Boinski et al., 2003), and the findings of other studies that evaluated the influence of habitat variables on anti-predator behaviors of other neotropical primates (Frechette, 2007).

Alternately, the higher frequencies of alarm vocalizations in denser cover could indicate the perception of lower risk. Because alarm vocalizations (and presumably the frequencies with which they are emitted) can be indicators of the urgency of the threat (Stanford, 2002) but also serve to reduce the inconspicuity of prey, primates may more effectively emit more alarm calls in denser cover without incurring additional risk while also diffusing the identity of the caller.

The low frequency of alarm vocalizations emitted in liana and low forest habitats may reflect a minimized perception of risk, but there are many variables that may confound useful analysis of these data. First, high frequencies of alarm vocalizations in high forest may reflect the high frequencies exhibited by spider monkeys and wedge-capped capuchins rather than the actual forest conditions. Further, the unexpectedly high alarm frequencies in bamboo and swamp forest habitats are from smaller sample sizes and exclusively at Raleighvallen, where the predation risk is thought to be higher, and therefore the sensitivities to harpy eagle playbacks were expected to be greater. There does appear to be a direct relationship between alarm frequency and maximum height, possibly indicating that higher-strata species emit more alarm vocalizations because they range higher in the canopy. Indeed, the four most vocal species (wedge-capped capuchins, spider monkeys, bearded sakis, and brown capuchins) are observed more frequently in mid- and upper-levels of the canopy (Fleagle, 1999; Mittermeier and van Roosmalen, 1981). These observations may oppose the hypothesis that predation risk (or perception thereof) decreases with an increase in ranging height (see review in Boinski et al., 2000).

4.6 - Learned and reinforced response

Owren and Rendall (2001) argue that sounds themselves do not have encoded meaning in the referential sense, but that continued exposure to stimulus, alarm vocalizations, and response patterns can condition an organism to appropriately react to subsequent vocal cues. Bachorowski and Owren (2003) further suggest that reactions to alarm calls are learned and reliant upon context. Therefore, one can extrapolate that primates may learn, through exposure and contact, how to appropriately respond to audio cues from potential predators in the same way they experientially learn proper responses to conspecific alarm vocalizations. Similar suggestions have been made in previous studies, in that exposure to predation attempts may benefit survivors by either reinforcing anti-predator behaviors (Friant et al., 2008; Boinski et al., 2000) or encouraging the rapid development of them (Gil-da-Costa et al., 2003).

Therefore, I expected differences in mean alarm vocalizations between the following primate populations: a) those with a significant rate of contact with a known population of harpy eagles and overlapping home ranges with the same, b) those with an unknown rate of contact ranging in an area without regular sightings or evidence of harpy eagle presence, and c) those born and reared in captivity with no prior exposure to predatory raptors. Significant differences were observed, further supporting Owren and Rendall’s assertions and indicating that severity and appropriateness of anti-predator response is, in part, dependent upon degree and regularity of contact between predator and prey.

That said, it is also suggested by my results that prey species respond with increased vigilance, increased alarm frequency, or both, to apparently unfamiliar sounds. These observations are also consistent with Owren and Rendall's (2001) perspective that vocalizations, and particularly alarm calls, are best explained as resultant from the caller's psychological state of arousal, and reactions to those calls reactions to that portrayed arousal rather than to encoded signals. Captive-born primate groups expressed anti-predator behaviors to both screaming piha and harpy eagle vocalizations, including alarm vocalizations, which is consistent with playback studies conducted on some captive-born groups but not others (see review in Friant et al., 2008). Therefore, it is suggested that the ability and capacity to emit alarm vocalizations in response to unfamiliar noises or otherwise stressful situations is not dependent upon exposure to predator species in the wild. In fact, as suggested by Boinski and colleagues (1999), alarm vocalizations in some species may be used to measure overall stress levels of captive primates.

Free-ranging primates at Raleighvallen and Brownsberg appeared to recognize piha vocalizations as non-threatening and did not react to them with anti-predator behaviors, but did respond to the broadcast vocalizations of harpy eagles. This further suggests that reinforcement is critical to the appropriateness of both the response to the innocuous piha vocalizations, as well as the hazard or unfamiliarity of the harpy eagle vocalizations, but that exposure to predators is not a necessary condition of behavioral anti-predator response. This is consistent with Janson's (1998) suggestion that animals need not be faced with predators to exhibit adaptive counter-strategies.

However, because alarm calls and other anti-predator behaviors are costly, the cognitive ability to distinguish potential threats from myriad other forest sounds is critical. Further, the ability to effectively gauge the riskiness of a given habitat and make appropriate subsequent decisions is paramount. Failure to appropriately evaluate the riskiness of a given habitat can result in the ultimate negative consequence: death.

4.7 - Explanations for non-responses

White-faced sakis in this study were routinely observed in lower canopy and understory habitats ($\bar{x}$=9.37 m; $\bar{x}^{min}$=4.86 m; $\bar{x}^{max}$=10.33 m), which is not unusual for the species (Fleagle, 1999; Mittermeier and van Roosmalen, 1981). Groups on which experiments were conducted were mostly found on the Brownsberg plateau, and no groups of sakis were located at Raleighvallen. Therefore, unlike with other groups that were observed along the slopes of the Brownsberg mountain, that allowed me to obfuscate the position or perceived height of the broadcast source, the perceived height of the speaker was assumed to be the true height. It is possible that the lack of response from white-faced saki groups is related to unrealistic portrayal of harpy eagle vocalization conditions due to the vertical proximity to the speaker.

However, many plateau groups occupying high and low canopy strata exhibited minimal responses to harpy eagle vocalization broadcasts, including groups of howler monkeys, tamarins, and brown capuchins. Therefore, positioning of the speaker is a less likely explanation for the lack of responses from these groups. It is possible that the frequency of other anthropogenic noises (chainsaws, water pumps, machetes, automobile engines) that have elicited alarm (or at least agitation) vocalizations in groups at Raleighvallen (pers. obs.) have dulled the response to the vocalizations of potential predators in groups at Brownsberg, that may lack the regular, consistent reinforcement for appropriate response provided by contact with real predators.

It is also probable that since cryptic foragers such as white-faced sakis (Boinski et al., 2000; Walker, 1996) are less likely to emit alarm vocalizations because alarm vocalizations announce their presence to a predator (Janson, 1998). This may be especially true when the predator in question is vocalizing, because a vocalizing ambush predator would be unlikely to be aware of the presence of the prey species (Janson, 1998). This may be the best explanation of why white-faced sakis were so reticent to respond to harpy eagle vocalizations. Alternately, some observations of response reactions that did not involve alarm vocalizations may have been responses to relatively "strong" threats, as described by Gleason and Norconk (2002).

Anti-predator responses appear to be highly variable, on a population, group, and even individual level across species. The only reliable, consistent alarm responses throughout the study were emitted by brown capuchins at Raleighvallen. Considering that brown capuchins are a major prey item of harpy eagles (Ford and Boinski, 2007) and that the groups measured at Raleighvallen closely neighbored a harpy eagle nest from at least 2002 (Boinski et al., 2003) through roughly 2007 (J. Frechette, pers. comm.), this is not unexpected.

Although highly variable alarm responses emitted by howler monkeys is documented elsewhere (Gil-da-Costa, 2007), howler responses at Raleighvallen were less intense than expected. Multiple “grunt” vocalizations were emitted each time harpy eagle vocalizations were broadcast at Raleighvallen, but no loud call vocalizations were emitted. This may suggest that some groups under extreme risk of predation alter their strategies, as Janson (1998) and Gil-da-Costa (2007) suggest is possible, or that there are few consistencies in anti-predator response between groups and populations. This is not unexpected, as a certain level of behavioral plasticity based on predation risk and predator density is anticipated to be beneficial, not only in terms of activity budget allocation, but also in terms of the strategies of the predators in question. For instance, ranging in high canopy strata with little overhead cover is likely to be an ineffective strategy in an area rife with soaring raptors (Boinski et al., 2000).

4.8 - Estimates of predator presence by response data

If regularity of contact with a given predator is one determinant of alarm response of a prey species, then likely territorial ranges of a given predator may be estimated by frequency of alarm responses in that area. If this assumption is accurate, and if harpy eagles do in fact exist at Brownsberg, then the alarm data, as proxy measures of perceived risk, suggest that the most likely area of regular occupation is along the slopes of the mountain near WK trail, where the most severe alarm and mobbing responses were noted. This is also the area where suspicious kill residue was found associated with a feather identified by park staff and researchers as belonging to a harpy eagle.

Although the last known harpy eagle nest site is now abandoned at Raleighvallen (J. Frechette, pers. comm.), one can infer by the reactions from the brown capuchins at the park that the raptors presence is either still established, which is supported by reports from researchers who observed harpy eagles at Raleighvallen several times during a week-long visit in 2009 (J. Frechette, pers. comm.), or that appropriate responses, once learned, are not easily forgotten, as suggest by Gil-da-Costa and colleagues (2003).

4.9 – Interspecific associations

This study attempted to compare responses between species, populations, and geographic locations. One peculiar anecdotal observation was that primate groups at Brownsberg were only found in mixed-species associations on one occasion (squirrel monkeys and bearded sakis), unlike the frequent mixed-species associations at Raleighvallen and elsewhere throughout the neotropics, particularly between squirrel monkeys and brown capuchins. Studies have shown mixed-species associations to be profitable in terms of potential reduced predation risk and actual reduced anti-predator activity responsibilities per individual among cercopithecines (Treves, 1999) and in the new world (Frechette, 2007; Terborgh, 1983).

CHAPTER FIVE
CONCLUSION

Clearly, predation is a significant factor in the behavioral and ecological repertoires of primates and other animals. The threat of being preyed upon has been a major factor in the evolution of behavioral and morphological traits, and even if the risk of predation is relatively slight, the selective pressure exerted on a population from it can be very strong. Animals are expected to react to the perceived risk of predation rather than the actual observed rate, and as such, correlates of perceived risk are expected to be high even when rate of predation is not. That said, anti-predator responses are variable between species, populations, and social groups, and may depend on several factors: a) presence of predator species, b) frequency of interaction between predators and prey, and c) reinforcement of ultimate predator-prey relationships by observation of successful predator attacks.

Animals in the neotropics may face a substantial threat of predation from intact, diverse predator guilds. Potential predators include several raptors (including harpy eagles, crested eagles, and ornate hawk eagles), felids (including jaguars, ocelots, and pumas), and other mammals (including tayras). All of these predators are suspected or documented at Brownsberg and Ralighvallen. The encounter rates of primates and primates within these parks is unknown, but it is presumed, through anecdotal, observational, and documented evidence, that some primates at Raleighvallen have regular, substantial contact with harpy eagles whose home ranges overlap with their own.

Therefore, it is presumed that primates at Raleighvallen likely experience higher risk of predation than many of those studied at Brownsberg, and the empirical evidence gather in this study may suggest that that presumption is warranted.

Habitat variables (understory density, overstory density, forest type) were found to be effective components of species' anti-predator strategy, as well as reasonable predictors of the severity of other responses. Further, a variety of social and behavioral variables appeared to influence anti-predator behavior (spatial positioning and dispersal) and be influenced by the perceived presence of predators (activity patterns).

Use of a densiometer in this study provided a way to measure habitat variables as they pertain to risk of predation and prey perception thereof. This is encouraging, and to my knowledge, few primate behavioral studies have employed the use of these devices to quantify habitat cover. Phillips and colleagues (1998) used densiometer measurements to calibrate the effectiveness of GPS signal acquisition in different environments, while Gross-Camp and Kaplan (2005) used them in a seed dispersal study. Vidal and Cintra (2006) are the only study that examined canopy density and attempted to relate it to predation risk in primates. Usefulness is not limited to predation studies, as densiometers may be effective for the quantification of ecological and phonological variables in a variety of research areas.

Alarm vocalizations are emitted in response to audio cues of predator presence or the presence of unknown, alarming noises. The production of alarm vocalizations by captive-born primates with no prior exposure to predators suggests that the production of alarm vocalizations in certain contexts has an instinctual basis. However, frequency and severity of response appears to be related to the prey species' ability to identify the predator vocalizations as such, and that likely depends upon frequency of interaction. If this is accurate, alarm responses elicited by broadcasts of predator vocalizations may provide information about the presence of predators in a given area. This is a useful measure for researchers studying predator-prey interactions, as it may be an additional inferential tool for estimating predator densities.

Alarm vocalizations probably serve multiple functions, possibly including signaling predator detection, encouraging an increase in neighbor proximity, and alerting close kin of danger. Overall frequency of alarm vocalizations is apparently related to group size, but not exclusively, as several medium-sized groups emitted no or infrequent alarm vocalizations.

Playback studies may be particularly effective means of studying prey response to specific predators, because a) the predator cue eliciting the response is selected by the observer, which allows measurement of predator-specific responses, b) measuring the response to perceived threats of predation may be more indicative of avoidance and deterrence strategies than the collection of baseline behaviors (such as vigilance), and c) the observer presents minimal risk of upsetting the natural predator-prey relationship by interfering with predation events. Therefore, playback studies featuring broadcasts of predator vocalizations can yield valuable information regarding the anti-predator responses within and between species.

Vigilance behavior decreased with areas of dense cover and limited visibility, suggesting that primates perceive lower visibility, lower predation risk, or both within dense habitats, and alter their strategies accordingly. This strategy would be adaptive for any animal, because even non-intensive anti-predator strategies may limit activity allocation to other activities, such as foraging or mating (Boinski et al., 2003; Janson, 1998; but see Treves, 1997 who argues that scanning for predators does not preclude an individual from looking for food or mates). Therefore, those animals that can selectively engage in differential anti-predator strategies based on the relative safety afforded by a given habitat will theoretically have increased fitness opportunities.

Further comparative studies between groups of primates at Raleighvallen and Brownsberg could shed additional light on the importance of intense predation threat on the behavioral ecology of prey species, and how the threat of being eaten can foster substantial behavioral differences between groups. This study is lacking reliable information of vigilance behaviors at Raleighvallen, due to brief study period and visibility issues. Bolstering of vigilance data would improve the overall comparative quality of the study.

Additionally, future directions for the primate-community-minded study of anti-predator strategies include attempting to use predator models to elicit response behaviors based on visual rather than auditory cues. Lack of responses in some primates (white-faced sakis, in particular) may indicate a stronger reliance on visual cues, which is suggested by some reports of their responses to perceived threat (Gleason and Norconk, 2002). Therefore, to attempt to understand the intricacies of anti-predator behaviors as completely as possible, auditory and visual stimuli should be presented to prey species, and in addition, the behaviors and population densities of predators themselves should be more intimately measured by whatever means possible.

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