

PRIMATE RESPONSE TO TOURIST PRESENCE AT RALEIGHVALLEN, CENTRAL
SURINAME NATURE RESERVE

By

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A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

2010

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To my family, friends and fellow students

ACKNOWLEDGMENTS

Many people contributed to the completion of this dissertation. I would like to thank my advisor, Sue Boinski and the rest of my committee; David Daegling, John Krigbaum and Brijesh Thapa. I would also like to thank Anna Vick and Jennifer Hotzman for support above and beyond the call of duty. Special thanks to Erin Ehmke, my wonder monkey twin, editor, sounding board and compatriot throughout this entire journey. Further thanks go out to the Raleighvallen field assistants: Miranda Davis, Andy Dosmann, Liz Fly, Julie Massicotte and Tory Shelley.

I am also grateful to the 365 tourists from the Netherlands, Suriname, Belgium, France, Austria, the United States and Ireland who allowed me to follow them. I also thank STINASU, Josta Schet, Marie Djosetro, the RV guides: Sandro, Donovan, Chafied, Sharif, Diego, Sergio, Kenneth, Apunte, Sabah, Vanski, Alma and Marcel and the Raleigh boys: Ronnie, Raymond, Sudanu, Benito, Gilly, Gordon, Sonny, Steven, Setman, Mano, Captain, Sampa and to Anna. Extra special thanks goes to my family for always believing in me and supporting me. Super extra special thanks to my husband, Rick, for being there for everything, loaning me to the jungle for six months, and helping me remember what is important in life.

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Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

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By

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December 2010

Chair: Sue Boinski
Major: Anthropology

This study explores the variables that predict the immediate responses of seven primate species to tourists at Raleighvallen in the Central Suriname Nature Reserve. This study adds a theoretical framework to research on the effects of wildlife tourism on animals by testing hypotheses informed by behavioral ecology. I use anti-predator responses of primates to tourists as a measure of the effect tourists have on normal primate behaviors. My results demonstrate that some primate species engage in anti-predator responses when exposed to tourists while other species do not seem to be bothered by tourist presence. Habituated monkeys alarm call less than unhabituated monkeys and smaller and faster tour groups result in more alarm calls than larger and slower groups. Species temperament can somewhat predict responses to tourists. Further, primates who are not threatened by tourists continue their natural foraging regime when in the presence of tourists—suggesting that feeding rates may be used as an indicator variable for primate disturbance.

I also measure predictors of tourist encounters with primates. Primate species known to be most abundant in the area were seen most frequently and more

encounters with these species occurred in dense versus open habitat. Results from this study can be used to make management and monitoring plans that will help keep wildlife tourism in Raleighvallen sustainable, minimizing its impact on the primates in the area as well as providing a satisfactory tourist experience that can lead to economic gains for the local people.

CHAPTER 1 INTRODUCTION

Habitat loss and species extinctions are serious threats to biodiversity (Awise et al., 2008; Brook et al., 2003; Koh et al., 2004; Pimm and Raven, 2000; Thomas et al., 2004). Many solutions are proposed to combat these threats, one of which is increasing conservation dollars and interest through wildlife tourism (WT); the tourism of experiencing wild animals in natural areas (Burger, 2000; Reynolds and Braithwaite, 2001; Roe et al., 1997; Walpole and Leader-Williams, 2002). In fact, tourism in general has become a significant part of the global economy. Tourism currently accounts for 9.6% of the world gross domestic product and it is expected to grow by 4.0% annually over the next ten years (World Travel and Tourism Council, 2009). Moreover, 20-40% of international tourists participate in WT and this high market share results in fierce competition among tour operators to provide more wildlife-related tourism experiences (Reynolds and Braithwaite, 2001).

Wildlife tourism is not without ecological impacts, however, and the ecological effects of such an industry must be considered. Increasing WT puts more people (tourists and tourist industry workers) into natural areas, possibly resulting in negative impacts on the ecology of the area that should be protected (Blamey, 2001). Furthermore, conservation based solely on the money from WT is susceptible to economic recessions and political instability (Clifton and Benson, 2006; Ormsby and Mannle, 2006). These issues necessitate research into the causes of wildlife changes associated with WT. Studies of the ecological impacts of WT to date are largely descriptive, and suffer from a lack of theoretical background (Backman and Morais,

2001; Buckley, 2001; Calver, 2005; Fennell, 2001; Frid and Dill, 2002; Rodger and Calver, 2005).

While there are numerous descriptions of wildlife responses to tourist presence, few of these studies situate their results in an explanatory framework (see Burger, 1998; Fairbanks and Tullous, 2002; Jacobson and Lopez, 1994). Burger (1998), for example, finds that common terns (*Sterna hirundo*) in New Jersey fly over their nesting area in greater numbers when approached by personal watercraft as compared to when approached by motorboats. Burger recommends that personal watercraft be kept away from tern nests, but does not go further and ask what it is about personal watercraft versus motorboats that leads to this flight response. The additional detailed knowledge of the characteristics of personal watercraft leading to the negative response would allow for more nuanced management plans, perhaps stating that a whole group of watercraft producing a certain noise level should be kept away from the tern nesting area. A number of researchers have noticed this need for more explanation of animal responses to WT (Backman and Morais, 2001; Fennell, 2001) and stated that more focus on underlying causes of wildlife responses to WT is needed to create more effective management plans (Calver, 2005; Frid and Dill, 2002).

This study investigates the immediate, short-term responses of primates when encountered by tourists at Raleighvallen, in the Central Suriname Nature Reserve. Hypotheses informed by behavioral ecology are used to investigate possible predictors of the immediate responses of primates to tourist presence. Hypotheses investigate a number of independent variables including rates of fleeing, alarm calls and feeding, primate species temperament, frequency of tour groups, habitat where encountered,

body size and tour group behavior. In testing these hypotheses I build upon prior studies of WT but add an emphasis on behavioral ecology—placing the immediate responses of primates to tourist in an evolutionary context. Addition of this theoretical context allows for a deeper understanding of wildlife response to tourists and, ultimately, more successful and sustainable management plans. In this introduction I provide a brief history of WT, discuss the need for a theoretical framework in studies of the impacts of WT, explain why effects of WT on primates should be studied and introduce the structure of the following chapters.

Description and Brief History of Wildlife Tourism

What is Wildlife Tourism?

Tourism can be divided into many subspecialties such as adventure tourism (Swarbrooke et al., 2003; Weber, 2001), heritage tourism (Nuryanti, 1996; Poria et al., 2003), sex tourism (Leheny, 1995; Oppermann, 1999) and medical tourism (Connell, 2006). Wildlife tourism (WT) is the tourism of experiencing wild animals in natural areas (Roe et al., 1997). Although the two are often used synonymously, WT is not the same as ecotourism. Ecotourism is “responsible travel to natural areas that conserves the environment and improves the well-being of local people” (The International Ecotourism Society, 2009) and may be considered a subset of WT. WT is not always held to the same environmentally beneficial standard as ecotourism, although researchers often consider WT to be benign as long as hunting does not occur (Ikiara and Okech, 2002).

WT is frequently seen as a remedy for habitat destruction and used as a conservation tool (Burger, 2000; Higginbottom et al., 2003). Increasing numbers of countries and NGOs are implementing tourism activities (Hawkins and Lamoureux, 2001) and these must be managed carefully to ensure they meet their goals. There is a

danger that in the rush to implement WT, provisions will not be made to monitor for possible serious impacts (Goodwin, 1996). The many stakeholders involved in WT, plus the lack of knowledge about how WT affects various components of ecosystems make implementing successful WT difficult (Goodwin, 1996; Weinberg et al., 2002).

History of the Study of Wildlife Tourism

Human interest in wildlife is nothing new, as humans have co-existed with wildlife since their earliest inceptions. Humans have always had to pay attention to the habits of wild animals for food and protection. In more recent times people began to observe wildlife for enjoyment (Newsome et al., 2005). In the last 200 years people began to travel to view wildlife with their own eyes as excursions such as safaris became popular (Adler, 1989).

The term “wildlife” is less than a century old (Hunter, 1990), and the study of WT is a relatively recent development (Rodger and Calver, 2005). Most WT studies focus on visitor management, visitor expectation and experiences, or business practices (Calver, 2005). A literature search on Google Scholar and the Web of Knowledge in July 2009 reveals that the earliest scholarly paper discussing WT appeared in 1975 (Gooders, 1975) and a number of 1970s and early 1980s papers discuss nature tourism based around wildlife without using the phrase WT (Duffie, 1981; Recher and Clark, 1974; Webster, 1980; Western and Henry, 1979). The phrase “wildlife tourism” does not find more widespread usage until the 1990s (Barnes et al., 1992; Valentine, 1992). Indeed, Backman and Morais (2001) surveyed three tourism journals, and found a rapid increase in studies dealing with ecotourism in the late 1990s. The fact that this is an emergent field partially explains the preponderance of descriptive studies and the lack of unifying theory found so far. In the next sections I will discuss why a theoretical basis

is needed to make sense of the currently disparate studies and how its implementation may facilitate predictions about wildlife responses to tourists. Ecological impacts of WT are not often discussed and when they are, the research tends towards the descriptive, not the theoretical.

Need for Research on Impacts of Wildlife Tourism

What Makes Successful WT?

Investigations of the impacts of tourism on specific taxa in particular habitats are used to measure the sustainability of wildlife tourism in each area. What is sustainability? The World Commission on Environment and Development (1987) describes sustainability as “development that meets the needs of the present without compromising the ability of future generations to meet their own needs.” Sustainable tourism should do the same (Butler, 1999a). Therefore, sustainable tourism must limit harm to the environment, be economically lucrative and minimize negative impacts on local people and cultures (Butler, 1999b). The many stakeholders involved in tourism endeavors (e.g., tour operators, tourists, governments, local people, and conservationists), however, differ in their ultimate goals and complicate the sustainability of WT (Backman et al., 2001; Blamey, 2001). WT planning needs to be a balancing act requiring advance planning and on-going management (Backman et al., 2001; Eagles, 2001; Newsome et al., 2005).

In order to be successful, ecotourism destinations must meet the expectations of tourists (Backman et al., 2001). Destinations recognize this customer demand and establish attractions that tourists want (Page and Dowling, 2002). While tourists interested in WT or ecotourism experiences are diverse (Page and Dowling, 2002), most of them want to learn about nature and be immersed in a wilderness experience

(Eagles and Higgins, 1998; Goeldner and Ritchie, 2003). Dissatisfied tourists neither return to natural attractions nor recommend them to others. Research demonstrates that tourist satisfaction increases as tourists are allowed more and more control over their encounters with wildlife (Reynolds and Braithwaite, 2001; Sparks, 1994) and close contact with wildlife (Backman and Morais, 2001; Valentine et al., 2004). Tourists also prefer experiences during biologically active times, such as birth or breeding seasons (Reynolds and Braithwaite, 2001). Most wildlife tour attractions provide such experiences through simple observation, but some involve closer contact such as touching or feeding—activities of high demand that can also have negative results such as disease transmission between animals and humans (Köndgen et al., 2008; Wallis and Lee, 2004), disruption of natural behaviors (Boutin, 1990; Roe et al., 1997) and aggression from animals towards tourists (Albert and Bowyer, 1991; Brennan et al., 1985; Fa, 1992).

Tourist preference for immersion in natural environments is often at odds with the objective of conserving the environment and improving the well-being of local people. Tourists introduced into an environment will affect both the ecological and cultural aspects of an area. Even presumably benign tours, such as those based solely around viewing wildlife, can have deleterious consequences. Effects of tourism on wildlife can vary from feeding and activity budget changes (Ikiara and Okech, 2002) to reproductive changes, (Jacobson and Lopez, 1994) ranging changes (Fairbanks and Tullous, 2002) and deaths of individual animals (Mathieson and Wall, 1982; Roe et al., 1997). Indeed, one review found that 81% of studies investigating the effects of WT on animals classified impacts as harmful (Knight and Cole, 1995). While most research finds WT to

have negative impacts, there is wide variation in the results of these studies from possibly mild effects whose influence on populations is unknown to clear cases where wildlife survival is threatened. Visitors to a state park in Utah, for example, have simply affected antelope ranging patterns (Fairbanks and Tullous, 2002). In contrast, increased tourism is associated with decreased penguin (*Megadyptes antipodes*) fledging survival (McClung et al., 2004) in New Zealand and with decreased fledgling survival of a rainforest bird (the hoatzin, *Opisthocomus hoazin*) in Ecuador (Müllner et al., 2004).

With proper management WT can produce a rewarding experience for the tourists, little effect on the animal and plant community as well as increased income for local stakeholders (Alexander, 2000; Kiss, 2004; Salafsky et al., 2001; Walpole and Goodwin, 2002). Examples of these positive outcomes can be found by examining dolphin (*Tursiops* sp.) encounters in Australia. At Monkey Mia in Australia, tourists were allowed to swim freely with wild dolphins but concerns grew about negative impacts caused by tourists in direct contact with the dolphins, at times touching the dolphins. A mandatory educational orientation was implemented and required of all tourists prior to interaction with the dolphins. Since the addition of education and monitoring programs, tourists have greatly reduced their harmful actions and tourist satisfaction has increased, leading to more income and sustainability for this project (Orams, 1994). A more recent study, however, indicates that tourists are still performing some unwanted behaviors towards the dolphins, and that even stricter monitoring is needed (Smith et al., 2008).

Creation of Management Plans for Successful Wildlife Tourism

The question then becomes: how do we create successful management plans to ensure the sustainability of WT as far as the wild animals are concerned? Many studies explore these goals (Burger, 1998; Burger and Gochfeld, 1998; Grossberg et al., 2003;

Lafferty, 2001; Matheson et al., 2006; Papouchis et al., 2001) but it is a slow and time consuming process to wait for each individual study to be carried out, published, and then possibly implemented by the management organization. Currently, there is no overarching theory present to explain wildlife responses to the presence of tourists (Fennell, 2001; Newsome et al., 2005). Studies of WT are based on one species in one specific area (Newsome et al., 2005) and have few conclusions that can be generalized to other taxa or habitats.

Much of the research on wildlife impacts of WT focuses on waterbirds. Researchers or managers interested in how introduction of tourists to an area will affect a bird species can find several studies on this topic (Beale and Monaghan, 2004; Burger, 1998; Burger and Gochfeld, 1981, 1998) and a review paper on the impacts of tourists on waterbirds (Carney and Sydeman, 1999). Different bird species respond to tourist presence differently—some species do not seem to be affected by tourist presence while others are strongly affected (Carney and Sydeman, 1999). In addition, response varies by the type of disturbance and the context. Some species respond more to direct approaches of people versus tangential approaches (Burger and Gochfeld, 1981). Also, birds are affected differently based on when the disturbance occurs in their life cycle and on the type of water craft they are exposed to (Burger, 1998).

Investigating bird response to WT within taxa does not necessarily result in any obvious patterns. Penguins are an oft-studied group and some studies find human presence to be related to decreased breeding success (Giese, 1996), while others find that the same species of penguin had less breeding success in an area free from

humans, and more breeding success when exposed to tourists (Fraser and Patterson, 1997). Such mixed results make it difficult to predict what will happen if penguins are exposed to tourists in a previously unstudied area.

Reviewing several studies of WT impacts on different waterbird species also demonstrates that these studies are generally descriptive and do not address the underlying reasons for the responses observed (Beale and Monaghan, 2004; Fennell, 2001). For example, Burger and Gochfeld (1998) investigate the effects of ecotourists on the behavior of five species of waterbirds in South Florida. They found that across species the presence of tourists decreased the time birds spent feeding and also that noise level decreased feeding time. No mention is made, however, of why birds respond to tourists in these ways. The authors state that their results can be used for management plans in other areas, and indeed the consistency of results across the five species helps this argument; other studies, however, conclude that some of the same species are not impacted by tourist presence (Carney and Sydeman, 1999; Goering and Cherry, 1971). Further understanding of which ecological variables are related to behavioral responses to tourists is needed in order to create more effective management plans for tourist areas.

Two important components of this dissertation are the use of a theoretical framework to understand the impacts of WT on primates and the testing of hypotheses based on the variables predicting animal response to tourists. These two additions to the WT literature will allow for conclusions to be generalized to other taxa and conditions which will in turn lead to more effective WT management.

Why Study Tourism's Effect on Primates?

Tourism affects different species in different ways. Because of each species' unique natural history, expected impacts may not be directly transferable across groups. This research is needed for three reasons: 1) primates are a common WT attraction (Newsome et al., 2005), 2) primates hold key positions in ecological communities as prey, predators, seed dispersers and pollinators (Caro and O'Doherty, 1999; Chapman, 1995; Chapman and Onderdonk, 1998; Lovett and Marshall, 2006; Sussman and Raven, 1978) and 3) primates have relatively long lives and contact with tourists may cause changes that are not immediately seen, but that could have a long-term effect on the population (Caldji et al., 2000; Essex et al., 2002). While results may not be directly transferable to other taxa, by investigating tourism's impacts on primates we can investigate methods of monitoring and management that can be translated for use with other species and in other WT contexts.

Primates are often the focus of tourist attractions (Cowlshaw and Dunbar, 2000; Dietz et al., 1994; Newsome et al., 2005), and may be sensitive to tourist impact due to their long lives (Charnov and Berrigan, 1993; Hennemann, 1983), complex social behavior (Eisenberg et al., 1972; Jolly, 1966), and high amount of parental investment (Harvey and Clutton-Brock, 1985). Primates have an extended life span which means that effects of tourist activities may only be apparent over a long time scale. Impacts of stress on a primate early in life, or in utero, may not be fully realized until later in life (Caldji et al., 2000; Essex et al., 2002) and can affect later development of motor skills (Schneider et al., 1992) or social behavior (Clarke and Schneider, 1993; Coplan et al., 1996).

Furthermore, WT impacts on primate social behavior could have important effects on survival. If tourism causes more or less intergroup aggression or more or less grooming, the effects could cascade to the population level. Increased inter or intragroup aggression may lead to stress and injury, resulting in smaller population numbers. Decreased grooming could affect social bonds in a group, possibly leading to group fragmentation, increased stress and lower reproductive rates. In addition, primates invest greatly in each individual offspring so they have less chance to recoup fitness losses if an offspring dies (Strier, 2007; Walters, 1987). Primates also put substantial energy into ensuring the survival of their infants, and time they may have to take away from parenting in order to guard against potential predators (e.g., tourists) could have serious effects (Frid and Dill, 2002).

Great apes in Africa are the focus of most published studies on the use of tourism for conservation of primates via the development of sustainable tourism (Blom et al., 2004; Kalpers et al., 2003; McNeilage, 1996). Tourism ventures in association with these taxa appear to be succeeding in attempts to both protect the threatened apes and provide economic opportunities for local people, possibly because tourists to these areas are tightly controlled in number and behavior (Litchfield, 2001; McNeilage, 1996). Thus, careful control, planning, and habituation seem to minimize negative impacts on the great apes (Blom et al., 2004; Johns, 1996). In addition, the establishment of the parks, popularity of the apes and presence of tourists helps safeguard these endangered animals by increasing local support for the protected areas. A 1995 census in the Virunga Volcanoes in Rwanda described a growing mountain gorilla (*Gorilla beringei beringei*) population, evidently in recovery from a steep decline in the 1960s

and 1970s (McNeilage, 1996). This population growth was associated with decreased signs of poaching, possibly attributed to increased presence of tourists and guides in the forest (McNeilage, 1996). A second survey of the entire Virungas region (situated in three countries: Uganda, Rwanda and the Democratic Republic of Congo) in 2000 estimated the gorilla population between 359-395 individuals, up from a low of 254 in 1981 (Kalpers et al., 2003). Some of this growth may be attributed to the increased monitoring of gorilla groups used for tourism, and a view of the gorillas as an important economic resource (via tourism) for the local people. During recent armed conflicts in the area different factions agreed on a commitment to leaving gorillas unharmed (Kalpers et al., 2003).

Aside from the example of great ape centered tourism, other destinations involving primates are less clear cut with respect to a benefit for the environment. In Belize, tourists at the Lamanai Archaeological Reserve negatively affected howler monkey behavior. Researchers observed increases in scattering and fleeing behavior, time on ground, vigilance towards tourists, vocalization rates and infant mortality in conjunction with tourist visits (Grossberg et al., 2003). Howler monkeys make a roaring sound to defend their territories, and guides and tourists sometimes attempt to elicit these noises by shaking branches and vocalizing at the monkeys. When the howlers roar in response other howler groups approach, as the sound indicates to them that the first group may be invading their territory. A violent intergroup encounter can follow, resulting in energy expenditure and possible injury to the monkeys involved (Grossberg et al., 2003). Other studies on primates and tourism have demonstrated changes in home range size, daily

travel routes, and amount of time spent feeding (Kinnaird and O'Brien, 1996; Koganezawa and Imaki, 1999; Saj et al., 1999).

Contribution of this Study

This study adds to the scant literature on primate-based WT by viewing the immediate responses of primates to tourists at RV, in the Central Suriname Nature Reserve, and interpreting the results within a theoretical framework of predator-prey interactions. Use of this framework allows for predictions to be made about the effects of WT on primates. By testing specific hypotheses about expected primate responses to tourists, generalizations can be made about the ways in which different primate species at RV behave when in contact with tourists (Table 1-1).

In the following chapters I explore the impacts of WT on a primate community in Suriname. First, I apply a much needed theoretical framework to studies of animals and tourism, resulting in clear, practical, and easily implemented method of monitoring primate response to tourists. I then explore the response of primates to tourists in more detail by investigating how responses are mediated through different ecological and biological variables. Finally I look at WT from the perspective of tourist behavior, explore how differently behaving tour groups affect primate responses, and discuss how to predict when primates are most likely to be seen. An outline of the following chapters can be found in Table 1-1.

In Chapter 2 I apply the theoretical framework of predator-prey relationships to interactions between tourists and primates in Raleighvallen, Suriname. I introduce predator-prey theory, discuss why it is applicable to the study of interactions between tourists and primates and then test three hypotheses regarding the short-term responses of primates in Suriname to the presence of tourists, indicating that predator-

prey theory can be used to understand these responses. As stated above, a theoretical basis founded in wildlife biology and behavioral ecology is needed to unify the disparate studies of WT that currently exist, which will allow more generalizations to be made from these studies. Once we can better predict how wildlife across taxa will respond to WT more effective management plans can be put in place to protect the wildlife that are the subject of WT. I conclude the chapter by discussing how the results of my study lead to a quick and effective method of monitoring effects of tourism on primates.

In Chapter 3 I examine how ecological variables affect primate response to tourists. I test three hypotheses investigating if and how primate responses to the presence of tourists change in different habitats, different contexts, and based on species size. This chapter fine tunes the results of the previous chapter and places these results in a more specific context. Conclusions can be used to help establish a management plan to limit disturbance of primate species. Furthermore, these conclusions can serve as a model for how to look at a specific location using the predator-prey theory.

Chapter 4 shifts focus to the behavior of the tourists. In this chapter I investigate how different tourist behaviors affect behavioral responses of the different primate species in Raleighvallen. I maintain the use of the predator-prey framework to measure how threatening primates find tourists but in this chapter I look at how tourist noise level, group size and speed affect primate responses. These results can again be used to manage tourist behavior with the goal of minimizing effects of tourism on the primates.

Lastly, Chapter 5 asks what variables predict whether or not tourists encounter primates. As discussed earlier, a WT destination cannot be successful in sustaining

itself if tourists do not get what they want out of the experience (Backman et al., 2001; Wight, 2001). Many tourists in other locations want to see wildlife (Chan and Baum, 2007; Chapman, 2003; Curtin, 2005), therefore knowledge of how to see wildlife can contribute to the sustainability of WT in RV. The results from this chapter can be used to help guides plan trips that are more likely to result in tourist satisfaction, therefore increasing the sustainability of WT.

As a whole, the importance of this dissertation is two-fold: (1) it provides much needed research on tourism impacts in a relatively undisturbed community where tourism is in its infancy, and (2) it adds to the empirical research thus far lacking in studies of WT (Newsome et al., 2005) by investigating the variables underlying primates' response to tourists. Management plans suggested by my research are more likely to be successful as they will be based in hypothesis-driven research leading to predictions about population effects that may arise from primate contact with tourists.

Table 1-1. Outline of the four data chapters to come.

Chapter title	Questions asked	Hypotheses tested	Results
Chapter 2: Tourists as predators: risk aversion in Surinamese primates when confronted by humans	Can primate responses to tourists in Suriname be viewed through the theoretical lens of predator/prey relationships? Do primates in Suriname respond to tourists as if the tourists were predators? What variables affect these responses?	<ol style="list-style-type: none"> 1. Primates will exhibit strong aversion to tourists, indicating that tourists represent high perceived risk. Primates in contact with tourists will devote their time to the following behaviors in the order listed: fleeing, alarm calls, displaying, feeding, playing, grooming. 2. Responses to tourists will lessen when tour group visits are more frequent. 3. Although all primate species are expected to exhibit predator avoidance responses to the presence of tourists, degree of these responses will differ by species and degree of response can be predicted based on species temperament. 	<ol style="list-style-type: none"> 1. Response differs by species. Not all species see tourists as representing high risk. 2. Supported only for displaying in spider monkeys. 3. Not supported for all species. Wedge-cap capuchins, howler monkeys and squirrel monkeys did not respond as predicted from the temperament literature.

Table 1-1.
Continued

Chapter title	Questions asked	Hypotheses tested	Results
Chapter 3: Ecological predictors of local wildlife response to tourism	How are the predator responses of Surinamese primates to tourists mediated by ecological and demographic variables?	<ol style="list-style-type: none"> 1. Animals encountered in open habitat will alarm call and flee more than those encountered in dense habitat 2. Long term habituation to a possible predator diminishes responses. 3. Smaller species, being at higher predation risk, will flee and alarm call more than larger species. 	<ol style="list-style-type: none"> 1. Only supported for alarm calling when species are pooled. 2. Supported in brown capuchins, and for alarm calling (but not fleeing) when species are pooled. 3. Not supported. Large species alarm call most followed by medium species and then small species.
Chapter 4: Primate response to predator (tourist) behavior	How does tourist behavior affect primate response? Are there characteristics of tourists groups that can be manipulated to minimize disturbance of primates encountered?	<ol style="list-style-type: none"> 1. Primates flee and alarm call less when in contact with quiet tourist groups as compared to noisy tourist groups. 2. Primates flee and alarm call less when in contact with small tourist groups versus larger tourist groups. 3. Primates flee and alarm call less when in contact with slow moving tourist groups as compared to faster moving groups. 	<ol style="list-style-type: none"> 1. Not supported. 2. Not supported. 3. Not supported.

Table 1-1. Continued

Chapter title	Questions asked	Hypotheses tested	Results
Chapter 5: Predictors of tourist encounters with primates	What variables predict tourist encounters with primate?	<ol style="list-style-type: none"> 1. Abundant primates will be encountered more often than less abundant primates. 2. Larger primates will be encountered more often than smaller primates. 3. Primates will be encountered more often in open habitats. 4. Primates will be encountered more often when study troop eats more fruit. 5. Primates will be encountered more often when study troop is traveling more. 6. Quiet tourist groups will encounter more primates than noisier tourist groups. 7. Tourist groups who spend more time "looking" will have more primate encounters. 	<ol style="list-style-type: none"> 1. Not supported when species pooled. Supported with wedge-cap capuchins and tamarins removed. 2. Not supported. 3. Not supported. 4. Supported. 5. Supported. 6. Not supported. 7. Supported.

CHAPTER 2 TOURISTS AS PREDATORS: RISK AVERSION IN SURINAMESE PRIMATES WHEN ENCOUNTERED BY HUMANS

Introduction

In Chapter 1, I discussed the need for increased study on the impacts of wildlife tourism and what is currently known about the effects of wildlife tourism on nonhuman primates and other animals. This chapter will further discuss the need for a richer, theoretically based examination of the impacts of wildlife tourism (WT) on wildlife. I demonstrate how this can be done by using the existing theory of economic decision making under predation threat to investigate the immediate responses of Surinamese primates to tourists.

As WT increases in popularity (Reynolds and Braithwaite, 2001), both as a choice for tourists and as a conservation tool, researchers and managers will benefit from the creation of predictive models of responses of wildlife to tourists (Calver, 2005). Predictive models of wildlife response to tourism will allow managers to coordinate and facilitate WT experiences that minimize disturbance of local wildlife, keeping the experience viable for future visitors while limiting negative ecological impacts caused by increased human visitation (Rodger and Calver, 2005).

As shown in Chapter 1, current research on human disturbance of animals by WT consists of disparate and descriptive studies of isolated and specific cases (Calver, 2005) (Fig. 2-1). Each study focuses on one species in its specific context and studies are undertaken after tourists have been introduced into an ecosystem. These studies investigate tourist impacts on wildlife by reporting what is currently happening and how it can be modified. They do not attempt to predict wildlife responses in advance of the introduction of tourists or explain variables contributing to wildlife responses. Negative

impacts of WT on wildlife discovered by these studies require changes to existing practices and structures (Eagles, 2001; Newsome et al., 2005). If the structures and practices are long-standing or entrenched, this task can be difficult or impractical. In sum, the lack of a theoretical background to many studies of WT results in limited utility of these studies to recommend empirically compelling management plans. Introduction of a theoretical background to the study of tourist impacts on wildlife is more likely to result in destinations planning for optimal protection and management of wildlife from the beginning of the WT endeavor.

Economic Decision Making

A current theory from the field of animal behavior and behavioral ecology fits in well with the need to predict wildlife responses to tourists—that of economic decision making by animals in the context of predator-prey interactions (Berger et al., 1983; Gill et al., 2001; Gill and Sutherland, 2000; Gill et al., 1996; Madsen, 1995). Animals can be seen as “decision making machines” (Stephens, 2008 , p. 483) who have to make complex choices on where to spend their energy in order to survive and reproduce. Further, the way in which animals make these choices is molded by natural selection (Stephens, 2008). According to economic decision making theory, animals have a finite amount of time in which to complete all the actions necessary to maintain life and increase reproductive success. Life-maintaining behaviors are referred to as long-term survival strategies and are assumed to be the behaviors animals will carry out when their immediate survival is not threatened (e.g., feeding, grooming, play) (Berger et al., 1983; Gill et al., 2001; Gill and Sutherland, 2000).

When a threatening stimulus is introduced into the environment, however, an animal must decide how to respond to the stimulus and economic decision making

comes into play. Without the stimulus, the animal might first spend its day feeding, then in social interactions, and later in time caring for offspring. Once a possible threatening stimulus is introduced, the animal must then decide if it should re-allocate any of its time from the above long-term behaviors towards short-term behaviors in response to the possible threat (Ydenberg and Dill, 1986). If the risk indicated by the stimulus is low, the animal may continue with its regular behaviors. If the threat stimulus is moderately high, the animal can move away from the stimulus somewhat, then go back to its normal behaviors. But if the threat is very high, the animal may flee altogether and become vigilant, not returning to its regular behaviors until much later. In this scenario, the animal is constantly weighing possible costs by straying from its regular long-term survival strategies (e.g., decreased caloric intake due to time away from feeding) versus risk presented by the stimulus (injury or death if the stimulus is a predator) (Gill et al., 2001; Ydenberg and Dill, 1986).

Examples of animals deciding where to allocate their energy in the face of predation risk are well documented. Abrahams and Dill (1989) experimentally investigated foraging decisions of guppies (*Poecilia reticulata*) when threatened by a predator. Guppies were first presented with food at two feeders, each with equal amounts of food. One feeder was in the presence of a predator and the other was not. When food amounts were equal between feeders, the fish were more likely to use the feeder without the predator. Animals, however, do not just make binary yes or no choices but rather weigh their options in terms of costs and benefits to reacting to risky stimuli in their particular context. When food in the feeder near the predator was increased, guppies more often risked proximity to the predator in order to reach the

greater food amount. When there was a greater reward to be gained in terms of more food, guppies were more likely to risk remaining in the presence of a predator (Abrahams and Dill, 1989).

Yellow marmots (*Marmota flaviventris*) are an example of a mammal that also uses these risk-reward trade-offs when faced with predation threat (Blumstein and Pelletier, 2005; Rhoades and Blumstein, 2007). These animals vary the amount of time they hide based on the approach speed of predators, and on the presence or absence of food. That is, when marmots had food available they spent less time hiding from predators (Blumstein and Pelletier, 2005). Hiding time is also affected by the speed of predators (Rhoades and Blumstein, 2007). These decisions also vary based on the condition and age of the individual marmots. The costs and benefits of avoiding predators must be weighed. Avoiding the predators can lead to less access to food, and when the food is available near the hiding spot, marmots will minimize their predator avoidance time (Blumstein and Pelletier, 2005).

Use of economic decision making as related to predation risk is also seen in primate species. Chacma baboons (*Papio cynecephalus*) are at risk of predation by lions and this predation risk affects the locations where the baboons groom, rest and feed (Cowlshaw, 1997a). The baboons groom and rest near refuges like trees and cliff faces. When the baboons need to feed, though, they will risk increased exposure to predators by moving away from refuges. In making this decision of where to carry out different behaviors, the baboons are weighing the costs and benefits of each. Only a more direct life-sustaining behavior such as the need to eat moves the baboons away

from their refuges. When possible, the baboons remain close to these refuges and therefore safer from predators (Cowlshaw, 1997a).

A more direct example of these trade-offs can be seen in captive populations of Geoffroy's marmosets (*Callithrix geoffroyi*) at the San Diego Wild Animal Park. On 24 occasions, marmosets were presented with either a freeze-dried rattlesnake in strike position, a cloth the same color and size of the snake or nothing. After the marmosets viewed the stimulus, it was removed. The next morning researchers recorded the number of vigilance checks from the marmosets to the location of the stimulus, how long it took the marmosets to leave their nest boxes after sunrise, and how quickly after leaving the nest boxes they approached the location of the stimulus. After viewing the snake the previous night the marmosets responded with more vigilance, a delayed start to foraging on the ground and a quicker approach to the presentation area than when presented with a cloth or with nothing (Hankerson and Caine, 2004). In this experiment, the marmosets responded to the possible danger of a snake by trading off foraging time in a specific location for additional vigilance. Marmosets adjusted their behaviors towards vigilance and reduced time spent foraging. The marmosets chose to limit their foraging in order to reduce the risk of being preyed upon.

Humans as Predators: The Risk-Disturbance Hypothesis

When humans are introduced into an ecosystem they may stand in for the predator stimulus under study and animals are expected to respond to humans following the same economic trade-offs discussed above. If tourists are not perceived as threatening to wildlife, the wildlife will put energy into long-term survival strategies having to do with parental investment, social bonds, learning or feeding. If tourists are perceived as threatening, animals will divert energy from these endeavors to more

short-term survival strategies such as fleeing, alarm calls and displays (Boinski et al., 1999). Frid and Dill (2002) suggest that these responses occur according to a risk-disturbance hypothesis in which “responses by disturbed animals track short-term changes in factors characterizing disturbance stimuli, with responses being stronger when perceived risk is greater” (Frid and Dill 2002, p. 2). That is, animals who perceive more risk from a stimulus will respond more strongly than animals who perceive less risk from a stimulus.

Are humans seen as predators?

The risk-disturbance hypothesis as applied to humans will not work if prey species evolve responses to specific predators. In this case, humans may not always have been historical predators to all species and it would be unlikely that animals would respond to human presences with anti-predator behaviors. Indeed, some research demonstrates that various species of animals cannot recognize introduced predators (McEvoy et al., 2008), but other studies show that prey species evolve generalized responses to signals that indicate the “predacious intent” of a possible predator (Dill, 1974, p. 711). Others have found that anti-predator responses have varying degrees of plasticity (Berger et al., 2007; Stankowich and Blumstein, 2005).

For example, marine iguanas (*Amblyrhynchus cristatus*) on the Galapagos Islands have lived isolated from natural predators for millions of years but in the past few decades began facing pressure from introduced domestic dogs and cats (Kruuk and Snell, 1981; Rassmann, 1997). Despite the lack of predation pressure for most of their history, Galapagos marine iguanas show increased flight initiation distances and increased levels of stress hormones when exposed to dogs and cats, indicating that they are able to recognize new, introduced predators (Berger et al., 2007). While it is

unknown how quickly these adjustments occurred, it is suspected that the responses are due more to learning than to natural selection. Due to the 30+ year lifespan of the iguanas, variability in individual responses and the relatively short history of exposure to dogs and cats it appears that each individual iguana is judging the threat of the introduced predators and responding based on their own experience (Berger et al., 2007).

There are few studies on the ability of primates to recognize introduced or novel predators and the studies that do exist have mixed results. Friant and others (2008) presented captive-born cotton top tamarins (*Saguinus oedipus*) with recorded calls from three natural tamarin predators and two non-predators. The tamarins responded most strongly to the call of the howler monkey, a non-predator, indicating that the tamarins are not responding to specific predators, but to other signals that could signify threat such as the low frequency sound of the howler monkey calls. Yorzinski and Ziegler (2007) observed stronger anti-predator responses for wild pigtailed langurs (*Simias concolor*) when presented with recorded vocalizations of unknown animals and humans (a current predator) than to felids, which were historical predators but not present on the islands currently inhabited by the langurs. Furthermore, while it is accepted that many primate species have specialized alarm calls in response to certain species such as felids or snakes (Boinski et al., 1999; Seyfarth et al., 1980; Wheeler, 2008) results also demonstrate that primates refine their knowledge of these categories over time (Seyfarth et al., 1980) and also use these specific calls to refer to possible predators (often including humans) that are not of the species usually indicated by the call (Boinski et al., 1999; Cowlshaw, 1997b). Other research on primates, however, has

demonstrated that captive-born primates do retain responses to historical predators (Barros et al., 2002) or that they use the fecal scent of possible predators in order to judge predation risk (Caine and Weldon, 1989; Sundermann et al., 2008).

Due to the fact that some species do adjust to novel predators and the fact that primates are known for their high level of behavioral plasticity (Fragaszy et al., 2004; Strier, 1994), I argue that the risk-disturbance hypothesis is likely to function in the current scenario. I expect that the primates subject to this study do not judge predators based on the species membership of the possible predator but by other behavioral characteristics that can indicate predacious intent. Thus, although humans are not a direct predator at RV, humans could act in ways that would signal danger to the primates. The primates would then respond with alarm calls and fleeing. Further evidence to this point is presented in Chapter 4 which investigates the effect of tour group behavior on primate responses. These risk-signaling characteristics are behaviors or features generally indicative of “predacious intent” across taxa (Dill, 1974, p.711). Some of these risk-signaling characteristics could be large size (Dill, 1974), predator speed (Burger, 1998; Dill, 1974; Hamr, 1988), predator approach (Frid and Dill, 2002) or sudden appearance (Thorpe, 1966).

Given that animals do not necessarily evolve specific anti-predator responses to specific predators, and that responses to possible predators are plastic, it is likely that primate species living in environments not previously inhabited by humans will respond to humans as if the humans are predators even if the primates have not been hunted. In areas where primates have had benign contact with humans, the primates may respond to humans as predators if the humans behave in unexpected ways, e.g., visiting new

areas, walking more quickly, making more noise. If these novel behaviors are similar to those that indicate predacious intent in other species, primates will respond with anti-predator behaviors.

Predictive power of the risk-disturbance hypothesis

Frid and Dill (2002) suggest that the risk-disturbance hypothesis can be looked at in an evolutionary framework and used more widely to predict impacts of human disturbance even up to a population level. That is, the rules animals use to make decisions about how to respond to possible risks result from natural selection (Stephens, 2008) and therefore, knowledge of an animal's natural and evolutionary history will allow us to predict the cascading effects of human disturbance. If we know that a certain species is more susceptible to predators than another, we can predict that the species in more danger of predation is more likely to respond to humans as predators. Other aspects of natural history can also contribute to these predictions. One species may be more food limited than another, and therefore less likely to flee from predators when at a food source. Knowing these details about different species and applying this knowledge under the risk-disturbance hypothesis will allow discovery of the underlying mechanisms accounting for wildlife responses to humans. By using rates of anti-predator behavior as a proxy measure for primates' perceived risk in the presence of humans, researchers can create more generalized predictions about wildlife response to human contact based on the evolutionary mechanisms behind such responses. With the theoretical background, we can start to answer both proximate and ultimate questions about why wildlife respond to tourist presence in different ways. Further, answers to these questions will allow for testable hypotheses to be generated about wildlife response to tourists in previously unstudied areas.

Application of the risk-disturbance hypothesis in Raleighvallen

This study accepts Frid and Dill's (2002) challenge to investigate wildlife response to humans using the theoretical framework of predator-prey interactions and the risk-disturbance hypothesis. Here, I treat tourists as predators in order to investigate the time allocation decisions wild primates make when faced with a potential predator. This will first test the risk-disturbance hypothesis by discovering whether or not primates respond to tourists with anti-predator behaviors by investigating if the rates of primate behavior in the presence of tourists match what would be expected if primates were viewing tourists as a threat. Second, I will investigate how responses to tourists differ based on rates of possible encounters with tourists. That is, are primates adjusting their responses based on short-term previous experience with tourists? Finally, I use the idea of behavioral syndromes (Sih et al., 2004) or temperament (Clarke and Boinski, 1995) to tie in primate responses to tourists with each species' evolutionary history. Using this framework, we can look at how the presence of tourists impacts the tradeoffs animals make between long- and short-term survival strategies and what might explain these decisions.

Hypothesis 1

Primates exhibit strong aversion to tourists indicating that tourists represent high perceived risk. Primates in contact with tourists devote their time to the following behaviors in the order listed: fleeing, alarm calls, displaying, feeding, playing, grooming.

When in the presence of tourists, wild monkeys weigh the risk indicated by the presences of the tourists in order to decide whether to engage in avoidance activities such as fleeing, displaying and alarm calling which take time from activities likely to contribute to the animals' survival (Frid and Dill, 2002; Yarmoloy et al., 1988). Thus,

activities likely to improve the animals' immediate survival take precedence over longer term, fitness enhancing behaviors. While the exact definition of fitness and how it can best be measured is under debate (Endler 1986; McGraw and Caswell 1996), I term long-term behaviors as fitness enhancing since animals who survive longer and are healthier are more likely to produce offspring than shorter lived, less healthy animals (Silk et al., 2010; Stearns et al., 2010). These animals will then pass on the genes that allowed the "more fit" individuals to survive longer, and these genes will become more prevalent in the population. Monkeys viewing tourist presence as risky will spend most time on behaviors which exist as an immediate and short-term response to a predatory threat, in order to improve their odds of surviving this threat. I predict that when monkeys are in the presence of tourists, behaviors of grooming, playing, feeding, displaying, alarm calling and fleeing are observed at different rates, according to their importance as short-term survival strategies. Primates not viewing tourists as a threat will not shift their behavior to anti-predator strategies. In addition, primates not using economic decision making will demonstrate a mix of long and short-term survival strategies.

I classify feeding, grooming and playing as long-term survival strategies. Animals obviously need to take in energy and nutrients to live, but for larger mammals like most primates, missing a meal does not immediately lead to death. Grooming and playing are also behaviors important to primates for long-term fitness reasons as opposed to short-term survival strategies and will be seen when perceived risk is low. Play is likely to have an adaptive advantage—it may help animals practice behaviors they will need later in life, or it may be a way to try out behavioral innovations (Biben, 1998; Fagen, 1974,

2002; Lancy, 1980). Grooming is important to primates for both social and hygienic reasons (Henzi et al., 2003; Schino, 2001; Seyfarth, 1977). Grooming may help protect primates from parasites and is known to be important in their social interactions. While grooming has been shown to have immediate benefits such as resulting in changes in endorphin levels (Keverne et al., 1989), neither it nor play are likely to be chosen over behaviors that will immediately deter a predator in a threatening situation. Fitness (an animal's ability to procreate and pass on their genes) and lifespan are enhanced by these long-term strategies, but generally only later in time than when the act is performed.

Displays, alarm calls and fleeing, on the other hand, are all responses to high predation risk. When contacted by a predator, prey species have to decide whether to evade the predator or attempt to deter the predator (Boinski et al., 2000b; Brodie et al., 1991; Kerfoot and Sih, 1987; van Schaik and van Hooff, 1983). Prey can either move away in order to avoid the predator, or they can act aggressively, alarm call, or charge in order to convince the predatory animal that it is risky to continue the predation attempt (Caro, 1995; Yeager, 1991; Zuberbuhler et al., 1997). Alarm calls may serve to alert the predator to the fact that they have been spotted (Woodland et al., 1980), or to alert the rest of the group to danger (Maynard Smith, 1965; Trivers, 1971). As these behaviors are mutually exclusive from other behaviors such as feeding, grooming and playing, in deciding to pursue an anti predator strategy animals are making a trade-off between long-term and short-term fitness enhancing activities.

I predict that when primates are in the presence of tourists they will decide to shift their energy expenditures to fleeing and alarm calls. Primates who spend more time on

these behaviors when in contact with tourists demonstrate that they view humans to be a predator worthy of these responses. This is illustrated in Figure 2-2 with most important survival strategies on the right of the threat continuum and least important strategies on the left. Behaviors on the left are more long-term survival strategies, and more likely to be seen when monkeys are not threatened by a possible predator. Behaviors on the right are short-term survival strategies, more likely to be observed when monkeys face a threat.

Hypothesis 2

Responses to tourists lessen when tourist group visits are more frequent.

If animals respond to characteristics of possible predators that may indicate risk, and given that many behaviors are plastic, then animals can also learn to not respond to some of these signals over short periods of time (Thorpe, 1966; Williamson and Feistner, 2003). This adjustment will occur as animals gather further information about a new stimulus that indicates the stimulus is not actually dangerous. No animal can have perfect information regarding the predation risk posed by other species, so they are predicted to err on the side of caution, responding as if tourists are a threat until they observe otherwise. Overestimating threat, however, can also be costly (Bouskila and Blumstein, 1992). Therefore, as animals are exposed to humans and are not harmed, their anti-predator responses should decrease. This behavior has been seen in various animal populations exposed to human disturbance including chamois (*Rupicapra rupicapra*) in Austria (Hamr, 1988), yellow-eyed penguins (*Megadyptes antipodes*) in New Zealand (Ellenberg et al., 2009), black-tailed godwits (*Limosa limosa*) in Denmark (Holm and Laursen, 2009), caribou (*Rangifer tarandus granti*) in Alaska (Haskell and

Ballard, 2008) and marmots (*Marmota olympus*) in Olympic National Park, Washington (Griffin et al., 2007). Learning that a seemingly dangerous stimulus is not in fact threatening is a common response throughout the animal kingdom as illustrated by the above examples. However, not every animal will decrease their fear responses to every stimulus (Boinski and Sirot, 1997; Feigley et al., 1972; Nair and Gonzalez-Lima, 1999).

In primate studies, researchers often slowly increase approach distances and contact time spent with their study animals in hopes of viewing more natural behaviors in the animals when in researcher presence, as opposed to behaviors based solely in response to the observers (Martin and Bateson, 1993). Although common practice, there are few published description of techniques and results (but see Cipolletta, 2003; Jack et al., 2008; Johns, 1996; Williamson and Feistner, 2003). Over time, animals perceive that the humans are not a threat and cease responding to them as such. As many species of primate have successfully learned to tolerate human presence, it is expected that as primates are more often in the presence of tourists they will follow this pattern and cease to see tourists as a threat.

Hypothesis 3

Although all primate species are expected to exhibit predator avoidance responses to the presence of tourists, degree of these responses differs by species and degree of response can be predicted based on species temperament.

Individual species evolve adaptations to a suite of environmental pressures. The resulting phenotype observed in individual members of a species is made up of multiple traits affected by natural selection as well as by phylogenetic constraints (Rose, 1983; Sih et al., 2004; Wolf et al., 2007). Each adaptive trait of an animal may be inherited singly or in concert with other traits (Cheverud, 1996). While this phenomenon is studied

most often in morphological traits (Cheverud, 1996; Lande, 1979; Lande and Arnold, 1983), it can also occur for behavioral traits and result in behavioral syndromes (Sih et al., 2004) or an animal's temperament (Clarke and Boinski, 1995). Sih and colleagues (2004) discuss behavioral syndromes, or suites of behaviors consistent across different contexts, while Clarke and Boinski (1995, p.104) define temperament as "Behavioral styles or tendencies that show continuity over time..." I will use the terms temperament and behavioral syndromes interchangeably. Temperament is often measured as reaction to novelty, with animals who avoid or act fearfully towards novel stimuli labeled as reactive (Clarke and Boinski, 1995) or neophobic (Day et al., 2003). Non-reactive, proactive, or neophilic animals, on the other hand, are attracted to novel stimuli (Clarke and Boinski, 1995; Day et al., 2003; Koolhaas et al., 1999). I will discuss primate responses to tourists in terms of neophilia versus neophobia (Table 2-1).

In primates, neophilia is often measured through interest in objects, and ability in object manipulation or tool use (Torigoe, 1985; van Schaik et al., 1999). Object manipulation requires individuals to demonstrate interest in objects. Species who react to novel situations with fear will not interact with objects enough to begin to manipulate them. While tourists are clearly not objects, the rationale behind these studies is that general temperament will affect how an animal responds to any stimulus, be it an object, a human, or a different species. Thus, I expect that due to overall temperament, an animal that behaves reactively or fearfully to novel stimulation will also demonstrate a strong reaction to the novel stimulus of tourists. By looking at published reports of primate responses to novel objects, we can predict primate responses to novel stimuli such as tourists. Table 2-1 shows predictions for each of the eight Surinamese species

based on earlier reports. Species are listed as neophobic, neophilic or equivocal, based on previous research.

All members of the genus *Cebus* are described as neophilic (Boinski et al., 2000a; Fragaszy et al., 2004). Other studies have found that capuchins have high interest in objects and demonstrate object manipulation in the wild and in captivity (Fragaszy et al., 2004; Torigoe, 1985; van Schaik et al., 1999). Therefore, both capuchin species (brown capuchins: *Cebus apella* and wedge-cap capuchins: *Cebus olivaceus*) are expected to have a relatively weak response to tourists compared to the other six species in this study. Reports on neophilia in squirrel monkeys (*Saimiri sciureus*) and howler monkeys (*Alouatta seniculus*), on the other hand, are ambiguous. Some have described squirrel monkeys as bold animals (Fragaszy and Mason, 1978) while others have found them to be disinterested in objects (van Schaik et al., 1999) and to demonstrate avoidance of humans (Boinski and Sirot, 1997). Results are similar for howler monkeys. Some studies indicate they have low manipulative abilities (van Schaik et al., 1999) while others have observed wild howler monkeys manipulating objects (Koch and Bicca-Marques, 2004; Richard-Hansen et al., 1998). Therefore I predict that these two species will show a medium response to tourist presence (Table 2-1).

The final four species in this study are all expected to react strongly to tourist presence. Spider monkeys (*Ateles paniscus*) do not exhibit neophilia (Torigoe, 1985; van Schaik et al., 1999). There is less information available for both saki species (white-faced sakis: *Pithecia pithecia* and bearded sakis: *Chiropotes satanas*), but van Schaik (1999) found both to have low skill in object manipulation. Similar results were found for

tamarins (*Saguinus midas*) (van Schaik et al., 1999) and Day and others (2003) found them to be less manipulative than other members of the family Callitrichidae. In this study, I expect spider monkeys, the two species of sakis and tamarins to exhibit the strongest predator responses when in contact with tourists.

I test the above three hypotheses using tourists in the Central Suriname Nature Reserve. The Central Suriname Nature Reserve is a relatively undisturbed habitat in the interior of Suriname, a country currently experiencing low rates of WT (Tropenbos International Suriname Programme, 2004). The area presents an ideal situation in which to investigate wildlife response to tourists, as tourism is just beginning and is still at low levels. Furthermore, the animals are not under any other human-caused threats or stresses, making tourism likely to be the only variable affecting changes in their behavior.

Tourism in Suriname

The country of Suriname is on the northeast coast of South America (Figure 2-3), has a population of 481,267 and is geographically slightly larger than the state of Georgia (CIA, 2009). Suriname contains a large sparsely inhabited and difficult to access interior made up mostly of tropical rainforest (Boinski et al., 2002) containing natural mineral resources (Sinclair, 2003). Currently, extractive industries such as aluminum, gold and oil make up 85% of the country's exports (CIA, 2009). These industries have been in decline in recent years, however, and the country is seeking alternative sources of revenue (Sinclair, 2003), one of which is nature based tourism. Although on the Caribbean ocean, Suriname was not involved in the earlier explosion of Caribbean tourism due to its lack of sandy coastal beaches (Sinclair, 2003). The need for alternatives to extractive industries plus the increase in alternative tourism or "off the

beaten track” tourism (Brohman, 1996; Foroohar, 2002; Gentry, 2007) has lead to Suriname’s interest in increasing WT in the country (Sinclair, 2003). Many have noted that tourism will be important to the economic survival of the Caribbean and the Guianan Shield (Jayawardena, 2002; Sinclair and Jayawardena, 2003) and tourism is also heavily promoted as a conservation tool in Suriname (Tropenbos International Suriname Programmme, 2004) in opposition to additional mining and logging. As these tourism promotion endeavors are just beginning, Suriname does not receive many foreign tourists. About 3,000 international leisure tourists per year currently visit the country (Tropenbos International Suriname Programmme, 2004) and most current visitors are Dutch (personal observation). The most visited natural area in Suriname is Brownsberg Nature Park, located near the capitol city, which receives about 13,000-19,000 visitors a year, most of whom are Surinamese (Tropenbos International Suriname Programmme, 2004; Westin, 2007).

This study took place in the interior of Suriname in the Central Suriname Nature Reserve (CSNR) (Figure 2-4), a 1.6 million ha World Heritage Site. The CSNR is isolated, accessible either by a one hour flight in a small plane, or by a total of 8 hours in bus and boat. The Foundation for Nature Conservation in Suriname (STINASU) manages the reserve and controls access for the tour groups that visit. Although no official counts of visitors to the park exist, I counted 557 tourists within the park between June 1, 2006 and November 30, 2006. This period constitutes the high tourist season. Other reports indicate that about 1000 tourists visited the park in 2004 (A. Vreedzaam, personal communication). Overwhelmingly, tourists only visit a small area of the CSNR,

a formerly separate and smaller nature reserve called Raleighvallen, near the northern border of the CSNR.

Methods

Study Site

The study site, Raleighvallen (RV) (4°0'N, 56°30'W), is situated in the 1.6 million ha Central Suriname Nature Reserve (CSNR) in the Coopename River drainage. The CSNR is located in west central Suriname and is comprised of lowland rainforest (Berrenstein, 2006). It receives annual average rainfall of 2300 mm (Reichart, 1993). The aerial and terrestrial predator complement of the forest is complete, and no significant hunting has occurred since the 1800s (Reichart, 1993; Trail, 1987). Eight species of primates are found at the site, brown capuchin (*Cebus apella*), squirrel monkey (*Saimiri sciureus*), wedge-cap capuchin (*Cebus olivaceus*), spider monkey (*Ateles paniscus*), howler monkey (*Alouatta seniculus*), white-faced saki (*Pithecia pithecia*), bearded saki (*Chiropotes satanas*) and golden handed tamarin (*Saguinus midas*). Additional descriptions of the site can also be found elsewhere (Boinski et al., 2005; Boinski et al., 2003; Boinski et al., 2002; Fleagle and Mittermeier, 1980; Mittermeier and van Roosmalen, 1981).

All primate species at the site are under risk of predation (Boinski et al, in prep). Predators seen in the area include harpy eagles (*Harpia harpyja*), crested eagles (*Morphnus guianensis*), puma (*Felis concolor*), jaguars (*Panthera onca*), margays (*Felis wiedii*), tayras (*Eira barbara*), ocelots (*Leopardus pardalis*) and boa constrictors (*Boa constrictor*) (Vath and Boinski, unpublished data; personal observation). All of the above have been observed to prey upon at least one of the seven primate species included in this study. Regular inspections of a harpy eagle nest in RV have yielded skeletal

material from all of the primate species present in RV (Boinski et al in prep).

Furthermore, successful harpy eagle predation events have been observed on squirrel monkeys, brown capuchins and howler monkeys. In addition, a puma was observed successfully killing a brown capuchin (Boinski, unpublished data).

Additional predation events have been observed elsewhere. Crested eagles have successfully preyed upon saddlebacked tamarins (*Saguinus fuscicollis*) and mustached tamarins (*Saguinus mystax*) in Peru (Vasquez and Heymann, 2001). Puma consume howler monkeys in Brazil (Ludwig et al., 2007) and have made attempts on spider monkeys in Colombia (Matsuda and Izawa, 2008). There is evidence of jaguars preying on howler monkeys in Venezuela (Peetz et al., 1992) and on spider monkeys in Peru (Emmons, 1987) and Colombia (Matsuda and Izawa, 2008). Margay predation has occurred on wedge-cap capuchins in Venezuela (Mondolfi, 1986), on tamarins in Brazil (de Oliveira Calleia et al., 2009) and brown capuchins in Guyana (Beebe, 1925). In Guatemala, both jaguars and pumas prey upon spider monkeys and howler monkeys (Novack et al., 2005).

Tayras attempt predation on squirrel monkeys and tamarins in Panama (Galef et al., 1976). In Brazil and Peru, examinations of ocelot feces show remains of brown capuchins, brown howler monkeys (*Alouatta guariba*), miquis (*Brachyteles hypoxanthus*) (Bianchi and Mendes, 2007), squirrel monkeys and saddlebacked tamarins (Emmons, 1987). While I could not find any published reports on the taking of spider monkeys by ocelots, miquis are much larger than spider monkeys, weighing 12-15 kilograms (Nishimura et al., 1988) in comparison to a spider monkey's 7-8 kilograms (Mittermeier and van Roosmalen, 1981), so it is likely that spider monkeys

are also at risk of predation from ocelots. Boa constrictors are known to prey upon white-faced capuchins (*Cebus capucinus*) in Costa Rica (Chapman, 1986; Perry et al., 2003), mustached tamarins in Peru (Tello et al., 2002) and bearded sakis in Brazil (Ferrari et al., 2004). From the above evidence, it is clear that primates at RV face predation pressure from a number of predators.

Since 1998 RV has been host to the Boinski Monkey-Forest Project, a long term focused study of the behavioral ecology of squirrel and capuchin monkeys, along with a broader program of ecological monitoring. Many aspects of the area are well-researched, including the populations of various animals, tree phenology and weather. My study is unique in that it reports on the activities of wildlife tourists on animals in a protected area not under threat of habitat loss or hunting. Animals under more extreme pressures such as from habitat loss or hunting are expected to exhibit more dramatic responses to tourists. Here I define a baseline of primate response to tourism which is needed before tourism further develops in RV. The tourist attraction of the Voltzberg trail allows an opportunity to encounter a number of different primate species and collect data on each.

Tourists generally visit the CSNR in order to hike to the Voltzberg (Figure 2-5), a 240 m tall inselberg (Berrenstein, 2006). The entire Guianan Shield sits on Precambrian igneous and metamorphic rock which has been stable for 1.9 billion years. Inselbergs are dome shaped Precambrian crystalline granite outcroppings (Berrenstein, 2006), characterized by distinctive vegetation (Grogger and Barthlott, 1996). Notable inselbergs include Stone Mountain in Georgia, Mount Katahdin in Maine and Uluru (Ayers Rock) in Australia. Similarly, the Voltzberg is an important tourist attraction, and most visits to the

CSNR are organized around a trip to “the mountain” as it is called. Tourists stay on Foengoe Island, upstream from the study site in the Coopename River. On the day of the hike to the Voltzberg tour groups arrive at Anjoemara Falls between 7:00 and 9:00 am. Groups walk a 6 km trail to an exposed granite area called the Western Plateau (Fig 2-6), from which they walk a further kilometer to the foot of the Voltzberg. Walking up the Voltzberg is challenging, as it is a steep incline with little shade. The entire round trip generally takes seven to eight hours, with about half the time spent getting to the Western Plateau and back and the other half spent climbing the Voltzberg itself. Tourists taking part in this expedition are the focus of my research.

Methodology

From July 8, 2006 through November 30, 2006 I completed 48 “tour follows” (equaling 365 individual tourists) along the trail from Anjoemara Falls to the Western Plateau of the Voltzberg (Figure 2-6). This equals 220.25 hours of tourist observation. All tourist groups combined spent a total of 8.2 hours in contact with primates. After receiving permission from the tourists and guides to make observations I noted the number of people in the group, and their age-sex distribution. The research was conducted under proper approvals from the University of Florida’s Institutional Animal Care and Use Committee (UF IACUC# E306), Institutional Review Board (UFIRB# 2005-U-1007), and with the permission of Surinamese authorities.

During tour follows, as I walked at the back of the tourist group, I completed an instantaneous group scan (Fragaszy et al., 1992; Martin and Bateson, 1993) every fifteen minutes. At each interval I recorded the number of tourists stopped, looking at the environment, taking photos, speaking and resting. When we reached the Western Plateau, I remained behind and waited while the tourists and guides climbed the

Voltzberg. I also noted the time spent in the forest traveling to the Plateau and back. Tour groups were defined as any group of people (aside from Boinski Monkey-Forest researchers) walking up the trail to the Voltzberg. Groups ranged in size from 4 to 23 people. Time spent traveling to and from the Voltzberg ranged from 3.25 to 5.75 hours. Table 2-2 summarizes terminology used and Table 2-3 contains definitions of tourist behaviors.

I define a “primate encounter” as an instance when I and at least one tourist and/or guide made visual contact with at least one individual primate. When primates were encountered I collected data on general troop characteristics such as location and movement as well as number of alarm calls heard. Via two minute instantaneous group scans I also recorded the number of individuals grooming, resting, participating in agonistic behavior, feeding and traveling (Table 2-4). Furthermore, the amount of time tourists spent in the presence of the monkeys was recorded.

Data were analyzed using Analyse-It for Excel (version 2.00). Data were not normally distributed and Analyse-It contains many nonparametric tests that permit hypothesis testing using non-normal data. I used Friedman’s method for randomized blocks (Sokal and Rohlf, 1995), also known as Friedman’s two-way analysis of variance (StatSoft, 2007) to confirm that within each species there were differences in the mean average time spent on each of the target behaviors. Friedman’s test is a nonparametric alternative to a repeated samples ANOVA (Sokal and Rohlf, 1995; StatSoft, 2007) and allows multiple comparisons among the mean time spent feeding, traveling, making alarm calls, and fleeing for each species. Kendall’s coefficient of rank correlation (Sokal and Rohlf, 1995) was used to test for associations between time since last tourist visit

and primate response to tourists. The tau statistic of Kendall's coefficient indicates the strength and direction of the association (Conover, 1999; Crichton, 2001). I used the Kruskal Wallis test to investigate between species differences in rates of alarm calls, travel and feeding. Kruskal Wallis is a nonparametric alternative to the ANOVA (Sokal and Rohlf, 1995) and allows for post-hoc tests to look for differences between pairs of species. Between species differences in presence or absence of fleeing were tested using Pearson's Chi Square. Fleeing was scored as either occurring or not occurring during each primate encounter, resulting in categorical data, making Pearson's Chi Square the appropriate test (Sokal and Rohlf, 1995).

Results

Over 48 tour follows I observed 86 separate primate encounters. That is, each tour group saw primates an average of 1.79 (s.d.=1) times. These 86 encounters consisted of 95 separate species sightings, for an average of 1.98 (s.d.=2) species seen per tour follow. Some primate encounters consisted of sightings of more than one species. On 10 tour follows (20.8%) no primates were encountered at all. The most commonly seen primates were brown capuchins followed by squirrel monkeys, spider monkeys, howler monkeys, bearded sakis, wedge-capped capuchins and tamarins (Table 2-5). Although white-faced sakis do inhabit the forest, they were never encountered with a tourist group.

The longest time tourists spent in a primate encounter was 18 minutes and the shortest was less than one minute. The mean primate encounter duration was 5.18 minutes (s.d.= 3.79). Out of the 95 different species sightings, the tourists were the ones to break contact in 87 instances (91.6%). Primates fled in 6.3% of the encounters and travelled away in 2.1%.

Significant differences were found between the behaviors for brown capuchins (Friedman's test, $p < .0001$), squirrel monkeys ($p < .0001$), and spider monkeys ($p < .005$). The remaining species (howler monkeys, bearded sakis, tamarins and wedge-cap capuchins) were seen too few times for statistical analysis, but I will examine patterns seen in their responses to tourists.

Hypothesis 1

Primates will exhibit strong aversion to tourists, indicating that tourists represent high perceived risk. Primates in contact with tourists will devote their time to the following behaviors in the order listed: fleeing, alarm calls, displaying, feeding, playing, grooming.

No species were observed playing or grooming in the presence of tourists. Using Friedman's two-way analysis of variance, I found statistically significant differences between the amounts of time three primate species (brown capuchins, squirrel monkeys and spider monkeys) spent on the target behaviors. Brown capuchins spent most of their time feeding, followed by fleeing, displaying and alarm calling ($n=45$, $p < .0001$). Squirrel monkeys were only seen feeding, then fleeing ($n=23$, $p < .0001$) and were never seen alarm calling. Spider monkeys spent time in contact with tourists alarm calling, then displaying, then feeding ($n=13$, $p=0.0014$).

Due to small sample sizes, anti-predator responses of howler monkeys, bearded sakis, tamarins and wedge-cap capuchins cannot be examined statistically. Howler monkeys were most often seen feeding, followed by alarm calls. Tamarins were only seen fleeing. Bearded sakis divided their time with tourists equally between fleeing, alarm calling and feeding. Finally, wedge-cap capuchins were observed fleeing, then in alarm calls. Results are presented in Table 2-6.

Hypothesis 2

Responses to tourists lessen when tourist group visits are more frequent.

The Kendall's tau correlation was used to compare time (in days) since a tourist group was last on the Voltzberg trail to percent of time spent on the various predator-aversion behaviors. Results are presented for brown capuchins, spider monkeys and squirrel monkeys as these were the three species with sample sizes large enough for statistical analysis (Table 2-7). Time since previous tour group did not correlate with rates of feeding (brown capuchin Tau= -0.10, $p=0.4$; squirrel monkey Tau= -0.15, $p=0.32$) for brown capuchins or squirrel monkeys. Time since previous tour group did not correlate with rates of display (Tau= 0.04, $p=0.58$) or alarm calling (Tau= 0.05, $p=0.32$) for brown capuchins. Squirrel monkeys were never seen displaying or alarm calling. For spider monkeys, there is a significant correlation of days since last tour group with rate of displaying (Tau= 0.44, $p=0.01$) but not between time since last tour group and rates of alarm call (Tau= -0.28, $p=0.22$). The more time that passed since tourists were in the area, the more the spider monkeys displayed when next encountered by a tour group.

Hypothesis 3

Although all primate species are expected to exhibit predator avoidance responses to the presence of tourists, degree of these responses will differ by species and degree of response can be predicted based on species temperament.

Significant differences were found between the species for all variables (feeding: $X^2=15.12$, $df=6$, $p=0.0193$; displaying: $X^2=16.21$, $df=6$, $p=0.0127$; alarm calling: $X^2=33.79$, $df=6$, $p<0.0001$; fleeing: $X^2=28.48$, $df=7$, $p=0.0002$), but strength of primate response did not completely align as predicted (Table 2-8). As predicted, brown

capuchins did not usually respond to tourists with anti-predator behaviors. Also as predicted, spider monkeys, bearded sakis and tamarins responded to tourists with alarm calls and fleeing. White-faced sakis were predicted to have a strong response to tourists, but were never seen. Predictions for squirrel monkeys and howler monkeys were ambiguous, as prior research found them to be both neophobic and neophilic (Boinski and Sirot, 1997; Fragaszy and Mason, 1978; Koch and Bicca-Marques, 2004; Richard-Hansen et al., 1998; van Schaik et al., 1999). Both species, however, demonstrated a weak response to tourists. Wedge-cap capuchins were generally expected to behave as their congeners, the brown capuchins, but these results demonstrate a dramatic difference between the two capuchin species.

Discussion

In this section I will first evaluate the utility of the economic decision making model in predicting primate response to tourists then I will discuss the theoretical applications of my research and finally I will mention the practical application of the research. Research on effects of WT on wild animals is currently not viewed within a unified theoretical framework. This study takes on the challenge posed by Frid and Dill (2002) and applies an extant framework from behavioral ecology of using economic decision making and the risk-disturbance hypothesis to understand the responses of wild primates when encountered by tourists. Application of this theoretical lens to primate responses to tourists at RV yielded mixed results: not all species view tourists as a threat, most predator response behaviors do not change with increased frequency of exposure to tourists and some, but not all, responses can be predicted based on prior investigations into species temperament (Tables 2.6, 2.7 and 2.8).

Application of Economic Decision Making Under Predation Threat

One goal of this research was to use the behavioral ecology theory of economic decision making in order to predict responses of primates to presence of tourists. I predicted that all species would respond to tourists as if the tourists were predators and shift their energies from long-term survival strategies like feeding to short-term survival strategies such as displaying, alarm calling and fleeing. Three species did as predicted, allocating more time to anti-predator behavior when in the presence of tourists: spider monkeys, tamarins and wedge-cap capuchins. Three species did not behave as predicted and allocated a higher percentage of their time in the presence of tourists to feeding and less to alarm calls, displays and fleeing: brown capuchins, squirrel monkeys and howler monkeys. One species, bearded sakis, did not fit into the model at all, evenly splitting their time in the presence of tourists between fleeing, alarm calls and feeding (Table 2-6). I will now address two questions related to these results: what is the utility of the economic decision making model when applied to tourist/primate interactions? And, what additional variables could explain these results?

Utility of the model

The economic decision making model worked for all but one of the primate species studied. Most species either spent time in the presence of tourists on long-term survival strategies or on short-term anti-predator behaviors, indicating that in most cases species were choosing one type of behavior or another (Table 2-6). If the model was not functioning in this scenario, I would have observed long and short-term behaviors intermixed, as occurred with the bearded sakis. Brown capuchins, squirrel monkeys, howler monkeys, tamarins, spider monkeys and wedge-cap capuchins all chose either short-term or long-term behavioral strategies when in the presence of

tourists. None of these species exhibited long-term survival behaviors concurrently with anti-predator behaviors. The one species who does not fit this pattern is the bearded saki who spent time with tourists equally feeding, alarm calling and fleeing (Table 2-6).

I propose that the apparent failure of bearded sakis to fit the model may not be due to a failure of the model, but instead to imperfect information on the part of the researcher. Animals making energy allocation decisions make these decisions based on information about risk and trade-offs (Frid and Dill, 2002; Stephens, 2008). When an animal decides to flee from a predator, they weigh the risk that the predator poses against the lost opportunity of continuing the behavior they were engaged in when the predator was detected (Bouskila and Blumstein, 1992; Stephens, 2008; Ydenberg and Dill, 1986). The behavior finally chosen will result from the immediate context in which the animal finds itself. Thus, animals are found to flee less quickly from predators when the animal is near a higher quality food source (Abrahams and Dill, 1989), curtail feeding more quickly when a predator appears more threatening (Helfman, 1989), or risk increased intraspecific competition by foraging in groups when predation risk is high (Berger et al., 1983; Cassini, 1991).

This study did not take into account any of these additional variables likely used by primates when deciding how to respond to a possible predator. Bearded sakis were only encountered three times and across all time observed in the presence of tourists they spent equal percentages fleeing, alarm calling and feeding (Table 2-6). As I did not record the context in which primates were encountered, the sakis possessed more information than I did on the variables contributing to their decision to continue feeding, even in the presence of tourists. It is possible that the sakis, like other species

mentioned in the research described above, weighed their current context as too beneficial to leave in the face of whatever possible danger the tourists represented. If the sakis were in an important food tree, the possible risk from tourists may not have reached a high enough level to compensate for the loss of an important food source (Brown and Kotler, 2004). Further research should investigate the behaviors in which animals are engaged when encountered by tourists and see if this context can more fully explain response to tourists.

Predictors of species response to tourists

In this section I will discuss the results of the current study and explore if these results can be explained by habituation level, abundance, encounter distance or social structure. The primates who were threatened by tourists vary greatly in size, as well as diet and even location in the canopy (Fleagle and Mittermeier, 1980). The same is true for the primates who did not perceive tourists as a threat. One of the most interesting results is that the two congeners, brown capuchins and wedge-cap capuchins had such different responses. It is true that the sample size for wedge-cap capuchins is small, but it is still suggestive that this species always responded by fleeing, whereas brown capuchins only fled once. It is also important to note that wedge-caps were seen so rarely while brown capuchins were the most commonly observed primate. Furthermore, wedge-cap capuchins are rarely seen in the area (Vath and Boinski, unpublished data) and other studies have found wedge-caps to be a shy and reclusive species (Fleagle and Mittermeier, 1980).

One might assume that the primate species that did not respond to tourists as a threat (brown capuchins, squirrel monkeys and howler monkeys) did so because they are simply more often encountered in the site, and therefore may be less susceptible to

viewing tourists as a threat. However this does not seem to be the case. This study found that tourists most encountered brown capuchins, followed by squirrel monkeys and then spider monkeys. Howler monkeys were the fourth most encountered species (Table 2-5). Additionally, other data from this same site indicates that brown capuchins are the most encountered primate followed by spider monkeys, squirrel monkeys, and tamarins with howler monkeys being the fifth most encountered species (Vath and Boinski, unpublished data)(Table 2-9). Aspects of species-specific habituation are reviewed in Chapter 3. It cannot be discounted, though, that brown capuchins and squirrel monkeys are the more habituated species, based on the long-term Boinski Monkey-Forest Project. Some individuals from habituated groups may have transferred to non-studied groups, decreasing these new groups' responses to humans (Jack et al., 2008). However, howler monkeys have not been subject to a long-term study at this location, so habituation to researchers cannot be an explanation for their lack of response.

Recent experience with tourists

For brown capuchins and squirrel monkeys no effect of time since tourists were last seen was found. Most spider monkey behaviors yielded the same result, although there was a significant correlation between time since last tourists and rate of display, indicating that spider monkeys spent more time displaying the longer it had been since they saw tourists. That is, spider monkeys seemed to respond more strongly to tourists when there had been less in the area.

It is interesting that although it was predicted that all species would respond more strongly to tourists when they were less frequently present, this was not supported at all for brown capuchins and squirrel monkeys. This might be explained by the fact that long

term studies have been completed in the area on these two species resulting in them being the most generally habituated of the species. Spider monkeys demonstrated more displays when tourist visits were infrequent, indicating that they may have become habituated somewhat to tourists when they came more regularly, but then lost this habituation when encounters with tourists decreased.

Social structure

Another possibility is that social structure somehow contributes to a primate's likeliness to view tourists as a threat. In French Guiana, Julliot (1994) observed a crowned eagle attack on neighboring groups of howler and spider monkeys. Each species responded quite differently to the attack, with the howler monkeys grouping together and making alarm calls while the spider monkeys did not form into a cohesive group and each individually vocalized and broke branches. The two adult spider monkeys left a young monkey undefended and alone, and the eagle was able to capture this individual. Julliot proposed that the cohesiveness of the howler monkey group was a better defense against the eagle than the spider monkeys' individualized attack. Spider monkeys do live in very flexible and variable fission-fusion social systems (McFarland Symington, 1988; van Roosmalen, 1980) whereas howler monkeys live in more cohesive groups (Crockett, 1985; Crockett and Eisenberg, 1987; Thorington and Ruiz, 1984). This explanation, however, is insufficient as fission-fusion social systems are rare amongst primate species in general and all of the other species found to respond negatively to tourist presence live in more cohesive groups (Kinzey and Cunningham, 1994; Symington, 1990; Terborgh and Janson, 1986).

Encounter distance also fails at explaining the species' differing response to tourists. While encounter distances were not recorded, knowledge of each species'

usage of the canopy exists. Among the species who did not respond to tourists as predators, both squirrel monkeys and brown capuchins are known to use the lower levels of the forest, while howler monkeys use the highest levels. For the other species, tamarins use the lower levels, as do wedge-cap capuchins while spider monkeys and bearded sakis use the highest levels of the forest (Mittermeier and van Roosmalen, 1981). Level of response to tourists cannot be explained by distance from tourists when encountered.

Theoretical Implications of Evolution of Decision Making

This research indicates that species temperament is not 100% successful at predicting responses to tourists. In this section, however, I will suggest that this result may be partly due to the fact that current research on temperament in primate species is so closely tied to manipulative ability and that further research should be undertaken in order to test the validity of this claim.

I predicted that the strength of each species' response to tourists could be anticipated based on previous research on temperament and neophobia. This held for four of the species observed (brown capuchins, spider monkeys, bearded sakis and tamarins), but was not true for three species: wedge-cap capuchins, squirrel monkeys and howler monkeys. Squirrel monkeys and howler monkeys may not be surprising, as literature on these two species is ambiguous. Neither squirrel monkeys nor howler monkeys show great interest in novel objects (van Schaik et al., 1999) and squirrel monkeys have been reported to avoid tourists in Costa Rica (Boinski and Sirot, 1997). In addition, the howler monkey diet is likely to contribute to high levels of neophobia (Tomblin and Cranford, 1994). Folivores such as the howler monkeys (Neville et al., 1988) are generally thought to be more neophobic due to restrictions in their diets

(Tomblin and Cranford, 1994). On the other hand, reports of howler monkeys manipulating objects in the wild do exist (Koch and Bicca-Marques, 2004; Richard-Hansen et al., 1998).

Furthermore, while squirrel monkeys are not described as neophilic and have shown aversion to tourists (Boinski and Sirot, 1997), others have described them as “bold” (Fragaszy and Mason, 1978). Because previous findings are so mixed, it is not necessarily surprising that neither of these species showed a strong response to tourists. These results indicate that howler monkeys and squirrel monkeys may not be as neophobic as previously considered, or that use of tools and object manipulation may not have such a strong correlation to temperament as often thought (Clarke and Boinski, 1995; Torigoe, 1985). Many studies on primate temperament use response to novel objects and tool-use abilities as proxy measures for temperament. While it makes sense that neophobia will limit a species’ ability to use tools, it does not immediately follow that because a species does not use tools or approach new objects with interest that they are neophobic in general. Adding the understanding of behavioral syndromes as expressed in the behavioral ecology literature (Bell, 2007; Sih et al., 2004) will enrich this understanding of temperament as a suite of evolved responses to evolutionary contexts.

Another piece of evidence for the possible lack of a direct correlation between object manipulation and temperament, especially in response to tourists, is the result found for the wedge-cap capuchins. Although there is a very small sample size for wedge-cap capuchins, they responded strongly to tourists, alarm calling 50% of the time observed and fleeing 100% of time observed (Table 2.6). This is in stark contrast to the

other capuchin species, brown capuchins who only alarm called 1.1% of the time and fled 7% of the time (Table 2-6). Although wedge-cap capuchins were only encountered for a total of 4 minutes, this result in itself is telling when considering that brown capuchins were contacted for 288 minutes. Wedge-cap capuchins were seen much less than brown capuchins. While no differences in the two species are seen in various personality tests in captivity (Fragaszy et al., 2004; Torigoe, 1985; van Schaik et al., 1999), it is clear they are responding differently in the wild. Furthermore, wedge-cap capuchins are rarely seen in the area (Vath and Boinski, unpublished data) and other studies have found wedge-caps to be a shy and difficult to encounter species (Fleagle and Mittermeier, 1980).

Response to predation by a species may be affected by other characteristics, such as rates of aggression, mating patterns (Sih, 1994), type of predator usually encountered (Rhoades and Blumstein, 2007) and territorial behavior. These responses can also vary based on individual characteristics such as condition, age and sex (Blumstein and Pelletier, 2005; Rhoades and Blumstein, 2007). That is, species actually have a limited amount of behavioral plasticity, which arises under many different selection pressures. Evolved response to one stimulus may limit possible responses to another stimulus. Therefore, although no clear similarities exist to explain why brown capuchins, howler monkeys and squirrel monkeys do not view tourists as threatening predators, some other evolutionary constraints may explain this.

Predictors of species response. What do brown capuchins, squirrel monkeys and howler monkeys have in common that causes them to not view tourists as a threat? At first glance, not a lot. To further complicate the issue, two closely related species,

wedge-cap capuchins and brown capuchins, had different reactions to tourists. This demonstrates that one species cannot be used as a barometer for the health of the primate population as a whole. Each species must be considered individually due to the economic decisions each one makes. Furthermore, researchers have to think about the characteristics of the most affected species when making management plans.

Managing tourism for brown capuchins, who do not appear to view tourists as a threat, could result in serious impacts on spider monkeys, who do see tourists as a threat.

Plans that work for one species will not necessarily work for all. Management based only on brown capuchins, for example, could result in higher numbers of tourists and different limits on tourist behavior, which could result in more impacts on a more sensitive species like the spider monkeys.

Management Implications

Two important lessons for management can be taken from this study: 1) primate species respond differently to tourists and 2) monitoring animals' response to tourism can be done quickly and effectively by monitoring feeding rates. Each primate species in this study responded differently towards the tourists. Three species: brown capuchins, squirrel monkeys and howler monkeys did not respond to tourists as if they were predators. Four species: spider monkeys, bearded sakis, tamarins and wedge-cap capuchins did respond as if tourists were predators by spending most of their time fleeing, alarm calling and displaying when in the presence of tourists. The three species who did not respond to tourists with anti-predator behaviors were all seen feeding in the presence of tourists. These patterns of inter-species response are not easily predicted although it is likely they arise from the unique evolutionary history of each species (Frid and Dill, 2002; Sih et al., 2004; Stephens, 2008).

When creating management plans for primate habitat areas managers must remember that the term 'primate' refers to a diverse Order. Indeed, primates are so diverse that even in one forest in Suriname, eight species exist that vary greatly in size, appearance, social organization and diet. The results from this study, demonstrating the variation in primate responses to tourists and the complexities that may constrain these responses, clearly shows that all primate species should not be lumped together when investigating their responses to tourists. The use of temperament or behavioral syndromes is one possible avenue of taking into account the whole natural history of a species when attempting to understand the species' responses to tourists. The temperament of an animal, like their responses to tourists, arises from a suite of adaptations that occurs in each species' unique evolutionary history (Bell, 2007; Sih et al., 2004). We need to investigate how each species responds to new situations, keeping in mind their diverse adaptations and evolutionary histories, as will be discussed in the next chapter. Doing so is imperative to successful management of WT based on primates.

In addition to being aware of species differences in creating management plans, tourist expectations can also be managed. As stated earlier, tourists who do not have a fulfilling experience are less likely to return to an attraction or recommend it to others (Reynolds and Braithwaite, 2001; Sparks, 1994). Tourists to RV should not be promised a definite encounter with a monkey, and they should be told that monkeys they are likely to see are brown capuchins or squirrel monkeys. Tourists knowing what to expect and having their expectations met will result in more sustainable tourism (Chan and Baum, 2007; Reynolds and Braithwaite, 2001). Because brown capuchins and squirrel

monkeys demonstrate little predator response to tourists, managers can also keep tourism focused on these two species, as opposed to others more sensitive to tourist presence. Squirrel monkeys and brown capuchins can be used in advertising to attract tourists, as they do not seem to be greatly affected by tourism at its present levels. If this helps maintain the reserve as a protected area, then benefits will also be felt by the other species more impacted by tourism.

Use of feeding as an indicator variable. One variable that cannot explain the variation, but that ties the differently responding species together is feeding. Of the three species found to not respond to tourists as if they were predators, all were also observed feeding (Table 2-10). As discussed earlier, feeding is an important long term survival strategy, but for most primates not an immediate one. That is, most primates can afford to spend a little less time feeding without immediately having their mortality affected. Animals under immediate predation threat will definitely not stop and feed. If animals have their feeding interrupted too often, however, this can eventually result in important and direct population effects. Animals may decrease in general physical condition, and not be able to reproduce as readily if not taking in the proper nutrients (Robinson and Redford, 1986; Tutin et al., 1997).

All of this means that if animals are observed feeding when in the presence of tourists, they likely do not see those tourists as an immediate threat to their survival. This is what was observed for brown capuchins, squirrel monkeys and howler monkeys, all of whom were observed feeding in the presence of tourists. Bearded sakis were also observed feeding in the presence of tourists but their story is not as straight forward. Bearded sakis alarm called and fled 33% of the time they were encountered. Bearded

sakis may have been at a very important food source when encountered and were less likely to flee or leave because of this. The bottom-line, however, is that the bearded sakis did continue eating to some extent, so tourism in RV is not depriving them of needed nutrients.

Current study of WT has not come up with many useful indicators to judge ecological impacts (Sirakaya et al., 2001). This study indicates that feeding can be used as a good proxy variable for amount of disturbance felt by each species. Indeed, other authors have also suggested feeding rates as a proxy variable for population health (Newsome et al., 2005). Out of the seven species in this study, three spent more of their time in contact with tourists feeding than in anti-predator behaviors, three were never seen feeding in the presence of tourists, and one (bearded sakis) equally divided time observed between feeding, alarm calling and fleeing (Table 2-6). To verify that these differences in time observed feeding were due to tourists and not to species-specific characteristics, I searched the literature for published activity budgets of each species (Table 2-11). As can be seen from Table 2-11, the three species not seen feeding in this study (spider monkeys, wedge-cap capuchins and tamarins) actually are known to spend a larger percentage of their time feeding than howler monkeys and squirrel monkeys. However in this study, howler monkeys and squirrel monkeys actually spent slightly more time feeding in the presence of tourists than expected from their published activity budgets (Table 2-11). This may be further evidence that tourism is causing disturbance to spider monkeys, tamarins and wedge-cap capuchins as these three species spend at least 15% of their day feeding, but in the presence of tourists this

decreases to zero, indicating that these monkeys may be giving up feeding time to respond to tourists with anti-predator behaviors.

In addition to its importance as a long-term life sustaining activity for primates (Robinson and Redford, 1986; Tutin et al., 1997), feeding is also a useful indicator due to its ease of recognition and recording. Untrained workers may not be able to detect a primate's presence before it flees or recognize the alarm calls of the various species, but anyone can recognize if a monkey is putting food in its mouth or not. With some basic training, workers can observe the primate populations and discover which species are feeding in the presence of tourists and which are not. This can be completed by guides already out with a tour, or by additional observers sent with tour groups. As long as species are feeding, animals are not viewing tourists as much of a risk, and population levels may not be greatly affected. This is not necessarily a very sensitive measure, but can be undertaken when time and resources are short to monitor basic primate community health.

In sum, this study can be used as a template for investigating the response of animal species to WT. Use of Frid and Dill's (2002) theoretical framework of predator-prey interactions allows us to easily measure the threat animals perceive from tourists. Diversity of responses and the need to monitor individual species are obvious, but the existence of feeding as a proxy variable makes this monitoring simple and possible with a minimum of effort. WT is not always benign and is not a panacea, but also does not always need to result in destruction of the site where it occurs.

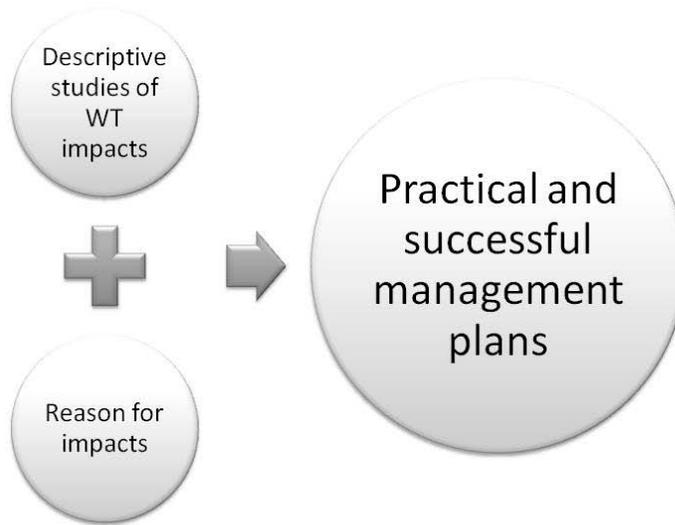


Figure 2-1: This study combines description of WT impacts with understanding of reasons for impacts. This combination will result in more practical and successful WT management plans.

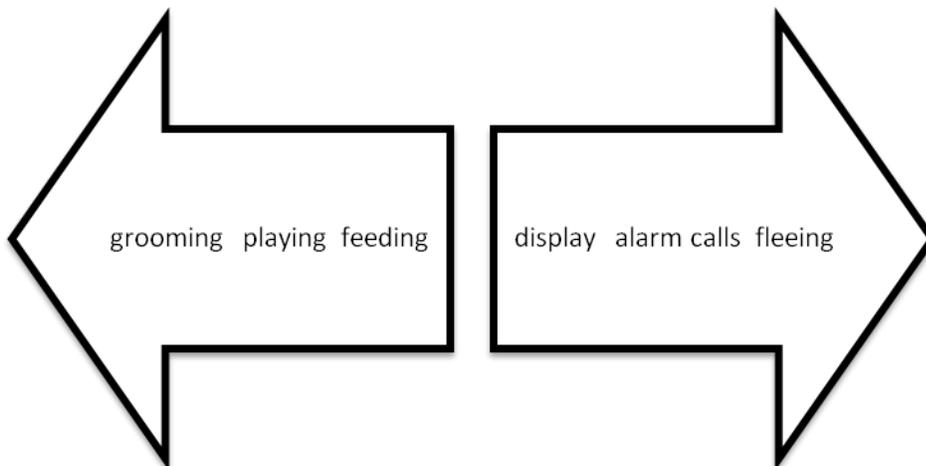
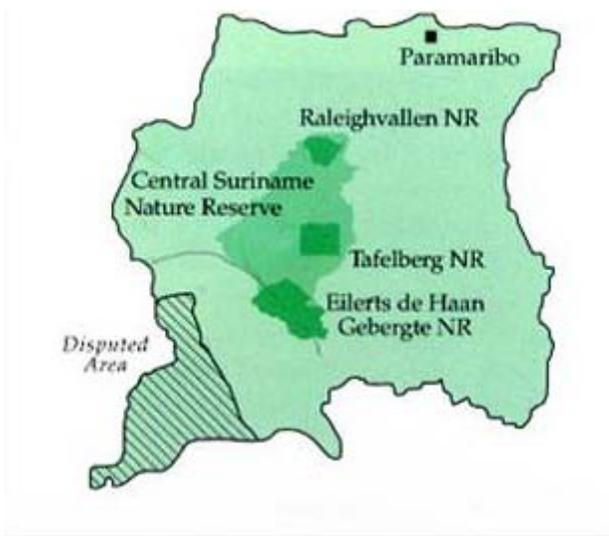


Figure 2-2: Continuum of proxy measures of threat response. Monkeys who perceive tourists as a risk are expected to spend more time on behaviors on the right, which are those most likely to lead to their immediate survival as compared to behaviors on the left, which are more long-term survival strategies.



Figure 2-3: Map of South America showing Suriname



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Figure 2-4: Map of Suriname indicating Raleighvallen and the Central Suriname Nature Reserve



Figure 2-5: The Voltzberg. View from the Western Plateau which can be seen in foreground.



Figure 2-6: Voltzberg trail map

Table 2-1: Predicted response to tourists based on species temperament.

Species	Temperament	Citations	Average Body Weight (grams)	Predicted Response*
Brown Capuchin	Neophilic	(Fragaszy et al., 2004; Torigoe, 1985; van Schaik et al., 1999)	2700	Weak response
Wedge Cap Capuchin	Neophilic	(Fragaszy et al., 2004; Torigoe, 1985; van Schaik et al., 1999)	2700	Weak response
Squirrel Monkey	Equivocal	(Boinski and Sirot, 1997; Fragaszy and Mason, 1978; van Schaik et al., 1999)	925	Some response
Howler Monkey	Equivocal	(Koch and Bicca-Marques, 2004; Richard-Hansen et al., 1998; Tomblin and Cranford, 1994; Torigoe, 1985; van Schaik et al., 1999)	7000	Some response
Spider Monkey	Neophobic	(Torigoe, 1985; van Schaik et al., 1999)	6000	Strong response
White-Faced Saki	Neophobic	(van Schaik et al., 1999)	1871	Strong response
Bearded Saki	Neophobic	(van Schaik et al., 1999)	3000	Strong response
Tamarin	Neophobic	(Day et al., 2003; van Schaik et al., 1999)	562	Strong response

Neophilia: Attraction to novel objects.

Neophobia: Revulsion or indifference towards novel objects

Equivocal: Neophilia or neophobia cannot be inferred from published studies

*strong response = species spends more than 25% of observed time fleeing or alarm calling; weak response = species spends less than 25% of observed time fleeing or alarm calling

Table 2-2: Explanation of terminology used in the data collection

Term	Definition
Tour follow	Observation of tourist group from Anjoemara Falls to Western Plateau and back. Researcher walked in the back of the group, generally maintaining a distance of one to three meters behind rearmost tourist.
Primate encounter	Any instance in which the group came within viewing distance of monkeys and at least one tourist or guide was aware of the monkeys.
Tour group	Any group of people (two or more) walking the Voltzberg Trail, not including Boinski Monkey-Forest researchers.

Table 2-3: Ethogram of tourist behaviors, data on these behaviors was collected via group scans

Behavior	Definition
Stop	Person not moving, is standing still, but not sitting or reclining.
Looking	Person is looking around, not only in front of them. Head is oriented somewhere other than the trail immediately in front of them.
Photo	Person using a still or video camera to take/record pictures.
Speaking	Person is talking, yelling, singing or emitting some noise out of their mouth.
Resting	Person is sitting or reclining, not standing upright.
Walking	Person is moving forward.

Table 2-4: Ethogram of monkey behaviors. Data on these behaviors was collected via 2 minute group scans during each primate encounter.

Behavior	Definition
Flee	Monkeys move away rapidly.
Alarm call	Varies by species, but is vocalization made in response to approach of a predator. All species alarm were known from prior experience.
Display	Varies somewhat by species. Consists of threat vocalization, shaking of branches, lunging or other threatening postures. Some species break and drop branches.
Feed	Monkey places some food item (fruit, insect, leaves) into their mouth.
Play	Wrestling, chasing.
Groom	One animal picks through another animal's fur.

Table 2-5: Number of times each species was encountered by tour groups.

Species	# of encounters	Percent of total encounters
Brown capuchin	45	47.4
Squirrel monkey	23	24.2
Spider monkey	13	13.7
Howler monkey	6	6.3
Bearded saki	3	3.2
Tamarin	3	3.2
Wedge-cap capuchin	2	2.1
White-faced saki	0	0

Table 2-6: Variation in species responses to tourists. Did species respond as if tourists were predators?

Species	Time observed (minutes)	Number encounters	Encounters Fled	Alarm calls	Displaying	Feeding	Playing	Grooming	Order of behaviors observed ¹	Hypothesis supported?
Brown capuchin	288	45	7%	1.1%	3.8%	30.3%	0%	0%	Feeding, fleeing, display, alarm calls	No*
Squirrel monkey	128	23	4%	0%	0%	14.9%	0%	0%	Feeding, fleeing	No*
Spider monkey	88	13	31%	24.3%	18.3%	0%	0%	0%	Fleeing, alarm calls, displaying	Yes*
Howler monkey	19	6	0%	6%	0%	10%	0%	0%	Feeding, alarm calls	No
Bearded saki	20	3	33%	33%	0%	33%	0%	0%	Fleeing, alarm calls, feeding	Yes
Tamarins	4	3	50%	0%	0%	0%	0%	0%	Fleeing	Yes
Wedge-cap capuchin	4	3	100%	50%	0%	0%	0%	0%	Fleeing, alarm calls	Yes

*statistically significant results at alpha value of .05

¹most observed to least observed

Table 2-7: Effect of time since last tourist group (in days) on wildlife response to tourists.

Species	Behaviors	Tau statistic	p value	Hypothesis supported?*
Brown capuchin (n=45)	Feed	-0.10	0.40	No
	Display	0.04	0.58	No
Spider monkey (n=13)	Alarm Call	0.05	0.32	No
	Feed	n/a	n/a	n/a
Squirrel monkey (n=23)	Display	0.44	0.01	Yes
	Alarm call	-0.28	0.22	No
	Feed	-0.15	0.32	No
	Display	n/a	n/a	n/a
	Alarm call	n/a	n/a	n/a

*Did response to tourists diminish with more frequent tour group visits?

Table 2-8: Results for Hypothesis 3. Strength of primate response can be predicted based on species temperament. A strong observed response is observed when a species spent more than 25% of observations either in alarm calls and displays or in fleeing.

Species	Temperament	Predicted Response	Observed Response	Hypothesis Supported?
Brown Capuchin	Neophilic	Weak response	Weak	Yes
Wedge Cap Capuchin	Neophilic	Weak response	Strong	No
Squirrel Monkey	Ambiguous	Some response	Weak	No
Howler	Ambiguous	Some response	Weak	No
Spider	Neophobic	Strong response	Strong	Yes
White-Faced Saki	Neophobic	Strong response	Never seen	Yes?
Bearded Saki	Neophobic	Strong response	Strong	Yes
Tamarin	Neophobic	Strong response	Strong	Yes

Table 2-9: Species responses to tourists as compared with amount encountered.

Species	Tourists seen as threat?	Encounter rank (current study)	Encounter rank (Vath and Boinski, unpublished data)
Brown capuchin	No	1	1
Squirrel monkey	No	2	*3
Howler monkey	No	4	4
Spider monkey	Yes	3	2
Bearded saki	Yes	*5	*5
Tamarin	Yes	*5	*3
Wedge-cap capuchin	Yes	6	6
White-faced saki	Not seen	Not seen	*5

*indicates a tie

Table 2-10: Relation of species view of predators and presence of feeding.

Species	Tourists seen as threat?	Feeding observed?
Brown capuchin	No	Yes
Squirrel monkey	No	Yes
Spider monkey	Yes	No
Howler monkey	No	Yes
Bearded saki	Yes	Yes
Tamarins	Yes	No
Wedge-cap capuchin	Yes	No

Table 2-11: Comparison of published time observed feeding to observed time (this study) spent feeding in the presence of tourists.

Species	% daily activity budget spent feeding	% seen feeding with tourists	Citations
Bearded saki	10-30 (average 20-25)	33	(Boyle and Smith; Port-Carvalho and Ferrari, 2004; Silva and Ferrari, 2008)
Brown capuchin	20-90	30.3	(Di Bitetti, 2003; Janson, 1985; Ross and Giller, 1988; Terborgh, 1983; Zhang, 1995)
Squirrel monkey ¹	11	14.9	(Mitchell et al., 1991)
Howler monkey	12.7	10	(Gaulin and Gaulin, 1982)
Spider monkey ²	15-25	0	(Wallace, 2001, 2005)
Tamarin ³	16-28	0	(Garber, 1988; Terborgh, 1983)
Wedge-cap capuchin	18-60	0	(Fragaszy and Boinski, 1995; Miller, 1996; Robinson, 1986)

¹ data for *Saimiri sciureus* not available. Estimates from *S. oerstedii* and *S. boliviensis*

² data for *Ateles paniscus* not available. Estimates from *A. chamek*.

³ data for *Saguinus midas* not available. Estimates from *S. fuscicollis*, *S. imperator*, and *S. mystax*.

CHAPTER 3 ECOLOGICAL PREDICTORS OF LOCAL WILDLIFE RESPONSE TO TOURISM

Introduction

The previous chapter investigated primate response to tourists in a theoretical framework of predator-prey relationships and illustrated the need to understand the behavioral ecology of individual species in order to best anticipate possible impacts of WT. Chapter 2 indicated that feeding rates could be used as a proxy variable for monitoring tourist impact on primate populations across sites and pointed out the importance of species differences in responses to tourists. This chapter asks: how are the predator responses of Surinamese primates to tourists mediated by ecological and demographic variables? Here I investigate the responses of primates to tourists in more detail, taking conclusions from the previous chapter and applying them to a particular area with its own unique ecology.

How do Animals Decide How to Respond to Possible Predators?

As found in the previous chapter, primate species do not have a unitary response to tourists. Squirrel monkeys, brown capuchins and howler monkeys rarely alarm call or flee when in the presence of tourists, while spider monkeys, wedge-cap capuchins, bearded sakis and tamarins often flee and alarm call when in the presence of tourists. Some of these responses could be predicted by each species' temperament (Clarke and Boinski, 1995) or behavioral syndromes (Sih et al., 2004), that is the unified set of behaviors an animal has in its repertoire, based on adaptations arising from that species' unique evolutionary history. Temperament/behavioral syndromes can be thought of as the general rules guiding how an animal responds to different circumstances it is presented with throughout its life.

Primates, along with other animals, are always making decisions on how to spend their time (Stephens, 2008). Each response of an animal to a stimulus arises from a decision made based on the costs and benefits of choosing one behavior over another. Animals must weigh the benefit obtained by a particular behavior with the opportunity costs of not being able to perform an alternate behavior. These decisions are not necessarily conscious, but are evolved responses to different circumstances. Further, the cost-benefit trade-off may change, based on the specific circumstances of the animal at each time a decision needs to be made. Thus the animal must decide what is most important to do in the context it is in (McFarland, 1977). This context consists of not only the ecological characteristics of the community, such as predation risk and resource availability (Stephens, 2008), but also the characteristics of the animal making the decision (Mangel and Clark, 1986) such as age, size, and sex.

In this chapter I test three hypotheses regarding primate response to tourist presence. One hypothesis deals with an intrinsic characteristic of primate species (body size) while the other two hypotheses are based on contexts of tourist encounters (habitat and habituation level). Using these hypotheses, I examine in detail how primates in the specific ecological milieu of the interior of Suriname respond to tourist presence. Each hypothesis consists of a general hypothesis, applicable to many species and situations, followed by a hypothesis specific to Raleighvallen, Suriname.

Hypothesis 1

General prediction: Animals encountered in open habitat will alarm call and flee more than those encountered in dense habitat.

RV prediction: Primates encountered in high forest will alarm call and flee more than those encountered in liana and/or low rain forest.

Animals use vegetation as refuge from predators (Amo et al., 2007; Boinski et al., 2003; Cassini, 1991; Cowlshaw, 1997a; Dill and Houtman, 1989). Studies in a number of taxa have found that animals under predation pressure prefer to remain near some sort of “refuge” site (Cowlshaw, 1997a; Dill and Houtman, 1989) where animals can attend to other needs such as foraging while at the same time be less detectable to predators (Pitt, 1999; Yasué et al., 2003). For chacma baboons (*Papio cynocephalus ursinus*) this may be a cliff face (Cowlshaw, 1997a), while for other animals like squirrel monkeys and wild guinea pigs (*Cavia aperea*) it is often more dense vegetation (Boinski et al., 2003; Cassini, 1991). Thicker vegetation protects animals from predation as predators will not be able to see prey well and also may not be able to penetrate the area in order to approach the prey species. Animals in thicker vegetation are therefore predicted to respond less strongly to possible predators due to the expected safety of their location. Gray squirrels (*Sciurus carolinensis*) begin flight from an approaching predator earlier when they are farther from refuge trees than when they are closer to trees (Dill and Houtman, 1989). Similar results have been found in woodchucks (*Marmota momax*) (Bonenfant and Kramer, 1996) and several species of freshwater fish (McLean and Godin, 1989). I predict that monkeys in denser habitats will not respond as strongly to tourists as those encountered in less dense habitats.

Hypothesis 2

General prediction: Long term experience with a possible predator diminishes responses.

RV prediction: Habituated animals (those seen within the Boinski Monkey-Forest study site) will flee and alarm call less than naïve animals (those seen outside the study site).

Habituation refers to the lessening of a response over time and with repeated exposures (Thorpe, 1966; Williamson and Feistner, 2003). Researchers conducting behavioral studies often habituate animals in hopes that this will lead to an ability to view more natural and normal behaviors in the animals, as opposed to behaviors based in responses to the observers. Over time, animals perceive that the humans are not a threat and cease responding to them as such.

Pros and cons of habituation

Opinions on the desirability of habituated animals for wildlife tourism vary (Shelton and Higham, 2007). Some studies have found that habituation can lead to increased aggression in the target animals and therefore more danger to tourists (Brennan et al., 1985; Fa, 1992). Furthermore, increased interactions between wildlife and humans can lead to disease transmission from humans to animals, especially in primates (Köndgen et al., 2008; Wallis and Lee, 2004). Others have found that it might be beneficial to habituate animals as habituation decreases stress responses. Comparisons of glucocorticoid concentrations in Galapagos lizards (*Amblyrhynchus cristatus*) demonstrate that lizards in a population regularly in contact with tourists have overall lower rates of stress hormones than those in a population not in contact with tourists (Romero and Wikelski, 2002). Similar results have been found in Magellanic penguins (*Spheniscus magellanicus*) (Fowler, 1999).

Close reading of these studies, however, indicates that not all define 'habituation' in the same way, and that a more fine-grained approach to looking at habituation is needed (Shelton and Higham, 2007). Many of the studies define habituation as not only increased non-reactivity to a stimulus, but increased interest in and approach towards a stimulus. For my purpose of evaluating the impacts of tourism on wildlife, separating

disinterest and non-responsiveness to humans from increased interest and approach is more useful than lumping these responses together under one term. Disinterest in tourists should limit changes in the wildlife population and increase tourist satisfaction. Increased interest in tourists, however, is more likely to lead to problems for tourists and wildlife in increased aggression and disease transmission (Brennan et al., 1985; Fa, 1992; Köndgen et al., 2008; Wallis and Lee, 2004). For this reason I use the term 'habituation' to refer to increased non-reactivity and 'over-habituation' (see below) to refer to increased interest and approach.

Habituation and primates

The first step of most primate studies is habituation: repeatedly introducing primates to non-threatening humans with the goal of decreasing rates of anti-predator responses. The goal is that after animals are habituated, researchers will be able to observe how the animals might behave if not observed (Cipolletta, 2003; Martin and Bateson, 1993; Williamson and Feistner, 2003). Habituation has been used as a tool to lessen primate responses to tourists, as can be seen with great apes in Africa (Blom et al., 2004). Blom and colleagues (2004) and Johns (1996) found that gorillas (*Gorilla gorilla*) and chimpanzees (*Pan troglodytes*) decreased fear responses to tourists and increased time ignoring tourists as habituation increased. The fact that the animals increased time spent ignoring humans indicates that they were able to continue with their regular behaviors, thus lessening tourist impacts. My study follows this accepted framework—I assume that habituated animals, ignoring human presence, are more likely to go about their regular behaviors (Crofoot et al., in press; Williamson and Feistner, 2003) and thus are less likely to be impacted by tourism. All species involved in this study have been successfully habituated, either at this site (Boinski et al., 2005; Boinski

et al., 2003; Boinski et al., 2000a), or at others (wedge-cap capuchin: Fragaszy and Boinski, 1995; Robinson, 1984, 1986; Robinson, 1981) (howler monkey: Peetz et al., 1992; Westin, 2007; Yumoto et al., 1999) (bearded sakis: Boyle et al., 2008; Boyle and Smith, 2010) (tamarins: Oliveira and Ferrari, 2000) (spider monkeys: Simmen and Sabatier, 1996).

In RV, a long term Monkey-Forest Project has been underway since 1998 (Boinski et al., 2005; Boinski et al., 2003; Boinski et al., 2000a; Boinski et al., 2002), investigating squirrel monkey and brown capuchin behavioral ecology along with the ecology of the entire forest community. The research is generally limited to the first 2 kilometers of the tourist trail and the surrounding area (Figure 3-1). Study groups of squirrel monkeys and brown capuchins rarely travel beyond this area, and researchers have not habituated any groups outside the study area. Therefore, for my study, animals seen in the Monkey-Forest study site are referred to as habituated, as they have been exposed to humans moving about the area daily since 1998 when the Boinski Monkey-Forest project began. Animals further along the trail see people less often and will be referred to as “naïve”. Because animals in the Monkey-Forest study site have more chance to interact with humans they are expected to demonstrate less predator responses to tourists. While it cannot be guaranteed that these are always different animals (i.e., animals may move from the habituated to naïve area), animals may respond differently to a stimulus (humans) depending on context (Mangel and Clark, 1986). That is, even habituated individuals may respond more strongly to humans when the humans are encountered in a different context.

Hypothesis 3

General prediction: Smaller species, being at higher predation risk, will flee and alarm call more than larger species.

RV prediction: Rates of fleeing and alarm calling will negatively correlate with average body size. In other words, small species (tamarins and squirrel monkeys) will flee and alarm call most followed in descending order by medium species (wedge-cap capuchins, bearded sakis and brown capuchins) and finally large species (howler monkeys and spider monkeys).

Body size is one of the factors that influences predation risk. Smaller animals have evolved to be more cryptic, and less likely to be spotted by predators. In trade off for their lack of detectability, however, small animals may be less likely to be able to defend themselves against potential predators (Broom and Ruxton, 2005; Maynard Smith, 1965). In addition, when predators have a choice, they are more likely to consume smaller prey animals (Benard, 2007; Shultz et al., 2004; St-Pierre et al., 2006; Wang et al., 2007) as they may be easier to catch. The above factors result in different predator responses based on body size. Animals who are smaller are more likely to flee from predators as they depend more on their crypticity than other defenses (Broom and Ruxton, 2005; Kissner et al., 1997). I hypothesize that when small-bodied RV primates are in contact with tourists they will flee and alarm call more than larger-bodied primates.

Methods

Study Site

The study site, Raleighvallen (RV) (4°0'N, 56°30'W), is situated in the 1.6 million ha Central Suriname Nature Reserve (CSNR) in the Coopename River drainage. The

CSNR is located in west central Suriname and is comprised of lowland rainforest (Berrenstein, 2006). It receives annual average rainfall of 2300 mm (Reichart, 1993). The aerial and terrestrial predator complement of the forest is complete, and no significant hunting has occurred since the 1800s (Reichart, 1993; Trail, 1987). Eight species of primates are found at the site, brown capuchin (*Cebus apella*), squirrel monkey (*Saimiri sciureus*), wedge-cap capuchin (*Cebus olivaceus*), spider monkey (*Ateles paniscus*), howler monkey (*Alouatta seniculus*), white-faced saki (*Pithecia pithecia*), bearded saki (*Chiropotes satanas*) and golden handed tamarin (*Saguinus midas*). Basic descriptions of the site can be found elsewhere (Boinski et al., 2005; Boinski et al., 2003; Boinski et al., 2002; Fleagle and Mittermeier, 1980; Mittermeier and van Roosmalen, 1981).

Since 1998 the site has been host to a long term focused study of the behavioral ecology of squirrel and capuchin monkeys along with a broader program of ecological monitoring. Many aspects of the site are well-researched, including the populations of various animals, the phenology, the climate and the weather. The current study is unique in that it reports on the activities of wildlife tourists on animals not subject to hunting or habitat loss. Animals under more extreme pressures, such as those listed above are expected to exhibit more dramatic responses to tourists. In this chapter I describe a baseline of primate response to tourism which is needed before tourism further develops in RV. The tourist attraction of the Voltzberg trail allows a unique opportunity to encounter a number of different primate species and collect data on each.

Methodology

From July 8, 2006 through November 30, 2006 I completed 48 “tour follows” (Table 3-1) (equaling 365 individual tourists) along the trail from Anjoemara Falls to the

Western Plateau of the Voltzberg (Figure 3-1). This equals 220.25 hours of tourist observation. The research was conducted under proper approvals from the University of Florida's Institutional Animal Care and Use Committee (UF IACUC# E306), Institutional Review Board (UFIRB# 2005-U-1007) and with permission and approval of Surinamese authorities.

During tour follows I walked at the back of the tourist group and recorded behaviors of the tourists and of any primates encountered. Whenever primate groups were encountered I collected data on general troop characteristics such as location and movement as well as number of alarm calls heard. Via two minute instantaneous group scans I also recorded the number of individuals grooming, resting, participating in agonistic behavior, feeding and traveling (Table 3-2). Furthermore, the amount of time tourists spent in the presence of the monkeys was recorded. After data were collected, I plotted locations of primate encounters onto a habitat map of the trail. The habitat map was created by mapping primary habitat type onto a map of the trail divided into a 100m x100m grid. Habitat categories (high forest, low rain forest, liana forest and pina swamp) followed Mittermeier and van Roosmalen (1981) (Table 3-3). Due to the small sample sizes of species encountered in each different habitat, habitats were later pooled by complexity into open (high rain forest and low rain forest) and dense (liana and piña swamp). A long term study has made use of the area for nearly 10 years, so animals encountered north of Stream A (within the long term study site) were determined to be habituated, while those south of Stream A, where researchers did not often venture, were referred to as naive. Body weights used in this chapter were taken from Mittermeier and van Roosmalen (1981).

Data were analyzed using Analyse-It for Excel (version 2.00). Data were not normal, and Analyse-It contains many tests for the analysis of non-normal data. Chi square tests were used to test all the hypotheses.

Results

Hypothesis 1

General prediction: Animals encountered in more open habitat will alarm call and flee more than those encountered in a denser habitat

RV prediction: Primates encountered in high forest will alarm call and flee more than those encountered in liana and/or low rain forest.

Overall, there were more primate encounters in dense habitat (65) than in open habitat (30). 67% of brown capuchin encounters were in dense habitat (n=45). Out of 13 spider monkey encounters, 7 (or 53%) were in open habitat while the remaining 6 were in dense habitat. Out of 23 encounters with squirrel monkeys, two or 9% were in open habitat with the rest in dense habitat (Table 3-4). Due to small sample sizes and the lack of alarm calling and fleeing in squirrel monkeys, only data for brown capuchins and spider monkeys could be statistically analyzed for this hypothesis. Brown capuchins had no significant differences in fleeing ($p>0.9$, $DF=1$, $\chi^2=0.01$) or alarm calling ($p>0.3$, $DF=1$, $\chi^2=0.73$) based on habitat. While there was no significant effect of habitat on fleeing in spider monkeys ($p>0.85$, $DF=1$, $\chi^2=0.03$), habitat did affect spider monkey alarm calls. Spider monkeys alarm called more in open habitat than in dense habitat ($p=0.0483$, $DF=1$, $\chi^2=3.90$).

Squirrel monkeys never alarm called and fled once. The one instance of fleeing was observed in dense forest. Squirrel monkeys were only seen in open forest twice and did not flee or alarm on either of those instances. Howler monkeys never fled. They

were seen 50% of the time in open habitat and 50% in dense. They alarm called once, in open habitat. Bearded sakis were seen three times, twice in dense habitat and once in open habitat, and they alarm called upon every encounter. Bearded sakis fled once, in dense forest.

Tamarins were seen twice in dense habitat and once in open. They alarm called twice—once in open habitat and once in dense. Tamarins fled twice, both instances when they were encountered in dense habitat. Wedge-cap capuchins were seen twice—once in dense habitat and once in open habitat and they alarm called and fled during both encounters.

When responses of all species are pooled, there was no significant effect of habitat on the percent of instances in which animals fled ($p > 0.9$, $DF = 1$, $\chi^2 = 0$). There was a significant effect of habitat on alarm calls ($p < 0.003$, $DF = 1$, $\chi^2 = 8.96$). Animals more often alarm called in open habitat than in dense habitat. However, it appears that this result is driven by the spider monkeys, as when spider monkeys are removed from the analysis, results are no longer significant ($p = 0.0669$, $DF = 1$, $\chi^2 = 3.36$).

Hypothesis 2

General prediction: Long term habituation to a possible predator diminishes responses.

RV prediction: Habituated animals (those seen within the Boinski Monkey-Forest study site) will flee and alarm call less than naïve animals.

Results are presented in Table 3-5. Due to sample sizes, statistical tests were only completed on brown capuchins and spider monkeys. Brown capuchins did demonstrate different rates of alarm calling and fleeing based on habituation status. Naive brown capuchins were observed fleeing or alarm calling while habituated brown

capuchins never fled or alarm called. These results are statistically significant (fleeing: $p < 0.003$, $DF=1$, $\chi^2=8.84$; alarm calls: $p < 0.0005$, $DF=1$, $\chi^2=12.03$). Squirrel monkeys never alarm called, regardless of habituation. They only fled once, when not habituated. There was no statistical difference between the amount of time spider monkeys alarm called ($p > 0.3$, $DF=1$, $\chi^2=0.93$) or fled ($p > 0.4$, $DF=1$, $\chi^2=0.48$) based on habituation. Habituated spider monkeys, however, were only seen once and did not flee or alarm call in that instance.

Howler monkeys were encountered six times and alarm called on one of these instances, when naïve. Howler monkeys never fled. Sakis were only seen in habituated areas and fled 33% of the time they were seen and alarm called 100% of the time. Tamarins were seen once while habituated and once when not. They fled when habituated, and alarm called when seen in the unhabituated area. Wedge cap capuchins were never habituated (i.e., seen within the Boinski Monkey-Forest study area), and always fled and alarm called.

When species are pooled, they are significantly more likely to flee ($p < 0.002$, $DF=1$, $\chi^2=10.55$) and alarm call ($p < 0.0001$, $DF=1$, $\chi^2=18.93$) when not habituated. Brown capuchins, however, appear to account for much of this difference. When they are removed from the analysis, there is no effect of habituation on fleeing ($p > 0.11$, $DF=1$, $\chi^2=2.48$), but animals remain more likely to alarm call when naïve ($p < 0.02$, $DF=1$, $\chi^2=6.13$).

Hypothesis 3

General prediction: Smaller species, being at higher predation risk, will flee and alarm call more than larger species.

RV prediction: Rates of fleeing and alarm calling will negatively correlate with average body size. That is, small species (tamarins and squirrel monkeys) will flee and alarm call most followed in descending order by medium species (wedge-cap capuchins, bearded sakis and brown capuchins) and finally large species (howler monkeys and spider monkeys).

Average species body weights are from Mittermeier and van Roosmalen (1981). Species were grouped into small (400-2000 g), medium (2000-5000 g) and large (5000 g and up). Small species are tamarins (492 g) and squirrel monkeys (688 g). Medium species are wedge-cap capuchins (2600 g), bearded sakis (2990 g) and brown capuchins (3450 g). Large species are howler monkeys (7275 g) and spider monkeys (7775 g). There were no significant differences in fleeing based on body size (Table 3-6) ($p > 0.5$, $DF=2$, $\chi^2=1.09$). There was, however, an association between body size and alarm calls ($p < 0.05$, $DF=2$, $\chi^2=6.14$). Smaller species alarmed less than medium species and large species. Large species alarm called 36% of the time they were encountered, medium species alarm called 18% of the time and small species only alarm called 8% of times encountered. However, this result was strongly driven by spider monkeys. When spider monkeys are removed from the analysis, the p value increases greatly, indicating no relationship between body size and alarm calls ($p=0.478$, $DF=2$, $\chi^2=1.48$).

Discussion

This chapter investigated the alarm and flight responses of primates based on habitat where encountered, habituation level as measured by location encountered and average species body size. The only variable to have a statistically significant effect across species was habituation level. When species were pooled, naïve species alarm

called more often than animals encountered in the long-term Boinski Monkey-Forest Project study site.

At a species level spider monkeys alarm called more than other species and alarm called more in open habitats than in dense habitats. Habituated brown capuchins fled and alarm called less than naïve brown capuchins. Across species, habitat where encountered and body size did not predict species responses to tourists and habituation level did not predict likelihood of fleeing. These results, like those of Chapter 2, demonstrate that the best predictor of primate response to tourists is species membership. As discussed in Chapter 2, each species' responses to various stimuli are shaped by natural selection, and each species has a limited plasticity within which to respond to stimuli. We can think of this group of evolved behaviors as a species-specific temperament (Clarke and Boinski, 1995) or a species' behavioral syndromes (Sih et al., 2004). Understanding the context in which each species lives and what environmental pressures may have contributed to these evolved behaviors can help us better predict how each species should respond to tourists. Next, I will explore how each species responded based on habitat, body size and habituation level in order to demonstrate the specific contexts that may have contributed to the evolution of each species' temperament.

Habitat

I predicted that primates encountered in open habitats would alarm call and flee more than those in dense habitats. This hypothesis was supported for alarm calls in spider monkeys but not for alarm calls in any other species or for fleeing in any species. I expected that animals in more open habitat would alarm call more as they may be more alert for predation or may be able to see approaching predators more clearly

(Chalfoun and Martin, 2009). As stated above, studies have shown that species such as squirrel monkeys and chacma baboons (*Papio cynocephalus ursinus*) use various refuges as protection from predators. In open habitats, a predator may spot the prey early in its approach, therefore negating any benefit the animals get from being hidden, so they add little risk by alarm calling and may also deter the predator (Zuberbühler et al., 1999). Why was there no effect of habitat on alarm calling in any other species or in fleeing across species? The following discussion of body size will begin to answer these questions, and also point out the importance of the entire context of an animals' encounter with possible predators.

Body Size

I predicted that large species (howler monkeys and spider monkeys) would flee and alarm call the least when in contact with tourists and that small species (tamarins and squirrel monkeys) would flee and alarm call the most. Larger animals are more able to defend themselves against predators and therefore can risk giving away their location through alarm calls (Cheney and Wrangham, 1987; Isbell, 1994). Smaller animals, on the other hand, depend more on being undetectable (Kerfoot and Sih, 1987) and therefore will not risk alarm calling and being spotted.

At RV, however, the effect of body size on behavioral responses to predators may be more related to general species temperament, as discussed in the previous chapter. The small sized species at RV are tamarins and squirrel monkeys. Tamarins were rarely seen and showed a predator-response to tourists. Squirrel monkeys, on the other hand, were seen more often (24% of encounters) and did not see tourists as predators (Table 2-9). Medium sized species are wedge-cap capuchins, bearded sakis, and brown capuchins. Of these species, both bearded sakis and wedge-cap capuchins respond to

tourists as predators, while brown capuchins do not. Finally, of the large size species, howler monkeys did not see tourists as predators while spider monkeys did (Table 2-6). As the rates of alarm calling in each group most relate to the species in the group with the largest sample size, a disproportionate bias was produced. Spider monkeys alarm called most frequently of all the species, making it appear as if larger animals alarm call more. This result further indicates that species' responses to tourists may be more related to general species characteristics (such as temperament) than variables that can be seen across species. Although both spider monkeys and howler monkeys have large body size, that alone does not explain their response to tourists.

These results also relate to the above discussion of habitat where encountered, in that species behaved similarly across habitats. For all species except spider monkeys, there was no effect of habitat on alarm calls. Each individual species alarm called at similar rates regardless of habitat where seen. Similar and more stark results are seen in fleeing, for which there was no effect of habitat in any species.

Habituation Level

I predicted that animals encountered in the Boinski Monkey-Forest Project site would flee and alarm call less than those encountered outside of the site. This hypothesis was supported for brown capuchins, who fled and alarm called less when encountered within the site. When species are pooled, they are also more likely to alarm call when encountered outside the Boinski Monkey-Forest site. Below I discuss the differences between fleeing and alarm calls and management implications of these results. Here I discuss these results in light of explaining the brown capuchins' unique response, and how these results further our understanding of habituation.

Why are brown capuchins the only species to adjust rates of fleeing based on habituation level? First, at the time of this study brown capuchins were also subject to a long-term observational study. Therefore several groups of brown capuchins in the Boinski Monkey-Forest site were used to seeing humans on a daily basis. While squirrel monkeys were previously studied, there was no active study concurrent with my data collection. Brown capuchins may show the most obvious effect of habituation due to their involvement with researchers.

These results also present a test of habituation—animals that were encountered in the area of the long-term study site did respond to tourists with less alarm calls than those outside the Boinski Monkey-Forest site. Thus long-term exposure to a possible predator does lessen the response to that predator in terms of rates of alarm calls, possibly because the stimulus is no longer seen as a predator. While only squirrel monkeys and brown capuchins have been specifically studied as part of the Boinski Monkey-Forest project, the fact that other species responded with less alarm calls to tourists in the project site indicates that other species were habituated to researcher presence. While many primatologists depend on habituation to gain access to their study animals' natural behaviors (Martin and Bateson, 1993; Williamson and Feistner, 2003) few studies have confirmed that habituated animals behave as they would without observers (but see Crofoot et al., in press).

This has important implications for tourism management and for researchers. While researchers or managers may set out to habituate one species, it is possible that other species in the area could also be habituated to humans. This could lead to unintended negative consequences if non-target species become aggressive to humans

(Brennan et al., 1985; Fa, 1992; Fuentes, 2006; Fuentes and Gamerl, 2005) are more susceptible to human-transmitted diseases (Jones-Engel et al., 2005; Wallis and Lee, 2004; Wolfe et al., 1998) or are more likely to be hunted (Kasereka et al., 2006).

Further, habituated animals may be learning two different things: 1) that humans are not predators and 2) that humans in a certain area behaving a certain way are not predators. Primates may be habituating to a certain context, and if this context changes they may respond with fleeing and alarm calls. Physiological responses to stressors in animals are known to change based on a wide variety of contexts including life history variables, what the animal is doing at time of exposure, if the animal is hungry or not and the predictability of the stressor exposure, among others (Wright et al., 2007). Predictability of a stressor is needed for habituation (Wright et al., 2007), so animals that are habituated to humans in one context may respond to humans with anti-predator behaviors if humans behave in unpredictable ways. I will discuss predictability further in Chapter 4.

Feeding Ecology

Again, most hypotheses were not supported for most species. Each species behaves towards humans in a consistent way not predicted by body size or habitat where encountered. By looking at some of the natural history of the species involved, we can begin to understand the underlying reasons for their behavior. Investigating spider monkey feeding habits may help explain why they alarm call at high rates when in the presence of tourists. Spider monkeys are frugivorous, which means they are limited in feeding by the availability of trees containing ripe fruit. The costs of leaving a fruiting tree can be high as there may not be a comparable food source available nearby. This constraint on spider monkey behavior may partially explain their decision

to alarm call rather than flee when in the presence of tourists. As the costs of them fleeing away from a fruit tree are high and the cost of alarm calling is smaller due to their large body size, alarm calling is the most optimal response to tourist presence. Other species that show less anti-predator response to tourists have more omnivorous diets, and may be able to more easily find alternative food sources. While brown capuchins and squirrel monkeys do eat fruit, they each have more dietary flexibility than spider monkeys. They both eat invertebrates and forage more widely throughout all levels of the canopy (Mittermeier and van Roosmalen, 1981; Simmen and Sabatier, 1996).

In comparison to spider monkeys, howler monkeys respond much less to tourist presence, rarely alarm calling or fleeing. Investigating the howler monkey diet can also illuminate some possible reasons why howler monkeys may not alarm call or flee when in the presence of tourists. Both alarm calling and fleeing have energetic costs (Bailey et al., 1993; Casey, 1992; Deecke et al., 2005; Fischer et al., 2004), although the immediate energetic cost of alarm calling is less. Howler monkeys in the Guianan shield eat mostly leaves (Julliot and Sabatier, 1993), a diet which is usually assumed to be of low quality resulting in animals more likely to conserve energy than spend it (Nagy and Milton, 1979; Pavelka and Knopff, 2004). Due to this evolved lifestyle of low energy expenditure, howler monkeys conserve energy and are therefore less likely to flee or alarm call when in the presence of tourists.

Are Alarm Calling and Fleeing Equitable Measures of Anti-predator Response?

According to these results, the predator response of alarm calling is more likely to be affected by variation in habitat, habituation and body size than is the response of flight. What might account for this difference and what implications might it have for the long term effects of tourism on the primates at RV? Alarm calling may indicate that

species perceive less threat than if they were to flee. In making the decision to alarm call, an animal risks discovery by the predator and loses any advantages it might have had from remaining unnoticed (Zuberbühler et al., 1999). Fleeing without alarm calling, on the other hand, shows that an animal perceives itself to be in such imminent danger that it needs to avoid the situation (Ydenberg and Dill, 1986). These results may indicate that as a whole, primates at RV do not feel imminently threatened by tourists.

Overall rates of alarm calling versus fleeing, however, are not radically different. Monkeys fled on 13 out of 95 encounters (13.7%) while they alarm called on 18 out of 95 encounters (18.9%). With species pooled, there is no statistical relationship between fleeing and alarm calling ($p < .005$, $\chi^2 = 11.94$, $DF = 1$). Trade-offs between foraging and predation risk may be coming into play here. If an animal is at a particularly valuable foraging spot, (s)he may not flee and instead solely alarm call, trading off the possibility of predation with the need to forage (Ydenberg and Dill, 1986). Further studies should more closely examine how tourist presence affects anti-predator responses in different and specific foraging situations.

Alarm calls and fleeing are also likely to have different effects on population health. While fleeing may indicate that an animal sees tourists as a greater threat, it may also be less disruptive, although more energetically expensive, as after it has fled an animal can return to its regular feeding and social behaviors. Increased alarm calls also result in animals allotting time to a short-term strategy over long-term maintenance behaviors but, depending on the strength of the response, animals may not return to regular behaviors so quickly as after fleeing. If animals flee in response to a strong perceived threat, they may remain vigilant or in hiding as opposed to immediately

returning to their maintenance behaviors (Cooper and Pérez-Mellado, 2004). The opportunity costs of such a prolonged reaction could affect the animals' health and nutrition, as well as interactions and relationships in the social group. For example, animals who alarm call more are known to demonstrate higher levels of stress hormones (Boinski et al., 1999). If higher stress is correlated with increased alarm calls, this could impact population health of wild primates in RV. Studies have shown that high stress over long periods as measured through increased corticosteroids leads to lower reproductive rates and higher metabolic costs (Sapolsky, 2005; Sapolsky et al., 2000). Increased stress resulting from tourist presence might physiologically impair reproduction, leading to decreases in population size of the affected animals.

In addition to energetic considerations and decreased population due to stress, increase of alarm calls may affect relationships with other species in the community. Alarm calls are a potentially risky behavior as they may alert a predator to the caller's location (Maynard Smith, 1965; Sherman, 1977, 1980) and are not generally used by smaller, more cryptic animals (Kerfoot and Sih, 1987). Animals may alarm to tourists, but then attract notice of another predator such as a harpy eagle or cat. Increased alarm calls may also affect intra-specific relationships. Grossberg and others (2003) found that howler monkeys calling in response to tourists at a Mayan archaeological site attracted other howler monkey groups who then began an aggressive interaction. Increased alarm calls could also cause more aggression between primate species competing for similar resources.

Management Implications

Results found in alarm call and fleeing responses of primates in RV have management implications for the various species. Further surveys should be done

investigating in detail the behaviors of the animals when encountered by tourists. First, what variables affect whether or not an animal flees in response to tourists? Animals may flee based on food resource or some other item beyond the scope of the present study. Second, as animals alarm called more often when naïve or when in open habitat, this indicates that animals were disturbed by tourists in these circumstances. Managers at RV should consider limiting the time tourists spend with primates in open habitat, and guide tourists seeking to view primates to more habituated groups. Managers may also want to consider habituating more species, but this should be done with care, as in other tourism ventures over-habituating has resulted in changes in primate behavior (Kauffman, in prep), increased aggression of primates towards tourists (Fa, 1992) or disease transmission between the species (Köndgen et al., 2008; Wallis and Lee, 2004). Over-habituating can be prevented by not providing food to the animals and slowly habituating them. Blom and colleagues (2004) habituated gorillas by approaching the animals little by little, allowing them to flee, and then approaching again. Habituation efforts should cease when animals reach the optimal level—that where they seem to ignore human presence, but do not approach. Further, guidelines can be put in place that indicate the minimum distance a tourist can approach the animals.

Conclusion

The results of this chapter provide further evidence that in order to create and manage a successful and non-invasive WT program each species must be managed separately, and that even traits such as species body size cannot be used to make generalizations about how primates will respond to tourists. Tourists in RV can be guided towards seeing brown capuchins, howler monkeys and squirrel monkeys, the primate species who do not show a predator response. This can be done by pointing

out these species over more reactive species, or by discovering where the squirrel monkeys, brown capuchins, or howler monkeys are most likely to be seen, and spending more time with tourists in those areas. Tourist time should be limited with wedge-cap capuchins, bearded sakis, spider monkeys and tamarins, especially when encountered in open habitats as all demonstrate predator responses. With limited time with tourists, the behaviors of these species will be less disrupted, and it is less likely that their populations will be adversely affected. In addition, if tourists are realistically told what animals to expect to see and told why they may not see others, tourist satisfaction should remain high.



Figure 3-1: Voltzberg trail map

Table 3-1: Explanation of terminology used in the data collection

Term	Definition
Tour follow	Observation of tourist group from Anjoemara Falls to Western Plateau and back. Researcher walked in the back of the group, generally maintaining a distance of one to three meters behind rearmost tourist.
Primate encounter	Any instance in which the group came within viewing distance of monkeys and at least one tourist or guide was aware of the monkeys.
Tour group	Any group of people (two or more) walking the Voltzberg Trail, not including Boinski Monkey-Forest researchers.

Table 3-2: Ethogram of monkey behaviors. Data on these behaviors was collected via 2 minute group scans during each primate encounter.

Behavior	Definition
Flee	Monkeys move away rapidly.
Alarm call	Varies by species, but is vocalization made in response to approach of a predator. All species alarm were known from prior experience.
Display	Varies somewhat by species. Consists of threat vocalization, shaking of branches, lunging or other threatening postures. Some species break and drop branches.
Feed	Monkey places some food item (fruit, insect, leaves) into their mouth.
Play	Wrestling, chasing.
Groom	One animal picks through another animal's fur.

Table 3-3 Habitat types of the Voltzberg trail (based on Mittermeier and van Roosmalen 1981)

Habitat Type	Description
High forest	Forest not affected by seasonal flooding, litter decomposition is good, three to four stories can be distinguished. Tallest trees can reach 60 m, understory consists of slender trees and samplings. Palms are abundant, especially <i>Astrocaryum sp.</i>
Low rain forest	A subcategory of high forest that does not exceed 20 m in height. Richer in lianas and with fewer palms than high forest.
Liana forest	Tall trees occur, but widely separated. Space between the trees is filled with dense tangles of lianas and vines.
Pina swamp	Forest in which the soil stays moist to wet for most of the year. Stilt roots on trees are common. In RV, this forest is categorized by the presence of <i>Euterpe oleracea</i> palms.

Table 3-4: Results for hypothesis 1. Responses of primates to tourists by habitat.

Species	Habitat	Behavior	% Time
Brown capuchin	Dense	Flee	6
		Alarm call	6
Spider monkey*	Open	Flee	7
		Alarm call	14
	Dense	Flee	33
		Alarm call	17*
Squirrel monkey+	Open	Flee	29
		Alarm call	71
	Dense	Flee	11
		Alarm call	0
Howler monkey+	Open	Flee	0
		Alarm call	0
	Dense	Flee	Not observed
		Alarm call	0
Bearded sakis+	Open	Flee	Not observed
		Alarm call	25
	Dense	Flee	50
		Alarm call	100
Tamarin+	Open	Flee	0
		Alarm call	100
	Dense	Flee	100
		Alarm call	50
Wedge cap capuchins+	Open	Flee	0
		Alarm call	100
	Dense	Flee	100
		Alarm call	100
All species pooled*	Open	Flee	100
		Alarm call	100
	Dense	Flee	14
		Alarm call	11*
All species pooled*	Open	Flee	13
		Alarm call	37*

*results significant ($p < 0.05$)

+statistical tests not possible

Table 3-5: Results for Hypothesis 2. Reactions of primates to tourists based on habituation level.

Species	Habituated?	Behavior	% Time
Brown capuchin*	Yes	Flee	0*
		Alarm call	0*
	No	Flee	25*
		Alarm call	33*
Squirrel monkey+	Yes	Flee	0
		Alarm call	0
	No	Flee	14
		Alarm call	0
Spider monkey	Yes	Flee	0
		Alarm call	0
	No	Flee	33
		Alarm call	50
Howler monkey+	Yes	Flee	0
		Alarm call	0
	No	Flee	0
		Alarm call	20
Bearded saki+	Yes	Flee	33
		Alarm call	100
	No	Flee	0
		Alarm call	0
Tamarin+	Yes	Flee	100
		Alarm call	0
	No	Flee	50
		Alarm call	100
Wedge-cap capuchin+	Yes	Flee	0
		Alarm call	0
	No	Flee	100
		Alarm call	100
All species pooled*	Yes	Flee	4 [#]
		Alarm call	4*
	No	Flee	27 [#]
		Alarm call	39*

*results significant ($p < 0.05$)

+statistical tests not possible

results are not significant when brown capuchins are removed from the analysis

Table 3-6: Results for hypothesis 3. Primate response to tourists based on primate body size.

Body size	Behavior	% Time
Small	Flee	21
	Alarm call	8*
Medium	Flee	12
	Alarm call	18*
Large	Flee	21
	Alarm call	37*

*results significant ($p < 0.05$)

CHAPTER 4 PRIMATE RESPONSE TO TOURIST BEHAVIOR

Introduction

This chapter investigates tourist-primate interaction in the Central Suriname Nature Reserve by examining the behavior of the tourists. How does tourist behavior affect primate responses? Are there characteristics of tourist groups that can be manipulated to minimize disturbance of primates encountered? Earlier chapters discussed primate response to tourists based on species membership and temperament, body size, habitat where encountered and habituation level. This chapter investigates how the behavior of tourists affects the anti-predator responses of the primates.

Predator Recognition

How do animals decide if another animal is a possible predator? There are two possibilities: 1) prey species recognize predators based on species membership or 2) prey species recognize predators based on characteristics that indicate the animal may be a predator, independent of species membership. If prey recognize predators based on species membership, these prey populations can be negatively impacted when faced with an introduced predator species that they do not recognize as a predator (Berger et al., 2007; Gill et al., 1996). Indeed, studies based on island communities have found that animals living without any natural predators are slow to respond to introduced predators (Iverson, 1978; Kruuk and Snell, 1981; McEvoy et al., 2008) which can affect population survival. This is of concern in areas with anthropogenically introduced predator species that can impact the survival of endangered prey species. The lack of response to introduced predator species indicates that these prey have evolved anti-

predator responses in response to certain species as opposed to general characteristics that could indicate a predator, such as odor indicating the animal is a carnivore (Caine and Weldon, 1989; Sundermann et al., 2008) or behaviors indicating danger (Bouskila and Blumstein, 1992; Dill, 1974; Helfman, 1989; Stankowich and Coss, 2006). In other words, the prey mainly use the fact of species membership to judge whether or not another animal is a possible predator. It is expected that a goal of predator recognition ability is to lessen the number of “mistakes” prey make, and reduce under- or over-estimation of predation risk. Both can be costly (Bouskila and Blumstein, 1992). Underestimation of predation risk can result in the animal’s death, while overestimation can result in unneeded energy expenditures. This specific evolution to recognize individual predator species will lessen mistakes in the judgment of danger facing prey species in less stochastic environments, but in environments with changing species compositions this would result in more misjudgments of danger resulting in more energetic costs.

Another possibility for animal recognition of predators suggests that prey respond to suites of characteristics that may suggest “predacious intent” (Dill, 1974) or other characteristics common among predators (e.g., odors that are common to carnivorous animals (see Bouskila and Blumstein, 1992; Roth et al., 2008; Sundermann et al., 2008). Having this plasticity allows the prey to less often under- or overestimate danger from possible predators. Predator-prey literature demonstrates that the behavior of potential predators has effects on the response of prey animals and is one of the factors that make up what we refer to as “predation risk” (Frid and Dill, 2002; Lima and Dill, 1990). Prey are likely to avoid animals whose behavior signifies danger. Such signals

may consist of novel stimuli, familiar stimuli that are more intense than usual (e.g. a stimulus that is louder, faster or more numerous than usual) or suddenly occurring stimuli (Thorpe, 1966).

Humans as Predators in Raleighvallen

As earlier chapters show that humans are seen as predators by some Raleighvallen (RV) primates, and since there has been no hunting in RV in modern times (Reichart, 1993; Trail, 1987), it appears that these animals are using the second method of predator recognition: monkeys are more likely responding to human actions that signify their predacious intent, such as noise level, group size, and speed of movement, as opposed to their species. Furthermore, primates are known for their behavioral plasticity (Boinski, 2005; Strier, 1994) and it makes sense that they, as a group, are less likely to respond solely to hard and fast rules about prey species. This can also be seen in the fact that many primate species have been observed making alarm calls to non-dangerous stimuli. Mustached tamarins (*Saguinus mystax*) and saddle-back tamarins (*Saguinus fuscicollis*) in Peru alarm call to non-threatening birds such as parrots and heron while at times not responding to the presence of dangerous raptors (Heymann, 1990). Vervet monkeys (*Cercopithecus aethiops*) also make alarm calls to non-dangerous birds and mammals, although juveniles do so more than adults (Seyfarth et al., 1980). I expect that primates will make decisions about how to respond to possible predators based on multiple variables, including where the predator is encountered and the behavior of the possible predator. These decision making variables are flexible and malleable to different contexts. In addition, primates at RV are subject to predation by both aerial (harpy eagle) and terrestrial (jaguars and pumas)

predators. With a variety of predators to respond to, it may be more parsimonious to evolve reactions to general characteristics, and not to different species.

As stated earlier, monkeys are expected to respond to four groups on the basis of perceived threat (Frid and Dill 2002). It is well known that sudden loud noises elicit a startle response in different animal species (Hoffman and Searle, 1968), including primates (Antoniadis et al.; Winslow et al., 2002). The startle response indicates that animals find these loud noises threatening and stressful, and animals will first respond by removing themselves from the stimulus if possible. If this is not possible, there will be an endocrine response resulting in increased levels of stress hormones (Wright et al., 2007). Regular exposure to threatening situations can have long term effects such as weakening of reflexes, lowering of learning abilities, and negative impacts on reproduction (Moberg, 1987; Sapolsky, 2005; Welch and Welch; Wingfield and Sapolsky, 2003).

Exposure to longer duration noisiness can also affect animal populations. Studies on the responses of animals to anthropogenic noise in both the wild and captivity have found negative effects that may cascade to the population level. One review found that marine animals generally acted as if noise levels indicated a threat (Myrberg, 1990) and another found that fishes exposed to periodic noise from ships secreted more cortisol, indicating elevated stress levels (Wysocki et al.). Increased exposure to airplane noise is associated with faster heart rates in ducks (*Anas rubripes*) (Trimper et al., 2003) and larger adrenal glands in mice (*Mus musculus*) (Chesser et al., 1975), indicating that both species were undergoing a physiological stress response. In addition, exposure to noise in captive settings has been found to increase stress responses and negatively

affect animal physiology. Rats (*Rattus norvegicus*) exposed to loud noises daily for limited periods of time had accelerated heart rates and damage to their gastrointestinal system (Baldwin, 2007). There are fewer studies of the impact of tourist-produced noise on wild animals, but several species of foraging birds were found to respond more strongly to faster and noisier boats in their vicinity and also to larger and noisier tourist groups (Burger and Gochfeld, 1998). Ruesto et al (submitted) also found that as decibel level of tourists viewing Tibetan macaques (*Macaca thibetana*) increased, so did the rate of threats made by the macaques.

In addition, larger tour groups may also be a high intensity stimulus (Thorpe, 1966) which will result in primates fleeing and/or alarm calling more. Animals of several different species respond negatively to larger groups of tourists. Ibis (*Plegadis falcinellus*), herons (*Egretta caerulea* and *E. tricolor*) and gallinules (*Gallinula chloropus*) decrease feeding time when in contact with larger groups of people (Burger and Gochfeld, 1998), macaques (*Macaca nigra*) in Indonesia flee from tour groups of over six or seven people (Kinnaird and O'Brien 1996) and Australian parrots (*Platycerus elegans*) are more likely to flee when approached by two people as opposed to one (Geist et al., 2005) although tour group size has no effect on bat (*Myotis velifer*) behavior in caves (Mann et al., 2002) or on Tibetan macaque behavior in China (Ruesto et al, submitted).

Finally, faster moving tour groups are also predicted to be more likely seen as a serious threat—a high intensity stimulus indicating danger (Dill, 1974; Thorpe, 1966). Through their quick approach, animals are signaling that they have a dangerous (to the prey) intent. Burger (1998) found that common terns (*Sterna hirundo*) responded more

strongly to fast approaching boats versus slow boats and chamois (*Rupicapra rupicapra*) in Austria flee more often when approached quickly (Burger, 1998; Hamr, 1988).

Thus, the behavior of possible predators, in this case, humans, is expected to have an impact on the anti-predator responses exhibited by primates in RV. Primates should view larger, louder and faster moving groups as a more serious threat and respond with higher rates of alarm calls and fleeing. It is predicted that groups who are noisier, move more quickly, and are larger will be perceived as more of a threat than quieter, slower and smaller groups. Increased noise and disruption in these tour groups will indicate more danger to the monkeys. Effects of tourist behavior on primate response are investigated through testing the following three hypotheses:

Hypothesis 1: Primates flee and alarm call less when in contact with quiet tourist groups as compared to noisy tourist groups.

Hypothesis 2: Primates flee and alarm call less when in contact with small tourist groups versus larger tourist groups.

Hypothesis 3: Primates flee and alarm call less when in contact with slow moving tourist groups as compared to faster moving groups.

Methods

Study Site

The study site, Raleighvallen (RV) (4°0'N, 56°30'W), is situated in the 1.6 million ha Central Suriname Nature Reserve (CSNR) in the Coopename River drainage. The CSNR is located in west central Suriname and is comprised of lowland rainforest (Berrenstein, 2006). It receives annual average rainfall of 2300 mm (Reichart, 1993). The aerial and terrestrial predator complement of the forest is complete, and no

significant hunting has occurred since the 1800s (Reichart, 1993; Trail, 1987). Eight species of primates are found at RV, brown capuchin (*Cebus apella*), squirrel monkey (*Saimiri sciureus*), wedge-cap capuchin (*Cebus olivaceus*), spider monkey (*Ateles paniscus*), howler monkey (*Alouatta seniculus*), white-faced saki (*Pithecia pithecia*), bearded saki (*Chiropotes satanas*) and golden handed tamarin (*Saguinus midas*). Additional descriptions of the site can be found elsewhere (Boinski et al., 2005; Boinski et al., 2003; Boinski et al., 2002; Fleagle and Mittermeier, 1980; Mittermeier and van Roosmalen, 1981).

Since 1998, the site has been host to a long term focused study of the behavioral ecology of squirrel and capuchin monkeys, along with a broader program of ecological monitoring. Many aspects of the site are well-researched, including the populations of various animals, the phenology, the climate and the weather. This study is unique in that it reports on the activities of wildlife tourists on otherwise undisturbed animals. Animals under more extreme pressures such as from habitat loss or hunting are expected to exhibit more dramatic responses to tourists. Here I describe a baseline of primate response to tourism which is needed before tourism further develops in RV. The tourist attraction of the Voltzberg trail allows a unique opportunity to encounter a number of different primate species and collect data on each.

Methodology

From July 8, 2006 through November 30, 2006 I completed 48 “tour follows” (equaling 365 individual tourists) along the trail from Anjoemara Falls to the Western Plateau of the Voltzberg (Figure 2-6). This equals 220.25 hours of tourist observation. After receiving permission from the tourists and guides to make observations, I noted the number of people in the group, and their age-sex distribution. The research was

conducted under proper approvals from the University of Florida's Institutional Animal Care and Use Committee (UF IACUC# E306), Institutional Review Board (UFIRB# 2005-U-1007), and with permission and approval of Surinamese authorities.

During tour follows, as I walked at the back of the tourist group, I completed an instantaneous group scan (Fragaszy et al., 1992; Martin and Bateson, 1993) every fifteen minutes. At each interval I recorded the number of tourists stopped, looking at the environment, taking photos, speaking and resting.

In addition, I measured how much time tourist groups spent making noise. Before meeting tourist groups I used a random number table to choose three fifteen-minute intervals during which I would record noises produced by tourist groups. I recorded this noise via an omni-directional lavalier microphone attached to a bandanna on my head and a battery-powered cassette tape recorder. At the beginning of each interval I set the tape recorder to record and let it run for approximately the next 15 minutes. If tourists were on top of the Voltzberg or not yet arrived at the trailhead for one of the intervals I recorded them as soon as possible after the missed interval. Furthermore, if it appeared we would complete the walk before the latest interval was reached, I recorded the last fifteen minutes of the hike. This measure of "noisiness" is used to estimate the disturbance caused by each tourist group. Decibel level of each tourist group would also be a possible measure of tourist group disturbance, but was not practical in these circumstances. To measure decibel levels, the microphone must be equidistant from all subjects. Thus, I would have had to walk in the center of the tour group which would have limited by ability to collect other data, or each tourist would have to have a microphone. This equipment was not available. However, percent time spent making

noise should still provide sufficient information about tour group disturbance levels, as very quiet noises were not picked up by the microphone, and I remained a consistent distance behind each tour group.

When we reached the Western Plateau, I remained behind and waited while the tourists and guides climbed the Voltzberg. I also noted the time spent in the forest traveling to the Plateau and back. Tour groups were defined as any group of people (aside from other researchers) walking up the trail to the Voltzberg. Groups ranged in size from 4 to 23 people. Time spent traveling to and from the Voltzberg ranged from 3.25 to 5.75 hours. Table 2-2 summarizes terminology used and Table 2-3 is an ethogram of tourist behaviors.

Whenever primate groups were encountered I collected data on general troop characteristics such as location and movement as well as number of alarm calls heard. Via two minute instantaneous group scans I also recorded the number of individuals grooming, resting, participating in agonistic behavior, feeding and traveling (Table 2-4). Furthermore, the amount of time tourists spend in the presence of the monkeys was recorded.

Sound data were analyzed by digitizing each tape of three approximately fifteen minute intervals using Audacity (version 1.2.6, <http://audacity.sourceforge.net/>). I then listened to each tape, and deleted all parts without human made noise (excluding footsteps). I was left with the total duration of human made noise for each tour group and these were converted to percentages of time spent making noise.

Data were analyzed using Analyse-It for Excel version 2.00 (<http://www.analyse-it.com/>). Data were not normal, and Analyse-It contains many tests for the analysis of

non-normal data. The Kruskal-Wallis test was used to test the relationships between the various variables and the presence and absences of fleeing or alarm calling. The Kruskal-Wallis test was chosen as it is powerful for small sample sizes of non-normal data, and can be used to compare variables of differing sample sizes (Sokal and Rohlf, 1995).

Results

I followed 48 tourist groups equaling 365 total tourists. The average number of tourists per group was 7.4, the average number of guides per group was 1.7, and the average number of total people per tour follow was 10.2 (including myself). The range of number of people per group was between 4 and 23. The range of tourists per group was from 2 to 20. The range of number of guides per group was 0 to 3. The shortest trip was 3.25 hours and the longest was 5.75, with an average of 4.57 hours. Data are analyzed for brown capuchins, squirrel monkeys and spider monkeys as other sample sizes are too small for statistical analyses.

I made tape recordings of 45 of the 48 tour groups. Tapes for three of the groups are not available due to equipment failure. Generally, recordings were made over 3 randomly selected 15 minute intervals. However, there was some variation in the exact number of minutes recorded for each group, so amount of minutes spent making noise was converted to percentages for analysis. The mean percentage time spent noisy was 41%. The quietest group made noise for 6% of the time and the loudest group was noisy 80% of the time recorded. The number of people in a group was correlated with percent of time noise was made (Spearman's rank correlation, $p < 0.02$, $r_s = .39$).

Hypothesis 1: Primates flee and alarm call less when in contact with quiet tourist groups compared to noisy tourist groups.

There were 88 instances where monkeys were encountered and noisiness of tour groups was recorded. There was no statistically significant difference between the results (Kruskal Wallis, $n=88$, $p>0.1$). The average noisiness of groups who did not elicit alarm calls in primates encountered was 39.9% while the average noisiness of groups who did elicit alarm calls in primates was 31.9% (Table 4-1). There was no effect of tour group noisiness on alarm calls, although there is a statistically insignificant pattern of animals in contact with noisier groups alarm calling less than those in contact with quieter groups.

For fleeing, the average noisiness of tour groups in instances where fleeing was observed is 35.5%. The average noisiness of tour groups where fleeing was not observed is 38.8% (Table 4-1). Although these values are more similar between responding and not responding animals than the results for alarm calls, there is a slight (although nonsignificant) trend for animals to flee less for noisier groups (Kruskal Wallis, $n=88$, $p>0.8$).

Hypothesis 2: Primates flee and alarm call less when in contact with small tourist groups versus larger tourist groups.

Percentage of alarm calls observed with differently sized groups were similar, and were not statistically significant (Table 4-2). Tour groups of eleven or more elicited alarm calls 18% of the time they contacted monkeys ($n=28$). Tour groups of five to ten people elicited alarm calls 20% of the time they contacted monkeys ($n=66$). For fleeing, there appeared a slight tendency to flee more for tour groups of five to ten people (15%, $n=66$) while monkeys only fled when in contact with large groups 11% of the time ($n=28$). However, none of these results are statistically significant. There was no

relationship between number of people in the tour groups and likelihood of alarm calls (Kruskal Wallis, $n=95$, $p>0.6$). There was also no relationship between number of tourists and likelihood of fleeing (Kruskal Wallis, $n=95$, $p>0.4$). Only one group had less than 5 people, and primates encountered by this group neither fled or alarm called. When looked at by species, there was also no relationship between alarm calls and tour group size in brown capuchins (Kruskal Wallis, $n=45$, $p>0.2$) or spider monkeys (Kruskal Wallis, $n=13$, $p>0.6$). Squirrel monkeys were never observed making alarm calls. For fleeing, there was again no relationship with tour group size for brown capuchins (Kruskal Wallis, $n=45$, $p>0.4$), spider monkeys (Kruskal Wallis, $n=13$, $p>0.4$) or squirrel monkeys (Kruskal Wallis, $n=23$, $p>0.2$).

Hypothesis 3: Primates flee and alarm call less when in contact with slow moving tourist groups as compared to faster moving groups.

The average time spent walking the trail for all tour groups who encountered monkeys was 4.62 hours ($n=38$, $s.d.=0.64$) (Table 4-3). In primate encounters when primates did not flee, the average time tour groups spent walking the Voltzberg trail was 4.63 hours ($n=83$, $s.d.=0.60$). In primate encounters when primates did flee, the average time tour groups spent walking the Voltzberg trail was 4.91 hours ($n=12$, $s.d.=0.69$). In primate encounters when primates did not alarm call, the average time spent walking the trail was 4.65 hours ($n=78$, $s.d.=0.61$). In primate encounters when primates did alarm call, the average time spent on the trail was 4.69 hours ($n=17$, $s.d.=0.65$). These results are not statistically significant. When species were pooled, there was no effect of speed of tour groups on fleeing (Kruskal-Wallis, $n=95$, $p>0.4$) or alarm calling (Kruskal-Wallis, $n=95$, $p>0.9$). Additionally, when analyzed by species there were also no effects

of speed of groups on alarm calls for brown capuchins ($n=43$, $p>0.8$) or spider monkeys ($n=13$, $p>0.8$). Squirrel monkeys were never observed alarm calling. There were also no effects of tour group speed on fleeing in brown capuchins ($n=43$, $p>0.7$), spider monkeys ($n=13$, $p>0.8$) or squirrel monkeys ($n=24$, $p>0.1$). There was, however, a correlation between the number of people and speed (Spearman, $r_s=0.18$, $p<0.04$). Larger groups were slower.

Discussion

None of the variables explored in this chapter explain the anti-predator response of primates encountered (Table 4-4). Part of this may be due to the low rate of response to tourists overall. Most tourist encounters were with brown capuchins, squirrel monkeys and howler monkeys, all of whom showed low rates of anti-predator response to tourists (Table 2.6, 2.9). In this section I will discuss how these results provide insights into how primates perceive anthropogenic noise, some sampling issues of the study and applications of these results to tourism management.

The Importance of Surprise

Although not statistically significant, these data indicate a slight pattern of larger and noisier tourist groups resulting in less anti-predator behavior (Tables 4-1 and 4-2). It may be that in RV primates are assessing risk of the tourists based on the predictability of the tourists, versus their loud or startling behaviors. That is, as larger groups are noisier, primate species at RV are more able to detect these larger tour groups and monitor their whereabouts—these groups are actually less startling than small, quiet tourist groups, resulting in fewer instances of alarm calls and fleeing. Larger and louder tour groups were more likely to be noticed by the monkeys earlier, giving the animals a chance to verify that the tour groups were not dangerous and thus negating the need for

alarm calls and fleeing. Smaller, quieter tour groups may surprise the animals, startling them into alarm responses.

Literature on the response of animals to the noisiness of tourists or other anthropogenic disturbances is scant and generally based on the assumption that noise level of tourists will be more disruptive to the animals in question. Furthermore, results of the studies are mixed. While some studies have found that noise level increased the antipredator behaviors of various taxa (Burger and Gochfeld, 1998; Myrberg, 1990; Wysocki et al., 2006), others found no such effect (Papouchis et al., 2001). Others found results similar to this study; that increased noise actually decreased antipredator responses (Blom et al., 2004; Hamr, 1988). Bighorn sheep (*Rupicapra rupicapra*) in Austria respond more to quiet hikers than to noisy vehicles, possibly due to the unpredictability of hikers when compared to vehicles (Hamr, 1988). The mixed results in the literature, in combination with the current study, indicate that noisiness may not always be perceived by animals as signifying predacious intent on the part of humans. Instead, it seems that sudden and unexpected noises are more likely to signal danger to the animals. Gorillas (*Gorilla gorilla*) also respond more strongly to humans who approach quietly, than to those who signal their presence via 'tongue clacks' (Blom et al., 2004). As long as animals know where a possible predator is, they can keep track of the predator's movements and will therefore lessen their predation responses. The primates at RV might be alarm calling and fleeing less in the presence of larger groups because they know where those groups are.

Further support for this can be found in the fact that noise level of tourist groups was positively correlated with size of tourist groups. Groups that are larger and noisier

are less likely to surprise animals and therefore less likely to elicit anti-predator responses. Finally, the speed at which groups walked the trail was not related to occurrences of alarm calls or fleeing. Size of groups, however, was correlated with speed of groups, indicating that larger groups walked more slowly. Variation in the speed of tour groups was not great (s.d.=0.64 hours). I believe that this low variation, plus the fact that larger groups were slower, indicates that the variable of speed is less important than those of tour group size and noisiness in this case. Speed was simply swamped by the importance of size and noisiness to the broadcasting of a tour group's presence.

It is also important to note that tourists in RV are limited to a very small area within a large reserve and that the monkeys can easily move to a different location away from tourists. If animals encountered in this study heard the tourists in advance, they may have already decided not to flee, thus allowing for the encounter to occur. Animals who have decided not to move away from the tourists are therefore prepared for and act unconcerned by, tourist presence. Therefore, anti-predator responses to tourists may be underestimated. Some of the primates encountered in this study may have decided to remain near the trail and encounter humans, while the alarm calls and fleeing of other primates may have occurred before observations could be made. For this reason, a future study that follows the primates instead of the tourists, would also be beneficial.

Frid and Dill (2002) point out that many factors can contribute to "predation risk" and among these are the behavior of the predator. This research shows that, contrary to the hypotheses, when primates at RV do react to tourists as predators, they do not see larger, noisier or faster tour groups as more disruptive or as indicating more danger.

Thorpe (1966) predicts that prey avoid danger signals which indicate novel or high intensity stimuli. While the loud, large and noisy tour groups may seem to be “high intensity”, the data show that primates do not perceive them this way. Instead, primates may be more attuned to sudden stimuli (Thorpe, 1966) which are personified here by smaller and quieter tour groups. As smaller groups are also faster, speed of groups does not end up having an impact.

Finally, these results correspond with known hormonal responses to unpredictable stressors and situations. Wingfield and others (1998) describe how unpredictable events can trigger a stress response in animals. This can be seen in long-lived animals (like primates) as one long-lived individual will have to respond to a variety of situations over their lifetime. Therefore they can be expected to be able to deal with instability within a certain limit, but unpredictable events, such as human disturbance, can result in a stronger stress response than expected, predictable events (Wingfield, 2003). Others have found increased levels of stress in unpredictable environments in snowshoe hares (*Lepus americanus*) (Boonstra et al., 1998) and in rats (*Rattus norvegicus*) (Haller et al., 1998).

Benefits of Larger and Noisier Tourist Groups?

In order to have successful wildlife tourism, two things must happen; 1) the environment must not be harmed and 2) tourists must have an enjoyable experience. Since primates have a slight tendency to alarm call and flee for smaller and quieter tourist groups, larger and noisier tour groups may actually be preferable. Blom and colleagues (2004) found similar results in gorillas which were more likely to respond to the presence of researchers when not alerted by the noise of the researchers. When researchers announced their presence by making tongue clacks, gorillas were less

likely to flee when approached (Blom et al., 2004). Johns (1996) also found no effect of tour group size on chimpanzee behavior, although she does recommend tour groups be capped at 10 people, not because of impacts on the chimpanzees, but because visitor satisfaction decreases when tour groups are larger (Johns, 1996).

Two kinds of additional research must be carried out before limits on tour group size can be set. First, we should understand the impact of tour group size and noisiness on other species in RV. While large and noisy tour groups do not result in more primate anti-predator behavior, we do not know of their impact on other animals such as smaller mammals, birds, or reptiles. Indeed, the mixed results of research on animal response to anthropogenic noise demonstrate that it is likely that tourist noise may affect other non-primate species. Secondly, research should be completed to discover what tourists to RV want from the experience. From the viewpoint of the welfare of the monkeys, fewer larger tour groups may be beneficial. That is, larger tour groups are less likely to take the animals by surprise, thus decreasing their disturbance. There is also most likely an upper limit to tour group size after which the benefit of the noise as a warning to animals is outweighed by the tourists' disturbance of the area. The largest number of people in a tour group in this study was 23. It is not reasonable to assume that much larger tour groups of 50 or 100 would have similar effects.

In addition, having larger groups in the forest less often may minimize disturbance of other plants and animals. It is not known, however, if tourists in RV prefer smaller groups over larger groups. If larger tour groups will decrease visitor satisfaction too sharply, negating the economic benefits of tourism in RV, then an optimal group size should be found which will be large enough to provide warning to the primates while still

maintaining visitor satisfaction. Alternatively, tourists could travel in smaller groups, as long as some sort of noise was made to alert the animals to their approach, as Blom recommends with tongue clacks for the gorillas (Blom et al., 2004).

Table 4-1: Results for hypothesis 1: Primates flee and alarm call less when in contact with quiet tourist groups compared to noisy tourist groups.

Alarm call observed?	Average time spent making noise
Yes	31.9%
No	39.9%
Fleeing observed?	
Yes	35.5%
No	38.8%

Results are not significant at $p=0.05$

Table 4-2: Results for hypothesis 2: Primates flee and alarm call less when in contact with small tourist groups versus larger tourist groups

Tour group size	primate encounters with alarm calls
11+	18% (n=28)
5-10	20% (n=66)
	primate encounters with fleeing
11+	15% (n=28)
5-10	11% (n=66)

Results are not significant at $p=0.05$

Table 4-3: Primates flee and alarm call less when in contact with slower tourist groups versus faster tourist groups.

Alarm call observed?	Average time spent on trail
Yes	4.69 hours (n=17, s.d.=.65)
No	4.65 hours (n=78, s.d.=.61)
Fleeing observed?	
Yes	4.91 hours (n=12, s.d.=.69)
No	4.63 hours (n=83, s.d.=.60)

Results are not significant at $p=0.05$

Table 4-4. Results for the three hypotheses.

Hypothesis	Supported?
Primates flee and alarm call less when in contact with quiet tourist groups compared to noisy tourist groups.	No
Primates flee and alarm call less when in contact with small tourist groups versus larger tourist groups.	No
Primates flee and alarm call less when in contact with slow moving tourist groups as compared to faster moving groups.	No

CHAPTER 5 PREDICTORS OF TOURIST ENCOUNTERS WITH PRIMATES

Introduction

Earlier chapters discussed the interest in wildlife tourism (WT) as a conservation tool. That is, instead of using resources in an extractive way, WT can promote economic development while simultaneously preserving habitat. Chapter 1 discussed two components to sustainable tourism: 1) protection and preservation of the environment and 2) economic sustainability resulting from tourists visiting and recommending the site to others. All of the chapters of this dissertation so far have focused on the effects of tourism on the behavior of primates in Raleighvallen (RV), in the Central Suriname Nature Reserve. This chapter will look at the sustainability of WT in RV in terms of the likelihood of tourist encounters with primates. What variables best predict the likelihood of encountering primates in RV?

What Do Tourists Want?

In order for tourism to be sustainable, it must be economically profitable and attract customers (Backman et al., 2001; Page and Dowling, 2002). There are two types of research investigating the opinions and experiences of wildlife tourists. One operationalizes tourist satisfaction as met expectations. Tourists are expected to rate their WT experience more highly if their expectations for the experience are met. These tourists will either return to the destination or recommend it to others (Akama and Kieti, 2003), increasing the sustainability of the tourism endeavor. Akama and Kieti (2003) measured tourist satisfaction in Tsavo West National Park, Kenya. Via questionnaires they found that tourists to this park had high rates of satisfaction due to the fact that their expectations for their trip were exceeded. In Litchfield National Park, Australia,

tourists who expected to see wildlife had better experiences when they actually experienced wildlife encounters (Ryan and Sterling, 2001). Furthermore, the tourists in this study varied in their expectations and their view of the success of the experience related to whether or not their expectations were met, regardless of the specifics of the expectations and the experience. People who wanted a relaxing time with little exertion were able to meet this goal and were therefore satisfied with their trip. Others who were interested in learning about aboriginal culture, which was not something the park provided, were dissatisfied with their experience (Ryan and Sterling, 2001). Also in a national survey of visitors to Australia, it was found that tourists' ability to see wildlife they were expecting to see correlated highly with their satisfaction with their trip (Fredline and Faulkner, 2001).

The second type of research investigating the opinions of wildlife tourists is more experiential and looks at the emotions resulting from wildlife encounters. These researchers point out that tourists often have vague expectations in advance of their trip, so that measuring whether expectations are met may not be the best measure of tourist satisfaction (Arnould and Price, 1993; Curtin, 2005). The experiential approach investigates tourist views of WT through participant observation during the event, along with interviews and surveys administered following the experience. Results from this research indicate that tourists most value authentic experiences, unexpected events, and close contact with certain kinds of wildlife (Arnould and Price, 1993; Chan and Baum, 2007; Chapman, 2003; Farber and Hall, 2007; Fredrickson and Anderson, 1999; Glaspell et al., 2003; Hammitt et al., 1993).

In several of these studies tourists mentioned the importance of an authentic wildlife experience. Tourists talked about getting away from crowds and really being in the wilderness (Cole and Hall, 2009). Women in the Boundary Waters in Minnesota and in the Grand Canyon repeatedly referred to the importance of real and direct contact with nature and the presence of “bona fide” nature when recounting what made their experiences special (Fredrickson and Anderson, 1999). Glaspell and colleagues (2003) found similar results when studying tourists at the Gates of the Arctic National Park in Alaska. They found that one indicator of a good wilderness experience at this location was “untrammelled wildlife” (p. 66). Similarly, visitors to Alpine Lakes Wilderness in Washington, and Three Sisters Wilderness in Oregon were looking for a lack of human impact in their WT experiences (Cole and Hall, 2009). In Malaysia, ecotourists wanted a “clean and undisturbed environment” (Chan and Baum, 2007 p. 581).

Unexpected and unique events can also result in a memorable experience and further satisfy the desire for an authentic experience. River rafters thought of spontaneous events as the most memorable (Arnould and Price, 1993) as did travelers on the Dalton Highway in Alaska (Farber and Hall, 2007). If the experience is truly authentic and “wild”, the unexpected is expected to occur.

Finally, contact with wildlife can improve the tourist experience, regardless of expectations. At Elk Island National Park in Alberta, Canada tourists most often mentioned three main characteristics of wildlife encounters: size, shape and movement (Chapman, 2003). These tourists found encounters with larger, moving and uncommon wildlife as more memorable than encounters with smaller, stationary and more common wildlife. About one fifth of the tourists in this study also found eye contact with wildlife to

be important to creating a memorable experience. A review of experiential studies of WT found that tourists enjoy encounters with species that are larger, beautiful, charismatic and similar to humans (Curtin, 2005). On the Dalton Highway tourists had the best experiences when they saw animals for a long time and at close range, with offspring and acting naturally (Farber and Hall, 2007) as did the tourists in the Boundary Waters and at the Grand Canyon (Fredrickson and Anderson, 1999), at Gates of the Arctic (Glaspell et al., 2003) and in the Smoky Mountains (Hammit et al., 1993).

These two approaches to studying tourist experience do not have to be mutually exclusive. Combined, they can illustrate a more complete picture of what makes a satisfactory WT experience. Seeing wildlife known to be common in the area did not improve the tourist experience at Elk Island (Chapman, 2003), as the tourists were hoping to see rare wildlife—something they viewed as more unexpected and authentic. In addition, lack of wildlife does not take away from the experience but presence of wildlife will add to it. In some settings, such as Alpine Lakes and Three Sisters, only about 10% of the tourists visiting were interested in wildlife and therefore did not have wildlife viewing expectations. For these tourists seeing wildlife added greatly to the experience while not seeing any only detracted moderately (Cole and Hall, 2009). Furthermore, tourists on whale watching cruises report satisfactory experiences even if whales are not seen (Orams, 2000). During the whale-watching trip, tourists had their expectations modified and other aspects of the trip, such as the experience on the boat, provided a satisfactory experience. Again, this overlaps the expectations research in that when tourists went on a trip in order to see scenery (as at Alpine Lakes and Three

Sisters), as opposed to wildlife, lack of wildlife did not disappoint although presence of wildlife could add to the experience.

Although studies of tourist satisfaction in regards to wildlife experiences differ in their methodologies, a few generalizations can be made. First, most tourists rate their experiences more highly when they involve some sort of contact with wildlife (Chan and Baum, 2007; Chapman, 2003; Farber and Hall, 2007; Glaspell et al., 2003; Hammitt et al., 1993) and especially with charismatic animals that are similar to humans, such as primates (Curtin, 2005; Myers et al., 2004). Second, even when the expectations of tourists are vague or not met, the tourists can still have a satisfactory experience if they feel something unique or unusual has occurred or if their expectations can be modified during the experience (Orams, 2000; Reynolds and Braithwaite, 2001; Ryan and Sterling, 2001). While no studies on the tourists at RV have been carried out to date, we can assume these general conclusions drawn from several studies of disparate tourists attractions still apply. Viewing wildlife should improve the experience, as should having unique and unusual experiences. The ability to predict and increase the chances of tourist encounters with primates will increase the sustainability of tourism at RV. This chapter tests hypotheses regarding variables that affect the likelihood of tourist encounters with primates. With this knowledge, the tourist experience at RV can be improved, leading to increased sustainability.

How to Increase Encounters with Primates

I am unaware of any studies addressing the issue of how to increase tourist encounters with any type of wildlife. There is, however, research on the use of line transect surveys to detect animal species and estimate population densities (Buckland et al., In press; Chapman et al., 1988; MacKenzie et al., 2002; Marshall et al., 2008;

Royle and Nichols, 2003; Strayer, 1999). Conclusions from this literature can be used to determine what variables are most likely to predict the detection of animals. Below, I will state the seven hypotheses of this chapter and explain how they originate from the transect survey literature.

Hypothesis 1: Abundant primates will be encountered more often than less abundant primates.

The abundance of individuals of a species in an area is highly predictive of encounter rates on transect surveys. Simply, species that have larger populations are more likely to be seen (Bailey et al., 2004; Gu and Swihart, 2004; Royle and Nichols, 2003). This is the assumption behind transects, which are used to estimate species abundance (Bailey et al., 2004). Studies have tested this assumption through simulations (Buckland et al., 2010, in press; Gu and Swihart, 2004; Lopez and Pfister, 2001; MacKenzie et al., 2002; Royle and Nichols, 2003; Strayer, 1999) or comparisons with population data from long term studies (Chapman et al., 1988; Defler and Pintor, 1985; Hassel-Finnegan et al., 2008).

Although there is debate as to the exact methods and mathematical models to be employed in order to best predict populations from transects, most studies find that rough presence/absence data is robust in determining relative populations of species in an area. Chapman and colleagues (1988) used transect data to estimate the populations of white-faced capuchins (*Cebus capucinus*) and howler monkeys (*Alouatta palliata*) and compared this result to known counts of the animals derived from long-term studies. The researchers found that transects with a large sample size (many transects walked at all hours of the day) most matched the known population densities

of the animals. In addition, even when there were discrepancies between the estimated populations and the actual populations, the relative density of each species remained the same. For example, if capuchins were over or underestimated the results still showed a consistently higher population of howler monkeys in the area (Chapman et al., 1988). Even those critical of transects as predictors of abundance state that presence/absence data on species can indicate how likely a species is to be encountered in an area (Buckland et al., 2010). Buckland and colleagues (2010) extensively discuss the mathematical and theoretical problems with the usual methods of predicting population densities from transects, but they do not criticize the usefulness of transects for general occupancy information (Buckland et al., 2010).

While there are valid concerns about identifying species and individual populations from transects, most do find that if one species is encountered more than other during a transect survey, that species has a generally larger population (Chapman et al., 1988; MacKenzie et al., 2002; Marshall et al., 2008; Royle and Nichols, 2003). Due to the robustness of transect surveys in predicting general relative abundance, I predict that species encountered more often in a transect survey of this study site as done by Vath and Boinski (unpublished data) will also be encountered more often by tour groups.

Hypothesis 2: Larger primates will be encountered more often than smaller primates.

Hypothesis 3: Primates will be encountered more often in open habitats.

Transect survey literature also makes it clear that animal body size and habitat where encountered affect detectability (Bailey et al., 2004; Gu and Swihart, 2004; Lopez and Pfister, 2001; O'Connell et al., 2006). Transect survey methodology contains

various methods for dealing with unequal visibility and habitat usage by calculating “detectability rates” which indicate how likely a species is to be spotted on a transect (Bailey et al., 2004; Gu and Swihart, 2004; O’Connell et al., 2006). Gardner and others (1999) experimentally placed models of the geometric tortoise (*Psammobates geometricus*) along a transect and found that observers failed to observe 50% of the models. The authors found that observers were more likely to see larger tortoise models than smaller models and when completing observations alone, observers saw fewer of the models placed in dense habitat (Gardner et al., 1999). Species who are smaller and more likely to depend on crypticity for predation avoidance (Broom and Ruxton, 2005; Maynard Smith, 1965) may hide in denser vegetation and have lower detection rates (Gu and Swihart, 2004). From this evidence, I predict that tourists will have more encounters with larger primates and with primates in more open habitats.

Hypothesis 4: Primates will be encountered more often when study troop eats more fruit species.

Hypothesis 5: Primates will be encountered more often when study troop is traveling more.

Seasonal changes should also affect encounter rates. Wild animals change their activity patterns based on the time of year (Doran, 1997; O’Farrell, 1974; Peres, 1994), and these activity patterns affect whether or not animals are likely to be encountered (O’Connell et al., 2006). For example, salamander species make seasonal movements from locations of high visibility (on the surface of the ground) to low visibility (subterranean burrows), and this choice of habitat had a strong effect on detection rates (Bailey et al., 2004). O’Connell and colleagues (2006) also found that seasonality

affects detection rates of mammals in Cape Cod. In this study, opossums (*Didelphis virginiana*) were most seen in late summer and fall while raccoons (*Procyon lotor*) were most seen in spring (O'Connell et al., 2006).

A long-term study of the behavioral ecology of brown capuchins ran concurrent to my study and data are available on the study troop's movements and rate of fruit eating. Monkeys may be more easily spotted when they are moving as they are often noisier at that time (Defler and Pintor, 1985) or may just be more likely to cross the tourist path. Furthermore, monkeys often travel more when fruit is in season (Norconk and Kinzey, 1994; Stevenson et al., 2000) and this may also bring them onto the tourist path at greater rates. Due to this knowledge of the behavior of primates and the above information on the importance of seasonality in predicting detection rates of mammals, I hypothesize that tourists will have more primate encounters when the study troop travels more and eats more species of fruit.

Hypothesis 6: Quiet tourist groups will encounter more primates than noisier tourist groups.

Hypothesis 7: Tourist groups who spend more time "looking" will have more primate encounters.

Finally, the importance of observer behavior on detection rates can be seen in the methodology for transect surveys. Peres (1999) recommends that transects be walked slowly, by one person at a time, and that transects be left undisturbed for one day after being cut in order to decrease detectability errors (i.e., not observing a species that is actually present). He also recommends that researchers along a transect stop regularly to look around and make sure they are not failing to observe any animals present.

Buckland (in press) seconds the importance of letting the transect rest before data collection while DeFler and Pintor (1985) point out the importance of being able to hear monkeys in order to register their presence. Marshall and colleagues (2008) also state the importance of researchers walking slowly and looking around. Researchers walking transects should be quiet not only to avoid disturbing animals, but also to make sure they observe all the animals present. In addition, a study in Southern India found that roads cannot be used as proxies for line transects, as the traffic lessens animal encounters when compared to continuous forest (Varman and Sukumar, 1995). From the above evidence, I predict that tourist groups that spend less time making noise and that look around them more will have more primate encounters.

Methods

Study Site

The study site, Raleighvallen (RV) (4°0'N, 56°30'W), is situated in the 1.6 million ha Central Suriname Nature Reserve (CSNR) in the Coopename River drainage. The CSNR is located in west central Suriname and is comprised of lowland rainforest (Berrenstein, 2006). It receives annual average rainfall of 2300 mm (Reichart, 1993). The aerial and terrestrial predator complement of the forest is complete, and no significant hunting has occurred since the 1800s (Reichart, 1993; Trail, 1987). Eight species of primates are found at the site, brown capuchin (*Cebus apella*), squirrel monkey (*Saimiri sciureus*), wedge-cap capuchin (*Cebus olivaceus*), spider monkey (*Ateles paniscus*), howler monkey (*Alouatta seniculus*), white-faced saki (*Pithecia pithecia*), bearded saki (*Chiropotes satanas*) and golden-handed tamarin (*Saguinus midas*). Additional descriptions of the site can be found elsewhere (Boinski et al., 2005;

Boinski et al., 2003; Boinski et al., 2002; Fleagle and Mittermeier, 1980; Mittermeier and van Roosmalen, 1981).

Since 1998, the site has been host to a long term focused study of the behavioral ecology of squirrel and capuchin monkeys, along with a broader program of ecological monitoring. Many aspects of the site are well-researched, including the populations of various animals, the phenology, the climate and the weather. The current study is unique in that it reports on the activities of wildlife tourists on otherwise undisturbed animals. Animals under more extreme pressures such as from habitat loss or hunting are expected to exhibit more dramatic responses to tourists. Here I describe a baseline of primate response to tourism which is needed before tourism further develops in RV. The tourist attraction of the Voltzberg trail allows a unique opportunity to encounter a number of different primate species and collect data on each.

Methodology

From July 8, 2006 through November 30, 2006 I completed 48 “tour follows” (equaling 365 individual tourists) along the trail from Anjoemara Falls to the Western Plateau of the Voltzberg (Fig 2-6). This equals 220.25 hours of tourist observation. After receiving permission from the tourists and guides to make observations, I noted the number of people in the group, and their age-sex distribution. The research was conducted under proper approvals from the University of Florida’s Institutional Animal Care and Use Committee (UF IACUC# E306), Institutional Review Board (UFIRB# 2005-U-1007), and with permission of Surinamese authorities.

During tour follows, as I walked at the back of the tourist group, I completed an instantaneous group scan (Fragaszy et al., 1992; Martin and Bateson, 1993) every fifteen minutes. At each interval, I quickly recorded the number of tourists stopped,

looking at the environment, taking photos, speaking and resting (Table 2-3). In addition, I recorded the noises made by each tour group. Before meeting tourists groups I used a random number table to choose three fifteen-minute intervals in which to record noises produced by tourist groups. I recorded noise made by tourists via an omni-directional lavaier microphone attached to a bandanna on my head and a battery-powered cassette tape recorder. At the beginning of each interval I set the tape recorder to record and let it run for the next 15 minutes. If tourists were on top of the Voltzberg or not yet arrived at the trailhead for one of the pre-determined intervals I recorded them as soon as possible after the missed interval. Furthermore, if it appeared we would complete the walk before the latest interval was reached, I recorded the last fifteen minutes of the hike. When we reached the Western Plateau, I remained behind and waited while the tourists and guides climbed the Voltzberg. I also noted the time spent in the forest traveling to the Plateau and back. Tour groups were defined as any group of people (aside from other researchers) walking up the trail to the Voltzberg. Groups ranged in size from 4 to 23 people. Time spent traveling to and from the Voltzberg ranged from 3.25 to 5.75 hours. Table 2-2 summarizes terminology used and Table 2-3 is an ethogram of tourist behaviors.

Whenever a primate encounter occurred I collected data on general troop characteristics such as location and movement as well as number of alarm calls heard. Via two minute instantaneous group scans I also recorded the number of individuals grooming, resting, participating in agonistic behavior, feeding and traveling (Table 2-4). Furthermore, the amount of time tourists spent in the presence of the monkeys was recorded. Abundance measurements were taken from Vath and Boinski (unpublished

data) while body size measurements are from Mittermeier and van Roosmalen (1981) (Table 5-1).

Sound data were analyzed by digitizing each tape of three fifteen minute intervals using Audacity (version 1.2.6; <http://audacity.sourceforge.net/>). I then listened to each tape, and deleted all parts without human made noise (excluding footsteps). I was left with the total duration of human made noise for each tour group and these were converted to percentages of time spent making noise.

Statistical Analysis

Hypotheses 1 and 2 were tested via resampling using Resampling Stats (version 4.0; <http://www.resample.com/content/software/excel/index.shtml>). Resampling, unlike parametric methods, does not make assumptions about the distribution of the population from which the sample is taken (Mooney and Duval, 1993). Instead, resampling methods use the observed data to estimate characteristics of the population. This is done by randomly drawing many more data points based on the test sample allowing one to judge how likely it is that you would see the observed results. I will say more about resampling in the results section. This method is appropriate due to the non-normal distribution of my data. Hypothesis 3 was tested using the Mann-Whitney U test. This nonparametric method was carried out using Analyse-It for Excel (version 2.00).

Factor analysis. Hypotheses 4-7 were tested using factor analysis. As it is likely that several of the variables in these hypotheses are correlated and interact to predict whether or not tourists see primates, I needed to use a multivariate method to analyze the data. Factor analysis (FA) was chosen as it is a multivariate method that does not require an assumption of normality and examines a set of variables for correlations

between them that are linked to an unknown or latent variable. FA can be used to identify causal factors behind correlations (Frane and Hill, 1976; Sokal and Rohlf, 1995). It reduces the variables into factors which are as yet unmeasured (or latent) variables affecting the measured variables (Bartholomew et al., 2002). Variables that contribute to the number of times each species was encountered or the likelihood of any particular tourist group encountering monkeys were explored using this method in PASW Statistics (formerly SPSS) version 17. In this study I ask: What variables predict tourist encounters with primates? FA can help answer this question by identifying the interactions and possibly complex relationships between my independent and dependent variables (Bartholomew et al., 2002; Sokal and Rohlf, 1995).

A varimax rotation was used for the FA, the varimax rotation is an orthogonal rotation that transforms the data, allowing for easier interpretation. The rotation does not change the relationships of any of the variables but simply clarifies the relationships (Bartholomew et al., 2002).

The variables used in this analysis were: number of primate encounters by each tour group, order of tour group (1st, 2nd, etc. tour group followed), daily number of species of fruit eaten by the long-term study group of brown capuchins, daily meters traveled by the long-term study brown capuchins, percent of time tourists spent looking, and percent of time tourists made noise.

Results

Hypothesis 1

Abundant primates will be encountered more often than less abundant primates.

This hypothesis was tested by using data from Vath and Boinski (unpublished data) on encounter rates of researchers with primates in RV along the Voltzberg Trail. I

expected that the abundance of each primate species—the number of times each species was encountered out of Vath and Boinski's samples—would be related to the number of times tourists encountered each species. Abundance is the independent variable and encounter rate per species is the dependent variable. If abundance is related to species encounter rate, then I should be able to predict relative tourist encounter rates of each species based on Vath and Boinski's (unpublished data) data. In other words, the two samples should come from the same population.

To test if my sample and Vath and Boinski's were from the same population I first calculated the expected rate of encounter out of 95 samples assuming Vath and Boinski's data as the baseline (Table 5-1). Next I calculated the absolute difference between these expected encounters and my observed encounter rates. I used urn resampling (Simon, 1997) to take 95 samples (my sample size) out of Boinski and Vath and Boinski's data. I then compared these observations to the earlier calculated expected observations. This was repeated 5000 times. Basically, I tested how many times samples of 95 out of Vath and Boinski's data match my data or are more different. Results are shown in Table 5-1. With all species pooled, there is only a 3/5000 (or 0.06%) chance that results drawn from the Vath and Boinski population will be as different, or more different, from the expected than mine are. In other words, the null hypothesis was that the populations were the same. $P=0.006$, so with an alpha value of $p=0.05$, I reject the null hypothesis. Thus, I conclude that my population is not equal to Vath and Boinski's.

I also calculated the likelihood of getting my results for each species, assuming Vath and Boinski's data as the population. The null hypothesis could not be rejected for

spider monkeys ($p=0.40$), white-faced sakis ($p=0.16$), howler monkeys ($p=0.84$) and bearded sakis ($p=0.72$). For brown capuchins ($p=0.06$) the null hypothesis can also not be rejected, although the p value is approaching 0.05. The null hypothesis is supported for tamarins ($p=0.0004$), squirrel monkeys ($p=0.04$) and wedge-cap capuchins ($p=0.0$) (Table 5-1). I was struck by the very low p values of tamarins and wedge-cap capuchins so I repeated the test with those two species removed (Table 5-2). Without tamarins and wedge-cap capuchins the null hypothesis of no difference between the populations cannot be rejected ($p=0.14$), meaning the populations are equal. The same holds true for each individual species (Table 5-2). Therefore, this hypothesis is not supported with species pooled, as if my population were truly drawn from Vath and Boinski's my result would be very unlikely. With tamarins and wedge-cap capuchins removed species abundance from Vath and Boinski (unpublished data) does predict encounter rate of the other 6 species with tourists.

Hypotheses 2 and 3

Larger primates will be encountered more often than smaller primates.

Primates will be encountered more often in open habitats.

Reported average weights of each species (Mittermeier and van Roosmalen, 1981) were used to divide them into groups of small (400-2000 g), medium (2000-5000 g) and large (5000 g and up). Small species are tamarins (492 g) and squirrel monkeys (688 g). Medium species are wedge-cap capuchins (2600 g), bearded sakis (2990 g) and brown capuchins (3450 g). Large species are howler monkeys (7275 g) and spider monkeys (7775 g). Medium species were most encountered (50 encounters) followed by small species (26 encounters) and large species had the least encounters (19). However, brown capuchins are the most encountered species in general and are

medium sized, so I needed to control for encounter rates. I needed to test if large, medium or small species were encountered by tourists more than predicted due to their abundance in the forest. I again used Vath and Boinski's data as the expected population, created a sample population matching hers (Simon, 1997) and then drew out 95 samples. This was repeated 5000 times and each time the difference between the observed value from the resample and the expected value was calculated (Table 5-3). Overall, there was no significant difference between the populations ($p=0.07$), meaning my result was expected assuming the population it was drawn from. That is, small, medium and large primates were encountered at rates expected due to their population sizes. There was no significant difference between observed and expected values for small and large species ($p>0.25$) but medium species are on the border ($p=0.05$). I saw medium species more than was expected (Table 5-3). When pooled, this hypothesis is not supported. For medium species, however, I may have encountered more medium species than expected (Table 5-3).

A Mann-Whitney U test looked for significant differences in number of primate encounters in open habitat versus dense habitat. There was no significant difference between number of encounters in dense versus open habitat ($p=0.8750$). This hypothesis was not supported—and the nonsignificant trend was opposite the prediction. There were 65 encounters in dense habitat and 30 in open habitat.

Factor Analysis Model Formation

In this section I will describe the formation of the FA model. Later, I will explain the interpretation of the FA results. The first step of FA is to create a correlation matrix (Table 5-4) which shows that several of the variables are correlated. This means the FA can move forward. But we do not yet know whether or not there is only one common

factor underlying these variables. In order to get at the latent factors underlying these correlations, we measure the distance between the observed correlation matrix and the one that would be predicted by the model (Bartholomew et al., 2002). This was done using the generalized least squares method resulting in a table indicating the amount of variance in the data explained by 6 latent factors (the number of factors equals the number of variables input) (Table 5-5). Next, the factors are transformed via a geometric rotation to be more interpretable. This helps demonstrate the patterns in the data more clearly. Finally, a goodness of fit test tests whether or not the measured variables appear in the form specified by the factor model. Failure to reject the null hypothesis that the observed measures match the predicted measures means the data fit the model (Bartholomew et al., 2002).

Number of Primates Seen

The model created through factor analysis looks at predictors of number of primate encounters for each tourist group. This is a different independent variable than in the above hypotheses, which dealt with number of tourist encounters per species. Primate encounters per tour group ranged from 0 to 5 with a mean of 2 (s.d.=1.35). Thirty-four tour groups had zero to three primate encounters, while only four had four or five encounters (Figure 5-2). The variables of number of fruit species eaten by the study troop, number of primates seen by tour group, number of meters traveled by the study troop, percent time tour group members spent looking, percent time tour group members made noise and order of tour group (1= beginning of study to 48= end of study) were put into a factor analysis with varimax rotation and eigenvalues set to > 1 . The Kaiser-Meyer-Olkin measure of sampling adequacy was 0.714, over the usual accepted minimum of 0.6 (Kaiser, 1974) and the Bartlett's test of sphericity had a p

value of 0.000, indicating that the data are appropriate for a factor analysis (Norusis, 1994). If the p value of the Bartlett's test of sphericity were greater than 0.05 this would indicate that the correlation matrix was an identity matrix, that is, that each variable was correlated only with itself (Norusis, 1994). Two factors emerge, which account for 62% of the variance (Table 5-5). The rotated factor matrix (Table 5-6) indicates that Factor 1 is made up of four variables (i.e. these four variables have strong, higher than 0.5, correlations with the factor): order of tourist group, daily fruit species consumption, daily travel distance and rate looking. Factor 2 consists of one variable: number primates seen. This analysis indicates that more primate encounters are associated with more fruit species eaten by the study troop, and with the travel distance of the study troop. Therefore hypotheses 4 and 5 are supported. The noisiness of tourists does not contribute to the latent factors, so hypothesis 6 is not supported. Finally, rate of looking is negatively correlated with the latent factors, so hypothesis 7 is also supported.

Discussion

Abundance, Body Size and Habitat

Abundance as taken from Vath and Boinski (unpublished data) does predict encounter rate for brown capuchins, squirrel monkeys, spider monkeys, howler monkeys, bearded sakis and white-faced sakis (who were not encountered in this study) but not for wedge-cap capuchins and tamarins. This fits in with the line transect census literature, in that primate species more often seen on a line transect survey were also more often seen by tourists walking in the same area (Bailey et al., 2004; Gu and Swihart, 2004; Royle and Nichols, 2003). Interestingly, for 5 of the species this result goes against assumptions that transects should be completed with a few quiet researchers (Peres, 1999; Varman and Sukumar, 1995). At RV, at least, similar

encounter rates were found between a census completed by two quiet, slow walking researchers and trips taken by four to 23 tourists who talked and made noise during 6-80% of their trip. In some locations, such as RV, shorter censuses may result in realistic abundance estimations, even when the usual protocols for transect censuses are not met. RV may have this result as it is relatively undisturbed (Reichart, 1993; Trail, 1987).

But why did the wedge-cap capuchins and tamarins respond differently? Tamarins were often seen on the transect survey (16% of the time) while I only saw them with tourists during 3% of the primate encounters. I saw tamarins much less often than expected. Both methods had low encounter rates for wedge-cap capuchins, 0.1% of encounters for Vath and Boinski and 2% of encounters for me. I actually saw the wedge-cap capuchins more often than expected. This may be evidence that tamarins are actively avoiding tourist groups and therefore tourism may be having an impact on this species. If tamarins are actively avoiding tourist groups, there may be impact on tamarin ranging and foraging patterns. Both species fled and alarm called upon all their encounters with tourists.

I found that body size did have an effect on encounter rate, but not in the direction predicted. Medium sized species were seen most often, and more than expected when controlling for abundance. Small species were seen second most often and large species were least seen. Both small and large species were seen as expected when controlling for abundance (Table 5-3). This result may be related to overall habituation level. Medium species were seen more than expected and brown capuchins were the most encountered medium species. Brown capuchins are also the only species subject

to a concurrent long-term study, and several brown capuchins troops encountered researchers on a daily basis.

There is no significant difference in encounter rate based on habitat. There were more encounters in dense habitat than in open habitat, but the difference is not statistically significant. This could occur for several reasons. Chapter 3 found that monkeys were more likely to alarm call in dense habitats and the alarm calls could have drawn my attention, leading me to spot more monkeys in dense habitat. This could also be an artifact of which species are seen more. Brown capuchins and squirrel monkeys were the species seen most often, and both prefer a more dense habitat (Boinski et al., 2003; Vath and Boinski, unpublished data). A summary of these conclusions can be seen in Table 5-8.

Effects of Fruit, Travel, Noise and Looking

Factor analysis interpretation. The above variables were analyzed using FA. The first step of interpreting the FA is to investigate and name the latent variables produced. The latent variables that emerge should be easily interpretable (Bartholomew et al., 2002). FA resulted in a model for primate encounters that included two factors. FA's purpose is to reduce the number of variables needed to explain the data (Bartholomew et al., 2002). Table 5-5 demonstrates that two unmeasured variables can explain 62% of the variation in the data. Table 5-6 shows the relationships between the measured variables and these newly discovered latent variables. Factor 1 is strongly positively correlated with order of tourist group, daily number of fruit species eaten, daily travel rate and negatively correlated with percent of time tourists spent looking around. We can say that these 4 variables are standing in for an unmeasured variable. As factor 1 is made up of 3 time-related variables (order of tour groups, fruit species eaten by a

study troop and rate of study group travel) and one tourist behavior variable (percent look)—I named this factor “Time/Look.” This factor alone accounts for 42.39% of the variance in the data (Table 5-5). The second factor only has one strong correlation—with number of primate encounters (Table 5-6). This indicates that the second factor which I will call Primates is most strongly correlated with the number of primates seen. Further, we must look at the communalities for each variable, which indicate the proportion of the variance explained by the common factors (Bartholomew et al., 2002). Here, we see that the two latent variables, Time/Look and Primates, are most highly correlated with the order of the tourist groups, second with the number of primates seen, third with rate of travel of the study troop and fourth with amount of fruit species eaten by the study troop (Bartholomew et al., 2002)(Table 5-7). The fact that the factor, Primates, is mostly created by the measured variable, number of primates seen, indicates that I am still missing an important variable that explains the number of primate encounters.

The results in this factor analysis shown by the rotated factor matrix (Table 5-6) can be used to test hypotheses 4-7 (Table 5-8). Hypotheses 4-7 have number of primate encounters as the dependent variable. 62.07% of the variance in the number of primate encounters per tour group is explained by the two latent variables of Time/Look and Primates. The positive correlations between number of fruit species eaten by the study troop (0.643) and travel distance of the study troop (0.651) indicate that tourists encountered more primates as when the study troop ate more fruit (hypothesis 4) and when the study troop traveled more (hypothesis 5). Therefore these two hypotheses are supported. I also hypothesized that quiet tourist groups would encounter more primates

than louder tourist groups (hypothesis 6). The noisiness of tourists does not contribute enough to be kept in the model, so this hypothesis is not supported. Finally, I hypothesized that tourist groups who looked around more would have more primate encounters (hypothesis 7). Rate of looking contributes negatively to the Time/Look factor (Table 5-6). To elucidate this, I looked again at the correlation matrix showing the correlations between all the variables (Table 5-4). Rate of looking is correlated with the number of primates seen ($r^2 = 0.071$) and although this is not a strong correlation, it is significant ($p = 0.036$). Therefore, hypothesis 7 is supported, although I am not sure it has a lot of biological significance.

As the study went on the study troop showed a general trend of both traveling more and eating more fruit species, although there was a dip in both in October (Fig. 5-5 and 5-6). In addition, the factor analysis shows that percent of time tourists spent looking is negatively associated with the other variables, indicating that as the study progressed tourists looked around less (Table 5-5).

Importance of Species Membership

This chapter examines the importance of species membership to primate interactions with tourists. In Chapter 2, species membership was an important predictor of how primates responded to tourist presence. In this chapter, we see that species membership also contributes to which primates are encountered by tourists. Tourists were more likely to see most abundant primates (a species-specific characteristic), indicating that the tourists encounter primates similarly to researchers on a census transect (Vath and Boinski, unpublished data). This is a good control for transect methods of estimating primate population. Similar rates of primate encounters occurred despite the larger size of tour groups when compared with transect samples.

Although I assumed larger primates would be easier to see, larger primates are not the ones most present in the forest (Table 5-9). In RV, it seems that the fact that the small squirrel monkeys are so present and unlikely to flee from tourists outweighs their size. The results of this study more closely echo those of Bailey and colleagues (2004) who found that in salamanders species size did not affect detection probabilities. In fact, they found that habitat and seasonal variables most explained detection probabilities, and that local abundance was the best predictor of detection rates. In cases where the smaller animals are more rare, it may be that they can be underestimated, but when they are common, the abundance outweighs the size (Bailey et al., 2004). In RV, when abundance is examined along with body size and encounter rate, we see that the most seen primates are small and medium sized (Table 5-9). If all other things were equal, larger primates would be easiest to see; this study shows that all other things are not equal, however, and that population density will affect how often each species is seen by tourists, except for medium species who are seen at higher rates than expected. Furthermore, species that are most seen are also most likely to occur in dense habitats. Again, characteristics of the species as a whole are contributing to its likelihood of being seen by tourists.

Tourist Control over Viewing of Primates

Regarding the two hypotheses about tourist behavior and its effect on viewing or not viewing primates, there were mixed results. Less noisiness was associated with number of primates seen, as predicted, but looking was also negatively associated with number of primates seen, opposite the prediction. As present in Chapter 4, I found that noise level did not cause primate anti-predator behavior. Peres (1999) suggests, however, that researchers make as little noise as possible to increase the chances of

properly estimating wildlife numbers during transects. In addition, various wildlife-viewing codes of conduct mention the need to minimize noise (Garrod and Fennell, 2004; Parsons and Woods-Ballard, 2003). Why, if noise does not result in fleeing or alarm calls, is a lower noise level associated with more primate sightings? Two things could be at work here: primates may be fleeing as they hear loud tour groups approaching or the relationship may not be causal in the direction expected. If the primates flee before tour groups are in view, they would not have made it into the data set presented in Chapter 4. Therefore I may not have detected an anti-predator response to loud tourists as the response occurred before I was able to observe the presence of any primates. Secondly, quieter tourists may be associated with seeing more primates, but primate presence may cause the tourists to be quiet, not vice versa. Tourists often became quiet once a primate encounter began. If this is the case, having tourists be quiet as they walk down the trail may not impact the number of primates seen. It might be beneficial to have tourists be quiet, even if the relationship is not causal, as it may improve the tourist experience (Cole and Hall, 2009; Reynolds and Braithwaite, 2001).

I also predicted that tourists who looked more would see more primates. Again, this hypothesis came from guidelines for transect surveys (Peres, 1999). Rate of looking was found to be negatively associated with order of tour group, number of fruit species eaten by the study troop and amount traveled. It is interesting that the rate of looking has a seasonal component. That is, as the study progressed the tourists looked around less, but this was not related to the number of primates seen.

How to See Primates

What can tour groups do to be more likely to see primates? The results of this study indicate that the answer is to look for abundant primates in dense habitat and look around. Although it is not certain that all these variables are causal. The factor analysis indicates the complex relationships between several variables that explain the variation in the number of primates seen by tourists. What does this mean for sustainable tourism? In order to be sustainable, tourist destinations need to provide satisfactory experiences for the consumers (Backman et al., 2001). In this case, when odds are good for encountering primates, but it is difficult to predict where and when and what behaviors of tourist groups can lead to these encounters, there are two options for managing tourist expectations and experience: be realistic about what the tourists can expect to see and modify the experience as it occurs to make it seem special and unique.

Since tourists have a more satisfactory experience when their expectations are met (Akama and Kieti, 2003; Ryan and Sterling, 2001), tourists should be given realistic expectations. Tourists can be told that it is likely they will see primates, but not guaranteed. They can be told which monkey species are most common in the area, and therefore more likely to be seen. This study provides information on which species a tour group can expect to encounter, and this information can be used to manage expectations. This can be done in other locations where species abundances are not known by first completing transects to get a rough idea of relative abundances in the area.

Secondly, as other research has indicated that tourists deem WT experiences as successful if they feel they had a unique or authentic experience (Arnould and Price,

1993), the experience can be constructed in a way to make it feel special. The uniqueness of the forest can be pointed out, and unique characteristics of the monkey species could be remarked on (Reynolds and Braithwaite, 2001). Although it is unclear if noise level is causally related to encounter rate, others suggest that tourists be asked to be quiet anyway, to increase the feeling that the experience is special and unique (Reynolds and Braithwaite, 2001).

Conclusion

There is no literature on how tourist groups can behave in order to encounter more wildlife species. Using transect survey literature, I proposed several hypotheses about variables that would predict tourist encounters with primates in RV. Through factor analysis it was found that abundance and time of year were related to primate encounter rate and that noise level and amount of time spent looking were related to number of primate encounters in groups that saw primates. This chapter reiterates the importance of species membership to various aspects of tourist interactions with primates. It also has implications for how tourist expectations can be managed in order to increase tourist satisfaction and therefore increase the sustainability of the tourism endeavor.

Hypothesis 1: Abundant primates will be encountered more often than less abundant primates.

Hypothesis 2: Larger primates will be encountered more often than smaller primates.

Hypothesis 3: Primates will be encountered more often in open habitats.

Hypothesis 4: Primates will be encountered more often when study troop eats more species of fruit per day.

Hypothesis 5: Primates will be encountered more often when study troop is traveling more.

Hypothesis 6: Quiet tourist groups will encounter more primates than noisier tourist groups.

Hypothesis 7: Tourist groups who spend more time "looking" will have more primate encounters.

Figure 5-1: Hypotheses about primate encounter rates

Table 5-1: Results of resampling analysis of relationship between encounter rate and abundance.

Species	# of encounters this study	Expected encounter #	observed difference	P value
Brown capuchin	45	36.08	8.92	0.06
Spider monkey	13	16.33	3.33	0.40
Squirrel monkey	23	15.76	7.24	0.043
Tamarin	3	15.53	12.53	0.0004
Howler monkey	6	6.85	0.85	0.84
Bearded saki	3	2.28	0.72	0.72
White-faced saki	0	2.06	2.06	0.16
Wedge-cap capuchin	2	0.11	1.89	0
Total	95			
Sum of differences			37.54	0.0006

Table 5-2: Results of resampling with tamarins and wedge-cap capuchins removed

Species	# of encounters this study	Expected encounter #	observed difference	P value
Brown capuchin	45	40.92	4.08	0.37
Spider monkey	13	18.52	5.52	0.14
Squirrel monkey	23	17.87	5.13	0.17
White-faced saki	0	2.33	2.33	0.15
Howler monkey	6	7.77	1.77	0.56
Bearded saki	3	2.59	0.41	1.0
Total	90			
Sum of differences			19.24	0.14

Table 5-3: Results of resampling based on body size, controlling for abundance.

Size	# of encounters this study	Expected encounter #	Observed difference	P value
Small	26	31.29	5.29	0.2534
Medium	50	40.53	9.47	0.0456
Large	19	23.12	4.12	0.3108
Total	95			
Sum of differences			18.88	0.074

Table 5-4: Correlation matrix for factor analysis.

		Order	Fruit	Travel	Look	Encounters	Noise
Correlation	Order	1.000	0.597	0.646	-0.394	0.323	-0.233
	Fruit	0.597	1.000	0.459	-0.265	0.151	-0.023
	Travel	0.646	0.459	1.000	-0.339	0.281	-0.168
	Look	-0.394	-0.265	-0.339	1.000	0.071	0.056
	Encounters	0.323	0.151	0.281	0.071	1.000	-0.224
	Noise	-0.233	-0.023	-0.168	0.056	-0.224	1.000
Significance	Order		0.000	0.000	0.005	0.018	0.069
	Fruit	0.000		0.001	0.045	0.171	0.443
	Travel	0.000	0.001		0.014	0.036	0.144
	Look	0.005	0.045	0.014		0.329	0.363
	Encounters	0.018	0.171	0.036	0.329		0.077
	Noise	0.069	0.443	0.144	0.363	0.077	

Table 5-5: Percent variance explained by each of the six latent factors.

Factor	Initial eigenvalues		
	Total	% of variance	Cumulative %
1	2.543	42.39	42.39
2	1.181	19.68	62.07
3	0.883	14.72	
4	0.622	10.37	
5	0.480	7.99	
6	0.291	4.85	

Table 5-6: Rotated factor matrix.

Factor	1	2
Order	0.857*	0.335
Fruit	0.643*	0.132
Travel	0.651*	0.286
Look	-0.507*	0.115
Encounters	0.056	0.827*
Noise	-0.142	-0.274

*variables with strong correlations contributing to the latent factor

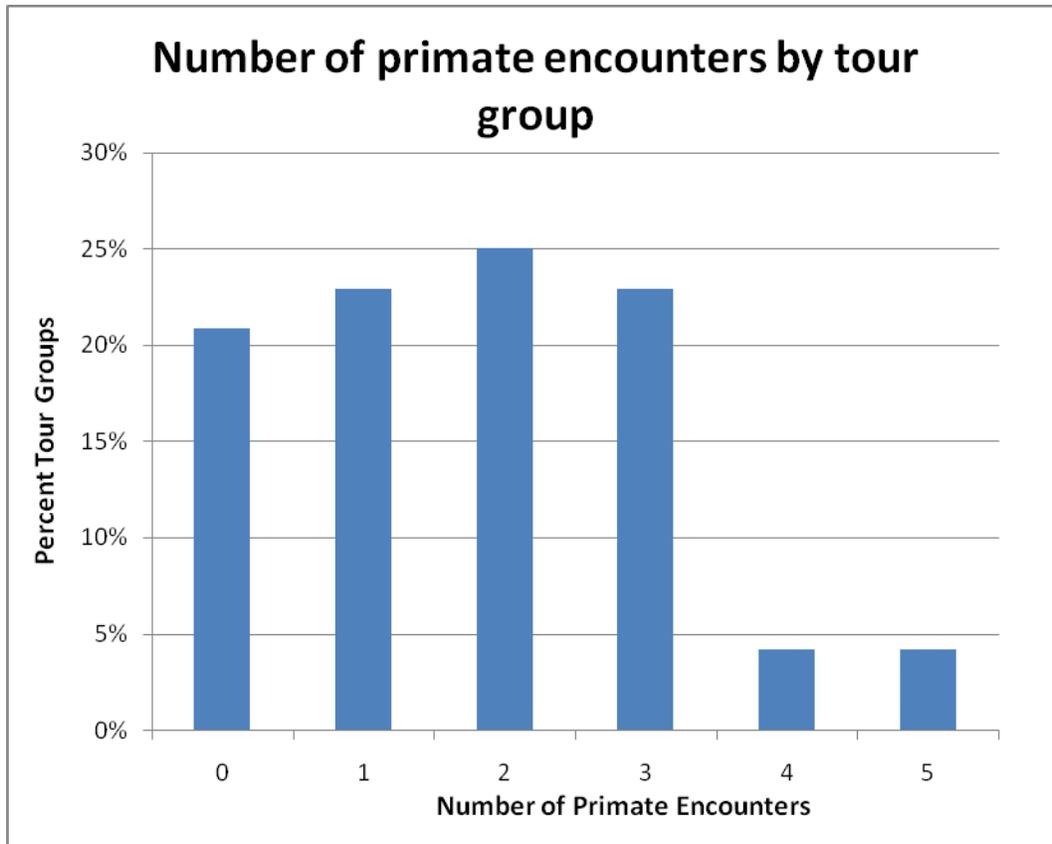


Figure 5-2: Number of primate encounters by tour groups.

Table 5-7: The proportion of the variance of each variable explained by the common factors.

	Proportion of variance explained
Order	0.848
Fruit	0.460
Travel	0.511
Look	0.285
Encounters	0.688
Noise	0.138

Table 5-8: Summary of results

Hypothesis		Supported?
1	Abundant primates will be encountered more often than less abundant primates.	No*
2	Larger primates will be encountered more often than smaller primates.	No
3	Primates will be encountered more often in open habitats.	No
4	Primates will be encountered more often when study troop eats more fruit.	Yes
5	Primates will be encountered more often when study troop is traveling more.	Yes
6	Quiet tourist groups will encounter more primates than noisier tourist groups.	Yes
7	Tourist groups who spend more time “looking” will have more primate encounters.	Yes

*This hypothesis is not supported when all species are pooled, but is supported when tamarins and wedge-cap capuchins are removed from the analysis

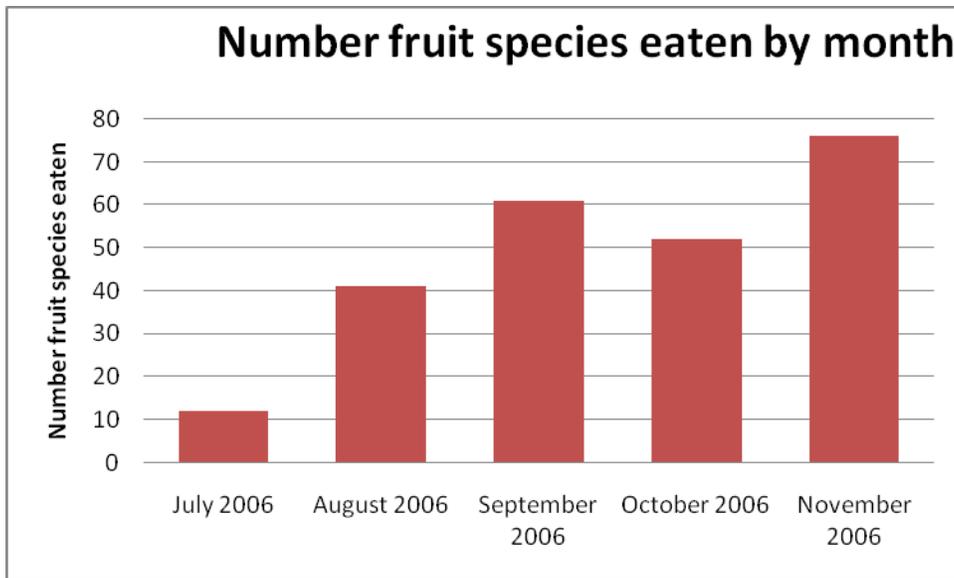


Figure 5-3: Number of fruit species eaten by study troop per month

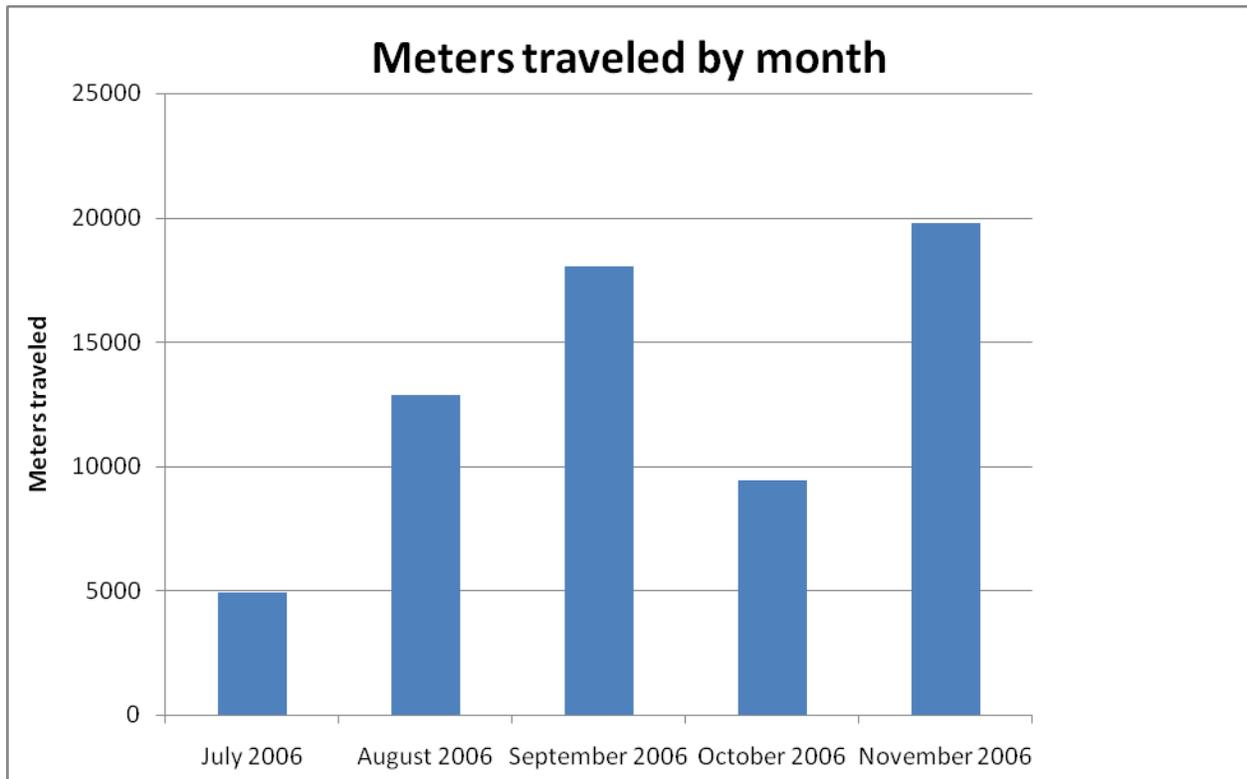


Figure 5-4: Meters traveled by study group by month.

Table 5-9: Species responses to tourists as compared with amount encountered.

Species	Average body weight (g) ¹	Body size ²	Encounter rank (current study)	Encounter rank (Vath and Boinski, unpublished data)
Brown capuchin	3450	Medium	1	1
Squirrel monkey	688	Small	2	*3
Howler monkey	7275	Large	4	4
Spider monkey	7775	Large	3	2
Bearded Saki	2990	Medium	*5	*5
Tamarin	492	Small	*5	*3
Wedge-cap capuchin	2600	Medium	6	6
White-faced saki	2000	Medium	Not seen	5*

*indicates a tie

¹ from Mittermeier and van Roosmalen 1981

² small=400-1999 g, medium=2000-5000g, large=5001 g and up

CHAPTER 6 CONCLUSION

With habitat loss increasing rapidly and mass extinctions of animal species occurring (Aulsebrook et al., 2008; Brook et al., 2003; Koh et al., 2004; Pimm and Raven, 2000; Thomas et al., 2004) wildlife based tourism (WT) is frequently seen as a panacea to habitat destruction and touted as a conservation tool (Burger, 2000; Higginbottom et al., 2003; Krueger, 2005). Increasing numbers of countries and NGOs are beginning to implement nature-based tourism activities as an alternative, non-consumptive way of making profits from various ecosystems. These activities must be managed carefully to make sure they meet their economic and conservation goals. There is a danger that areas may rush to implement WT without making provisions to monitor for possible serious impacts. The many stakeholders involved in WT, plus the interconnections and complexity present in ecosystems makes implementing successful WT difficult. Numerous researchers in diverse fields from anthropology to zoology investigate impacts of tourism on various levels of human and ecological communities, but few connections are made across disciplines. This dissertation investigates impacts of tourism on primates in RV, from both the view of the primates (do they perceive tourists as a predator?) and the tourists (does tourist behavior affect primate response and encounter rate?).

A number of studies have found negative effects of tourism on both non-primate (Giese, 1996; Knight and Cole, 1995; Lafferty, 2001; Müllner et al., 2004; Wysocki et al., 2006) and primate wildlife (Grossberg et al., 2003; Kinnaird and O'Brien, 1996). The literature on impacts of tourism on primate species is much less than that for other animals. Even though primates are charismatic animals often appealing to tourists

(Eddy et al., 1993; Myers et al., 2004; Nakajima et al., 2002; Newsome et al., 2005) there are many gaps in our knowledge of their response to tourist presence. In addition, the complex social structure, long life, and long infant and juvenile period of primates may make them particularly susceptible to tourist disturbance. Finally, primates are also important member of the biological community, as predators and seed-dispersers among other roles (Caro and O'Doherty, 1999; Chapman, 1995; Chapman and Onderdonk, 1998; Lovett and Marshall, 2006; Sussman and Raven, 1978) and disturbances to their population may cascade out into the ecosystem.

Few studies of the impacts of WT are grounded in a theoretical background and most report on individual species at individual locations. Due to this it is difficult to make predictions about how WT may impact any specific species at any one location. This study set out to investigate the immediate, short-term responses of primates when contacted by tourists at Raleighvallen (RV), in the Central Suriname Nature Reserve (CSNR) through the testing of hypotheses based in behavioral ecology. Use of predator-prey theory (Frid and Dill, 2002) should help create larger scale guidelines that can be used to manage WT at various locations. Furthermore, a better understanding of primate response to tourists, and of the behavior of the tourists themselves, can be used to make sure WT in RV remains sustainable.

To reach these goals, I studied the immediate responses of primates to the presence of tourists and investigated which variables predict these responses. I found that some species (spider monkeys, wedge-cap capuchins, tamarins and bearded sakis) responded to tourists with anti-predator responses such as alarm calls and fleeing while other species (brown capuchins, howler monkeys and squirrel monkeys)

did not. There was no single characteristic of each species that predicted their response to tourists, but by using the literature on temperament or behavioral syndromes, some predictions that were supported could be made. Primate species known to respond negatively to unknown stimuli responded to tourists with anti-predator behaviors such as alarm calls and fleeing, while species known to be interested in new stimuli did not. If this information is available for non-primate species it could be used to predict those animals' responses to tourists as well. All species who did not have anti-predator responses to tourists were seen feeding at some point, while the others were generally not seen feeding. This suggests that presence or absence of feeding could be used as a quick and easy method of monitoring animals populations involved in tourism.

Species body size and location where encountered did not affect rates of anti-predator behavior in the direction expected, while habituation level did. Habituated animals alarm called less than unhabituated animals. Again, no single variable such as species body size or habitat where encountered predicted anti-predator behavior. Furthermore, these results indicate the need for more understanding of how and when primates decide to flee. Alarm calls were better predicted than fleeing. Animals alarm called less in open habitat and larger and medium sized animals alarm called more than small animals. Fleeing was not related to any of these variables. Alarm calls may indicate that animals are not so stressed that they need to move away from the perceived predator, but there is clearly something additional going on in the animals' decision making process when determining whether or not to flee. Additional research on what the primates are doing when encountered by tourists will help us better predict when primates decide to flee versus remain in the presence of tourists.

The second half of the dissertation investigated primate response to tourist behavior and variables that might predict the likelihood of tourist encounters with primates. Tour group size, speed and noisiness did not have any statistically significant effects on primate anti-predator behaviors. Unexpectedly, smaller, faster and quieter tour groups elicited more anti-predator responses than did larger noisier tour groups (although results are not significant). I suspect that the faster and quieter groups were more likely to take primates by surprise, eliciting an anti-predator response. Whenever a slower, larger, noisier group encountered primates it is likely that the animals heard the tour group approaching and decided to remain in view along the trail. Therefore, I may have missed any anti-predator response of animals not seen as they fled out of view, and did not see a response from animals encountered as they had already decided that the tourists were not indicating a large enough threat to necessitate leaving the area. This is similar to results found in studies of great ape reaction to tourists (Blom et al., 2004). RV managers may want to consider allowing fewer, but larger tour groups into the forest. Fewer, larger groups may have less impacts on other aspects of the ecology, although further research is needed on this topic.

The last chapter investigated predictors of tourist encounters with primates. When species were pooled, abundance in the forest did not predict species encounter rate. But when wedge-cap capuchins and tamarins were removed from the analysis, abundance did predict encounter rate. Wedge-cap capuchins were encountered more often than expected and tamarins were encountered less often than expected. This is more evidence that tourism in RV may be affecting tamarin behaviors, as they are seen on researcher-walked transects, but not by larger tour groups. There was no effect of

average primate species body size on species encounter rates, nor was there an effect of habitat on species encounter rates.

I also looked at how best to predict how many times each tour group would encounter primates. I found that tour groups were more likely to encounter primates when a troop of capuchins from a long-term study at the same location at more fruit species and traveled more. Tourists were also more likely to see primates on trips where they spent more time looking around, but this may not be causal. In creating a satisfactory experience for tourists at RV, managers should be aware of the importance of tourist expectations. Expectations can be managed so that tourists are told which species they are most likely to see. Results from concurrent studies on primate behavioral ecology can also be used to predict when primate species are most likely to be encountered in the forest.

Results from this research suggest one main take-home lesson relating to monitoring and three related to management. Each individual primate's response to tourists and likelihood of being seen by tourists is best predicted by species membership and therefore each species must be monitored separately. While characteristics that differentiate each species from another (such as size) do not predict primate response or likelihood of being seen, unique responses to tourists from all the aggregate responses of each species arise. Each species consists of something beyond the characteristics that make it up. That is, a species is more than the sum of its parts. We may be able to refer to this as "behavioral syndromes" or "temperament", but more research needs to be done on these issues to see how applicable they are across contexts. There are a few variables that can cross species to demonstrate or change

responses to tourists. All species who did not see tourists as predators (brown capuchins, squirrel monkeys and howler monkeys) were seen feeding at one time or another. Three of the species who saw tourists as a threat were never seen feeding (spider monkeys, wedge-cap capuchins and tamarins) while bearded sakis behaved as if tourists were a threat by alarm calling and fleeing, but were also observed feeding. Feeding can be used as a good indicator variable for quick and dirty monitoring of the health of a primate species. If primates exposed to tourism are still feeding, they are secure enough to spend time on these long term maintenance activities, and are not at an immediate risk.

This research also suggest two lessons for management of wildlife tourism at RV: 1) the species that do not see tourists as a threat and that are already habituated can be used for tourism and 2) management of tourists can concentrate more on tourist expectations than on tourist behavior.

Brown capuchins, squirrel monkeys and howler monkeys did not have an anti-predator responses to tourists, indicating that they did not view tourist groups as a threat. Furthermore, the brown capuchins and squirrel monkeys are habituated, due to their use in a long-term behavioral ecology study. This suggests that as these three species are least disturbed by tourists, they would be good to direct the tourists towards. Tour groups can try to encounter these species in areas they are known to frequent and groups could perhaps also be allowed to stay longer with these species. As two of the species are already habituated, they can also be more of a focal species for tourism. Habituation is a possible tool for successful WT, as it decreases disruption and therefore possible stress in the animals, and may also provide a better experience

for tourists. Limiting habituation to those species already used to human presence may also help decrease some of the negative effects habituation can cause.

Secondly, the behavior of tour groups does not affect the responses or the rate of encounter for the primates. At current levels, it does not seem as if caps on tourist number or management of number and occurrence of tour groups need to be implemented. The park is very large and the tourists are constrained to a small area. If tourism begins to use more space in the park, or increases greatly in number, however, this would need to be re-evaluated. Tourist expectations can best be managed by stating which species they are most likely to see, and giving them information to invest them in seeing these species. Tourists can also be alerted to the fact that they are most likely to see primates in dense habitat, and can be lead to spend more time in these areas. While tourist behavior does not seem to need management at this point, tourist expectations could be managed to increase customer satisfaction. Research finds that tourists have a better time when their expectations are met (Akama and Kieti, 2003; Ryan and Sterling, 2001). However, it is also known that tourists have satisfactory experiences even when their expectations are unclear or not met as long as they feel they had a unique, special, and out of the ordinary experience (Arnould and Price, 1993; Cole and Hall, 2009; Orams, 2000).

This study presents baseline information on interactions between primates and tourists at Raleighvallen, in the Central Suriname Nature Reserve. It introduces the use of theory to look at human disturbance on wildlife, and suggests management plans to protect the primates and to increase tour enjoyment. More should be known about tourist affect on other plants and animals in the site. This study also gives a basis for

further studies of the decisions made by primates when encountering tourists. More will be understood if the primates could be followed before and after encounters with tour groups, or with more data collected on the details of what primates do when encountering tourists. How much do they abandon one behavior for another? Does this change based on context? Further research should also be done on what tourists want. Only with additional, complete knowledge can RV (or any other wildlife tourism destination) be managed for truly successful ecotourism.

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BIOGRAPHICAL SKETCH

Laurie Kauffman was born in southern California and grew up in Northern Idaho and St. Louis, Missouri. She decided to study primates after viewing the movie *Gorillas in the Mist* at the age of twelve and has carried out primatological field work in Costa Rica and Suriname. She received her Bachelor of Arts in anthropology from Grinnell College and her Master of Arts in anthropology from the University of Florida.