EFFECTS OF TOURISM ON THE BEHAVIOR AND HEALTH OF RED HOWLER MONKEYS (*ALOUATTA SENICULUS)* IN SURINAME

by

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ABSTRACT

Ecological changes and habitat degradation have measurable effects on nonhuman primate group size, but little is known about their effects on the behavior and health of primates. Specifically, ecological change caused by the implementation of tourism projects can impact nonhuman primates. In this project I assess the impact of tourism on the health and behavior of free-ranging red howler monkeys (*Alouatta seniculus*) in Suriname. I evaluated the health of subjects through observations of external indicators of poor health such as wounds, scars, and bot fly lesions, and through the analysis of non-invasively collected urine and feces. Urine samples were screened for indicators of poor health such as the presence of protein, glucose, or blood, and fecal samples were analyzed for the presence of intestinal parasite eggs and larvae. I also conducted behavioral observations to assay the effects of tourists on monkey behavioral patterns and responses to human activities. I monitored changes in weather and resource availability as other potential sources of stress. Results of this study suggest that monkeys living in areas of high tourist use altered their behaviors in response to tourism, while monkeys living in areas with little tourist presence responded more to specific disturbances imposed on them by the tourists. Health parameters were not as strongly affected by tourist presence, though in general, monkeys in areas of high tourist presence suffered slightly poorer health than other monkeys. These results contribute to our understanding of how nonhuman primates respond to human actions and ecological changes, and have important implications for conservation and tourism programs in tropical forests. Moreover, these results indicate that responsibly managed tourism programs may only minimally affect howler monkeys, and may provide the economic incentive needed for local managers to keep parks and reserves intact rather than degrade them through extractive harvesting or mining.

Chapter I

Introduction

A. Statement of Purpose

Nonhuman primate populations are in decline everywhere (Strier 2007, Chapman and Lambert 2000, Mittermeier and Cheney 1987). One reason for this decline is that primate conservation often clashes with the economic needs of people living in host countries. Humans frequently encroach upon nonhuman primate habitat through commercial activities. Concomitant changes in forest ecology potentially affect the health and behavior of animals. What can be done to provide for people while still protecting natural resources?

Ecotourism is commonly promoted as a potential solution, and a few notable successes exist. For instance, the Mountain Gorilla Project generated significant revenue for Rwanda prior to the civil war there (Weber and Vedder 2001), and the Community Baboon Sanctuary has been instrumental in increasing the black howler monkey population in Belize, while allowing local farmers to stay in business and earn extra income through ecotourism (Horwich 1998). Ecotourism projects can also allow local inhabitants to earn a stable income while being employed near their families, as is the case with Las Islas de los Changos (the Monkey Islands) in Los Tuxtlas, Veracruz, Mexico. The availability of employment near to home can reduce the migration of local people away from their region (Serio-Silva 2006).

Despite cases such as these, the potential deleterious effects of tourism on primate populations are seldom investigated. Tourists alter the environments they visit in multiple ways. To accommodate tourists, trails are created, buildings are constructed, and wastes are disposed. To survive and reproduce, animals

must respond to these environmental changes through changes in their behavior and physiology. In this thesis, I present the results of a systematic study of the impact of tourism on the health and behavior of wild primates. Specifically, I investigate the relative impacts of human encroachment through tourism and environmental factors such as forest structure, weather, and food availability, on the behavior and health of red howler monkeys (*Alouatta seniculus*) in the Brownsberg Natuur Park, Suriname.

B. Background

1. Literature review of the effects of general habitat disturbance on primates

Habitat destruction is a major threat to populations of wild nonhuman primates (Strier 2007, Fedigan and Jack 2001, Zinner and Butynski 1998). Forest degradation and fragmentation, due to logging, mining, agriculture, and medicinal plant harvesting are hazards encountered by monkeys at my research site, Brownsberg Natuur Park, in Suriname. Considerable attention has been given to the effects of habitat loss and fragmentation on primate densities and behavior. These effects are well-documented, though not always well-understood. One such effect is a decrease in the number of individuals in a particular area. For example, in Costa Rica, squirrel monkey, *Saimiri oerstedii*, populations were much smaller than what would be considered minimal to maintain genetic viability (Boinski et al. 1998). Habitat destruction, due to agriculture and tourism development, was the explanation for such losses in animals. Chapman et al. (2000) found that heavy logging activities in Kibale National Park in Uganda still had effects on primate populations decades later. Populations of blue monkeys, *Cercopithecus mitis*, and red-tailed monkeys, *C. ascanius*, continued to decline in response to heavy logging that had occurred in the past. In contrast, primates living in areas that were only slightly logged were able to recover in numbers and did not show a population decline (Chapman et al. 2000). In Indonesia, Sulawesi crested macaques, *Macaca nigra*, were found to live at relatively high population densities in logged forests, but their densities were much lower than those found in primary forest (Rosenbaum et al. 1998). Food resources in the logged forests

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were lower in quality and quantity than in the primary forest; and canopy cover, tree species richness, and tree density were lower, which may explain the lower densities found there (Rosenbaum et al. 1998). Similarly, in the Kibale National Forest, Uganda, densities of pottos, *Perodictus potto*, and galagos, *Galago demidovii* and *G. inustus*, were lower in logged areas than in unlogged forest (Weisenseel et al. 1993). In addition to forest destruction, hunting can also negatively impact primate populations at some sites, especially when logging roads open up the forest interior to hunters. For example, in the Korup Project Area, south-west Cameroon, populations of Preuss' red colobus, *Procolobus pennantii preussi*, mainland drill, *Mandrillus leucophaeus leucophaeus*, chimpanzee, *Pan troglodytes vellerosus*, and several species of guenon, *Cercopithecus* spp., have declined in number or exhibited decreased densities in areas with high hunting and logging pressure (Waltert et al. 2002). The decrease in numbers could also be due to death of the animals by causes other than hunting, or by animals moving to adjacent habitat. Further observations at Korup are necessary to determine the ultimate cause of the loss in primate numbers.

Troop demographics can also be influenced by habitat disturbance or fragmentation, hunting, and disease (Chapman and Balcomb 1998). In Mexico, troops of black howlers, *Alouatta pigra*, in small forest fragments (10 ha) were smaller, and included fewer adult males when compared with troops found in the nearby protected Palenque National Park (17.7 km²) (Estrada et al. 2002). The formation of smaller groups may be a way for these monkeys to reduce within-group competition for resources in smaller than average habitat-islands. In Costa Rica, troops of mantled howlers, *Alouatta palliata*, decreased in numbers during and after a period of deforestation (Clarke et al. 2002a). Numbers of both adult females and adult males decreased significantly during the course of the study, while juvenile numbers stayed the same. These monkeys also exhibited longer daily path lengths and altered daily activity patterns after deforestation (Clarke et al. 2002a). These behavioral changes were most likely due to the loss of preferred food trees and increased patchiness of resources (ibid.), suggesting that habitat quality and/or resource availability was altered.

Another, immediate effect of habitat destruction on primate populations is an initially high population density (Clarke et al. 2002b, Chapman and Lambert 2000). Presumably, when habitat is destroyed around a group of primates, individuals will crowd together in the small patches of forest that are left. This crowding may not be sustainable over the long term as competition over resources may become intense, habitat may be further degraded through crowding, and disease may spread quickly and decimate populations (Lafferty and Gerber 2002). A disease epizootic may be an even greater problem if the environment is degraded and resources are scarce resulting in decreased disease resistance. Howlers, *Alouatta caraya*, live at high densities in forest fragments in Northern Argentina (Kowalewski and Zunino 1999). Populations of howlers were monitored both before and after a forest disturbance. The number of troops of monkeys was the same before and after the disturbance, though they were more concentrated in smaller forest patches after the disturbance. Accompanying the change in patch size was a change in patch composition; howler food trees were heavily exploited by loggers (Kowalewski and Zunino 1999). This is likely to affect the diet of the howlers in the future.

Forest disturbance may also lead to body mass and behavioral changes in primates. Logging in Kibale National Park, Uganda, may have been the cause of a reduction in the body mass of male grey-cheeked mangabeys, *Lophocebus albigena*, (Olupot 2000). Male mangabeys living in unlogged forest were significantly heavier than those living in logged areas, and these differences could not be attributed to differences in age or skeletal size. The logged areas had a reduced tree density, a change in species composition, and lower fruit production. Thus, the change in body mass may have been due to a change in quantity or quality of food resources in the logged forest. The differences in male mangabey body composition, probably signifying decreased nutritional status, may lead to lower fertility and survivorship in individuals living in logged areas (Olupot 2000).

Primates may also respond behaviorally to habitat change. Johns (1986) found that the activity patterns of lar gibbons, *Hylobates lar*, and banded leaf

monkeys, *Presbytis melalophos*, in the Sungai Tekam Forestry Concession, Pahang, West Malaysia, changed after logging. Both species spent more time resting and less time feeding and traveling. This could have been due to a loss of preferred fruits and seeds after logging, and a need to conserve energy while high quality foods were scarce. Additionally, the gibbons may have rested more due to the energetic costs of digesting leaf matter. After a hurricane in Belize, black howlers were forced to rely almost completely on young leaves while the affected forest produced new leaves exclusively (Behie and Pavelka 2005). The monkeys spent more time resting after the hurricane, which may have been due to the greater reliance on leaves, which are difficult to digest and provide less energy than higher quality foods. Additionally, new leaves were more abundant than other food types throughout the forest, so they did not need to travel far to find food.

Not all primate species are negatively affected by human activities. Vervet monkeys, *Cercopithecus aethiops*, in Kenya routinely raid crops when available, and females at one site were found to be heavier than their wild-feeding counterparts (Turner et al. 1997). This may have been due solely to the higher availability of human food at this site, and to the decreased energy expenditure needed to find food when agricultural crops were readily available. Tarsiers, *Tarsius dianae*, in Indonesia may have benefited from agro-forestry areas because insects were very abundant in plantations (Merker and Mühlenberg 2000). Tarsiers preferentially fed on insects and may have also provided a natural pesticide for plantation owners. The authors did not mention, however, whether chemical pesticides were used in the plantation; tarsiers would be exposed to high levels of chemicals from their insect diet if farmers sprayed their crops. Alternatively, tarsiers were negatively affected by logging and avoided logged areas, probably due to a reduced density of locomotor supports and potential sleeping sites, and the noise of the tree cutters (Merker and Mühlenberg 2000). Additionally, low-intensity logging may have been beneficial to folivorous colobines in Uganda. Trees found along forest patch edges in lightly logged areas of Kibale National Park, Uganda, produced leaves with a higher protein-to-

fiber ratio than trees in the forest interior. Colobus monkeys, *Colobus guereza* and *Procolobus badius*, were able to take advantage of this food and thus maintain a high biomass in fragmented areas (Chapman et al. 2004). Black and white colobus monkeys, *Colobus guereza*, were also encountered more frequently in regenerating forests than in old growth forests in Kibale, indicating that these monkeys were able to take advantage of areas of forest recently logged by humans (Lwanga 2006). Similarly, in the Budongo Forest Reserve, Uganda, black and white colobus monkeys were found at higher numbers in logged forest when compared to unlogged forest (Plumptre and Reynolds 1994).

Increased forest patchiness can also affect primate populations in complicated ways. Cotton-top tamarins, *Saguinus oedipus*, in Colombia, living in forest patches smaller than 300 ha suffered higher rates of adult and infant mortality, lacked stable social groups, and exhibited more frequent emigration and immigration in comparison with tamarins living in forest areas larger than 3000 ha (Miller et al. 2004). Inter- and intraspecific competition for limited resources in the forest patches was the possible cause for this higher mortality and social instability. Primate distributions may have been affected by forest patchiness in Kibale National Park, Uganda. Of six common diurnal primates, two species (blue monkeys, *Cercopithecus mitis*, and grey-cheeked mangabeys, *Cercocebus albigena*) were absent from forest patches ≤ 10 ha (Chapman and Onderdonk 1998). Chimpanzees, *Pan troglodytes*, entered patches only occasionally. In Mexico, mantled howler monkeys were absent from 17 out of 38 forest patches investigated (Estrada et al. 1999a). Patches lacking monkeys were the smallest of those surveyed, ranging from 1 to 30 ha (mean 3.2 ha). Howler troops were not sustainable in these small forest patches. Composition of forest patches, and thus food resources found in them, may change over time as certain larger-bodied species of primate seed dispersers avoid small forest patches. Forest fragments therefore will have a greater proportion of tree species with small seeds that may not require primate dispersers. Because of the fragmentation of the forest and the elimination of large-bodied seed dispersers such as primates, the forest's ability to regenerate will be diminished, and the

composition of the forest will change (Chapman and Onderdonk 1998). These are just a few examples of how human activities can seem very specialized in their impact, but can in fact upset the balance of the habitat for many kilometers around.

As illustrated above, primate communities are affected by habitat alteration caused by humans. There is debate regarding the proximate causes of these changes in primates, but evidence points to ecological changes due to edge effects (Medley 1993) and loss of food resources (Chapman and Onderdonk 1998) as two possibilities. Individual trees that survive habitat alteration may be over-browsed, resulting in long term loss of food resources. Logging projects, even small-scale ones, increase forest edge and change forest composition in ways that have been seldom studied. Microclimate conditions along forest edges are different than those of interior forests; temperatures are higher, humidity is lower, and solar radiation and wind penetration are higher (Estrada et al. 1999b, Murcia 1995). Initially, high tree mortality may be a factor along forest edges as shallow-rooted trees are newly exposed to wind. Later, new growth along forest edges includes early-successional species, which consist of different plants and trees than usually grow in older forests. Edge forest is also younger with a shorter canopy than forest interior (Murcia 1995). Certain early-successional species, such as *Cecropia* spp., provide fruits that are favorite foods of primates in the Neotropics, but many edge species may not be part of primate diets. Additionally, changes in food availability may force monkeys to eat less preferred foods, such as mature leaves (Pavelka et al. 2003), which may impact overall nutritional status and health. Microclimate changes (higher temperatures, lower humidity, and increased solar radiation) due to increased edge also affect habitat dynamics (Estrada et al. 1999b).

Pollution can also be a factor in the loss of food resources for primates, and air and water pollution, as well as light and noise pollution, can contribute to cases of non-infectious diseases (Deem et al. 2001). Air pollution from cities or water pollution from wastewater treatment can cause die-offs of native plants and animals in the forest. Species that depend on these plants and animals suffer in

turn. Thus primates are affected by plant and animal die-off when some of their food options are eliminated. Over-exploitation of a particular species of plant or insect can have a similar impact on the natural cycling of nutrients and forest regeneration, which can negatively affect primates that indirectly rely on that particular plant or insect.

In sum, the effects of habitat disturbance on primate populations are complicated and variable among geographic regions and primate species. Primates are most often negatively impacted by human destruction and fragmentation of their habitat through logging, agriculture, and mining. Population decline, changes in animal density, reduced group size or composition, reduced body size, behavioral changes, or changes in species distribution are all known to occur as a result of human alteration of habitat. In contrast, very little is known about the effects of habitat destruction on primate health, or the effects of tourism on the behavior and health of primates, and how direct contact with humans affects them.

2. Literature review of the effects of human disturbance on primates

This thesis addresses the impact of tourism on the behavior and health of primates. Only a few studies on this subject exist. The situation can be complicated due to the many ways in which tourism alters the habitats of primates. Some of these include, but are not limited to, the following: (1) areas of forest must be cleared for tourist lodges and trails; (2) human garbage and bodily waste must be disposed; and (3) transportation of tourists brings air and noise pollution into formerly pristine landscapes. Despite these drawbacks, the actual forest areas remain mostly intact, which is why tourism is one way to maintain forests while providing economic alternatives for local people. Nevertheless, through tourism, nonhuman primates directly encounter people, water, refuse, and other resources used and left behind by them. This can affect primate behavior and health in unforeseen ways.

Tourism may provide an alternate source of income for people and governments of countries that are home to nonhuman primates. Forests may be

spared from logging and other forms of extractive harvesting if money is made available to local people from tourism projects (Horwich 1990). If, however, a tourism program is not properly managed, financial benefits to local people may be small, and certain wildlife species may actually suffer (Crockett 1998). Tourists also bring diseases into the forest, and these diseases can be transmitted to wildlife, especially nonhuman primates. Often, tourists are warned about the dangers of getting too close to wildlife, in an attempt to protect the tourists, not the animals (Wallis and Lee 1999). Also, waste disposal plans are aimed at keeping the parks clean, not at keeping animals from foraging in human trash heaps. In most cases of tourism, human visitors are not effectively made aware of their roles as potential threats to wildlife health (Wallis and Lee 1999).

Direct contact with tourists may explain changes in primate group structure and reproductive rates. In China's Nanwan Reserve, tourist presence increased 70% from 1985 to 1989. This increase in tourism may have been the cause of the decreased reproductive rate and the increased juvenile mortality rate of rhesus monkeys, *Macaca mulatta*, at that site (Jiang et al. 1994). In contrast, reproductive rates may have been accelerated in provisioned groups of macaques, *Macaca* spp., at other tourist sites in Asia (Takahata et al. 1998). Nutritional constraints are relaxed when monkeys are provisioned, which may help to increase their reproduction. Troops in some areas of Asia have increased in numbers up to several times the average troop size of 40-50 individuals, with some troops containing several hundred individuals (Nakamichi and Shizawa 2003, Kurita 1999). The macaques generally were able to recognize all members of their social group, but in artificially large groups, most members were probably strangers. Stress levels were probably elevated as social structures, kin systems, and coalition networks became vastly more complicated in a group many times the normal size. Additionally, competition over provisioned foods often increased in these artificial conditions (Nakamichi and Shizawa 2003, Ram et al. 2003, Berman and Li 2002, Hill 1999). Low ranking female Japanese macaques, *Macaca fuscata*, were observed to avoid conflicts with high ranking females over provisioned foods by eating more natural foods when in season (Soumah and

Yokota 1991). A higher proportion of the low ranking females' diets were made up of natural foods, meaning that they had to forage longer to find foods, and rest and socialize less than high ranking females (ibid.). Thus, energy expenditures as well as social networks were disrupted by provisioning. Excessive provisioning will also harm the health of primate individuals when energy expenditure to procure food is minimized and caloric intake is maximized. Heavily provisioned monkeys in certain areas are likely to become obese (O'Leary and Fa 1993).

Primate behaviors can also be affected by the presence of tourists. Wild Tibetan macaques, *Macaca thibetana*, at Mount Emei, a tourism and Buddhism center in China, were given food handouts, which provided them with an incentive to attack and injure tourists (Zhao and Deng 1992). In fact, the monkeys were more likely to attack people who fed them than people who did not (Zhao 1991). The macaques have also changed their ranging patterns to be near food-carrying humans. The monkeys showed no fear of tourists, and begged from tourists or robbed them. Visitors lacking understanding of macaque behavior responded inappropriately to the monkeys' advances and were often harassed or injured as a result (ibid.). Consequently, disease transmission between monkeys and humans was a real possibility, and stress levels of monkeys were affected by these violent interactions. Tourists also killed monkeys that were looking for handouts on the roads, often just for amusement (Zhao and Deng 1992). The situation at Hindu temples in India was similar. Monkeys were given food handouts by local people and tourists at many sites. The macaques often became aggressive and tore clothing or bit people when food was denied them (Wolfe 2002). Additionally, monkeys entered pantries and hotel rooms looking for food. Such close contact could increase incidences of disease transfer. At tourist sites in Bali, Indonesia, long-tailed macaques, *Macaca fascicularis*, have been "trained" by people to steal personal items from tourists in exchange for a food reward. Additionally, the local people snapped Polaroid photographs of the monkeys with the tourists and sold them for a few dollars (Small 1994). In Ngorongoro Crater, Tanzania, vervet monkeys waited at picnic and toilet stations to ambush unsuspecting tourists and rob them of the leftovers

of their boxed lunches. These interactions could result in direct contact between monkeys and tourists thus increasing the possibility of injury, attack, or disease transmission. Additionally, foods found by the monkeys in lunch boxes and vehicles were often still wrapped in cellophane, which could be ingested by the monkeys (personal observation). The altered nutritional intake of monkeys eating human foods will potentially negatively affect the health of these animals, which may have long-term consequences for survival and reproduction.

Monkeys in the New World are not averse to these aggressive and destructive behaviors, though their arboreality minimizes direct contact with humans. When food handouts are provided, Neotropical monkeys may also learn behaviors that bring them in close contact with humans. Capuchin monkeys, *Cebus capucinus*, in Costa Rica were often given food handouts for the amusement of resort guests (Hal Wyss personal communication). The monkeys were lured to the backyards of the tourist facilities, and came within a few meters of human visitors. Monkeys may also become aggressive when food is involved. For example, I observed spider monkeys, *Ateles fusciceps*, in Nicaragua, bite humans who carried food. Although those incidences involved monkeys in artificial settings (one captive monkey on a chain, and three monkeys restricted to a small island), they illustrate the potential for negative interactions with human tourists. Additionally, tourists may not visit a particular destination for the specific purpose of viewing monkeys, but for other reasons such as exploring archaeological sites as is the case at the Lamanai Archaeological Reserve in Belize (Grossberg et al. 2003). Tourists may inadvertently come into contact with endangered black howler monkeys and potentially transfer diseases to them or cause them stress by yelling at them or trying to elicit roars (ibid.).

Indirect impacts of tourism can also affect primates, including alteration of the environment through noise pollution, compaction of the soil, and use of resources such as water. Construction projects, waste disposal, trail creation, use of flash photography, and loud parties are additional ways that tourists may disturb primates. Local populations of animals must respond to these changes in the environment through their behavior and physiology. Often this means

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changing ranging patterns to avoid human activities or fighting off infections transmitted by human visitors.

Primate health can be affected by contact with humans. Anthropozoonotic disease transmission can potentially cause significant illness and death of wild primates, especially as humans encroach ever further into primate habitat (Jones-Engel et al. 2001). Because humans, apes, and monkeys are closely related, human to nonhuman primate disease transmission is a common occurrence in areas of contact. Pathogens are easily transmitted due to close interaction (Wallis and Lee 1999). Even if measurable illness or death is not the result of these parasite outbreaks, parasites can often affect a population indirectly, reducing foraging efficiency or affecting the ability to conceive (Stokstad 2004a, Gunn and Irvine 2003). Nonhuman primates are also known reservoirs for human diseases such as malaria (Volney et al. 2002, de Thoisy et al. 2000, Fandeur et al. 2000, Davies et al. 1991), yellow fever (de Thoisy et al. 2001), hepatitis B (Vartanian et al. 2002), trypanosomiasis (de Thoisy et al. 2001, de Thoisy et al. 2000), and schistosomiasis (Weyher et al. 2006, Legesse and Erko 2004, Phillips et al. 2004, Murray et al. 2000, Wallis and Lee 1999, Muriuki et al. 1998). A group of wild red howlers captured for translocation in French Guiana tested positive for human diseases including trypanosomiasis and microfilariasis (Vié 1999). Baboons in Gombe Stream National Park, Tanzania, using the same water source as nearby humans had higher *Schistosoma mansoni* infection rates than other baboon troops without similar contact with humans (Müller-Graf et al. 1997). Population density may also have played a role in the concentration of the parasites and levels of exposure. The baboon troop with the highest parasite loads lived at high densities as did the nearby humans. Intense *S. mansoni* infections can result in death, and less intense infections may have subtle impacts on survival and reproduction (Müller-Graf et al. 1997). In Jaipur, India, all water sources for the resident macaques were also used for human activities, and most of the water was contaminated to some degree by industrial run-off, human sewage, and/or soap (Wolfe 2002). Contaminated drinking water and unnatural foods may have adverse effects on the health of

these monkeys. Likewise, in Polonnaruwa Nature Sanctuary, Sri Lanka, toque macaques, *Macaca sinica sinica*, gray langurs, *Semnopithecus priam thersites*, and purple-faced langurs, *Trachypithecus vetulus philbricki*, living in areas contaminated by human and livestock feces, were found to harbor higher levels of *Cryptosporidium* sp., a common human intestinal protozoan parasite, as well as several other species of protozoa and nematode, than monkeys living in clean areas (Ekanayake et al. 2006). On Ometepe Island, Nicaragua, two troops of mantled howler monkeys were screened for intestinal parasites. The troop living closer to humans in a recently disturbed patch of forest harbored species of nematode not found in the troop living farther from humans in a less disturbed area (Kahre 1999). Proximity to humans and domesticated animals, and habitat disturbance may have been the causes for this increased parasite richness.

Tourist presence can affect the health of primates through the introduction or spreading of infections to wild primate populations (Fuentes 2006, May 1988). Gorillas, *Gorilla beringei beringei*, habituated to tourist presence in Bwindi Impenetrable National Park, Uganda, exhibited higher fecal egg counts of parasites compared with non-habituated gorillas (Kalema-Zikusoka et al. 2005). Furthermore, all nematode eggs identified in these gorillas have been recorded in humans, though there has been no recorded evidence of direct disease transmission. Many human diseases can be fatal to gorillas, while others affect behavior and reproduction (Woodford et al. 2002). Villagers living near Bwindi passed through the park on their way to other villages or markets, or worked in the park, and often encountered gorillas (Guerrera et al. 2003). These Ugandans often had malaria, intestinal parasites, and probably tuberculosis, all of which could be transmitted to gorillas, often with devastating effects. In Indonesia, wild and pet macaques, *Macaca tonkeana*, were found to carry antibodies to measles, and several different human parainfluenza viruses, probably due to indirect or direct exposure to infected humans (Jones-Engel et al. 2001). Additionally, older macaques possessed antibodies against more of the viruses than younger macaques, suggesting that the animals may be exposed to these viruses over time. Such exposure can be in the form of direct contact with

humans, or contact with human trash or contaminated water sources. All infants in a troop of Barbary macaques, *Macaca sylvanus*, on Gibraltar were killed during a single viral pneumonia outbreak in 1987 (O'Leary and Fa 1993). Tourist presence was common on Gibraltar and contact between humans and monkeys could have resulted in the occurrence of pneumonia there, or could result in a similarly devastating outbreak in the future. In Suriname, brown capuchin monkeys, *Cebus apella*, and squirrel monkeys, *Saimiri sciureus*, have been observed to exhibit symptoms of the common cold, possibly due to presence of sick tourists (Boinski personal communication).

Human activities create situations in which primates come into direct contact with humans or human waste. Additionally, tourism projects result in degradation of forest due to the building of lodges and tourist trails. The extent of this degradation is smaller than large-scale logging or agricultural projects, but it may still affect daily primate behaviors, health, or even reproductive success and intergroup relations (Grossberg et al. 2003). Few data exist concerning the effects of habitat degradation on the health of primates, and equally unclear is the point at which the health of individuals starts to decline in response to altered environmental conditions. Stress is also a factor; habituated great apes are known to be susceptible to diseases carried by tourists, researchers, and park managers, and their susceptibility is exacerbated by the stress caused by the presence of humans (Stokstad 2004a, Woodford et al. 2002). Stressors, such as human encroachment through tourism or habitat degradation, also play a role, and can affect an individual primate's ability to fight off disease. Monkeys are exposed to stressors throughout the year, which may have indirect effects on their health. They must cope with seasonal weather fluctuations, pollution, noise, and habitat alteration by human activities such as tourism. Animals that are exposed to stressful conditions may experience immunological, gastrointestinal, or cardiovascular changes that may make them more susceptible to disease (Deem et al. 2001, Laudenslager and Boccia 1996, Caldecott and Kavanagh 1983). Stress resulting from a poor diet, low food availability, and/or aggression from established groups, may have increased the disease susceptibility and

death of members of new red howler groups in Venezuela (Rudran and Fernandez-Duque 2003). In the same population, stress resulting from a drought-related food shortage, combined with disease, may have led to a population crash in the early 1990's (ibid.) In mantled howlers on Barro Colorado Island, Panama, stress due to food shortage possibly resulted in decreased resistance to bot fly infestations; especially bad bot fly infestations were associated with emaciated animals (Otis et al. 1981). The combination of nutritional stress and bot fly infestation, occasionally coupled with infected bot sores or screwworm infestation, dramatically contributed to mortality rates in the population (Milton 1996).

Human alteration of forest habitat can also affect wildlife disease ecology through the disruption of habitat dynamics, especially macro- and microclimate changes and environmental contamination. Forest fragmentation caused by human activities can result in "island ecosystems" in which populations are isolated and more susceptible to extinction when exposed to a new disease (Daszak et al. 2000). Groups of animals may also be displaced by habitat fragmentation, and could carry their pathogens to new areas and new groups or species (Meffe 1999). Furthermore, once a disease has been transmitted to a dense and isolated population of nonhuman primates it can spread quickly and decimate the group. Although a relatively closed group will have minimal risk of disease transmission among its members, a group with a high population density will be more susceptible to disease outbreaks (Scott 1988). Decreased availability of food resources and stress due to high population densities will also exaggerate the effects of disease, even to the point of death of the animal (ibid.). Infants are most at risk due to their less-developed immune systems; and they may not be able to fight off an infection that comes from repeated exposure. Additionally, infants are at risk due to their need to invest much of their energy intake into rapid growth, which often comes at a cost to immune function. The same can be said for adult females who invest in pregnancy and lactation, with little energy left over for their immune system (Coop and Kyriazakis 1999). Also, the high concentration of individuals in one area can result in contamination of

the environment (Freeland 1976). Group sizes are therefore expected to be smaller in more sedentary species, as fecal contamination of the site happens faster when the group stays in one place. Capture and transportation of primates, through hunting or the pet trade, or for conservation reasons, also allow for the transportation of diseases into new areas where livestock and wild animals may not be resistant (Deem et al. 2001, Cunningham 1996). Parasite densities have also been found to be higher in forest fragments (Stokstad 2004a). A study from Kibale National Park, Uganda, analyzed more than 1000 fecal samples from monkeys, and found that monkeys from forest fragments had significantly higher parasite loads than monkeys from undisturbed forest (ibid.). Transmission was thought to be from people or livestock, and many of the parasites found in the feces from animals in fragmented landscapes were previously known only to infect humans and livestock (Stokstad 2004a). The increased edge of forest fragments also increases the opportunity for animals to come into contact with humans or domestic animals, with this increased exposure resulting in greater disease transmission, often from humans to nonhuman primates.

Human activities have profound effects on wild populations of non-human primates; this occurs through habitat loss and disease transmission, as illustrated above. Social structure, reproductive rates, body sizes, behavior, and health of non-human primates can be impacted by these human activities. Additionally, ecological factors, such as forest composition, weather patterns, and food availability, can also play roles. For example, the size of trees in the forest through which the monkeys must travel, and the availability of preferred food sources such as fruit can affect ranging and activity patterns. Seasonal weather fluctuations, particularly the hot and humid conditions favoring parasite survival, can affect parasite loads and parasite transmission, as well as non-human primate activity patterns. When attempting to determine whether the behavior or health of non-human primates is influenced by human activities, it is also important to characterize the impact of these ecological factors, as ranging behavior, activity patterns, and health status can vary in response to natural

cycles. For this reason, I also investigated whether ecological factors could have had an impact on red howler monkey behavior or health.

In this thesis, I investigated whether the presence of tourists had an adverse effect on the behavior and health of red howler monkeys. Second, I addressed whether three factors, forest structure, weather patterns, and food availability influenced the relationship of human tourism with monkey behavior and health. These three factors, as well as tourism, may play a role in the seasonal fluctuations of behavior and health status in howler monkeys. To test the hypothesis that tourism affects the monkeys, I also monitored the general ecology as well.

C. General Goals of the Thesis

1. Research Questions

Given the potential effects of tourism on the health and behavior of primates, it is crucial to know answers to the following questions: Are nonhuman primates able to cope with the stress of living in a tourist region? Do nonhuman primates alter their behavior in response to human presence? Does the general health of monkeys suffer due to the presence of humans and the alteration of habitat caused by humans? Do monkeys living in tourist areas contract more diseases and carry more intestinal parasites than monkeys living outside tourist areas? I will address these questions in this thesis.

2. Assumptions

The assumption of this study is that the influence of tourism on the behavior and health of red howler monkeys can be investigated without also investigating the physiological mechanisms by which this influence is occurring. Whether monkeys come into direct contact with contaminated human or livestock feces, trash, or water (Wallis and Lee 1999, Stuart et al. 1990), or whether the human influence on primate health is indirect via habitat alteration or crowding (Stuart and Strier 1995), a potential exists for disease transmission from humans to nonhuman primates. Stress caused by tourist presence may also affect the health of the monkeys (Deem et al. 2001). Physical stressors such as loud music

or bright lights are common during the height of the tourist season at my study site, Brownsberg Natuur Park, Suriname.

An investigation into the physiological mechanisms by which tourism affects monkey health and behavior is outside the scope of this thesis. Rather, I focus on illustrating the relationships between human presence and aberrant or unusual behavioral patterns and deleterious health. Through behavioral observations, urinalysis, and fecal analysis, I investigated whether the behavioral profiles and the health status of monkeys differed between areas with tourist presence and areas with no tourists. I also controlled for possible confounds that might affect the relationship of tourist presence and altered behavior or deleterious health, including forest structure, weather, and food availability. If statistically significant differences in the behavior or health between the two groups could be shown, and if confounds could be eliminated, tourist presence would be implicated as a major factor influencing the monkeys.

3. Hypotheses and Predictions

My working hypothesis for this research was that human tourism changes the behavior of, and impacts the health of wild red howler monkeys. This general hypothesis can be broken down into two specific hypotheses.

1. Monkeys living in the tourist area will exhibit different behavioral profiles and lower overall health status when compared to monkeys living outside the tourist area, as evidenced by indicators of poor health such as wounds, scars, or bot fly lesions, urine parameters, and greater prevalence and intensity of intestinal parasite infections.

2. During the time of peak tourist attendance in the park, monkeys exposed to tourists will exhibit different behavioral profiles and lower overall health status, when compared to other times of the year.

Specifically, I predicted that increased travel and decreased resting would characterize monkeys in the tourist areas, and reactions to humans would be stronger in monkeys exposed to tourists and during the height of the tourist season. Alternatively, the monkeys may have become habituated to the presence of tourists, and therefore I would expect stronger reactions to come

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from the monkeys with little exposure to people. I also predicted more indicators of poor health in the tourist area, urine measures indicative of poor health, and intestinal infections higher in prevalence and intensity for monkeys exposed to tourists and during peak tourist seasons.

4. Significance of this Study

Understanding how human tourism affects primate health is crucial for the proper management of animals, resources, and tourists. The goal of this project was to monitor the behavior of monkeys, as well as utilize a simple, novel, and noninvasive technique to obtain direct information regarding primate health as influenced by tourists, climate changes, and food availability. Results of this project, either negative or positive, promise to have significant implications for future primate conservation plans. Results will be shared with Stinasu (The Foundation for Nature Conservation in Suriname) with whom I worked during the course of my research. Managers of the Brownsberg Natuur Park can thus be informed of the impact of tourism on the monkeys and management plans can be reassessed.

Chapter II

Methods

A. Study Site

Suriname is located on the northeast coast of South America, north of Brazil, between Guyana and French Guiana (Map 2.1). The country is slightly larger than the U.S. state of Georgia. Suriname is part of the Guiana Shield, which includes French Guiana, Guyana, northern Brazil, and eastern Venezuela. Suriname's forests are adjacent to and historically part of the Amazon rainforest, though the Amazon River watershed does not extend north into Suriname.

Map 2.1: Location of Suriname (Vandeputte 1993)

Suriname is one of the few countries in the world with large undisturbed ecosystems, mainly due to its small population size (Fitzgerald 2003). Suriname has an area of 163,270 km^2 and a population of only 470,784 people (July 2007 estimate, The World Factbook 2007). The majority of Suriname's land is unpopulated and not subject to development pressure and most (80 to 90%) of the Surinamese people live along the coast, and especially in the capital city of Paramaribo (Heemskerk 2002, Peterson and Heemskerk 2001). The forest interior houses many Amerindian (est. 10,000 people) and Maroon (est. 50,000 people) ethnic groups, living in different forest territories (Heemskerk 2003, Heemskerk 2002). Most of these groups hunt monkeys for food, and although hunting is not allowed in nature reserves, exceptions are made for indigenous forest peoples (Vreedzaam personal communication).

Suriname has only been independent from the Netherlands since 1975, and yet has an outstanding nature conservation system that ranks among the best in South America (Fitzgerald 2003). According to the World Resources Institute (2005), about 85% of Suriname's land area has greater than 50% tree crown coverage. Deforestation is generally low, but foreign logging companies have large-scale concessions, and there are no government controls for logging operations, which results in more trees being felled than permitted (Fey 2003). As of 2002, the amount of land protected in parks or reserves totaled 1,959,180 ha, which is nearly 12% of the country's total land area. These protected areas include 11 nature reserves, 1 nature park, and 3 multiple-use management areas, ranging in size from 100 ha to 1.6 million ha, and including forest and coastal areas (Fey 2003, Fitzgerald 2003). In 1998, Conservation International assisted with the creation of the Central Suriname Nature Reserve, a protected area of 1.6 million ha that represents nearly 10% of the country, and is one of the world's largest reserves (Fey 2003). Despite this impressive conservation record, it is worth noting that much of the actual conservation of natural areas in Suriname has been due to low human population densities in the interior of the country. Currently, hunting, mining, logging, and human encroachment are all

increasing, which may prove to be a serious threat to natural areas in the future (Norconk et al. 1996).

Suriname has several major extractive industries, including bauxite, oil, gold, and timber (Fey 2003). The Aluminum Company of America (Alcoa) began mining bauxite in Suriname during World War I. The building of the hydroelectric dam at Afobaka, and the creation of the Brokopondo Reservoir at the edge of Brownsberg Natuur Park are direct results of the bauxite industry in Suriname. Oil production is currently over 10,000 barrels per day from offshore oil reserves, and is increasing. Gold mining has existed in Suriname since the late 1800's, when mercury extraction was the common method. Gold was not plentiful and mining slowed during the early 1900's (Fey 2003). Mining concessions have recently increased again due to the high price of gold on the global market. The main concession near Brownsberg is owned by a Canadian company, Cambior. Small-scale gold mining by village-dwelling locals and Brazilians is currently damaging the fringes of Brownsberg Natuur Park, and is encroaching on the main areas of the park at alarming rates (Norconk personal communication). Entire watershed areas have been polluted with mercury, creeks have been rerouted, large areas of forest have been cleared, and wildlife has been over-hunted (personal observation). Logging of the rainforest has been a profitable business for some time (Fey 2003). Most timber concessions are owned by Asian countries, and these are monitored by the Foundation for Forest Management (SBB). Logging is not permitted inside reserve areas, though enforcement is always a problem.

I conducted my study at the Brownsberg Natuur Park in Suriname. Brownsberg Natuur Park was established in 1970 and is the first and only national park in Suriname. The park is located northwest of the 1560 km^2 Brokopondo Reservoir, in the northeastern part of Suriname. It lies about 90 km south of Suriname's capital city, Paramaribo (i.e. about 100 km south of the Atlantic coastline, Map 2.2). The current park encompasses 12,200 ha, which is most of the Brownsberg hill, a 500-meter-high tabletop range. This "inselberg" is a remnant granite outcrop of the Guayana Shield (Norconk et al. 1996). The park

straddles a long and narrow crescent-shaped laterite plateau that is a watershed divide between the Suriname and Saramacca river systems (Fitzgerald et al. 2002). The park is dominated by seasonal evergreen rainforest and is characterized by steep slopes and gullies on all sides of the plateau. Brownsberg is biologically diverse due to its rapidly rising slopes, which contain various habitat types. The park is home to all eight of the primate species occurring in Suriname: the red howler, *Alouatta seniculus*, the brown capuchin, *Cebus apella*, the wedge-capped capuchin, *Cebus olivaceus*, the Guianan saki monkey, *Pithecia pithecia*, the brown bearded saki monkey, *Chiropotes satanas*, the black spider monkey, *Ateles paniscus*, the golden-handed tamarin, *Saguinus midas*, and the common squirrel monkey, *Saimiri sciureus sciureus* (species names as found in Emmons 1997).

Map 2.2: Location of Brownsberg Natuur Park (BNP)

Research at the Brownsberg site has been minimal, though in 2001, park staff implemented a research and monitoring program to provide current information on vegetation and wildlife for the purpose of aiding management

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decisions (Fitzgerald et al. 2002). The goals of the research and monitoring program for the park included assessment of the park's ecosystem and the conservation status of animals and plants within the park, documentation of the species of flora and fauna for the purpose of visitor education, improvement of the potential of the site for domestic and international ecological research, and facilitation of research and methodology sharing across the Guianas (ibid.). The protocol for the program included monitoring of climate and hydrology, water quality, vegetation and wildlife.

This site offers an unusual opportunity to investigate the impact of tourists on the behavior and health of monkeys. Brownsberg is a site of tourism, where monkeys in areas of contact with tourists can be easily compared with monkeys who have limited contact with humans. Stinasu (Stichting Natuurbehoud Suriname or the Foundation for Nature Conservation in Suriname) has been instrumental in promoting Brownsberg as a recreation destination for Surinamers. In 2003, the park hosted 19,700 visitors, most of whom were Surinamese. This represents more than 4% of the total population of Suriname. Several thousand foreign ecotourists also visit each year. Brownsberg is the most popular nature destination in Suriname and thus offers opportunities for nature education, exposure of the public to nature research, and promotion of respect and appreciation for nature (Fitzgerald et al. 2002).

Brownsberg has clearly demarcated tourist seasons with some areas open to tourists and others that are restricted. The research area for this project was concentrated on top of the Brownsberg plateau, around the main tourist facilities and trails extending approximately twelve km from the tourist area. For the purposes of this study, I designated a "tourist area" as the area including the most popular trails and all facilities for tourists, researchers, and workers. The tourist area was approximately 130 ha, though some of the popular tourist trails continued outside this range. The area designated as the "non-tourist" site included all forest along trails outside and to the southwest of the tourist area (Map 2.3). I also created additional trails in the non-tourist area to facilitate observation of the monkeys. The tourist and non-tourist areas were contiguous,

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and were connected by the main plateau road, off of which, additional trails extended. To distinguish tourist monkeys from non-tourist monkeys, I primarily used geographic location unless I could recognize individual animals. Because red howlers are folivorous, they have small home ranges, rarely more than 40-50 ha, and they often do not travel more than 100 to 200 m per day (Boinski 2002, 16- and 23-ha home ranges on islands in Venezuela: Lopez et al. 2005, 5.5- and 25-ha home ranges in Venezuela: Pope 1992). As a result, monkeys probably crossed the boundary between the tourist and non-tourist areas only rarely. The study area for this project was also primarily restricted to the top of the plateau. To minimize the effect of altitude as a possible confound, I focused my observations on the flat areas of the plateau. As howlers had very small home ranges, monkeys that I encountered on the plateau spent little, if any, time down the slopes.

Map 2.3: Non-Tourist and Tourist Areas
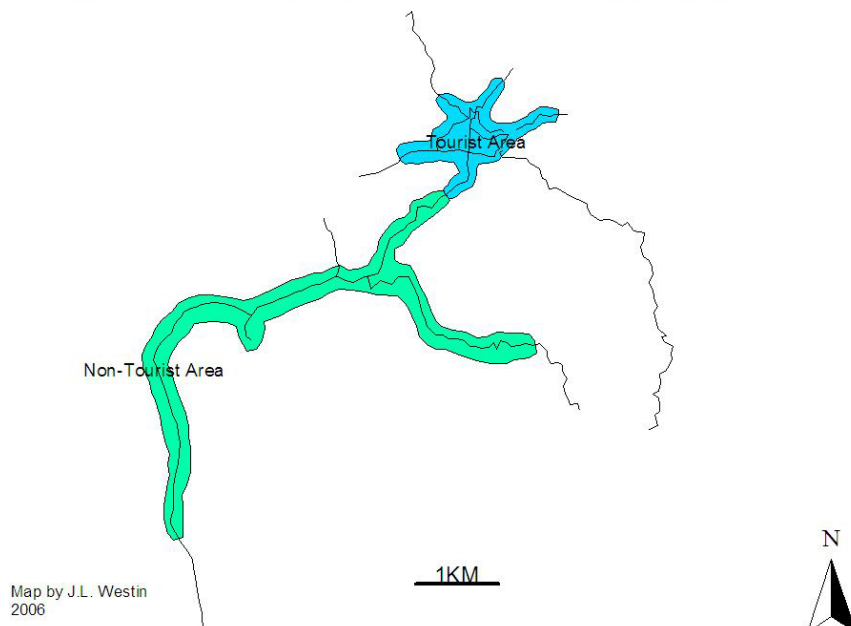
B. Study Subjects

Of the eight species of monkeys living in the Brownsberg Natuur Park, the most appropriate for this project was the red howler monkey due to the adaptable nature of these monkeys when faced with habitat disturbances (Clarke et al. 2002b, Horwich 1998, de Thoisy and Richard-Hansen 1996). Howlers are known to be flexible in diet and behavior in response to habitat alteration, and if I found that they are in fact affected by tourism, it would mean that other less adaptable species are also likely to suffer.

The red howler monkey is one of the largest primates of the Neotropics, with adults weighing between 3.6 and 11.1 kg (Emmons 1997). Howlers are sexually dimorphic in size, with males larger than females. Red howlers are red-orange in color ranging from golden to maroon, with adults sexually monochromatic (Crockett and Eisenberg 1987). Howler monkeys possess enlarged hyoid bones, which help resonate and amplify long distance calls. Hyoids are larger in males than females, and red howlers have the largest hyoids of any species in the genus *Alouatta* (ibid.). Howler monkey long calls are generally initiated by males, which is typical for most primate species (Wich and Nunn 2002), but other group members usually join them (Chiarello 1995). Calls are most common in early morning hours, and probably function to announce location and communicate information about group composition, especially the minimum number of males present. Alpha males may use other groups' calls to assess their odds of winning a physical contest with a neighboring group, and base their response (call back, approach, retreat, etc.) on the information conveyed by the other group's call (Kitchen 2004). Another notable feature of howler monkeys is their prehensile tail. The tail is used as a fifth limb, and aids in support while feeding and moving. Bridging is also common in red howlers in which the monkey uses all four limbs and the prehensile tail to grasp both the branches of the tree it is leaving, and the branches of the tree it is entering in order to maximize stability and minimize the risk of falling (Youlatos 1993). Occasionally, an adult female holds branches of adjacent trees while her offspring walks across her back to traverse the gap (personal observation).

Howlers are almost completely vegetarian, and the most folivorous of the New World primates, though they have been considered "as frugivorous as possible...and as folivorous as necessary" (Silver et al. 1998, p. 273). Howler diet consists of a wide variety of new leaves, fruits, and flowers (Milton 1980). Red howlers in French Guiana eat a substantial amount of new leaves, although fruits can comprise up to half of their monthly diet (Julliot and Sabatier 1993). These monkeys are opportunistic foragers, but prefer to eat fruits and flowers when they are seasonally available; new leaves are always available and are consumed all year. Red howlers also eat some mature leaves, though they are lower in protein and digestible nutrients and higher in fiber and secondary compounds than new leaves (Estrada and Coates-Estrada 1986, Estrada 1984, Milton 1980). Termite nests and soil are also occasionally eaten by howlers, presumably as a way to detoxify a diet of leaves containing secondary compounds (Julliot and Sabatier 1993). Howlers do not have highly specialized digestive tracts for the digestion of leaves, however, their colon is somewhat enlarged. Howlers tend not to range widely or quickly on a daily basis. This is due to the low amount of energy available from a leafy diet, the fact that more rest time is needed to digest cellulose, and the relative abundance of leaves in the forest (Milton 1980). Red howlers also rest for long periods often several times a day (personal observation), presumably to digest their bulky diets. Howlers also tend to focus on a limited number of food species for the majority of their diet. This is probably because of their need to balance nutrition with known trees containing minimal levels of secondary compounds. Tree species diversity is also a factor in howler monkey diet, and monkeys living in sites with higher availability of food trees have broader diets (Julliot and Sabatier 1993).

Red howler troops range from three to nine individuals, but I most commonly observed them in troops of four to six. Groups consisted of one to three adult males, two to five adult females, and their offspring (Pope 1998, personal observation). Mean group size was around five for groups I was fairly certain were distinct and not just subsets of larger groups (mean = 5.26, SD = 1.22, *N* = 35). Allogrooming occurs infrequently in the species, and grooming

bouts are very short. Adult females are the most common groomers, and although males rarely groom others, I witnessed several cases where adult males groomed females and occasionally immatures. Red howlers exhibit a single-male harem breeding structure (Pope 1992), in which both sexes disperse upon reaching maturity (Crockett and Eisenberg 1987). Females emigrate because of reproductive competition with other females, and they are more likely to emigrate from groups already containing several adult females (Pope 1998). The daughters of a single, presumably dominant female sometimes are allowed to remain in the natal group, but in general, females try to evict each other's daughters. These evicted females are often prevented by resident females from joining other groups, and therefore form new groups with other extragroup males and females rather than enter an existing group (ibid.). Infanticide by invading males has been reported for red howlers, and some males die of injuries sustained while fighting other males (Crockett and Eisenberg 1987).

Howlers use the middle and upper levels of the main canopy and emergents of mature and disturbed forest, and travel quadrupedally on the tops of branches (Fleagle and Mittermeier 1980). They occasionally come to the ground to cross roads or move from one vegetation clump to another (Crockett and Eisenberg 1987). Though not strictly territorial, red howlers often confront neighboring troops when sighted. Usually, one troop howls at the other, and the other troop either howls in response, or leaves the area. A few times I witnessed extreme confrontational behavior in which both troops retreated from each other slightly and urinated and defecated as a group, after which, the approaching troop left the area. This defecation response has been interpreted as unconscious and due to fear (Racenis 1952). Occasionally, three troops were involved in a howling confrontation, suggesting considerable overlap of home range areas (personal observation).

Howler monkeys are often thought to be fairly adaptable when faced with habitat disturbances (Clarke et al. 2002b, Horwich 1998, de Thoisy and Richard-Hansen 1996). This makes them a good choice to study the effects of tourism because if they are in fact affected, other less adaptable species are also likely to

suffer. Howlers have been shown to adapt to food shortages by decreasing their diet breadth and relying more heavily on leaves rather than fruits in small patches of forest (Lopez et al. 2005). The howler monkeys' ability to increase the proportion of leaves in their diet after a forest disturbance may itself be a key adaptation that allows them to survive despite experiencing a loss of food resources due to logging (Johns and Skorupa 1987). After a hurricane in Belize, black howlers altered their diet to match the foods available in the severely disturbed forest; the absence of fruit and flowers and the abundance of new leaves forced the monkeys to adopt a completely folivorous diet (Behie and Pavelka 2005). In Venezuela, red howlers live at very low densities and travel over one kilometer per day. This is presumably to compensate for the poor soil quality and resulting low food tree density found in their habitat (Palacios and Rodriguez 2001). There is some evidence that birth rates are much lower in groups of howlers suffering from severe nutritional stress in very small forest patches in Venezuela. However, despite poor nutrition, these troops of howlers were able to persist for decades (Lopez et al. 2005).

Howlers are also relevant study subjects because they play an integral role in the ecosystems in which they live (Estrada et al. 1999a). Howler monkeys are important seed dispersers, specialized for dispersing seeds of trees in the Sapotaceae family (Julliot 1996a). Red howlers in French Guiana have been observed to disperse seeds up to 550 m from the parent tree (mean 260 m), and over the course of a year, a troop of six individuals was estimated to have dispersed 1.3 million seeds (Julliot 1996b). Seeds processed by howlers may be better able to germinate than those dropped under the parent tree for several reasons: 1) seeds are transported to suitable microsites and out from under the shadow of the parent tree, 2) seeds passed through the gut of a monkey are scarified by stomach acid, reducing latency time to germination (Chapman 1995), and 3) seeds are deposited in abundant piles of fertilizer. Seed dispersal by howler monkeys is not only important for forest regeneration for the forest's sake, but also for the sake of the humans relying on the natural regeneration of primate-dispersed tree species for wood products. Many commonly used timber

species of Suriname, such as *Tetragastis altissima, Ocotea* sp., and *Virola* spp. (Hammond et al. 1996) are regularly dispersed by howlers (personal observation).

The seeds passed in howler monkey dung can also be further dispersed by dung beetles (Andresen and Levey 2004, Vulinec 2002). The presence of howler monkeys is positively linked to numbers of dung beetles (Estrada et al. 1999a), and the loss of either the monkeys or the beetles from a habitat causes a disruption in the ecosystem, which may result in a loss of forest diversity (Stokstad 2004b, Vulinec 2000). Thus the regenerating capacity of small forest fragments may be weakened by the absence of howler monkey and dung beetle seed dispersers (Estrada et al. 1999a). Additionally, dung beetles may decrease the numbers of viable nematode parasite eggs in dung through mastication of the eggs, resulting in fewer eggs on the forest floor to infect other animals (Bergstrom et al. 1976). They also aid in nutrient recycling and aeration of the soil (Vulinec 2000). Seed predators also take advantage of howler monkey defecation patterns; large dung piles make easily found seed sources for agoutis and other rodents. Rodents cache and eat seeds found on the forest floor, including those found in howler dung. Howler dung is also an important factor in nutrient recycling of tropical forests, and it contains a higher concentration of nutrients than leaf litter (Feeley 2005). A six-monkey red howler troop in French Guiana was estimated to deposit an average of 1.5 kg of nitrogen- and phosphorus-rich fecal material per day (Julliot 1996b). Soil underlying red howler latrines in Venezuela was found to have higher concentrations of bioavailable nitrogen and phosphorus, and plants seemed to be taking advantage of these high levels of nutrients by increasing their root production under latrine sites (Feeley 2005).

Howlers are also food for other species including large raptors, such as the harpy eagle, *Harpia harpyja* (Gil-da-Costa et al. 2003, Peres 1990), cats, such as ocelots, *Leopardus pardalis* (Bianchi and Mendes 2007), or jaguars, *Panthera onca* (Peetz et al. 1992), and occasionally by a member of the weasel

family, the tayra, *Eira barbara* (Camargo and Ferrari 2007, Vreedzaam personal communication), all of which can be found at Brownsberg Natuur Park.

There are many troops of red howlers at the Brownsberg site, and tourists often stopped to watch them. The Brownsberg monkeys were fairly well-habituated to human presence and could be followed for observation, though those in the non-tourist areas had less exposure to human presence and were less well-habituated. I spent my first several months at Brownsberg looking for monkeys in the non-tourist areas to habituate them to my presence. These groups were scarce and I was only able to find a few groups repeatedly. Therefore, habituation for many groups was never fully accomplished, which I had to keep in mind when examining their reactions to human presence, including my own. I also attempted to acquaint myself with the individuals in each group to ensure that behavioral observations and urine and feces were collected from different monkeys. This proved to be difficult due to the high canopy where howlers spent most of their time, and the sedentary nature of the howlers, which prevented me from getting even a glimpse of many individuals. Additionally, I found during my observations that the monkeys had an uncanny knack for disappearing into tree canopies, and on more than one occasion I lost individuals or groups completely. Individual markings and scars were also lacking for most individuals, and pelage color differences were too subtle to be used for distinguishing individuals. Bot fly lesions on the face and neck helped me to identify individuals within groups over short terms, but these healed and individuals were presumably re-infected during the course of the year. All of these factors prevented me from accurately identifying many individuals, and therefore, I chose to focus on observing "adult male" and "adult female" monkeys rather than specific individuals.

During four months of preliminary field observations from mid-August to mid-December 2003, and during subsequent data collection during 2004, I tentatively censused 20 and 15 groups in the non-tourist and tourist areas, respectively. Around twenty groups of red howlers had been previously censused in the park area (Norconk et al. 2003). This included groups found on two sloping

trails, which I did not utilize for observations, but it did not include monkeys found on a newly opened trail in the non-tourist area. Because I was unable to identify individuals reliably, and because there is a high degree of overlap in red howler home ranges (Pope 1992, personal observation), I was only able to obtain tentative counts for each age-sex class during my observations, thus making it difficult to determine whether subsequent sightings of monkeys in similar geographic areas were the same or distinct groups. My tallies of group numbers therefore were likely to be overestimates. On at least eight occasions I witnessed encounters by two to three groups at a time, in both the non-tourist and tourist areas (four encounters in each area). Given those encounters, and taking into account other distinct groups throughout the park, while keeping in mind possible home range sizes and overlap, I suggest that a more conservative estimate of group numbers, and the absolute minimum number of red howler groups at BNP were 16 and 11 in the non-tourist and tourist areas, respectively. These counts reflect the number of groups of which I was confident were distinct, whereas the above estimates may have counted one or more groups twice.

Most groups I observed consisted of three to nine individuals with an average of about five. I calculated mean group size from low and high estimates of individuals from all groups observed, and separately using only groups I was more confident were distinct. The median and mode for all group size observations were five individuals, and the mean for the most conservative estimate of distinct groups, which did not include observations of solitary individuals, was 5.25 (SD = 1.22, n = 35 groups). Groups consisted of one to three adult males, two to five adult females, and their offspring (personal observation). I infrequently encountered a group of two individuals (one adult male and one adult female), and only six times did I observe a solitary individual (four solitary males, and two solitary females). These could have been emigrants, or individuals whose groups I did not detect near them. Occasionally, I observed a group of eight or more, always along the same 400 to 500 m stretch of road, presumably the same group each time. Often complete counts of all individuals in

a group were not possible due to the cryptic nature of group members who rested high in the tree canopy.

I evenly divided my observations between the non-tourist and tourist areas. Starting with the non-tourist area, I observed monkeys for approximately two weeks before switching to the tourist area, and back and forth for the duration of the year of study. It was more difficult to find and follow monkeys in the non-tourist area, so I devoted proportionally more time to observations there to keep the quantity of observations approximately equal between the two areas. My aim was to stagger observations of one or more groups throughout the day, starting at 06.00 and ending at 19.00. Starting at 06.00 was easier in the tourist area because monkey troops lived near the research station, and often could be heard howling early in the morning. It turned out to be much more difficult to locate monkeys in the non-tourist area, even when I was there to hear their morning howls. Usually, the duration of the howl was not sufficient to allow me to locate them in the dense canopy. This was the case in the middle of the day when I had the help of the sun in looking for the monkeys, and was especially difficult in the early morning darkness. Consequently, observations of non-tourist monkeys rarely began before 07.30 or 08.00. I followed troops when possible, and usually followed at least one or two troops for a part of each day. If troops left the plateau or moved quickly away, I left them to find other troops. Because of the high density of red howlers at Brownsberg, it was better for me to leave and troop I was having trouble viewing and find another, which I occasionally encountered within minutes of leaving the previous troop. Upon completion of my year-long project, I had observed monkeys for 422 hours, almost equally divided between the non-tourist and tourist areas; I had searched unsuccessfully for monkeys for an additional 845 hours, mostly in the non-tourist area, and had covered almost 2000 km of trails and roads. I also observed 371 long calls and 358 short calls in the two areas, and collected 370 fecal samples and 73 urine samples on over 200 days of observations.

C. Tourism

I worked closely with park managers to monitor the tourist activity and presence at Brownsberg. The park office recorded the number of tourists, the dates of their visits, length of stays, houses used, and vehicles driven. Three to four troops of howlers lived in the area directly behind and next to three of the tourist lodges. Visitors often played loud music near the houses, talked and laughed loudly, drove their vehicles, used flashlights or fires to cook, and observed and took flash photographs of the monkeys in their backyards. The tourists also most often used one particular trail, *Ireneval*, which leads to a waterfall and was visited by nearly one hundred tourists per day during the peak season of August and September (see Map 2.4 of all trails). I paid especially close attention to the monkeys near the housing, and along the *Ireneval* trail, monitoring their behavioral responses to human presence.

Map 2.4: Main Trails and Tourist Buildings

Brownsberg Natuur Park Trails

LEGEND
IV- Ireneval
RW- Rond Wandeling
AKP- Agwago Kun Pasi
MT- Mazaroni Top
MW- Mazaroni Weg
WK- Wittiekreek
KV- Kumbuval
MV- Mazaronival
TE- Telesur
JT- Jeep Trail
PP- Pedrekoe Pasi

Map by J.L. Westin 2006
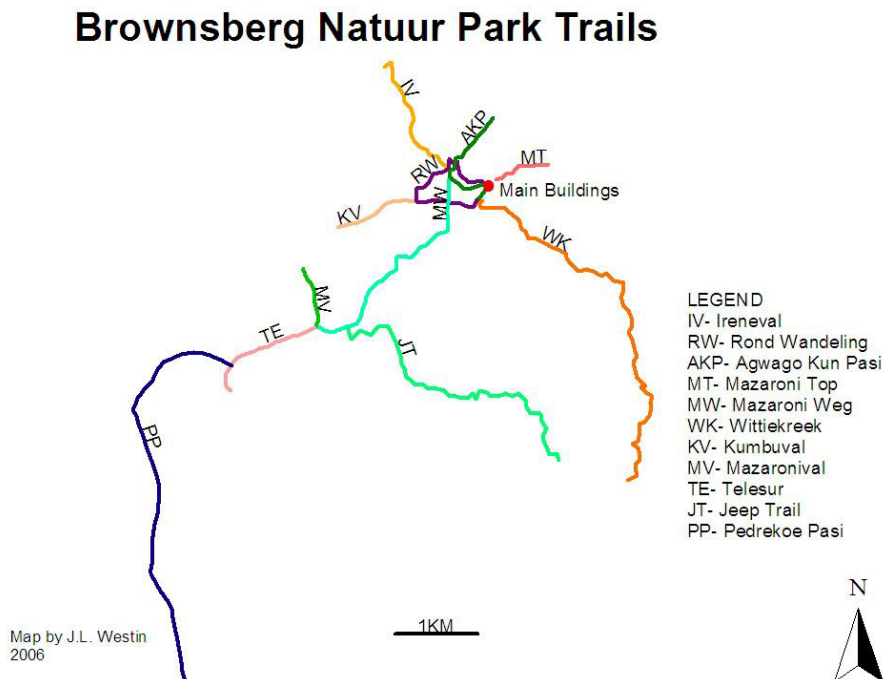
The height of the tourist season at the Brownsberg Natuur Park coincided with the dry season in Suriname, primarily August and September. This was also

the hottest time of year, and the time when schools were out and Surinamese families took vacations to the interior. European visitors, including those traveling from French Guiana, visited throughout the year, with a peak in visits during July and August. I was not able to record the nationalities of the visitors to Brownsberg, but my impressions of the difference between Surinamese and foreign visitors are described below. In general, tourists from Suriname visited the park for only the day, brought food with them, and trekked only to the main waterfall, *Ireneval*. Litter was frequently dropped along the *Ireneval* trail, which exceeded the litter dropped on other trails (Djosetro et al. 2005). Litter included plastic cups and food containers, plastic and glass bottles, wrappers of all sorts, and the occasional flip flop sandal. No howler monkeys have been witnessed to descend to the ground to investigate or eat pieces of litter, though the pollution, when left on the forest floor, presumably has an impact on tree health and growth.

In addition to day trips, many Surinamers remained on the mountain overnight, and rented one of the houses available for tourists. They usually packed it full with family members, cooked on several of the outdoor fire pits, and played loud music from their cars, which they parked near the houses. During the height of the tourist season, it was not unusual to have three groups at three different houses playing three separate radio stations loudly from their cars. The tourist houses were only 50 to 100 m apart and the research station was in the middle of them. Needless to say, many afternoons and evenings were quite loud on the plateau. The overnight guests also visited *Ireneval*, as well as the main plateau road, *Mazaroni Weg*, and a more distant creek, *Wittiekreek*. The latter was not included in my study area because the elevation of the trail dropped precipitously and drastically.

Foreign visitors were similar in many ways to Surinamese visitors, though they rarely came just for day trips and usually stayed at least one night, often occupying hammock shelters or renting houses. Foreign groups tended to be less tightly packed in the houses than Surinamese groups, and it was not unusual for a couple or family of three or four to rent a house with space for eight

to twelve. Foreigners traversed the same trails as Surinamers, with possibly less emphasis on the *Ireneval* trail, and they also tended to have loud parties at night. Behavior on the trails differed slightly between the two groups. Surinamers were less concerned than foreigners with searching for wildlife, but were very focused on reaching the waterfall to "go bathing." Consequently, groups of Surinamers were more vocal and rambunctious than foreigners.

Unfortunately, I do not have records of the geographic origins of the guests at Brownsberg beyond the first three months of my data collection. I intended to explore whether the two "tourist styles" affected the monkeys differently, but considering that the differences in visitor behavior were subtle, it may not have been possible to compare them. I do however have observations of particular trail-walking behavior and noise levels, and the corresponding responses of the monkeys. Additionally, Surinamers were the more frequent guests on the mountains at all times of the year, and visitor effects on the monkeys would be influenced mostly by Surinamese guests.

To evaluate the highs and lows of tourist presence, I recorded "visitor-days." A visitor-day was 12 visitor-hours, and 2 visitor-days equaled one calendar day. It was important to divide the calendar day in half because most visitors to the park were day-trippers, while others stayed overnight. I also recorded the total number of individuals at the park per day, based on the records kept by the front desk workers, regardless of whether or not they spent the night, and calculated the total number of people in the park over time. The category of "total people" included the calculations for visitor-days, the number of researchers in the park per day multiplied by two because researchers stayed overnight in the research lodge, and number of workers multiplied by one. Although a few workers spent the night, most only came to the park for the day, and I had no record of how many did which on a daily basis. Both researcher presence and worker presence were linked with tourist season: researchers were more common during the temperate zone summer vacation months of June, July, and August, and more workers were on hand when more tourists were present. I calculated the numbers of visitors to the park to determine the period of peak

tourist activity (Figure 2.1). Using these figures and a calculation of the mean number of visitors per week over the course of the year, I was able to determine the weeks of high and low tourist presence. The mean number of people visiting the park per week was 650 (s.d. = 315). Any week above one standard deviation from the mean (i.e. 965 individuals) was considered to be the "high tourist season." This included one week from the 5th through the 11th of April (week 10), and eleven weeks from the 12th of July to the 26th of September (weeks 24 through 34), all in 2004. Because there was a clear tourist season between weeks 24-34, the high number of tourists during week 10 seemed anomalous. Therefore, I deleted all observations during week 10, which comprised 74 scan observations over two days in the tourist area. I did not make any observations in the non-tourist area during that week. All other weeks (1-23 and 35-53) were considered "low tourist season." I used these high and low tourist seasons to compare human impact at two different intensities (see Chapter 4).

Figure 2.1: Total People per Week at BNP
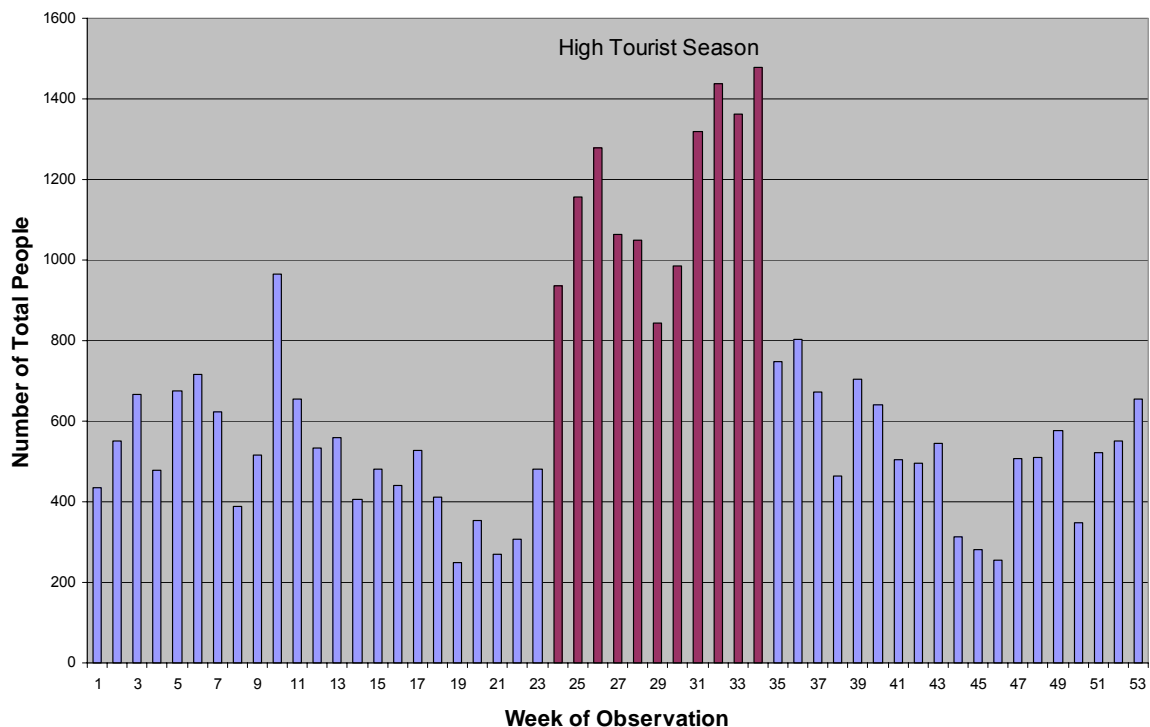
D. Analyses

All statistical analyses were conducted using either Microsoft Excel software (Copyright © 1985-2001 by Microsoft Corporation) or SAS software, Version 9.1 (Copyright © 2002-2003 by SAS Institute Inc., Cary, NC, USA). All independent samples and paired t tests were conducted using Excel software, and were used to compare measurements directly between areas. All figures were created with Excel. Rao-Scott Adjusted χ^2 tests, Fisher's Exact tests, and the ordinal logistic model were conducted using SAS software. Rao-Scott Adjusted χ^2 tests were used for scans of behavioral data that were compared between areas. The null hypothesis for these tests was that there was no association between the behaviors and the treatments of area, season, sex, etc. The observed and expected counts for these tests were calculated in the same way that they are in Pearson χ^2 tests, but the data were clustered into statistically independent sets. Subsequent scan records are not statistically independent because the behavior of a monkey during one scan is likely to be the same behavior exhibited by the monkey in the next scan. The Rao-Scott χ^2 test allowed for a design correction of the Pearson χ^2 test, resulting in the clustering of scans for analysis (Rao and Scott 1992). I clustered scan data by group and day to give a higher weighting to daily behavior bouts per group than to individual scan records. For most tests, I compared the two areas to determine whether behavior was independent of location, but the tests also allowed me to investigate whether behavior was independent of tourist, weather, or fruit seasons. The use of Rao-Scott χ^2 tests versus Pearson χ^2 tests results in a smaller Type I error rate (ibid.). The Fisher's Exact tests were used to investigate health parameters, which in all cases had observation sample sizes small enough to necessitate the use of the Exact test. Health parameters were analyzed with Fisher's Exact tests to determine whether there was an association between area and health status. The ordinal logistic model was used to investigate which parameters had a significant influence on the likelihood of monkeys responding to human disturbances. All maps were created using ArcView GIS software, Version 3.3 (Copyright © 1992-2002 by Environmental Systems Research Institute, Inc.).

Chapter III

Ecology

A. Potential Confounds

Before beginning data collection for this project, I sampled forest structure, including tree diameter at breast height and tree height, in the tourist and non-tourist areas for comparison. If the forest structure differed significantly between the two areas, then monkey travel routes, feeding patterns, or parasite exposure may vary as well; if the structure did not differ significantly, it could be ruled out as a confound. I also monitored two other variables possibly influencing the behavior and health of the monkeys: weather patterns and food availability. I gathered data regarding climate and food resources to determine their possible effects on health and behavior, and whether these two differed significantly between the non-tourist and tourist areas. If weather patterns and food availability did not differ significantly between the areas, I could rule them out as confounds. If weather patterns and food availability were found to be different, I would consider their impact on monkey behavior and health. Due to the geographic proximity of the non-tourist and tourist areas in the park, I predicted that forest structure, weather patterns, and food availability were similar between the non-tourist and tourist areas and thus did not affect the relationship between behavior, health, and tourists.

1. Forest Structure

Forest structure, as measured by tree diameter at breast height and tree height, could affect mobility patterns and canopy usage of monkeys. Additionally, forest type and degree of structural heterogeneity of the forest can affect howler densities (Peres 1997). Howler monkeys may prefer certain sizes of trees or

types of forest canopy, and thus preferentially utilize certain areas of forest over others. This preference may influence the monkeys' exposure to parasites, especially if travel routes through the canopy exposed the monkeys to areas where they or other monkeys have defecated onto the leaves and branches (Gilbert 1997). Tree heights may also influence the possibility for direct disease transmission between tourists and monkeys, especially where trees are short and the monkeys come close to the ground to feed. This was especially problematic at the Brownsberg Natuur Park when monkeys came closer to the ground near the park restaurant and tourist houses (personal observation). Furthermore, red howlers in the Brownsberg Natuur Park occasionally came to the ground to cross roads or paths (Mondo and Satyawan personal communication), and this may have been especially true in areas of the park that had been greatly disturbed for the construction of tourist facilities or views of the lake. One area in particular had wide swaths of trees missing to allow tourists an uninterrupted view of the lake. Howlers lived in that area, and may have needed to descend to the ground to cross through the logged areas. Black howlers in Belize were observed to cross roads on the ground more frequently after a hurricane disturbed the area (Pavelka et al. 2003). Mantled howlers in Costa Rica traveled and foraged on the ground more frequently after deforestation than before, once deforestation made their favorite food trees inaccessible (Clarke et al. 2002a). In areas where monkeys descend to the ground, tree heights and diameters can influence the monkeys' ability to reach the ground and thus come into contact with tourist waste and water facilities. If the forest structure found in the non-tourist and tourist areas was found to differ significantly, the travel patterns and disease exposure of the monkeys may have varied between the two areas, which in turn could result in area-specific differences in their behavior or health.

To assess the forest structure of the two areas of forest, I created transects throughout the tourist and non-tourist areas. The tourist area transects were a mix of transects cut into the forest at right angles to the preexisting trails (one-fourth of the total transect distance: 425 m out of 1625 m of transects), and

transects running along the length of trails (three-fourths of the total transect distance: 1200 m out of 1625 m of transects). I used preexisting trails for transects, partly to reflect the main areas where monkeys were seen by humans, and partly to reflect areas with most tourist presence. I only used sections of trail for transects if the establishment of the trail did not result in disturbance of the forest and the cutting of trees, generally trails with a width of one meter or less. I did not utilize trails used as roads with obvious successional or edge characteristics, including smaller diameter, shorter trees flanking the road edges, or early successional species including *Cecropia* spp. Before taking measurements, I plotted transects and sections of trails used for transects on a map to ensure even spacing across the tourist area. This allowed me to thoroughly sample the forest (Map 3.1).

Map 3.1: Tourist Area Transects

BNP Tourist Area Transects
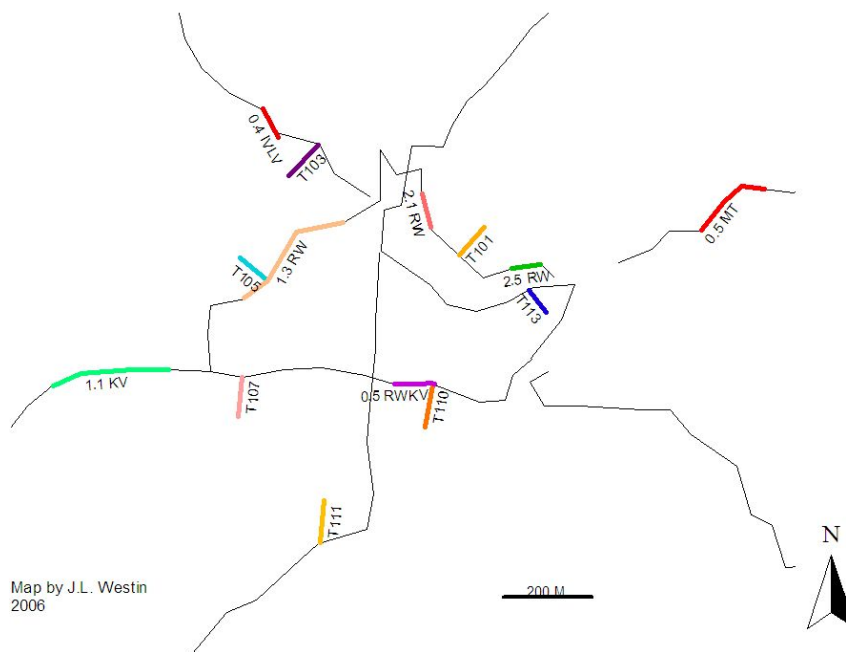
I created transects in the non-tourist area differently. The research trails in the non-tourist area were old roads with too much disturbance to allow for the measuring of trees along them, so I cut transects into the forest to minimize the

effects of disturbance. I created the non-tourist transects to run perpendicular to the established trails and roads, and spaced them 500 m apart along more than seven km of trails found outside the tourist area (Map 3.2). This ensured systematic sampling of the forest. I cut 26 transects at 13 points along the trails (one transect perpendicular in each direction at a given trail marker). The transects ranged from 15 to 140 m in length, depending on the terrain and whether I ran into a tree fall. The average length of a non-tourist area transect was 70 m. I later used the transects to search for monkeys and occasionally followed monkeys beyond the end of a transect, but for the measurements of forest structure I chose to limit the sample area to a manageable size, while also reflecting the most likely places for monkey sightings.

Map 3.2: Non-Tourist Area Transects

BNP Non-Tourist Area Transects
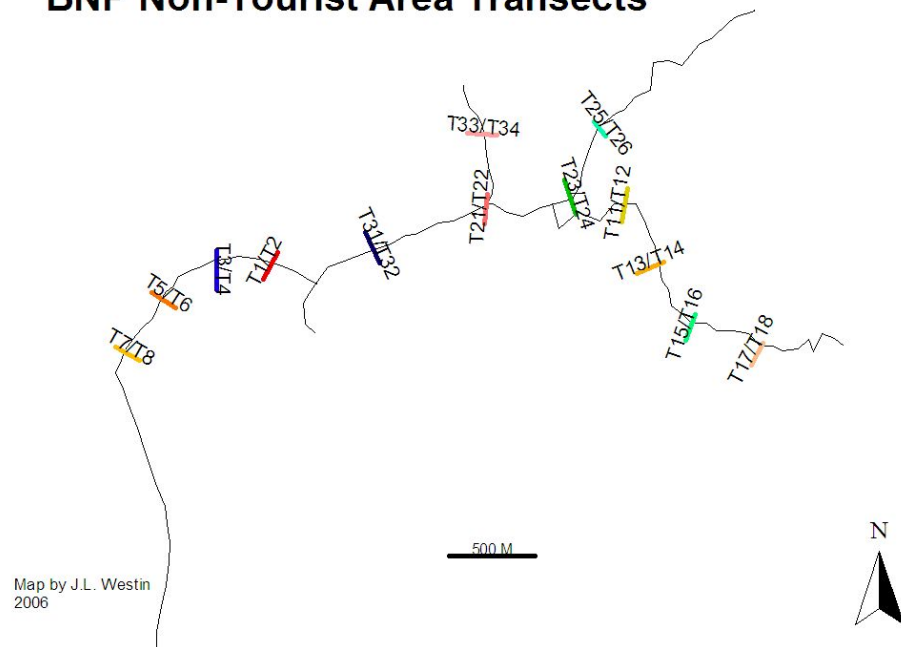
During four months of pilot field research, I established transects as described above, and sampled 2.5% of the target research area. The tourist area covered about 130 ha (see Map 2.3 above), from which I sampled 3.25 ha of forest along 1625 m of transects (see Map 3.1 above). The non-tourist area

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covered about 146 ha (as I delimited it for the purposes of transect creation, see Map 2.3 above), from which I sampled 3.65 ha of forest along 1825 m of transects (see Map 3.2 above). I measured 1562 trees along the tourist transects, and 1635 trees along the non-tourist transects. I marked transect lines with flagging tape so that they were easily seen and traversed, and measured the width of transects at 20 m (ten m on either side of the center line). Along each transect, I measured the diameter at breast height (dbh) in cm for all trees greater than 10 cm in diameter, and estimated tree height in m.

a. Diameter at Breast Height (dbh)

Tree diameter at breast height and tree height provided a measure of the size of the trees in the forest, and these measures could be compared to determine whether forest structure differed significantly between the two areas. I measured tree diameter at breast height (dbh) according to the following established forestry guidelines: measurements of buttressed trees and trees on slopes were taken above the buttress and on the high side of the slope, respectively. I considered trees that split below breast height to be two separate stems and measured each stem accordingly, while trees that split above breast height were measured as a single stem (Avery and Burkhart 1994). Due to various factors (excessive vine coverage; buttressing, stilt, or plank roots above breast height; biting ant nests; or bee hives, for example), I was forced to estimate the dbh of several trees. Because I could not verify their accuracy, I decided to remove these estimates from my analysis. I eliminated 106 measurements out of 1635 (6.5%) from the non-tourist area, and 104 measurements out of 1562 (6.7%) from the tourist area. I then compared the remaining dbh measurements for 1527 non-tourist area trees, and 1456 tourist area trees (Table 3.1). There was no difference in dbh measurements between the non-tourist and tourist areas (independent samples t test: $t = 1.38$, $df = 2981$, $P = 0.17$).

Table 3.1: Tree DBH and Height Measurements by Area

	DBH (cm)			Height (m)		
Area	# Trees	Mean	SD	# Trees	Mean	SD
Non-Tour	1527	24.17	15.50	1560	17.50	6.32
Tourist	1456	23.41	14.64	1498	17.09	6.15

b. Height

I estimated tree height in meters for all trees greater than ten centimeters dbh along my research transects. To improve my estimates, I first measured several dozen trees with a clinometer, and then checked my estimates against the measured values. During the weeks in which I measured the forest trees, I also periodically checked my accuracy with the clinometer. I estimated tree heights by visually breaking trunks into two meter pieces going up the trunk as is commonly done by foresters when estimating standing timber measurements (Edgington personal communication). These estimates were probably slightly lower than actual heights due to the fact that I needed to stand very near to the trunk to be able to see the top of the crown. Estimates taken from this perspective tend to shorten the height of the tree. This bias occurred in both the non-tourist and tourist areas, and therefore, was consistent across all estimates. Due to poor crown visibility in some areas of the forest, I was unable to estimate tree heights for every tree in my census. In the non-tourist area, I was able to estimate heights for 1560 out of 1635 trees (95.4%), and in the tourist area I was able to estimates heights for 1498 out of 1562 trees (95.9%) (see Table 3.1 above). There was no difference in the heights of trees in the non-tourist and tourist areas (independent samples t test: $t = 1.82$, $df = 3056$, $P = 0.07$).

2. Weather Patterns

Suriname has distinct wet and dry seasons, with associated changes in humidity and temperature. December and January usually comprise the short rainy season, and February and March the short dry season, though this is variable. The long rainy season usually lasts from April through July, and the long dry season stretches from August through November. At the peak of the rainy

season, trails were flooded, branches and trees fell in storms, and the park waterfalls were massive. Usually by the end of November, and often again at the end of March, the park water reserves for the human visitors ran out, days were hotter and sunnier, and the waterfalls were reduced to trickles.

Hot and wet forests are especially good habitats for the infective forms of intestinal pathogens; eggs, cysts, and larvae are less likely to dry out (Stoner 1996, Stuart et al. 1990). Rainfall patterns and forest structure also may influence monkey density (Peres 1997), and density, especially in narrow corridors of forest, in turn may also be a factor in the transmission of intestinal diseases (Stoner 1996, Scott 1988). Howler monkeys in Belize have been shown to exhibit a higher prevalence of intestinal parasite larvae in the wet season compared to the dry season (Eckert et al. 2006). Additionally, primate species living in wetter habitats have been shown to have increased circulating concentrations of leucocytes, which indicated a heightened immune response to the higher parasite prevalence in wetter areas (Semple et al. 2002). If monkeys in the non-tourist area were exposed to the same amounts of rainfall, temperatures, and relative humidities, as those in the tourist area, I could conclude that the conditions were not significantly different between the two habitats. Because intestinal parasites are found throughout wide geographic ranges, it is likely that the monkeys in both groups were exposed to the same species and intensities of naturally occurring pathogens.

To assess weather patterns during the year of my study, I measured weekly rainfall, weekly temperatures, and weekly relative humidity in both the non-tourist and tourist areas. To monitor the weekly rainfall in both areas, I used two manual rain gauges (Figure 3.1), one in each research area, both mounted in clearings to collect rainfall without obstruction. To measure weekly temperature and weekly relative humidity, I used two HOBO® Pro Temp/RH data loggers (Figure 3.2), one in each area. To ensure that I measured the rainfall, temperature, and humidity consistently in an area frequented by the monkeys, I placed the weather equipment directly in the forest in an area where monkeys

had been observed. The data loggers were programmed to record temperature and percent humidity at two-hour intervals over the entire year of observation.

Figure 3.1: Manual Rain Gauge (photo by Forestry Suppliers, Inc.)

Figure 3.2: HOBO® Pro Temp/RH Data Logger Mounted on a Tree Trunk in the Tourist Area

Because the monkeys experienced temperatures nearer the tops of trees, rather than at their trunks where I could consistently reach the equipment, I

checked whether temperatures recorded at these locations were different. I measured temperatures using two manual max/min thermometers (Figure 3.3), one at the trunk and one ten meters off the ground in the canopy for the month of October 2004. I then averaged the maximum and minimum temperatures for the trunk and canopy (Table 3.2). There was a difference between the means of the paired average trunk and canopy measurements (paired t test: $t = -3.47$, $df = 30$, $P = 0.0016$), but not for the unpaired means (independent samples t test: $t = -1.24$, $df = 60$, $P = 0.22$). Daily maximum temperatures were different between the trunk and canopy thermometers by 0 to 1 ºC, and on average, the canopy measurements were the higher values, possibly reflecting the influence of higher insolation. Additionally, the means of the averaged trunk and canopy values were different by only 0.2 ºC. Differences as small as these are not likely to be biologically significant, and only reflect degree of sun exposure. Because of the results of this temperature test, I chose to mount my data loggers on the trunks of the trees rather than in the canopies, thus ensuring easy access to the equipment.

Table 3.2: Max/Min Temperatures for Trunk and Canopy Thermometers

	Max (°C)		Min (°C)		Ave. (°C)	
	Mean	SD	Mean	SD	Mean	SD
Trunk	27.03	0.86	21.95	0.54	24.49	0.60
Canopy	27.42	1.07	21.98	0.58	24.70	0.73

Figure 3.3: Max/Min Thermometer Mounted on a Tree Truck in the Non-Tourist Area

In the tourist area, I used the official Stinasu manual rain gauge for my measurements. This rain gauge was located in a clearing in front of the research station, and was part of an extensive weather station (Map 3.3). The rain gauge was checked and emptied at the same time each day by myself or one of the Stinasu staff or volunteers, and the amount of rainfall in the previous 24-hour period was recorded. I mounted the tourist-area HOBO® Pro Temp/RH data logger (labeled "Temp" on maps) in the orchid garden area of the plateau near the research station (Map 3.3). I placed the data logger on the trunk of a howler monkey food tree in the middle of the orchid garden patch of forest. The orchid garden was relatively undisturbed forest at the edge of the tourist housing. The temperatures experienced by monkeys in the orchid garden may have fluctuated more than the temperatures in deeper recesses of the non-tourist area for two reasons. First, cooler breezes traveled up and over the edge of the mountain and into the orchid garden. Second, the orchid garden was possibly more exposed to higher temperatures during the day due to the fact that it was more recently disturbed and possibly exhibited a more open canopy. I did not expect either of

these possible temperature fluctuations to affect the monkeys significantly. I chose to mount the data logger in the forest understory rather than in an open area, because I wanted to measure the temperatures and humidities experienced by the monkeys who live in the trees and not in open areas. The data logger was protected from the rain by a rain shield (see Figure 3.2 above).

Map 3.3: Tourist Area Buildings and Weather Equipment
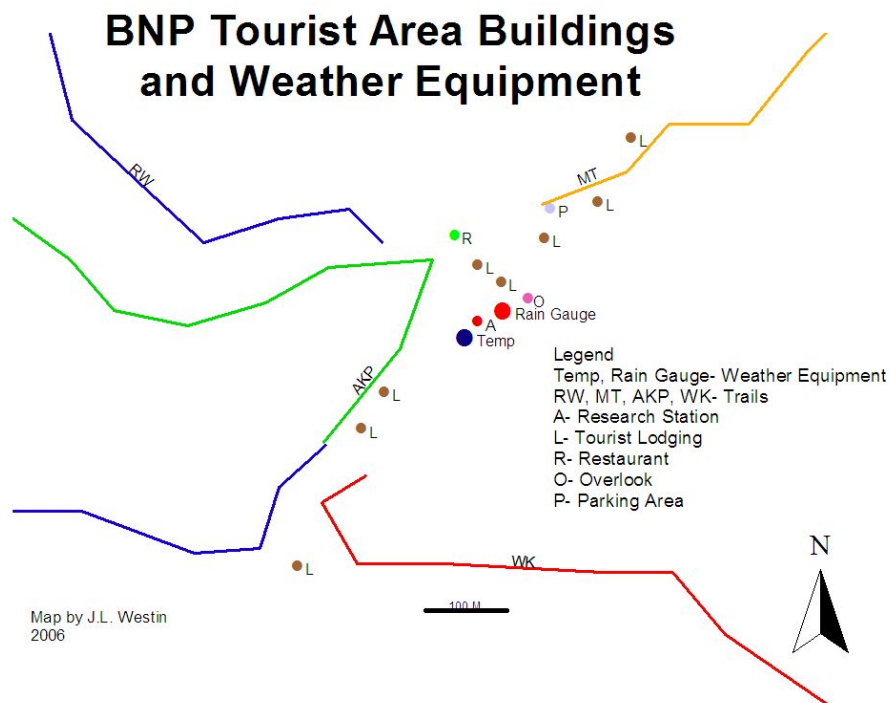
In the non-tourist area, I placed the weather equipment in an area in which I had observed at least two troops of howlers. I mounted the manual rain gauge approximately 200 m down the research trail, Jeep Trail (JT) (Map 3.4). The trailhead of Jeep Trail connected with the plateau road, *Mazaroni Weg*, and was 1.6 km from the start of the non-tourist area (Map 3.4; see Map 3.5 for a comparison of the two areas' weather equipment locations). I chose this location because it is well into the non-tourist area, but not too far that it could not be reached quickly by bicycle when I needed to check the weather equipment. Additionally, because JT was restricted from tourists, the rain gauge was

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protected from disturbance. I mounted the gauge in a clearing, and tested to make sure rain fell uninterrupted into the funnel. I mounted the HOBO® Pro Temp/RH data logger on the trunk of a tree just to the side of the trail and about ten m away from the rain gauge (Map 3.4). For the reasons mentioned above, I placed the weather equipment on the trunk of the tree rather than in its canopy. During the year, I emptied the rain gauge at least once per week and more often during the rainy season. I also recorded the date, time, weather, and any notes. I unloaded the logged data from both the non-tourist and tourist area data loggers at the end of my year of observations.

Map 3.4: Non-Tourist Area Weather Equipment
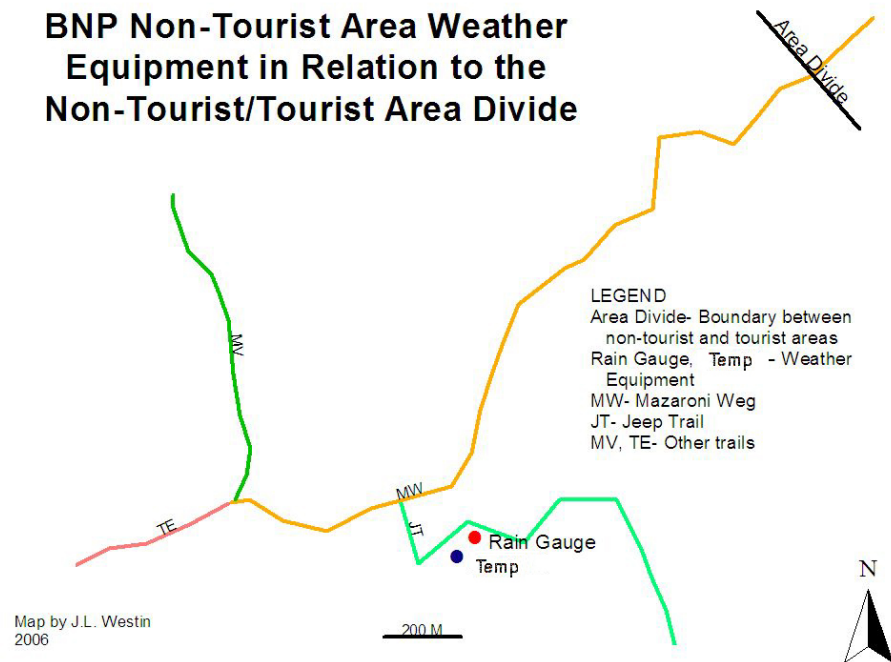
Map 3.5: Non-Tourist and Tourist Area Weather Equipment
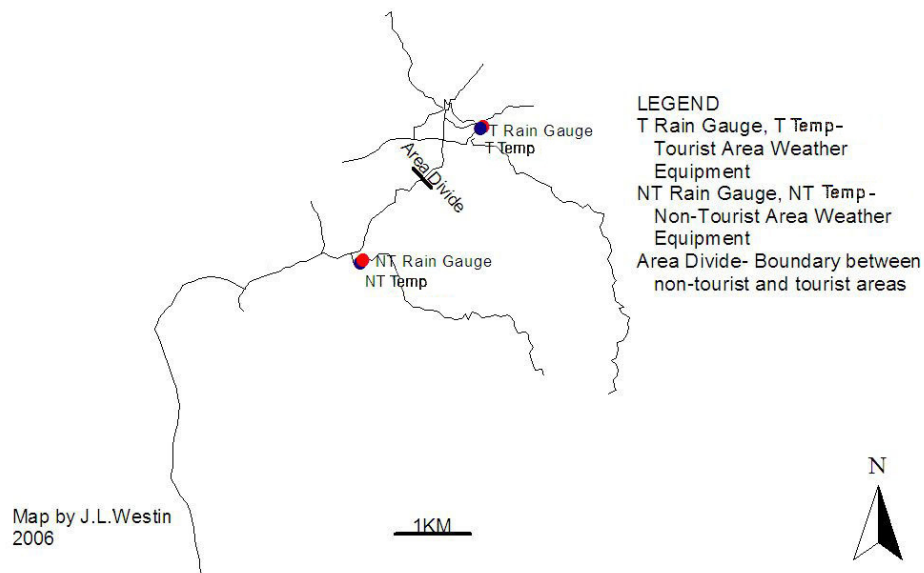
a. Weekly Rainfall

I collected 53 weekly measurements for rainfall (mm) from each site over the course of the year. I acknowledge that subsequent data points were not truly independent of each other, and because of this, I also graphed the weekly amounts of rainfall throughout the course of the study for comparison between sites (Table 3.3 and Figure 3.4). Although the area with the most weekly rainfall alternated throughout the year, there was no difference in the average weekly amount of rainfall between the non-tourist and tourist areas (paired t test: t = 1.06, df = 52, P = 0.29).

Table 3.3: Weekly Rainfall, Temperature, and Relative Humidity by Area

	Rain (mm)		Temp (ºC)		RH (%)	
Area	Mean	SD	Mean	SD	Mean	SD
Non-Tour	45.28	43.15	**22.19**	0.50	99.79	2.49
Tourist	47.45	44.78	**22.72**	0.70	100.39	2.53

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Figure 3.4: Amount Rainfall (mm) per Week
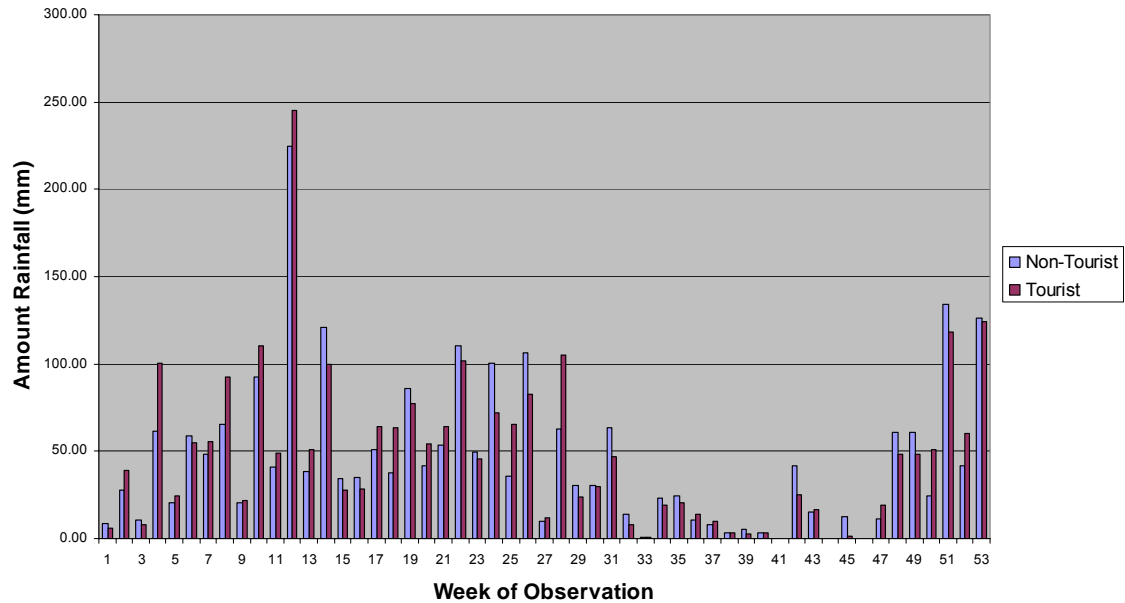
b. Weekly Temperature

I collected over 4500 data points for temperatures and relative humidities over more than 53 weeks in both the non-tourist and tourist areas using HOBO® Pro Temp/RH data loggers. The data loggers recorded temperatures and relative humidities every two hours around the clock. I then averaged the measurements to reflect weekly values over the 53 weeks of my study (see Table 3.3 above and Figure 3.5). There was a significant difference in the average weekly temperatures between the non-tourist and tourist areas (paired t test: t = -10.77, df = 52, P < 0.0001). However, the means were only 0.53 ºC apart with the tourist area only slightly warmer on average, which is unlikely to be of biological significance to the monkeys themselves.

Figure 3.5: Average Temperature (ºC) per Week
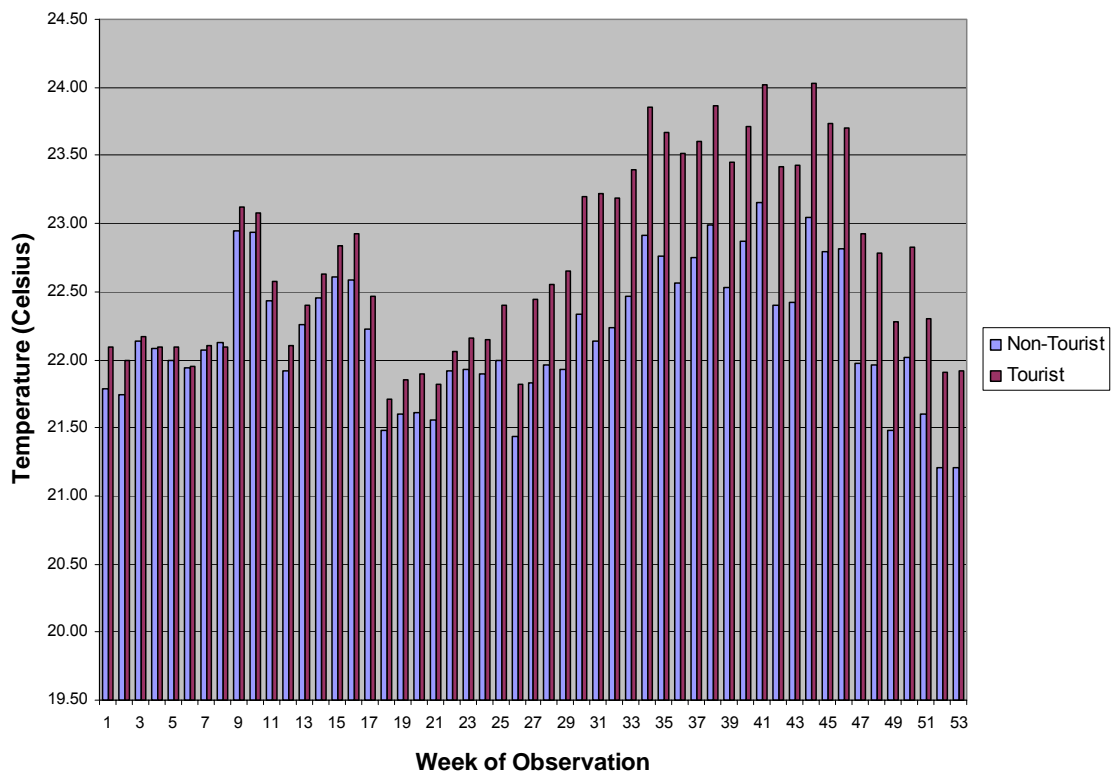
c. Weekly Relative Humidity

Despite having the rain shield on the data logger, the recordings of relative humidity in the tourist area got stuck on one measurement (104.2%) for the majority of the final recordings, and especially during the cooler and wetter nights. I therefore threw out the final three months of relative humidity measurements (see Table 3.3 above and Figure 3.6). For the remaining nine months of reliable measurements, I found no significant difference between the average weekly relative humidities in the two areas (paired t test: t = -1.38, df = 39, P = 0.17).

Figure 3.6: Average Relative Humidity (%) per Week
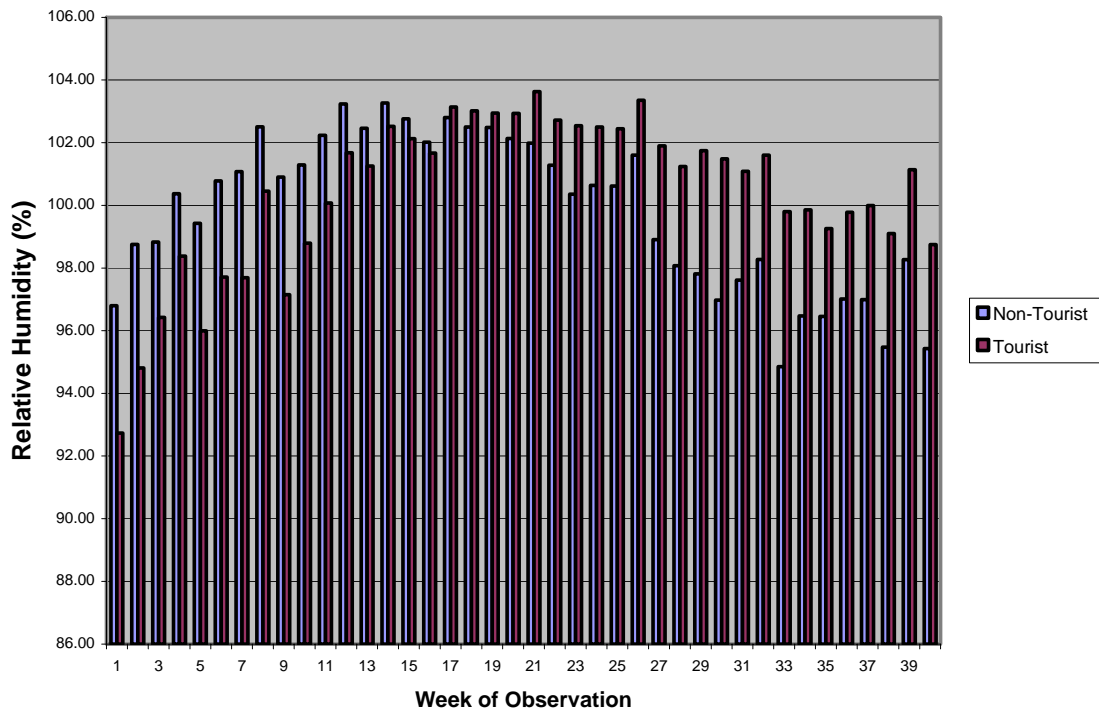
3. Food Availability

Food availability could also potentially influence both the behavior and health of monkeys. Different species of food tree flower and fruit at different times seasonally. Howler monkeys are generally considered to be folivorous, but will consume fruits and flowers opportunistically (Crockett and Eisenberg 1987). The diet of howler monkeys includes young and mature leaves, ripe and unripe fruits, and flowers, though the exact dietary composition varies among studies (Pinto and Setz 2004). In French Guiana, red howlers are known to include a substantial percentage of fruit in their annual diet, and it has been proposed that howlers there are specialized frugivores, feeding selectively on species in the family Sapotaceae (Julliot 1996a). Howlers need fruits for easily digested sugars, and leaves for protein, and flowers may substitute for fruits as a source of carbohydrates and occasionally protein (Milton 1980). For a non-specialized digestive system, the nutritional value of flowers and fruits is higher than that of leaves, and differential consumption of these foods may affect the behavior and

health of the monkeys. Additionally, poor nutrition is associated with disease and loss of immune function, especially when available energy is invested in growth or reproduction rather than in body maintenance (Norris and Evans 2000). Furthermore, chronic nutritional or psychological stress can result in long-term immune suppression and recurring infections, and stressful situations may exacerbate and expose subclinical diseases (Scott 1988, Caldecott and Kavanagh 1983). The immune system can be given a boost with certain foods, especially those high in protein, and helminth infections are more manageable when the individual eats foods high in protein (Coop and Holmes 1996).

To evaluate food availability, I monitored the fruiting, flowering, and leafing cycles during the year of known (or suspected) food species of the howler monkeys distributed throughout the research area, and sampled the available food biomass of both the tourist and non-tourist areas. Additionally, during my behavioral observations, I noted parts of plants and food species eaten, when known. I compared these observations between the two areas over the year of study. Not only did I monitor which foods were available throughout the year, but also which were actually being utilized by the groups of monkeys in each area. Aside from the center of the tourist camp where trees have been removed to build housing, the forest within the tourist area was likely to be similar to that of the forest outside of the tourist area, due to its close proximity. Species composition and location of important food trees were likely to differ between the two sites, but I predicted that overall, food availability would be comparable between the two areas. If the monkeys in the tourist and non-tourist areas had access to the same species and parts of plants for food during the year of observations, I could conclude that food availability does not explain any differences found in health or behavior between the two groups of animals.

a. Phenology

I collected information on seasonal changes in preferred red howler food sources on a biweekly basis using phenology monitoring (Estrada et al. 1999b, Silver et al. 1998, Estrada and Coates-Estrada 1986). Presumably, as is common in neotropical sites, fruiting and leafing at Brownsberg occur out of

phase with each other, with the result that the howlers have food resources year-round (Heymann 2001). Neotropical species also tend to produce flowers and fruits with some degree of intraspecific synchrony as well (Augspurger 1983), resulting in a patchy distribution of one or more species of preferred food throughout the forest. When fruits are abundant, they make up 50-70% of the red howler monkey diet (Julliot and Sabatier 1993). When fruits are scarce, howlers utilize flowers, leaves from trees and vines, and aroids such as *Heteropsis* and *Philodendron* to satisfy their nutritional needs. My phenology monitoring at Brownsberg tracked seasonal fluctuations of flowers, fruits, and new leaves eaten regularly by howler monkeys. Although red howlers eat fruits and leaves from lianas and vines, it is very difficult to quantify the relative importance and abundance of vine and liana species. Therefore, I chose to limit my food availability investigations to forest tree species.

I monitored phenological cycles of the forest trees to compare the non-tourist and tourist areas regarding the availability of fruit, flowers, and leaves throughout the year. I chose tree species to monitor based on observations of other troops and species of howlers in Mexico (Estrada et al. 1999b, Estrada and Coates-Estrada 1986, Estrada 1984), Belize (Silver et al. 1998), French Guiana (Julliot 1996a, Julliot and Sabatier 1993, Forget personal communication), Brazil (Pinto and Setz 2004), Panama (Milton 1980), Costa Rica (Glander 1975), and my own and volunteer observations in Suriname (Leupen and Yoder personal communication). Because many of these studies occurred in areas where tree species composition differed from that of Suriname, I considered trees of the same genus as those in the aforementioned studies to be possible food species for the red howlers in Suriname. I was able to confirm that many of the genera I chose did in fact make up part of the howler diet at Brownsberg, however, other genera and species were not confirmed as food sources. For example, one tree known to be a favorite fruit source of red howlers in Venezuela, *Talisia* sp. (Grafton and Norconk 2002), was abundant at the Brownsberg site, yet no single tree that I monitored ever fruited during the course of my 12-month study, nor during 5 months of prior and subsequent research. I included unconfirmed

genera and species in the phenology monitoring program, however, because I could not rule them out definitely as food species for the monkeys in Suriname.

To maximize the number of trees I could monitor for this project, I worked in conjunction with the Stinasu staff member in charge of the Vegetation Monitoring Project, sponsored by the World Wildlife Fund (WWF). Many of the tree species I chose from diet studies of other howler groups were already monitored by the Stinasu staff. I therefore gleaned data on my target tree species from the Stinasu database. In addition, I found, identified, and monitored trees along a separate transect. My phenology transect spanned both the tourist and non-tourist areas of the park, beginning outside the research station and ending 1.6 km down Jeep Trail (Map 3.6). I monitored 10 trees in the tourist area and 44 trees in the non-tourist area. I identified most of the trees myself, but some of the trees on Jeep Trail were already labeled though not monitored. I checked the trees every two weeks for their phenology status as described below. Trees chosen for my transect were chosen to supplement those genera and species already monitored by Stinasu staff. I included multiple individuals from several species even though many individuals of a given species flower or fruit at the same time as each other (Milton 1980).

Map 3.6: JLW Phenology Transect

JLW Phenology Transect

LEGEND
Area Divide- Boundary between
    non-tourist and tourist areas
JLW Transect- Phenology Transect
Overlook- Starting Point
1.2 JT- Ending Point

Map by J.L. Westin
2006

200 M

Overlook

1.2 JT

N
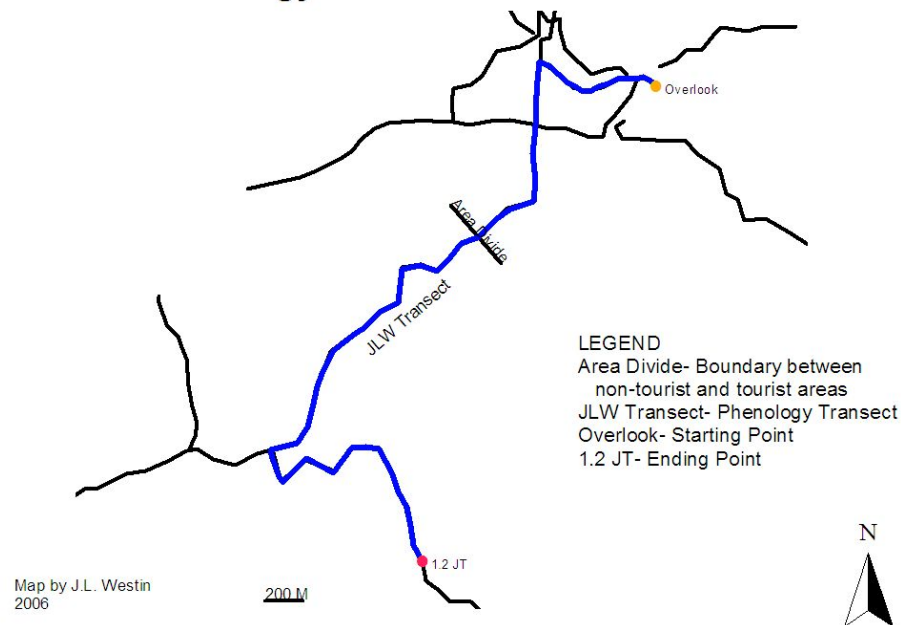
I and the Stinasu staff recorded the following information while monitoring the phenological states of trees: date, trail, tree species, identification number of individual tree, and phenology status: flower buds; flowers or old flowers; fruit or old fruit; new leaves (just fully refoliated); defoliating or refoliating; bare or dead tree. The presence of the above items was recorded for all applicable categories. Ripe and unripe fruit were not distinguished and no estimates were made regarding the percent coverage of fruit or flowers on the trees. The monitoring was kept simple so that my observations were compatible with the Stinasu staff and volunteers working on the Stinasu project. Trees were considered to be fully foliated unless "bare tree," "defoliating," or "refoliating" were recorded. "Old fruit" or "old flowers" referred to fruits and flowers not consumed by the howlers anymore. Flowering or fruiting trees were often favored food sources, as well as refoliating trees, due to their abundance of young leaves.

In total, I, along with Stinasu staff members, monitored 114 trees in the non-tourist area and 120 trees in the tourist area. Trees monitored in the non-tourist area included 59 species from 45 genera and 30 families. Trees monitored

in the tourist area included 79 species from 58 genera and 32 families (Table 3.4). A greater diversity of trees was sampled in the tourist area because most of the previous botanical work had been done near the facilities, and more trees were already labeled and monitored in the tourist area. The non-tourist and tourist areas shared 79 percent of families with individual tree species monitored; likewise, 63 percent of genera and 46 percent of species were shared between the two areas. Ideally, I would have had 100 percent overlap of species monitored between the two areas; unfortunately, this was not the case. However, the tree species used for the phenology monitoring were in similar proportions between the two areas as far as the plant parts they provided for monkey consumption. In both the non-tourist and tourist areas I monitored similar numbers of tree species providing fruit to the monkeys as providing leaves (43 fruit species to 37 leaf species, a 1.00 to 1.16 ratio, and 57 fruit species to 50 leaf species, a 1.00 to 1.14 ratio, in the non-tourist and tourist areas, respectively), with slightly more species providing fruit. I also monitored flower-providing species totaling just over one-fifth the numbers of fruit and leaf species combined. In this way I hoped to dilute the effect of disparate species monitored between the two areas by maintaining similar proportions of plant parts provided to the monkeys. Thus, through time, on average, I would expect similar amounts of fruit, leaves, and flowers to be available to the monkeys in both the non-tourist and tourist areas.

Table 3.4: Tree Species Monitored for Phenology in each Area (listed by family)

Family	Area	Species	Area
Anacardiaceae	both	*Anacardium spruceanum*	T
		Spondias mombin	T
		Tapirira guianensis	both
Apocynaceae	both	*Aspidiosperma marcgravianum*	T
		Parahancornia fasciculata	both
Araliaceae	both	*Schefflera decaphylla*	both
Arecaceae	both	*Astrocaryum paramaca*	both
		Astrocaryum vulgare	T
		Socratea exorrhiza	NT

Bignoniaceae	both	*Jacaranda copaia*	both
		Tabebuia capitata	T
		Tabebuia serratifolia	both
Bombacaceae	both	*Quararibea duckei*	both
Boraginaceae	T	*Cordia sagotii*	T
Burseraceae	both	*Protium* sp.	T
		Tetragastis altissima	both
		Tetragastis panamensis	T
Caesalpiniaceae	both	*Bocoa prouacensis*	NT
		Eperua falcata	both
		Vouacapoua americana	both
Cecropiaceae	both	*Cecropia obtusa*	both
		Cecropia sciadophylla	both
		Pourouma "deep lobes"	NT
		Pourouma mollis	both
Chrysobalanaceae	both	*Licania macrophylla*	NT
		Licania micrantha	T
		Licania octandra	T
		Licania ovalifolia	T
Clusiaceae	both	*Clusia grandiflora*	both
Combretaceae	both	*Terminalia amazonia*	both
		Terminalia dichotoma	T
Euphorbiaceae	both	*Croton matourensis*	both
		Drypetes variabilis	both
Fabaceae	both	*Dipteryx odorata*	both
		Dipteryx punctata	T
		Ormosia coccinea	T
		Swartzia amshoffiana	T
		Swartzia benthamiana	T
Flacourtiaceae	both	*Laetia procera*	both
Goupiaceae	NT	*Goupia glabra*	NT
Lecythidaceae	both	*Gustavia hexapetala*	T
		Lecythis zabucajo	both
Malpighiaceae	NT	*Byrsonima stipulacea*	NT
Melastomataceae	both	*Bellucia grossularioides*	both
Meliaceae	both	*Cedrela odorata*	both
		Guarea glabra	T
		Trichilia quadrijuga	T
Mimosaceae	both	*Abarema jupunba*	both
		Balizia pedicellaris	T
		Enterolobium schomburgkii	both
		Inga alba	both
		Inga leiocalyina	T
		Inga sp.	NT
		Parkia nitida	both

		Parkia pendula	NT
		Parkia ulei	T
		Zygia racemosa	T
Moraceae	both	*Bagassa guianensis*	both
		Brosimum parinarioides	both
		Brosimum rubescens	T
		Ficus nymphaeifolia	both
		Ficus sp.	both
		Maquira sclerophylla	both
		Sp. indet.	T
Myristicaceae	both	*Iryanthera sagotiana*	T
		Virola michelii	both
		Virola sebifera	both
		Virola surinamensis	NT
Myrtaceae	T	*Eugenia coffeifolia*	T
Nyctaginaceae	T	*Neea floribunda*	T
Olacaceae	T	*Minquartia guianensis*	T
Rubiaceae	both	*Coussarea paniculata*	both
Rutaceae	NT	*Zanthoxylum rhoifolium*	NT
Sapindaceae	both	*Talisia megaphylla*	T
		Talisia "sp. A"	both
Sapotaceae	both	*Chrysophyllum cuneifolium*	both
		Chrysophyllum eximium	NT
		Chrysophyllum prieurii	T
		Chrysophyllum sp.	NT
		Manilkara bidentata	both
		Micropholis guyanensis	both
		Pouteria engleri	T
		Pouteria guianensis	both
		Pouteria melanopoda	T
		Pouteria speciosa	NT
		Pouteria sp.	NT
Simaroubaceae	both	*Simarouba amara*	both
Sterculiaceae	both	*Sterculia excelsa*	both
		Sterculia pruriens	both
Tiliaceae	both	*Apeiba glabra*	both
		Apeiba petuomo	both
		Apeiba tibourbou	NT
Vochysiaceae	T	*Qualea caerulea*	T
		Qualea rosea	T

To analyze these data, I combined the information for all trees in the tourist area and all trees in the non-tourist area and quantified the percentage of all sampled trees flowering, fruiting, etc., for a given observation period. For example, if out of 100 trees in the tourist area, ten were flowering during the observation period ending on 1 January, I quantified that as 10% for that period. Percentages of monitored trees bearing fruits, flowers, or new leaves during each phenology period did not differ between the non-tourist and tourist areas (Table 3.5) (paired t test for fruit: $t = 1.99$, $df = 27$, $P = 0.06$; flowers: $t = -0.09$, $df = 27$, $P = 0.93$; and new leaves: $t = 1.70$, $df = 27$, $P = 0.10$), and a combined total percentage of trees bearing one or more of the three categories also did not differ between areas (paired t test: $t = 1.61$, $df = 27$, $P = 0.12$). I then graphed the cycles of fruiting, flowering, young leaves, and total food availability for both the tourist and non-tourist areas for comparison (Figures 3.7-3.10).

Table 3.5: Percentages of Phenology Trees Exhibiting Fruit, Flowers, New Leaves, and Total by Area

	% Fruit		% Flower		% New Leaf		Total %	
Area	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Non-Tour	20.13	8.39	10.22	3.75	5.46	2.76	35.81	10.57
Tourist	18.78	6.82	10.29	3.91	4.70	2.99	33.77	7.37

Figure 3.7: Percentage of Fruiting Trees per Phenology Period
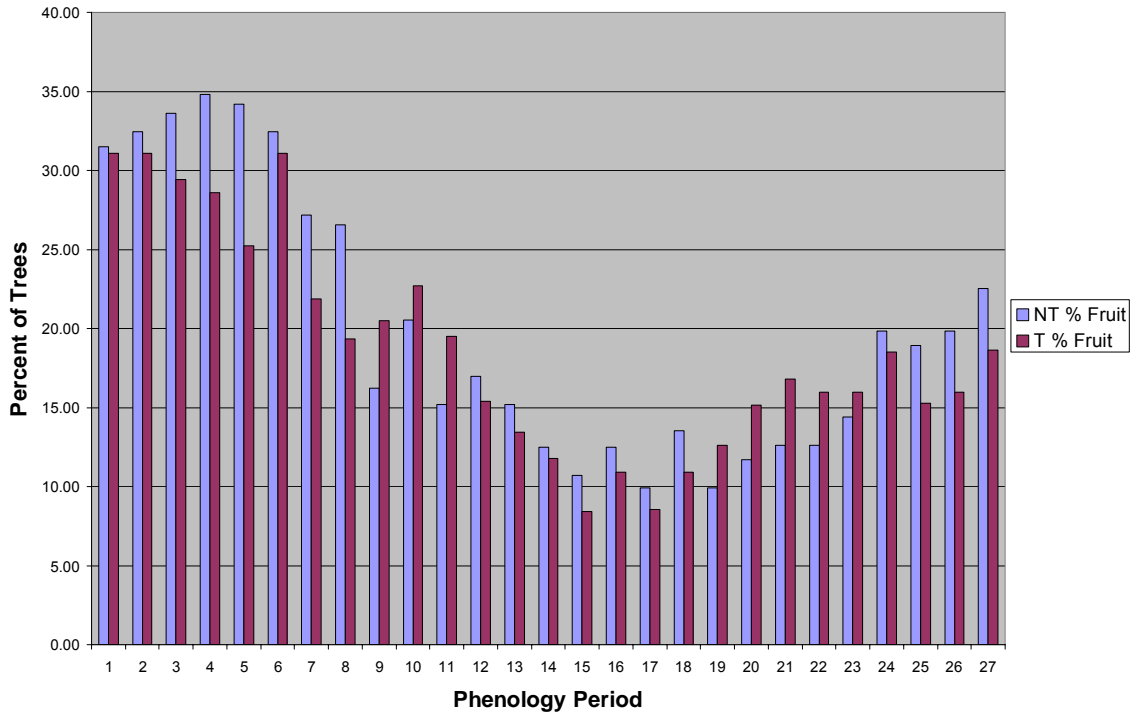
Figure 3.8: Percentage of Flowering Trees per Phenology Period
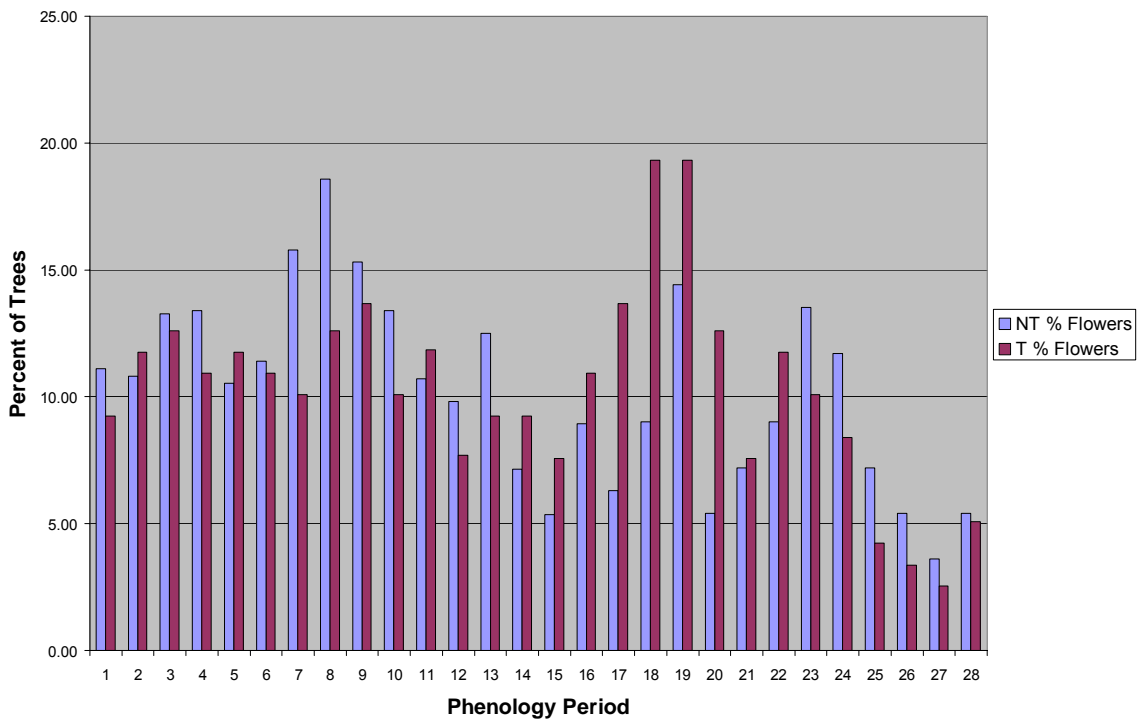
Figure 3.9: Percentage of Trees with New Leaves per Phenology Period
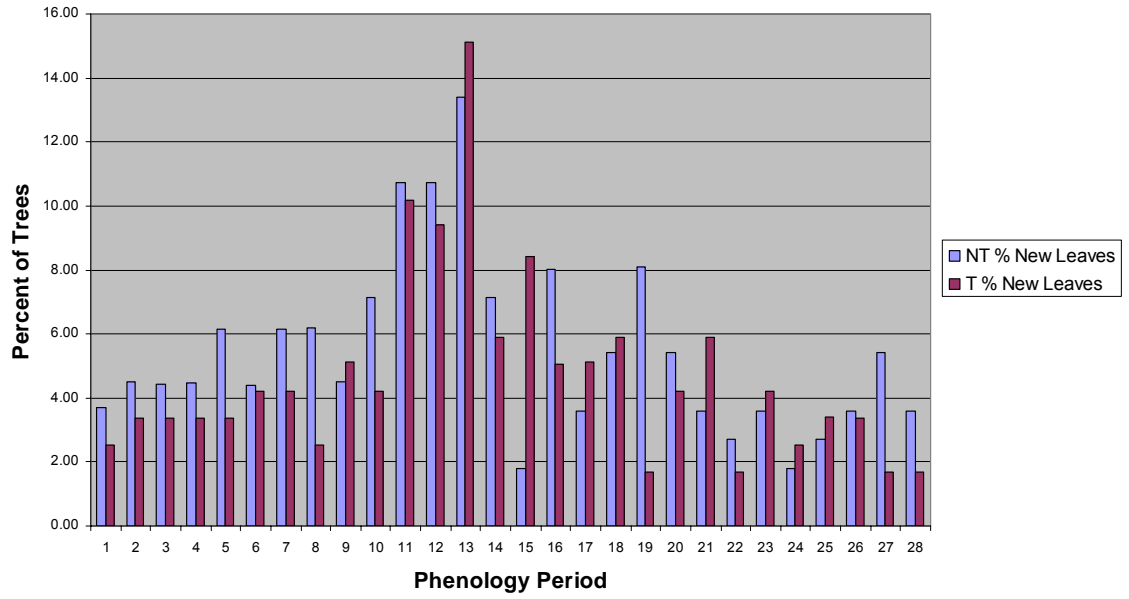
Figure 3.10: Percentage of Trees with All Food Types Combined per Phenology Period
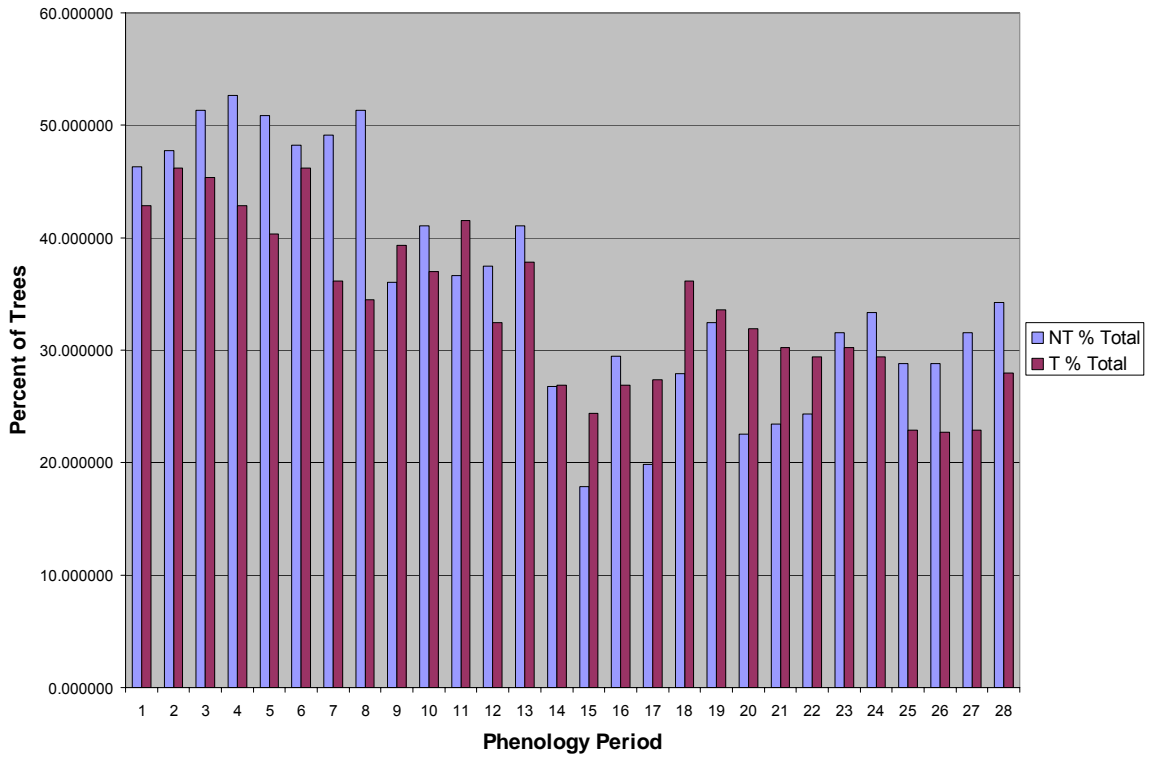
b. Biomass Calculations

To sample food biomass, I measured the diameter at breast height (dbh) of individuals of food tree species as an indirect way of estimating food availability. Leaf (Meadows and Hodges 2002, Singh and Yadava 1991, Clough and Scott 1989, Negi et al. 1983, Whittaker and Woodwell 1968, Kittredge 1944) and fruit biomass (Adler and Kielpinski 2000, Niklas 1994, Niklas 1993, Peters et al. 1988, Leighton and Leighton 1982) are known to be power functions of dbh. Additionally, studies of tropical trees have shown that the fruit and leaf biomass of several species can be explained by a single regression equation (for example: Peters et al. 1988), and the relationship is applicable to trees of different sizes, crown classes, and ages (Kittredge 1944). I therefore calculated food biomass estimates using the following equations: $Fr = 47dbh^{1.9}$ ($r^2 = 0.78$ for wild trees and shrubs, Peters et al. 1988, similar to Niklas 1993), and $L = 38.4dbh^{1.65}$ (Sorensen and Fedigan 2000, derived from equations in Whittaker and Woodwell 1968). Fr is the mass of fruit in grams, L is the mass of leaves in grams, and dbh is the diameter at breast height in centimeters of the feeding tree. Total food biomass for each tree is the sum of the fruit and leaf biomass estimates.

Trees measured for this estimate include those monitored for phenology (as mentioned above; tourist area: $n = 120$, non-tourist area: $n = 114$) as well as additional food trees used by the monkeys during the study (tourist area: $n = 50$, non-tourist area: $n = 29$). From those numbers I eliminated any trees for which I estimated the dbh measurements, and several trees due to dioecy (see below). The total numbers of trees used for the biomass estimates were therefore 116 trees in the non-tourist area and 143 trees in the tourist area. The smallest tree in which I observed howlers feeding was 19 cm dbh and the largest was almost 2 m. Howlers rarely feed in trees smaller than 25 cm dbh (Leighton and Leighton 1982), and less than 5% of the time in trees smaller than 20 cm dbh (Chapman 1990); therefore, I included only trees greater than or equal to 19 cm dbh in the biomass calculations.

In addition to revealing food availability, a comparison of leaf biomass between the two study areas could also serve as a proxy for measuring intestinal parasite presence to which the monkeys might be exposed. Leaf biomass is a contributor to humidity in the forest canopy, which relates to the prevalence of intestinal parasites with which the monkeys come into contact (i.e. the more humidity, the less desiccation of eggs and larvae, and the more infectious material to be contacted by monkeys). Transpiration and evaporation from leaves determines the amount of humidity present, and the more leaves there are, the more humidity (Kittredge 1944). Although I measured understory humidity directly, a comparison of leaf biomass between the two sites also gave me an indirect comparison of moisture in the canopy, which is of course where the monkeys would encounter parasites.

With the equations relating dbh and leaf and fruit biomass, I determined whether the non-tourist and tourist areas differed significantly in amount of food that they provided the monkeys. Many of the food species of the howlers are dioecious (Croat 1978, Bawa and Opler 1975, Glander 1975). For that reason, I used only half (assuming a balanced sex ratio) of the calculated fruit biomass of these species in my estimates of food availability because only gynoecious trees of these species produce fruit. About 26% of tree species used for the biomass calculations in both the non-tourist and tourist areas exhibited dioecy. This was a similar percentage to that found in other neotropical locales (20-22% in Costa Rica: Bawa 1979, Bawa and Opler 1975, 14-35% in Brazil: Matallana et al. 2005) I therefore eliminated the measurements of 18 and 19 trees in the non-tourist and tourist areas, respectively, which represented 50% of the measurements of dioecious trees. Howlers also consume the flowers of many tree species, but there is little information on the relationship between dbh and flower biomass for trees (shrubs have been studied by Armstrong and Marsh 1997, Le Maitre and Midgley 1991, Midgley and Bond 1989). I therefore used the biomass estimates for leaves in place of a calculation for flower biomass for the 15% of tree species from which howlers consistently consumed flowers. This may have been a slight overestimate of the biomass of flowers, but I was consistent in my substitutions

between the non-tourist and tourist areas. Any overestimate would therefore occur in both areas and would still be comparable between the two.

I acknowledge that the howlers do not feed equally from every food tree, and that they are limited by toxins in the leaves, which vary from tree to tree (Glander 1975), but with a thorough and diverse sample of the food trees of the forest, and with the majority of sampled trees being known food trees, an appropriate comparison could be made. There was no difference in the average combined fruit, flower, and leaf biomass between the non-tourist and tourist areas (Table 3.6) (independent samples t test: $t = -0.0092$, $df = 257$, $P = 0.99$). Additionally, there was no difference between the two areas as far as individual biomasses for fruit, flowers, and leaves when considered separately (independent samples t test for fruit: $t = 0.30$, $df = 157$, $P = 0.76$; flowers: $t = -0.66$, $df = 52$, $P = 0.51$; and leaves: $t = 0.90$, $df = 181$, $P = 0.37$).

Table 3.6: Biomass Estimates in Kilograms by Area

	Fruit		Flower		Leaf		Total	
Area	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Non-T	113.2	113.4	32.88	17.69	28.95	29.06	93.99	122.1
Tourist	106.9	139.5	39.74	45.11	25.80	17.67	94.15	144.2

I also combined the phenology data (see above) with the biomass calculations by calculating the biomass availability for each phenology period from the actual trees monitored and compared them between areas (Figure 3.11). I included all phenology observations made during the year of study even though the howlers did not consume fruits, flowers, and new leaves from every tree available. I however did not analyze the presence of mature leaves, assuming that in general, mature leaves were readily available, and that they constituted a smaller percentage of the howler diet when compared with new leaves. At any one time, an average of less than 1.5% of trees in both areas were defoliated, leaving 98.5% of trees fully foliated. The sample of estimated biomass of howler monkey foods available during each phenology period did not

differ between the two areas, though there was more food available in the non-tourist area at the start of the study, and more in the tourist area for the rest of the study (Table 3.7) (paired t test: $t = -1.81$, $df = 27$, $P = 0.08$).

Figure 3.11: Biomass Availability per Phenology Period
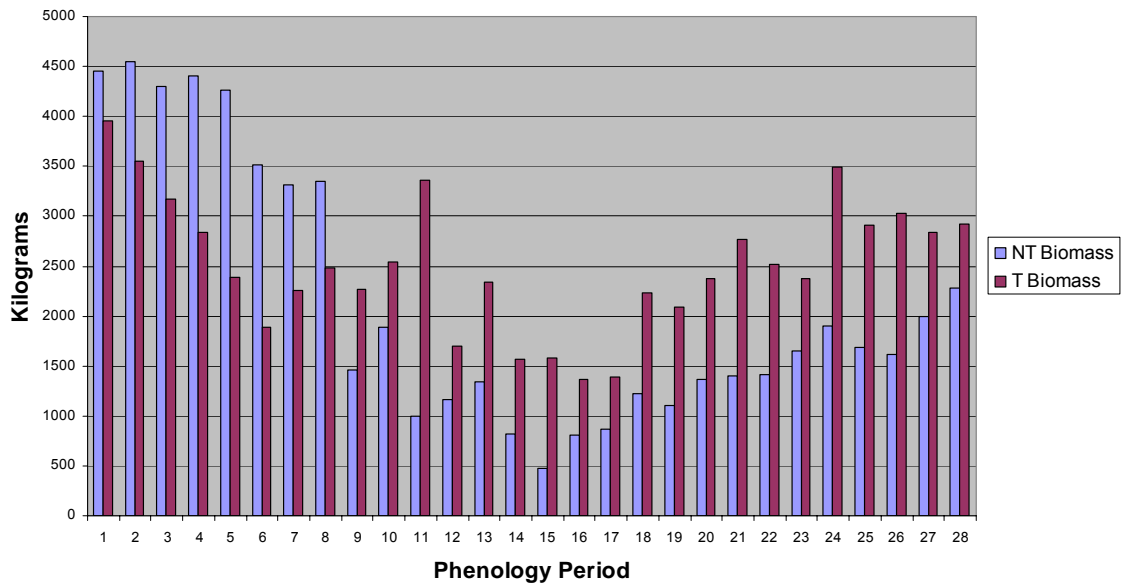
Table 3.7: Biomass Availability by Area

	Total Biomass Available (kg)	
Area	Mean	SD
Non-Tourist	2128.17	1305.70
Tourist	2507.48	666.13

B. Discussion and Conclusions

Forest structure (including dbh and height of trees), weather patterns (including rainfall, temperature, and relative humidity), and food availability (including phenology cycles and biomass availability), could all confound the relationship between human tourism and howler monkey behavior and health. I found no difference in the dbh or heights of trees sampled in the non-tourist and tourist areas. My sampling of the forest was extensive, and I measured

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approximately 1500 trees in both areas. This was to ensure that I had a thorough sampling of the forest. The measuring of dbh is generally sufficient for determining the structure of a given forest, and is often the only measurement taken when sampling a forest plot (ter Steege et al. 2004). I, however, also measured tree heights to make sure that the forest was not significantly taller or shorter in one area, and found that neither dbh nor height differed significantly between the two areas.

My only concern with these comparisons of forest structure is that I set up my plots and measured trees in areas of the forest with minimal disturbance. I wanted to quantify the typical undisturbed forest structure, and I did not quantify the extent of disturbance in either the non-tourist or tourist areas. I would guess that although the non-tourist area was disturbed along the current and former roads, the tourist area had more disturbance or disturbance of a higher magnitude in the areas surrounding the tourist facilities. The building of houses and parking areas for the tourists created more forest edge, which may have resulted in different species composition, and more solar radiation than what was found in interior forests. However, this is only my assumption since I did not measure this disturbance directly.

I also compared weather patterns between the two areas. I found no difference in the amount of weekly rainfall at each site, but I did find a difference in the paired weekly average temperatures. However, the means were only 0.53 degrees apart with the tourist area only slightly warmer on average. The increased temperatures in the tourist area may have been due to the possibly more open canopy of the orchid garden. The biggest disparity in weekly average temperatures between the two areas occurred during weeks 31 to 47 of the study (September, October, and December, 2004). These were weeks in which the difference between the two areas was greater than the mean (plus s.d.) of all the weekly differences, which also coincided with drier and sunnier conditions during the long dry season. During that time, the temperature disparities between the two areas may have been heightened by seasonal effects, namely the lack of cloud cover and thus more sunlight reaching and heating the understory in which

the data logger was positioned. Despite the statistical differences, the differences in mean weekly temperatures between the tourist and non-tourist areas were unlikely to be of biological significance to the monkeys themselves.

I also measured relative humidity in both the non-tourist and tourist areas. I found no difference in the average weekly relative humidities between the two areas for the remaining nine months, but it appeared that the tourist area humidities were higher than would be expected during the latter part of the observations, and especially during the dry season. This may have thrown off the paired statistical comparison, even though the differences were found not to be significant. Possibly, higher humidities coincided with the higher temperatures of the dry season due to the increase in solar radiation and thus evaporation of soil moisture. More evaporation of water from the forest floor could have resulted in higher humidities in the understory near the data logger, though as I recall, the top layer of soil and the leaf litter on the forest floor were both quite dry, with little moisture available to increase the air's humidity. That being said, the difference in the means of the relative humidities of the two areas is one percent, which is unlikely to be of biological significance. In general, I would have liked to have had many more data loggers and rain gauges to better measure the average rainfalls, temperatures, and relative humidities at multiple locations throughout both study areas. This would have resulted in a more balanced and thorough picture of weather patterns in general.

Finally, I compared food availability between the two areas both by looking at phenological data and by sampling estimated food biomass. This particular aspect of the forest ecology was especially difficult to measure. Due to a limited number of identified tree species in the non-tourist area, I monitored fewer species of tree there than in the tourist area. I did not have 100% overlap in monitored tree species between the two areas, but I tried to standardize the food types provided by these species to the howlers. The percentage of monitored trees bearing food during each phenology period was not statistically different between the two areas; however, in each plant part category the tourist area had slightly lower percentages of trees bearing food items. I found that 21 out of 114

trees (18.42%) and 27 out of 120 trees (22.50%) never had fruits, flowers, or new leaves in the non-tourist and tourist areas, respectively. The lower percentages of food-bearing trees found in the tourist area therefore may have been due to the fact that more monitored trees in the tourist area did not produce anything all year. This discrepancy in percentage of non-producing trees between the two areas may have been partially a result of the incomplete overlap among species between the non-tourist and tourist areas. The sampling of trees for phenology monitoring was supposed to be representative of howler monkey food species, but I would have liked to have had a higher diversity of species in both areas and complete overlap in species monitored between the two.

Compared to the phenology analysis, the estimates of howler monkey food biomass were drawn from larger samples of trees, and thus were more representative of what was truly available for the monkeys, assuming the calculations were correct for the amount of fruit and leaves on the average tree. I found no difference in the available biomass from sampled trees as far as fruit, flowers, leaves, or total available biomass. I only calculated the biomass of plant parts which were commonly, or presumably, eaten by the monkeys, and I accounted for dioecy in my estimates. The tourist and non-tourist areas did not appear to provide different amounts of food on average. Additionally, I looked at the phenology data to see if the trees that were actually being monitored offered similar amounts of food throughout the year between the two areas. These estimates were not significantly different; however, the non-tourist area provided more food compared to the tourist area during the first couple of months of observations, and then the tourist area had more food from the third month onward. This may have been due to random factors such as larger trees in the tourist area, but smaller trees in the non-tourist area producing food later in the study. Larger food-producing trees in the tourist area would explain why there was more food biomass produced in the tourist area in the latter part of the study (larger diameters equal a higher biomass estimate), and why the percentages of trees producing food in the tourist area were lower than in the non-tourist area throughout the study (fewer trees individually producing more food).

In conclusion, the general ecology of the non-tourist area did not differ significantly from that of the tourist area. Aside from some minor procedural issues that I would do differently if I could conduct the research again, I am confident that I can rule out the proposed confounds to the relationship between tourism and howler monkey behavior and health from being the explanation for any differences I found between the areas in behavior patterns or health parameters. The next chapter investigates the influence of tourist presence on monkey behavior.

Chapter IV

Behavioral Responses to Tourist Presence

A. Introduction

Howler monkeys are well-known to be excellent loungers, spending 60 to 80% of their time resting each day (Pavelka and Knopff 2004, Estrada et al. 1999b, Travers 1999, Silver et al. 1998, de Thoisy and Richard-Hansen 1996, Chiarello 1993, Milton 1980). Other common behaviors include foraging and traveling, while only small amounts of time are devoted to vocalizing, grooming, playing, and eliminating wastes (personal observation). To assess behavioral responses to the presence of tourists, I observed monkeys in the non-tourist and tourist areas, alternating between them every two weeks. I observed the behavior of almost all groups that I encountered at least for a short period of time. I recorded typical daily behaviors including those mentioned above (see Appendix: Ethogram). Additionally, I recorded behaviors that I interpreted as being responses to human presence. Possible responses to disturbance by humans included: no response, turning the head towards a human-made noise, grunting, retreating to better cover, displaying aggressively to human visitors, howling, and fleeing, among others (see Appendix: Ethogram). It was impossible to predict the actual levels of behavioral response monkeys in each area would show to human disturbance. Monkeys living in areas of frequent tourist activity may have been responsive to humans because of frequent contact, while monkeys in the non-tourist areas thus would exhibit lower responsiveness due to minimal human presence. In contrast, monkeys experiencing constant human disturbances may have become habituated to them, and thus exhibited fewer response behaviors.

Monkeys with less human presence and lower levels of habituation would react with higher intensity to the infrequent human disturbance.

In addition to investigating behaviors exhibited in direct response to human disturbance, I also examined daily patterns of common behaviors to determine whether the tourist troops exhibited different activity budgets compared with the non-tourist troops, possibly due to increased human presence. Because I could not identify individuals and thus account for individual variation, I monitored troops of monkeys using instantaneous scan sampling at five-minute intervals, noting behavioral states of visible group members every five minutes. I observed only adult females and/or adult males during scans; I did not record the activities of juveniles. Due to the high activity level of juveniles and the frequency of juveniles leaving my sight, I knew that it would be especially difficult to record their behavior. Their exclusion minimally impacted results because juveniles did not leave the proximity of the group, and did not engage in very different activities from the adults in the group, aside from increased play time (personal observation). Furthermore, studies have shown that daily activity patterns of juveniles do not differ significantly from those of adults (Clarke et al. 2002a). For these reasons, I decided to focus observations only on adults.

When possible, I recorded the behaviors of adult males and adult females, though a male and a female were not always in sight, and occasionally I encountered solitary animals. Every five minutes I recorded the behavioral states of visible adults, as well as other relevant information such as weather conditions, location, proximity to other individuals, and height in the tree. I recorded additional information when the animals foraged: species of tree or plant, if known, plant part eaten, and whether the tree had served as a food tree before. In this way, I was able to add new food trees to the food biomass estimates mentioned in Chapter 3. I continued recording group behavior in this manner every five minutes for the duration of my contact time with the group. Many times, especially when the animals were resting, I chose adult males and adult females that I could only partially see. The howler monkeys I observed during my study often disappeared while I was observing them. They usually did

not leave the area or even the tree, but retreated quietly to a hidden spot to continue resting. When this happened, and when I was certain that the monkeys remained resting in the tree, I continued to record resting behavior every five minutes for animals out of sight, rather than leave the area or cease data collection until the monkeys reappeared. This was also the case for travel through the trees. After initial unsuccessful attempts to visually follow a particular adult male or adult female as it traveled through the tree canopy, I decided instead to follow the group as it traveled and record my scans as "travel" as long as the majority of the group was on the move. The troops of howlers I observed generally traveled with many pauses to either sit still or feed on leaves. As long as most members of the troop were traveling, I considered the behavior to be "travel" even if the monkeys paused for a few seconds in between. I also recorded when monkeys eliminated wastes. I included this behavioral category even though, in other non-human primate species, it is usually considered an event and not a behavioral state. In howler monkeys however, the act of eliminating waste can take up to ten minutes or more, thus the monkeys were often engaged in this behavior when I conducted scans.

B. Common Behaviors

To simplify the long list of behaviors (see Appendix: Ethogram), I lumped together certain behaviors into categories (Table 4.1). All behavioral categories were mutually exclusive. I calculated percentages of scans for each type of behavioral category to determine activity budgets for all monkeys in the non-tourist and tourist areas, as well as both areas separated by sex. I further divided the non-tourist and tourist areas into 3 locales each to analyze human impact on common behaviors (see below). I designated these locales based on my impressions of intensities of exposure to human disturbance. I also investigated the effects of high and low tourist seasons, rainy and dry seasons, and high and low fruiting seasons on behavioral patterns for each study area. I considered seasonal change not as a potential confound, but instead as an influence on monkey behavioral and dietary adaptability. I conducted χ^2 tests to determine the

effects of these factors, with the added Rao-Scott design correction to allow for the clustering of scan observations by locale, group, and day.

Table 4.1: Categories of Monkey Behavior

Category	Included Behaviors
Remain Stationary	Rest, Sit Alert
Forage	Forage (including all plant parts & species eaten)
Locomote	Travel, Move, Flee
Vocalize	Roar, Bark, Rumble, Grunt
Eliminate Wastes	Both Types of Waste Elimination
Interact with Others	Groom, Fight, Play

1. Non-Tourist Area versus Tourist Area Patterns

I recorded a total of 3306 behavioral scans for adult females and adult males together in the non-tourist area, and 3930 scans for both sexes in the tourist area, during the observation hours of 06:00 to 19:00. I calculated the percentages for each behavioral category for the non-tourist area monkeys and the tourist area monkeys for the study (Table 4.2 and Figure 4.1).

Table 4.2: Activity Patterns by Area

Behavioral Category	Non-Tourist Area % (# Scans)	Tourist Area % (# Scans)
Remain Stationary	76.53% (2530)	61.65% (2423)
Forage	12.73% (421)	20.41% (802)
Locomote	6.90% (228)	14.17% (557)
Vocalize	2.69% (89)	2.34% (92)
Eliminate Waste	0.67% (22)	1.07% (42)
Interact with Others	0.48% (16)	0.36% (14)

Figure 4.1: Activity Patterns by Area
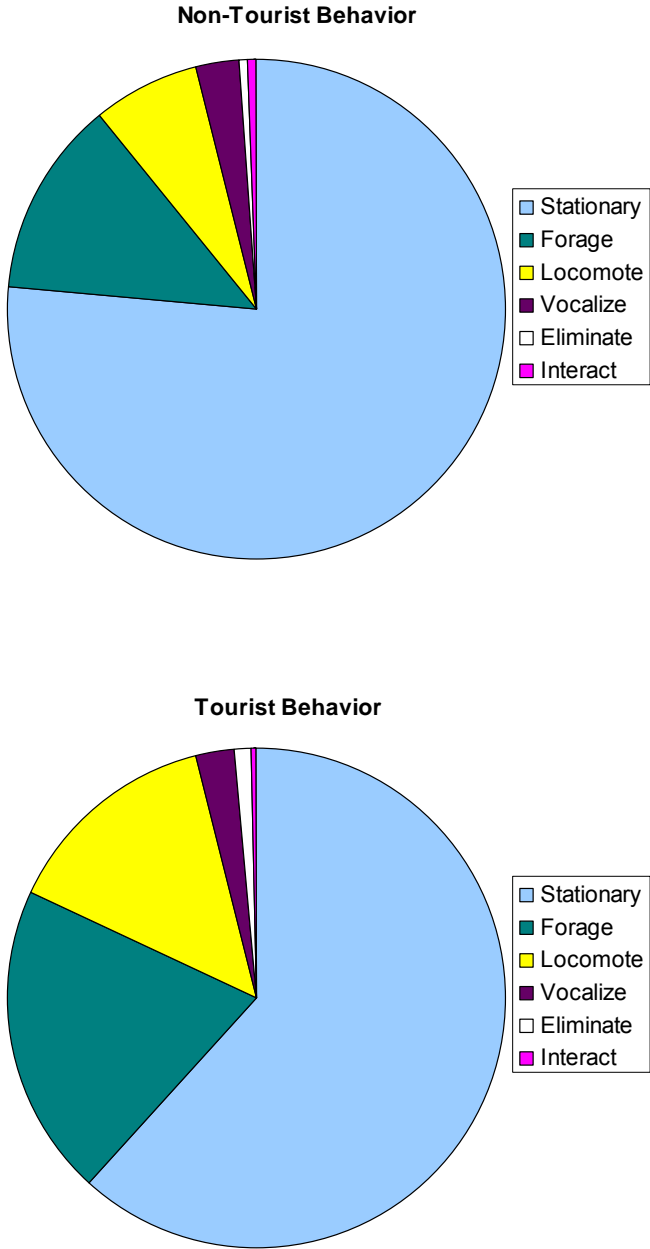
The monkeys' activity patterns did not seem to differ from other howler species at different sites, with the one exception that Brownsberg howlers socialized less often than howlers at other sites (Behie and Pavelka 2005, Pavelka and Knopff 2004, Chiarello 1993). When comparing the monkeys in the

two areas, I found that monkeys in the non-tourist area spent more time stationary and less time foraging and locomoting, on average, than monkeys in the tourist area. However, successive scans were not fully independent; if monkeys were resting during one scan it was likely that they would remain resting during subsequent scans, rather than change behavior every five minutes. For this reason, I analyzed these data further. By using a Rao-Scott Adjusted χ^2 test, I was able to cluster scans according to locale, date, and group per day, yielding data that could be considered independent for statistical purposes (see Chapter 2 above). I found behavioral patterns to be significantly associated with area (Rao-Scott Adjusted χ^2 test: $\chi^2 = 51.65$, $df = 5$, $P < 0.0001$). I also analyzed each behavioral category individually to see which behaviors were actually different between the two areas. I investigated the association of area with each behavior in turn, and found that remaining stationary, foraging, and locomoting were significantly influenced by area, but vocalizing, eliminating waste, and interacting with others were not (Table 4.3). It is also interesting to note that in both areas of study, I recorded more scans for the elimination of wastes than for interactions between individuals. Presumably the heavy reliance on foliage as well as the lengthy resting periods both influenced this result.

Behavioral Category	χ^2 (*df*)	*P*
Remain Stationary	23.18 (1)	**<0.0001**
Forage	9.94 (1)	**0.0016**
Locomote	21.82 (1)	**<0.0001**
Vocalize	0.22 (1)	0.64
Eliminate Waste	2.06 (1)	0.15
Interact with Others	0.34 (1)	0.56

An additional indicator of tourist influence on monkey behavior is duration of behavior bout; shorter resting or foraging bouts with greater traveling bouts in

between may indicate a need to avoid human presence. I looked at whether the tourist area monkeys did indeed move more frequently, or forage, sit, or rest for shorter durations than non-tourist area monkeys. Presumably, switching from one behavior to another after only a short period of time, and especially resting for only brief periods before moving on, could have been a way to avoid tourists. To investigate whether tourist area monkeys were doing this, I went back through my behavioral observations and looked at foraging, resting, and sitting bouts of at least ten minutes duration in both areas. I then compared the durations overall, and for each behavior between areas. I found that there was a difference in overall bout length between the two areas, but not a difference for each behavior separately (Table 4.4) (independent samples t test for all behaviors: $t = 2.26$, $df = 132$, $P = 0.03$; for foraging bouts: $t = 0.48$, $df = 60$, $P = 0.63$; for resting bouts; $t = 1.84$, $df = 49$, $P = 0.07$; and for sitting bouts: $t = 0.83$, $df = 19$, $P = 0.42$). The difference between the areas for resting bout duration approached significance, and for all behaviors, the tourist area monkeys had more bouts in total than the non-tourist area monkeys leading me to conclude that they changed behaviors more often than the non-tourist area monkeys did. Tourist activities may have interrupted the rest of the tourist area monkeys, and may have influenced their behavioral pattern of changing behaviors frequently. Increased travel by the tourist area monkeys would also mean a greater need to forage to replenish the energy used, and resting would be minimized as the opportunity cost of increased traveling and foraging. Thus tourist presence cannot be ruled out as an influence on the altered activity patterns seen in the tourist area compared to the non-tourist area.

Table 4.4: Duration (min) of Behavior Bouts by Area

	Forage		**Rest**		**Sit**		**All**	
Area	Mean	SD	Mean	SD	Mean	SD	Mean	SD
NT	25.79	12.50	145.23	93.79	28.33	20.16	**78.80**	86.21
Tour	23.60	18.01	102.24	79.98	22.50	12.15	**50.60**	58.34

2. Non-Tourist and Tourist Locale Patterns

Additionally, I divided the non-tourist and tourist areas each into 3 locales and investigated whether there was an effect of tourist proximity on behavior patterns. Locales 1-3 were in the tourist area and 4-6 were in the non-tourist area (Map 4.1). The creation of the locales was based on my impressions of intensities of exposure to human disturbance. Locale 1 centered around the main tourist buildings around which could be found the highest volumes of music and shouting, cars driving and idling, and general human activity. Locale 2 included the most popular trails (IV and MT), and the main plateau road (MW- the portion in the tourist area) and was only slightly removed from the noises heard in Locale 1. Locale 3 included trails less often visited by tourists (KV and portions of RW), and portions of Locale 2 trails located more remotely from the Locale 1 commotion. In the non-tourist area, Locale 4 consisted of the main plateau road (MW- the portion in the non-tourist area, and TE), which was the only part of the non-tourist area in which tourists were allowed, though rarely ventured. Locale 4 also saw the most vehicle traffic of the non-tourist area, though far less than was seen in the tourist area. Locale 5 included JT, which did not see vehicle or pedestrian traffic, but which was used by Stinasu staff and volunteers for the ecological monitoring program (2-3 individuals walked the trail 4 times per month). Lastly, Locale 6 included the majority of PP, which was only used by the volunteers two times per month, but was off limits to all tourists and all but the occasional research vehicle (see Map 2.4 for the names of all trails).

Map 4.1: Locales in the Study Area

Locales in the Tourist and Non-Tourist Areas
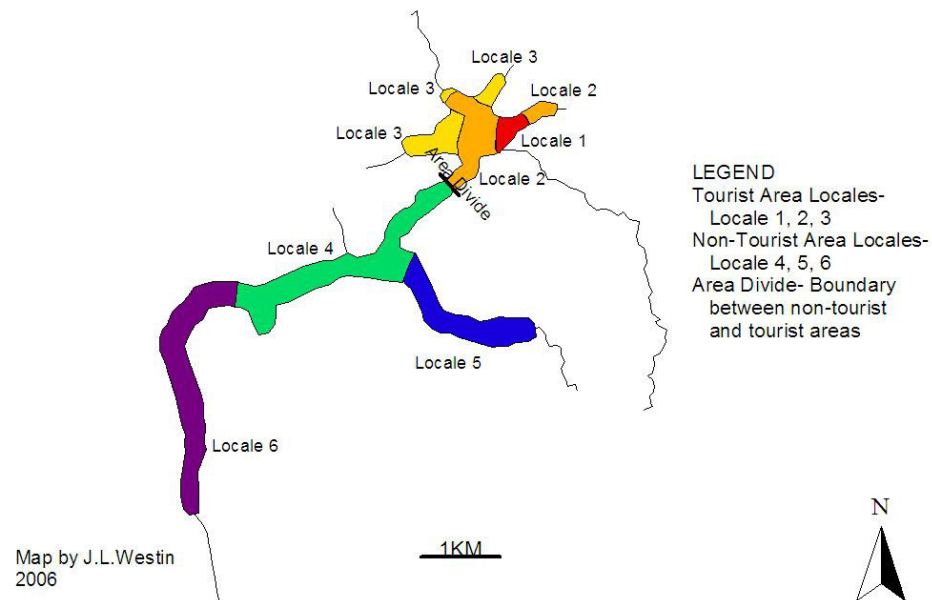
For the analysis of activity patterns by locale, I combined the behavioral categories "eliminate" and "interact" into another category called "other" because there were too few observations of waste elimination and social interaction in the non-tourist area to conduct a χ^2 test (Table 4.5). Among the behavioral categories "remain stationary," "forage," "locomote," "vocalize," and "other," I found no association of activity patterns with locale in the non-tourist area or in the tourist area (Rao-Scott Adjusted χ^2 test for the non-tourist area: χ^2 = 12.27, *df* = 8, *P* = 0.14; and for the tourist area: χ^2 = 13.97, *df* = 8, *P* = 0.08).

Table 4.5: Activity Patterns by Locale and Area

NT	Behavior	% (# Scans)	T	Behavior	% (# Scans)
4	Stationary	77.75 (2020)	1	Stationary	62.60 (1473)
	Forage	11.93 (310)		Forage	20.44 (481)
	Locomote	6.62 (172)		Locomote	12.20 (287)
	Vocalize	2.46 (64)		Vocalize	2.93 (69)
	Other	1.23 (32)		Other	1.83 (43)
5	Stationary	66.50 (272)	2	Stationary	59.48 (778)
	Forage	21.52 (88)		Forage	19.57 (256)
	Locomote	8.56 (35)		Locomote	19.11 (250)
	Vocalize	2.20 (9)		Vocalize	1.07 (14)
	Other	1.22 (5)		Other	0.76 (10)
6	Stationary	79.60 (238)	3	Stationary	63.94 (172)
	Forage	7.69 (23)		Forage	24.16 (65)
	Locomote	7.02 (21)		Locomote	7.43 (20)
	Vocalize	5.35 (16)		Vocalize	3.36 (9)
	Other	0.33 (1)		Other	1.12 (3)

3. Adult Male versus Adult Female Patterns

I recorded behaviors separately for adult males and adult females, and I occasionally encountered solitary individuals of both sexes. For these reasons, I also investigated the possibility of sex differences in behavior patterns, both within areas (Table 4.6) and overall. I found a significant association between behavioral patterns and sex both within areas and overall (Rao-Scott Adjusted χ^2 test for the non-tourist area: $\chi^2 = 24.85$, $df = 5$, $P = 0.0001$; tourist area: $\chi^2 = 29.59$, $df = 5$, $P < 0.0001$; and overall: $\chi^2 = 51.71$, $df = 5$, $P < 0.0001$). In both areas, females remained stationary and vocalized slightly less than males, and foraged slightly more, though remain stationary was not significant in the non-tourist area (Rao-Scott Adjusted χ^2 test for the non-tourist area: stationary: $\chi^2 = 0.93$, $df = 1$, $P = 0.34$; vocalize: $\chi^2 = 11.51$, $df = 1$, $P = 0.0007$; and forage: $\chi^2 = $

7.09, $df = 1$, $P = 0.0078$; and the tourist area: stationary: $\chi^2 = 4.02$, $df = 1$, $P = 0.045$; vocalize: $\chi^2 = 12.28$, $df = 1$, $P = 0.0005$; and forage: $\chi^2 = 13.62$, $df = 1$, $P = 0.0002$).

Table 4.6: Activity Patterns by Sex and Area

Females	Behavior	% (# Scans)	Males	Behavior	% (# Scans)
NT	**Stationary**	76.03 (1221)	NT	**Stationary**	77.00 (1309)
	Forage	**13.76 (221)**		**Forage**	**11.76 (200)**
	Locomote	7.22 (116)		**Locomote**	6.59 (112)
	Vocalize	**1.93 (31)**		**Vocalize**	**3.41 (58)**
	Eliminate	0.56 (9)		**Eliminate**	0.76 (13)
	Interact	0.50 (8)		**Interact**	0.47 (8)
T	**Stationary**	**60.87 (1190)**	T	**Stationary**	**62.43 (1233)**
	Forage	**21.43 (419)**		**Forage**	**19.39 (383)**
	Locomote	14.22 (278)		**Locomote**	14.13 (279)
	Vocalize	**1.94 (38)**		**Vocalize**	**2.73 (54)**
	Eliminate	1.07 (21)		**Eliminate**	1.06 (21)
	Interact	0.46 (9)		**Interact**	0.25 (5)

4. High and Low Tourist Season Effects

As mentioned in Chapter 2, I recorded tourist presence in the form of "visitor-days," and included the visitor-day totals with researcher and worker presence to calculate a measure of "total people" in the park per week. Using data from Figure 2.1 (see above) and the mean plus standard deviation of total people in the park each week over the course of the year, I determined the periods of high and low tourist presence. "High tourist season" comprised eleven weeks in 2004 from the 12th of July to the 26th of September (weeks 24 through 34) (see Chapter 2 above for more details). All other weeks were considered "low tourist season." I then investigated the impact of tourist season on behavioral patterns. Again I combined the behavioral categories "eliminate" and "interact" into another category called "other" because there were too few observations of

social interaction in the non-tourist area to conduct a χ^2 test (Table 4.7). Among the remaining behavioral categories, I found no association between overall activity patterns and tourist season in the non-tourist area (Rao-Scott Adjusted χ^2 test: $\chi^2 = 5.54$, $df = 4$, $P = 0.24$), but a significant association overall in the tourist area (Rao-Scott Adjusted χ^2 test: $\chi^2 = 10.14$, $df = 4$, $P = 0.04$). Of the six behavioral categories, only "locomote" and "eliminate waste" were significantly associated with tourist season in the tourist area (Rao-Scott Adjusted χ^2 test for locomote: $\chi^2 = 4.16$, $df = 1$, $P = 0.04$; and eliminate waste: $\chi^2 = 4.38$, $df = 1$, $P = 0.04$). Monkeys in the tourist area moved less and eliminated waste more during the high tourist season. Neither result was highly significant, and I would be surprised if a difference in waste elimination was due to tourist presence rather than stochastic sampling error. The difference in locomotor behavior may indicate a tendency to "freeze" around highly bothersome groups of tourists during the high tourist season. Alternatively, the tourist area monkeys may have spent less time moving during the high tourist season because the high tourist season coincided with the dry season when monkeys in general spent less time moving. Incidentally, even though activity patterns overall were not different in the non-tourist area due to tourist season, there was a significant association of locomotion with tourist season by these monkeys (Rao-Scott Adjusted χ^2 test: $\chi^2 = 7.10$, $df = 1$, $P = 0.0077$). Non-tourist area monkeys spent less time locomoting during the high tourist season (the same trend found in the tourist area monkeys). Activity patterns were not different between tourist seasons for both areas together and when "eliminate" and "interact" were considered separate behavior categories (Rao-Scott Adjusted χ^2 test: $\chi^2 = 9.30$, $df = 5$, $P = 0.10$).

Table 4.7: Activity Patterns by Tourist Season and Area

High	Behavior	% (# Scans)	Low	Behavior	% (# Scans)
NT	Stationary	77.54 (473)	NT	Stationary	76.30 (2057)
	Forage	13.77 (84)		Forage	12.50 (337)
	Locomote	**3.44 (21)**		Locomote	**7.68 (207)**
	Vocalize	4.75 (29)		Vocalize	2.23 (60)
	Other	0.49 (3)		Other	1.30 (35)
T	Stationary	63.21 (627)	T	Stationary	61.13 (1796)
	Forage	23.59 (234)		Forage	19.33 (568)
	Locomote	**8.97 (89)**		Locomote	**15.93 (468)**
	Vocalize	1.71 (17)		Vocalize	2.55 (75)
	Other	2.52 (25)		Other	1.06 (31)

5. Rainy and Dry Weather Season Effects

Seasonal effects, though similar between the non-tourist and tourist areas, could also impact monkey behavior overall. I analyzed activity budgets for both areas according to weather season to see if weather patterns could help explain the activity patterns I had thus far quantified. To assign weather seasons to the year of observations, I used rainfall and temperature data for the year to quantify these seasons specifically for 2004 and early 2005. My procedure was to average the rainfall and temperature data between the two areas and then calculate the mean weekly rainfalls and temperatures for the entire 53 weeks of study. Rainfall amounts above the mean, and temperatures below the mean to signified "rainy," and rainfall amounts below the mean, and temperatures above the mean to signified "dry." Hot temperatures generally coincided with the long dry season, and cooler temperatures with the long and short rainy seasons. I did not put as much weight on temperature readings during the short dry season (February and March) because it was technically winter and temperatures tended to be lower on average (compared to the long dry season) despite being drier and sunnier. High rainfall with low temperatures, and low rainfall with high temperatures of course did not overlap perfectly into four weather seasons, but

with the help of the actual measurements and graphical representations (Figures 3.4 and 3.5 above), I assigned weather seasons study period (Table 4.8).

Table 4.8: Weather Seasons in Suriname

Weather Season	Observation Weeks	Dates Included
Short Dry	1-7	end of January through 21 March 2004
Long Rainy	8-28	22 March through 15 August 2004
Long Dry	29-47	16 August through 26 December 2004
Short Rainy	48-53	27 December through 7 February 2005

For purposes of analysis, I combined the short and long dry seasons, and the short and long rainy seasons into dry versus rainy. I found no association between overall activity patterns and weather season in the non-tourist area (Rao-Scott Adjusted χ^2 test: $\chi^2 = 4.87$, $df = 5$, $P = 0.43$), but a significant association in the tourist area (Rao-Scott Adjusted χ^2 test: $\chi^2 = 17.08$, $df = 5$, $P = 0.0044$) (Table 4.9). Of the six behavioral categories, only "stationary" and "locomote" were significantly associated with weather season in the tourist area (Rao-Scott Adjusted χ^2 test for stationary: $\chi^2 = 4.78$, $df = 1$, $P = 0.03$; and locomote: $\chi^2 = 9.98$, $df = 1$, $P = 0.0016$). Monkeys in the tourist area spent more time stationary and less time locomoting during the dry seasons. Possibly this was due to the high temperatures associated with the dry season and the monkeys' need to minimize body heat production by remaining still. In the non-tourist area, the percentage of time spent locomoting was almost exactly the same in both weather seasons, but there was a slight, but statistically insignificant, trend towards more time spent stationary during the dry season, possibly due to the reasons mentioned above for the tourist area monkeys. In addition, monkeys in both areas foraged less during the dry seasons, though this was not a significant difference. The pattern of less foraging and more often stationary was also found during the dry season for red howlers in Venezuela (Sekulic 1982a). I found no difference in behavior due to weather season overall,

when area was not taken into account (Rao-Scott Adjusted χ^2 test: χ^2 = 6.89, *df* = 5, *P* = 0.23).

Table 4.9: Activity Patterns by Weather Season and Area

Dry	Behavior	% (# Scans)	Rainy	Behavior	% (# Scans)
NT	Stationary	78.74 (1278)	NT	Stationary	74.39 (1252)
	Forage	11.46 (186)		Forage	13.96 (235)
	Locomote	6.90 (112)		Locomote	6.89 (116)
	Vocalize	2.09 (34)		Vocalize	3.27 (55)
	Eliminate	0.68 (11)		Eliminate	0.65 (11)
	Interact	0.12 (2)		Interact	0.83 (14)
T	**Stationary**	**65.65 (1546)**	T	**Stationary**	**55.68 (877)**
	Forage	19.24 (453)		Forage	22.16 (349)
	Locomote	**10.96 (258)**		**Locomote**	**18.98 (299)**
	Vocalize	2.68 (63)		Vocalize	1.84 (29)
	Eliminate	1.02 (24)		Eliminate	1.14 (18)
	Interact	0.47 (11)		Interact	0.19 (3)

6. High and Low Fruit Season Effects

Fruit availability could also affect the movements and activity patterns of howler monkeys. I found reasonable similarity between the availability of fruit, flowers, and new leaves in the non-tourist and tourist areas; however, I was interested in investigating how fruit availability affected behavior and food preferences overall. I divided the observation year into seasons of high and low fruit availability by first averaging the percentages of monitored phenology trees bearing fruit for each phenology period (see Table 3.4 above). I then considered phenology periods with greater than the mean percent of fruiting trees to be seasons of high fruit availability and phenology periods with less than the mean percent of fruiting trees to be seasons of low fruit availability. High fruit seasons were from the beginning of the study through the 2nd of June, 2004 (approximately weeks 1-17 of observation), and again from the 13th of January

through the 9th of February, 2005 (approximately weeks 50-53 of observation). The low fruit season lasted from the 3rd of June, 2004, through the 12th of January, 2005 (approximately weeks 18-49 of observation) and included the entire high tourist season. The high fruit season coincided with the short rainy and short dry seasons and the first half of the long rainy season. The low fruit season coincided with the second half of the long rainy season and the entire long dry season.

I found no association between behavior and fruit season in the non-tourist area (Rao-Scott Adjusted χ^2 test: $\chi^2 = 5.27$, $df = 5$, $P = 0.38$), but an association in the tourist area and overall (Table 4.10) (Rao-Scott Adjusted χ^2 test for the tourist area: $\chi^2 = 19.79$, $df = 5$, $P = 0.0014$; overall: $\chi^2 = 12.40$, $df = 5$, $P = 0.03$). Of the six behavioral categories, only "stationary" and "locomote" were significantly associated with fruit season in the tourist area (Rao-Scott Adjusted χ^2 test for stationary: $\chi^2 = 4.63$, $df = 1$, $P = 0.03$; and locomote: $\chi^2 = 13.00$, $df = 1$, $P = 0.0003$). Tourist area monkeys spent less time stationary and more time locomoting during the high fruit seasons. This may have been due to the increase in available dietary energy from a diet high in fruit, thus allowing the monkeys to travel longer and rest less. It also could have been due to the need to travel further and longer between fruit trees which tend to be patchy in space, and thus the monkeys would have had less time to rest in between feeding bouts. In the non-tourist area, the same trends of less rest and more travel when fruit was abundant were seen; however, they were not statistically significant.

Table 4.10: Activity Patterns by Fruit Season and Area

High	Behavior	% (# Scans)	Low	Behavior	% (# Scans)
NT	Stationary	74.26 (981)	NT	Stationary	78.04 (1549)
	Forage	13.85 (183)		Forage	11.99 (238)
	Locomote	7.19 (95)		Locomote	6.70 (133)
	Vocalize	2.73 (36)		Vocalize	2.67 (53)
	Eliminate	0.91 (12)		Eliminate	0.50 (10)
	Interact	1.06 (14)		Interact	0.10 (2)
T	Stationary	**54.69 (770)**	T	Stationary	**65.54 (1653)**
	Forage	21.24 (299)		Forage	19.94 (503)
	Locomote	**20.45 (288)**		Locomote	**10.67 (269)**
	Vocalize	2.84 (40)		Vocalize	2.06 (52)
	Eliminate	0.57 (8)		Eliminate	1.35 (34)
	Interact	0.21 (3)		Interact	0.44 (11)

7. Behavioral Comparisons within each Season

To conclude that tourist presence rather than weather or fruit seasons was, in fact, the causal influence on different behavioral patterns seen between the two areas, and because I did find significant differences in behavioral patterns due to weather and fruit seasons, especially in the tourist area, I further analyzed the differences between the non-tourist and tourist area behaviors while controlling for weather and fruit seasons. To control for seasonal effect, I compared the behavioral patterns of monkeys in each area during each season. I first conducted four analyses comparing overall behavioral patterns between areas for dry, rainy, high fruit, and low fruit seasons. I then conducted twelve analyses representing four seasons each for the main three behavioral categories (remain stationary, forage, and locomote). In each analysis, I investigated whether there was an association between behavior and area within each season. I found that behavioral patterns were significantly associated with area in each weather and fruit season (Rao-Scott Adjusted χ^2 test for the dry seasons: $\chi^2 = 22.75$, *df* = 5, *P* = 0.0004; rainy seasons: $\chi^2 = 52.93$, *df* = 5, *P* = <

0.0001; high fruit seasons: $\chi^2 = 39.79$, $df = 5$, $P = < 0.0001$; and low fruit season: $\chi^2 = 27.79$, $df = 5$, $P = < 0.0001$). Furthermore, I found the same significant associations between area and the behaviors remain stationary (more often stationary in the non-tourist area), forage (less foraging in the non-tourist area), and locomote (less moving in the non-tourist area), when I analyzed them individually as those that I found in my original analysis. Remaining stationary, foraging, and locomoting were all significantly associated with area when weather and fruit seasons were controlled for, with the one exception of foraging during the high fruit season (Table 4.11). In all cases but the high fruit season, monkeys in the non-tourist area remained stationary more and foraged and moved less than monkeys in the tourist area, which is the same as what I found when I did not control for seasonal influence. Though it was not significant, during the high fruit season, monkeys in the non-tourist area foraged less than those in the tourist area, fitting the same pattern as all the other seasons. The influence of weather and fruit seasons on the behavioral differences seen between the non-tourist and tourist area monkeys is therefore minimal, and does not significantly affect the overall differences seen between these two areas. This lends further support to the idea that tourism influences behavior in red howler monkeys.

Table 4.11: Rao-Scott Adjusted χ^2 Analyses of Non-Tourist versus Tourist Area Differences in Behavior while Controlling for Season

Dry	χ^2 (*df*)	*P*	High Fruit	χ^2 (*df*)	*P*
Stationary	10.34 (1)	**0.0013**	**Stationary**	17.89 (1)	**< 0.0001**
Forage	6.12 (1)	**0.01**	**Forage**	3.34 (1)	0.07
Locomote	3.87 (1)	**0.05**	**Locomote**	35.26 (1)	**< 0.0001**
Rainy			**Low Fruit**		
Stationary	21.34 (1)	**< 0.0001**	**Stationary**	10.55 (1)	**0.0012**
Forage	5.36 (1)	**0.02**	**Forage**	7.13 (1)	**0.0076**
Locomote	36.20 (1)	**< 0.0001**	**Locomote**	4.53	**0.03**

8. Feeding Patterns

To analyze what the monkeys were eating, I monitored their feeding behavior. I noted plant parts and plant species consumed on a daily basis, whenever possible, as well as times of feeding, for monkeys in both the tourist and non-tourist areas during the course of the year of observations. I was able to identify fruits and flowers as food categories, as well as leaves, though the maturity of leaves was often difficult to determine. When the monkeys ate from a tree which was completely defoliated and was growing a new crop of leaves, it was easy to conclude that the leaves eaten were immature. Likewise, the new leaves of many species of tree were reddish, including the favored food species, *Inga alba*. New leaves also tended to grow primarily on the tips of twigs, and the location of leaves eaten helped me to determine the relative maturity of these food sources. However, many times I could not determine leaf maturity, and I subsequently combined all leaf feeding observations to eliminate this ambiguity. Food types analyzed included leaves, fruit, flowers, and unknown. I investigated whether differences existed in plant parts eaten under different conditions, including non-tourist versus tourist area, adult female versus adult male, high versus low tourist season, dry versus rainy season, and high versus low fruit season. As with the analyses of activity patterns mentioned above, I clustered all observations from one feeding bout, to minimize the problem of sequential observations not being statistically independent. I found no association between types of foods eaten and area (Table 4.12) (Rao-Scott Adjusted χ^2 test: χ^2 = 1.60, *df* = 3, *P* = 0.66). I did not look at feeding behavior differences by locale for several reasons: I did not standardize the land area among locales to insure the same access to food resources; I did not have consistent foraging observations among locales, resulting in wildly variable counts of foraging scans; and I did not expect there to be any particular difference in food types eaten in different locales, especially since behavior did not differ among locales.

Table 4.12: Food Types Eaten by Area

Food Type	Non-Tourist Area	Tourist Area
Leaves	46.12% (196 scans)	54.53% (439 scans)
Fruit	37.41% (159 scans)	35.53% (286 scans)
Flowers	11.29% (48 scans)	7.21% (58 scans)
Unknown	5.18% (22 scans)	2.73% (22 scans)

I found no association between food types eaten and sex, either within each area or overall (Table 4.13) (Rao-Scott Adjusted χ^2 test for the non-tourist area: χ^2 = 1.44, df = 3, P = 0.70; tourist area: χ^2 = 5.42, df = 3, P = 0.14; and overall: χ^2 = 5.36, df = 3, P = 0.15). Males and females in both areas consumed the same proportions of leaves, fruit, and flowers year-round.

Table 4.13: Food Types Eaten by Sex and Area

Females	Food Type	% (# Scans)	Males	Food Type	% (# Scans)
NT	Leaves	45.74 (102)	NT	Leaves	46.53 (94)
	Fruit	38.12 (85)		Fruit	36.63 (74)
	Flowers	11.66 (26)		Flowers	10.89 (22)
	Unknown	4.48 (10)		Unknown	5.94 (12)
T	Leaves	54.63 (230)	T	Leaves	54.43 (209)
	Fruit	36.10 (152)		Fruit	34.90 (134)
	Flowers	7.13 (30)		Flowers	7.29 (28)
	Unknown	2.14 (9)		Unknown	3.39 (13)

Tourist seasons were not significantly associated with types of foods eaten within in the tourist area (Rao-Scott Adjusted χ^2 test: χ^2 = 4.76, df = 3, P = 0.19), but they were associated in the non-tourist area and overall (Table 4.14) (Rao-Scott Adjusted χ^2 test for the non-tourist area: χ^2 = 17.75, df = 3, P = 0.0005; and overall: χ^2 = 9.25, df = 3, P = 0.03). The specific food types that were associated with tourist season in the non-tourist area were leaves (Rao-Scott

Adjusted χ^2 test: χ^2 = 6.69, df = 1, P = 0.0097), and probably fruit. I could not test whether fruit reliance during the tourist seasons was in fact different because there was only one observation of fruit foraging during the high tourist season. Non-tourist area monkeys ate more leaves during the high tourist season, though this could have been due as much to weather patterns as tourist presence.

Table 4.14: Food Types Eaten by Tourist Season and Area

High	Food Type	% (# Scans)	Low	Food Type	% (# Scans)
NT	Leaves	**82.14 (69)**	NT	Leaves	**37.24 (127)**
	Fruit	1.19 (1)		Fruit	46.33 (158)
	Flowers	13.10 (11)		Flowers	10.85 (37)
	Unknown	3.57 (3)		Unknown	5.57 (19)
T	Leaves	61.54 (144)	T	Leaves	51.66 (295)
	Fruit	23.08 (54)		Fruit	40.63 (232)
	Flowers	13.68 (32)		Flowers	4.55 (26)
	Unknown	1.71 (4)		Unknown	3.15 (18)

I found no association of food types eaten with weather season in the tourist area (Rao-Scott Adjusted χ^2 test: χ^2 = 5.63, df = 3, P = 0.13), but a significant association in the non-tourist area and overall (Table 4.15) (Rao-Scott Adjusted χ^2 test for the non-tourist area: χ^2 = 10.84, df = 3, P = 0.01; and overall: χ^2 = 12.68, df = 3, P = 0.0054). Monkeys in the non-tourist area ate less fruit and more flowers during the dry season (Rao-Scott Adjusted χ^2 test for fruit: χ^2 = 5.12, df = 1, P = 0.02; for flowers: χ^2 = 6.16, df = 1, P = 0.01). In the tourist area, the same trends were seen for fruit (not significant) and flowers (Rao-Scott Adjusted χ^2 test: χ^2 = 8.47, df = 1, P = 0.0036), and this was supported by the analysis of weather seasons overall. In general, the monkeys were eating food types based on what was seasonally available, though monkeys in the non-tourist area may have been subject to availability more so than monkeys in the tourist area, possibly due to them being less flexible behaviorally regarding time

spent traveling to find preferred fruit (see comparisons between non-tourist and tourist monkey behavioral patterns above).

Table 4.15: Food Types Eaten by Weather Season and Area

Dry	Food Type	% (# Scans)	Rainy	Food Type	% (# Scans)
NT	**Leaves**	46.77 (87)	**NT**	**Leaves**	45.61 (109)
	Fruit	**23.12 (43)**		**Fruit**	**48.54 (116)**
	Flowers	**22.04 (41)**		**Flowers**	**2.93 (7)**
	Unknown	8.06 (15)		**Unknown**	2.93 (7)
T	**Leaves**	53.73 (245)	**T**	**Leaves**	55.59 (194)
	Fruit	31.14 (142)		**Fruit**	41.26 (144)
	Flowers	**11.40 (52)**		**Flowers**	**1.72 (6)**
	Unknown	3.73 (17)		**Unknown**	1.43 (5)

As would be expected, I found a significant association between food types eaten and fruit season, both within areas and overall (Table 4.16) (Rao-Scott Adjusted χ^2 test for the non-tourist area: $\chi^2 = 37.29$, $df = 3$, $P < 0.0001$; tourist area: $\chi^2 = 10.41$, $df = 3$, $P = 0.02$; and overall: $\chi^2 = 28.73$, $df = 3$, $P < 0.0001$). Overall, not taking area into account, each of the three main food types was eaten in different proportions between the high and low fruit seasons (Rao-Scott Adjusted χ^2 test for fruits: $\chi^2 = 16.06$, $df = 1$, $P < 0.0001$; leaves: $\chi^2 = 7.40$, $df = 1$, $P = 0.0065$; and flowers: $\chi^2 = 6.93$, $df = 1$, $P = 0.0085$). However, while fruits and leaves were significantly associated with fruit season in the non-tourist area, flowers were not (Rao-Scott Adjusted χ^2 test for fruits: $\chi^2 = 77.92$, $df = 1$, $P < 0.0001$; leaves: $\chi^2 = 7.63$, $df = 1$, $P = 0.0058$; and flowers: $\chi^2 = 2.77$, $df = 1$, $P = 0.096$), and only flowers were significantly associated with fruit season in the tourist area (Rao-Scott Adjusted χ^2 test for fruits: $\chi^2 = 3.65$, $df = 1$, $P = 0.06$; leaves: $\chi^2 = 1.88$, $df = 1$, $P = 0.17$; and flowers: $\chi^2 = 6.10$, $df = 1$, $P = 0.01$).

Table 4.16: Food Types Eaten by Fruit Season and Area

High	Food Type	% (# Scans)	Low	Food Type	% (# Scans)
NT	Leaves	**23.78 (44)**	NT	Leaves	**63.33 (152)**
	Fruit	**69.73 (129)**		Fruit	**12.5 (30)**
	Flowers	3.78 (7)		Flowers	17.08 (41)
	Unknown	2.70 (5)		Unknown	7.08 (17)
T	Leaves	44.70 (135)	T	Leaves	60.44 (304)
	Fruit	49.67 (150)		Fruit	27.04 (136)
	Flowers	**1.66 (5)**		Flowers	**10.54 (53)**
	Unknown	3.97 (12)		Unknown	1.99 (10)

9. Howling

The common names for members of the genus *Alouatta* in many modern Indo-European languages (*mono aullador*, *brulaap*, *singe hurleur*) relate to the fact that these animals produce impressive vocalizations (Emmons 1997, Ybarra 1986). Even the generic name *Alouatta* derives from the 17th-century Carib names for "throat animal" (Ybarra 1986), and the modern Carib name, *alawata*, illustrates this derivation (Vreedzaam personal communication). The unusual vocalizations of the howler monkey are achievable due to the enlarged hyoid bone, especially prominent in males, which acts as a resonator (Boscarol et al. 2004, Sekulic and Chivers 1986). The hyoid imposes an upper frequency limit to the vocalizations resulting in an absence of high-pitched howling capability, unlike many other species of platyrrhines (Cornick and Markowitz 2002). Lower-frequency loud calls are more effective for long-distance propagation (Mitani and Stuht 1998, Whitehead 1995), and howler monkey loud calls can be heard from at least one kilometer away (Ybarra 1986, personal observation). Howlers, however, have very small home ranges (Lopez et al. 2005, Pope 1992), and this contradicts the idea that primates with larger home ranges will need to have farther-reaching loud calls (Mitani and Stuht 1998). Howling style and timing of howls during the day differ among species and populations of howlers (Cornick and Markowitz 2002). At least two different loud calls have been described in

howlers, the long call or roar, and the short call or bark (Drubbel 1993, Ybarra 1986). The long calls of the red howler last several minutes, and usually occur at dawn or in late afternoon (Emmons 1997). Roars are loud (88 dB at 5m), and roaring bouts can last up to an hour or more (Kitchen et al. 2004). As they are often accompanied by physical displays, roar bouts can be energetically costly (ibid.). The roar usually starts as an accelerating series of deep grunts or rumbles by a male, called the introduction, which often continues for up to a minute or more, and probably is caused by the increasing inflation of the air sacs (Drubbel 1993, Ybarra 1986, personal observation). These grunts grade into long deep roars and the females and subordinates join after a minute or two with higher-pitched roars (Emmons 1997, Sekulic 1982b). At the conclusion of the howl, the male emits one or two discrete blowing sounds or grunts. These sounds, which I named "stop grunts" seem to signify the end of the long call, and are probably produced through the emptying of the air sacs (Drubbel 1993). Additionally, many howls are finished with a rapid series of acoustic units during both inhalation and exhalation, called an *Oodle* (Boscarol et al. 2004). These are very quiet and are not heard in farther-away howls (personal observation).

The second type of howler vocalization is the short call or bark, seen infrequently in disturbed howlers (Sekulic 1982b). The bark may function as an alarm call both to warn group members of a nearby predator or other threat, and to warn the predator that it has been detected (Gil-da-Costa et al. 2003, Zuberbühler et al. 1997). Barks in red howlers are often characterized by a single individual, usually the adult male, producing a short series of grunts (Drubbel 1993). I considered these grunts, as well as any sudden, fast, and short vocalization by an individual or a group to be a bark. Often these short calls lasted only 10 to 20 seconds, but were repeated up to 20 or more times over the course of several hours (ibid., personal observation).

The practice of howling is most likely used as a spacing mechanism among howler groups (Milton 1980, Chivers 1969, personal observation). Howlers are most likely not strictly territorial due to the high degree of overlap of home ranges (Gómez-Marín and Veà 2001), and the high energetic costs of

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boundary defense for fairly immobile folivores (Grant et al. 1992); leaves are an abundant food resource and the need to defend them is low (ibid., Mitani and Rodman 1979). Groups do, however, tend to avoid using overlapping areas at the same time (Cornick and Markowitz 2002, Milton 1980, personal observation), and howling at conspecifics may be a way to defend their current location. A group encounter may result in one group being supplanted by another group from a feeding tree or home range, or a resident male may be evicted by a take-over male (Kitchen et al. 2004). Red howler groups howl most often early in the morning, during the "dawn chorus", with fewer howls throughout the day and night (Oliveira and Ades 2004, personal observation). Presumably, this early morning practice helps the groups start the day knowing where other conspecifics are. Groups can then decide where to travel in relation to others. Additionally, sound transmission may be better during the early mornings, and from the tops of sleeping trees (Drubbel 1993), and any limitations imposed by high temperatures would be minimal in the cool morning hours (Sekulic 1982a). The group howl may also serve as a signal of group size and therefore strength (Kitchen 2004), and may give another group the information necessary to assess whether to approach an occupied feeding tree. The ability to demonstrate a large number of males may also deter an extra-group male from invading (Crockett and Eisenberg 1987, Sekulic 1982b). Howling may advertise the number of adult males in the group, which allows other groups to assess the strength of their competitors, and avoid a contest they are likely to lose (Kitchen 2004, Kitchen et al. 2004). A howl is also probably an honest indicator of the minimum number of males in the group; a single male is not able to mimic many howling males because the howls of individuals are staggered (Kitchen et al. 2004). Most of the few howls that I personally witnessed seemed to be prompted by the presence of another group in the vicinity, and often involved both groups howling, with one group leaving the area after the bout. Several times, I had both groups in my sight while howling was taking place, or at least I had one group in my sight while I heard the second (and sometimes third) group howling nearby. Although many of the afternoon howling bouts proceeded in this manner, there were also several

occasions in which I had two or three groups in my sight, but none seemed concerned about the proximity of the other group(s). Why the groups did not howl at these times remains a mystery to me, but, for the most part, howling seems to have been used as a spacing mechanism.

In addition to howling being used as a spacing mechanism for resource control, maintaining distance from neighboring groups can have health implications as well. The composition of and interactions among primate social groups can have profound impacts on levels of infection and disease pathogenicity. Individual primates should pattern their social interactions in ways so as not to increase their risk of acquiring new pathogens, and to minimize the effects of pathogens they already carry (Freeland 1976). Primate groups are expected to be relatively closed as far as interactions with other conspecifics. Travel to previously unexplored areas, and interactions with non-group members increase the risk of disease acquisition, and group members should be selected to minimize these exploratory behaviors. If group members travel to new areas or interact with non-group members, new diseases not previously known in the group may be introduced. These new diseases may cause problems for group members ranging from decreased fertility to increased susceptibility to predation (Freeland 1976). Territorial behavior may be related to this phenomenon as well. Small, more sedentary groups may be selected for territoriality, not for protection of a food source, but for the exclusion of disease-carrying non-group individuals (ibid.). Hence, it is possible that howling has a disease transmission minimizing component.

When howler monkey troops were unsuccessful at maintaining distance from conspecifics, intergroup encounters occurred. Several of the intergroup encounters I witnessed involved not only vocalizing, including roaring, grunting, and barking, but also a sudden but brief retreat of the group coupled with a group defecation and urination upon arrival of a second group. The second group then usually halted, perhaps retreated a bit in the direction from which they came, and defecated and urinated as a group as well. Incidentally, on at least three occasions, my approach and/or presence prompted the same defecation

response from a few particularly skittish individuals, and two times I had reason to believe that my presence or approach incited a howl. Interestingly, the defecation response to my approach and presence happened in the non-tourist area, twice with one group on the distant Pedrekoe Pasi (PP trail, see Map 2.4 above) and once from a single individual on Telesur trail (TE); but the howl response to my presence/approach happened in the tourist area, once with a group on the Ireneval trail (IV), and once on the Kumbuval trail (KV). I may have misinterpreted the reason for the howl on the IV trail, but on all other defecation and howling occasions, I was fairly certain that I was the disturbance that resulted in the response.

Red howlers have been observed to vocalize for as long as ten minutes without a pause (Drubbel 1993), and I observed roars by howlers in Suriname as long as nine minutes or more (maximum 9 minutes and 44 seconds). Although I did not expect howling behavior to be drastically different between the two areas, I thought that perhaps call duration would differ due to interruption by human activities. In fact, only once in the non-tourist area but eleven times in the tourist area, did I observe monkeys possibly stopping a howl early due to human presence. Therefore, I predicted that call duration would be shorter on average in the tourist area due to interruption by humans. On the other hand, in order for the information communicated by a howl to reach the ears of other conspecifics, it has to be louder or perhaps longer than the other noises in the area. In the tourist area, it may therefore have been the case that howl duration was longer due to the need to out-compete the din of tourist activities. I observed the entire duration of 122 and 136 roars, and 178 and 137 barks in the non-tourist and tourist areas, respectively. I found that there was no difference in either roar or bark duration between areas (Table 4.17) (independent samples t test for roar duration: $t = -1.57$, $df = 256$, $P = 0.12$; and bark duration: $t = -1.44$, $df = 313$, $P = 0.15$). I also report mean durations overall in order to characterize vocalization behavior of red howlers in Brownsberg Natuur Park (Table 4.17). Even though they were not significant differences, both roar and bark durations were actually longer in the tourist area, which meant that howls were not being interrupted by human

disturbance as predicted, but were in fact longer, possibly in order to get the intended message across to conspecifics above the noises of the tourists.

Table 4.17: Roar and Bark Duration (sec) by Area

Area	Roar Duration		Bark Duration	
	Mean	SD	Mean	SD
Non-Tourist	229.55	103.13	16.39	7.96
Tourist	249.99	105.91	17.85	10.11
Both	240.32	104.90	17.03	8.98

I also was interested in the timing of vocalizations, and recorded the time of day at the start of all loud calls for which I also observed duration. I only noted times for vocalizations for which I recorded the entire duration; I did not record times for howls if I did not hear the start of the vocalization. Halfway through my data collection, I realized that by not at least recording the time of a vocalization, even if I could not record its duration, I was biasing the howl times to vocalizations for which I had complete durations. This may have eliminated vocalizations heard while doing another activity such as biking to the non-tourist area. Therefore, I began noting the times of all roars and barks heard, regardless of whether I was able to hear the entire vocalization and thus record the duration. For the second half of the year of observations, I therefore had a relatively complete record of the time of day for all roars and barks heard. I only considered vocalizations between the hours of 06.00 and 19.00, and tallied all vocalizations per hour (Table 4.18). I recorded times for 229 and 137 roars, and 111 and 82 barks in the non-tourist and tourist areas, respectively. The higher numbers of vocalizations in the non-tourist area may not have been an accurate representation of true vocal behavior for two reasons. I may have been less likely to hear loud calls in the tourist area above the human-made noises; and the non-tourist area was more expansive than the tourist area, so I was exposed to the vocalizations of more groups as I traveled through it. That being said, I did find a difference in number of roars per hour by area, but not a difference in number of

barks (Table 4.19) (paired *t* test for roar times: $t = 3.26$, *df* = 12, $P = 0.0068$; and bark times: $t = 1.12$, *df* = 12, $P = 0.28$). The difference in numbers of roars throughout the day by area may have been due to the fact that I observed more roars overall in the non-tourist area.

Table 4.18: Vocalizations per Hour by Area

Time of Day	NT Roars	T Roars	NT Barks	T Barks
6:00-7:00	47	35	3	0
7:00-8:00	31	12	3	6
8:00-9:00	36	17	7	3
9:00-10:00	9	10	1	0
10:00-11:00	20	2	19	3
11:00-12:00	7	6	15	1
12:00-13:00	8	2	1	3
13:00-14:00	8	2	1	9
14:00-15:00	11	6	10	0
15:00-16:00	18	14	17	17
16:00-17:00	13	10	23	24
17:00-18:00	20	14	11	11
18:00-19:00	1	7	0	5

Table 4.19: Roars and Barks per Hour by Area

	Roars per Hour		Barks per Hour	
Area	Mean	SD	Mean	SD
Non-Tourist	**17.62**	13.24	8.54	7.89
Tourist	**10.54**	8.85	6.31	7.30
Both	14.08	10.56	6.96	5.48

I was not able to standardize my counts of monkey calls per listening duration, but when looking at all calls witnessed, I found that red howler long calls appeared to have a bimodal temporal pattern in both areas (Figure 4.2). As

is typical for howler monkeys, there was a strong peak in roars during the morning hours of 06.00 to 09.00. The monkeys also roared before 06.00, but I did not include these howls in my observations. It would be interesting to investigate whether the morning peak would be greater with earlier howls included. Additionally, a smaller afternoon peak was evident from 14.00 until the end of the day. Presumably, the monkeys were less likely to howl during the hottest part of the day (from 09.00 until 14.00) as they may have been resting in the shade (Sekulic 1982a). After a midday nap, however, the monkeys may have been signaling their locations to other groups before commencing afternoon foraging. Barks lacked the morning peak seen with roars, but were especially common during the afternoon starting around 14.30 (Figure 4.3). Aside from excessive barking in the non-tourist area from 10.30 to 11.00 and 11.30 to 12.00, there were consistent but infrequent barks during the rest of the day. Because the barks were presumably produced in response to a disturbance, it makes sense that the monkeys would have had to have been up and moving through their home ranges after their morning rest before encountering a disturbance. Others have investigated seasonal patterns in howling (Sekulic 1982a), and found that the red howler monkeys in Venezuela howled more often during the dry season due to the increase in intergroup encounters around the few fruit sources available. In French Guiana, red howlers howled less often as rainfall increased (Drubbel 1993), which fits the pattern found in Venezuela. My analyses of behavior (see Chapter 4 above) illustrated a mixed seasonal pattern. Non-tourist area monkeys vocalized less during the dry season, but tourist area monkeys vocalized more during the dry season (see Table 4.9 above). Neither difference was statistically significant, and the analysis included all vocalizations and not just roars and barks. Furthermore, monkeys in both areas vocalized more during the high fruit season, which is the opposite of what Sekulic (1982a) found in Venezuela. Again these differences were not statistically significant and included all vocalizations. I would have liked to look more deeply into seasonal patterns of roar and barks only, but I thought my vocalization data were not quite rigorous enough to analyze further than what has been presented here.

Figure 4.2: Roar Times (Aug. 2004 - Jan. 2005)
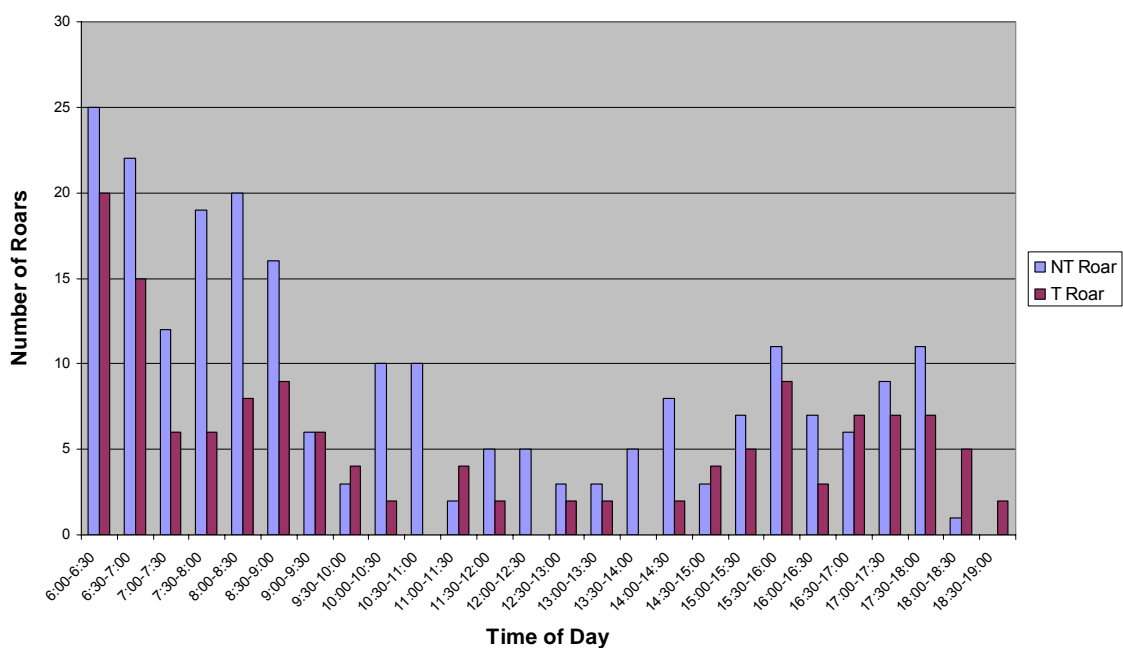
Figure 4.3: Bark Times (Aug. 2004 - Jan. 2005)
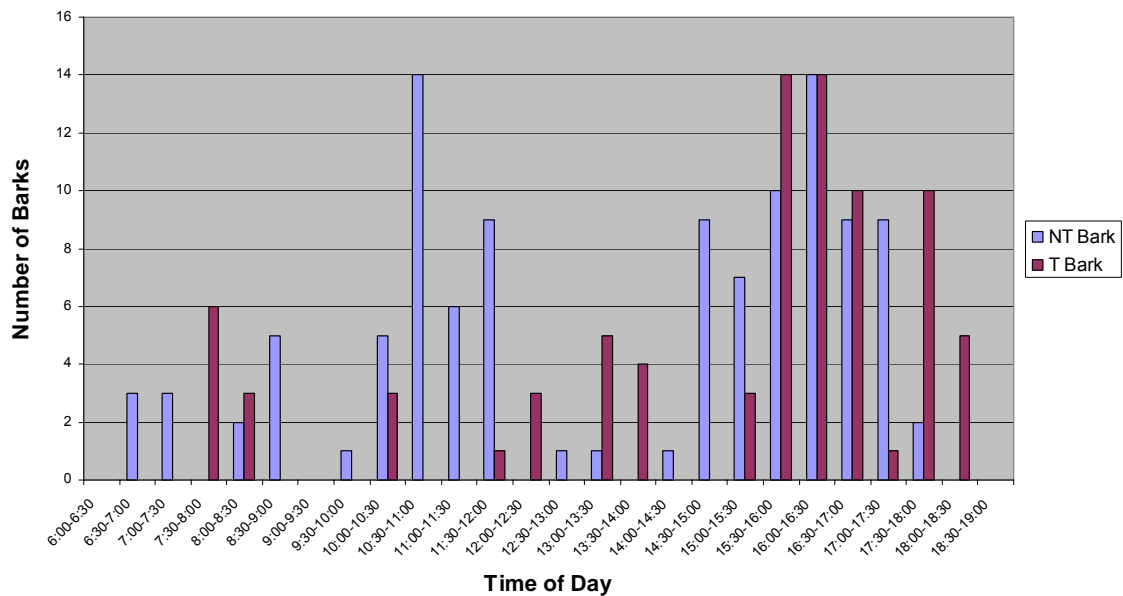
C. Responses to Humans

To quantify both the magnitude of human disturbance, and the magnitude
of monkey response, I assigned rankings to both human activities and monkey

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responses. When considering the assignment of rankings to various monkey responses, I took into account energy expenditure primarily, as well as perceived emotional state. A turn of the head to investigate a disturbance was clearly a lower response than that of fleeing frantically. Likewise, other possible responses were also assigned their relative ranks along a continuum from no response to flee/defecate/intense vocalization (Table 4.20) (see Appendix: Ethogram for more detail).

Table 4.20: Possible Monkey Responses to Human Disturbance by Rank

Response Rank	Monkey Response
0	No Response
1 (Mild Physical Response)	Look at me, look towards noise, shift position, or sit alert
2 (Moderate Physical or Vocal Response)	Generally nervous behavior (including pacing), join another monkey, retreat to cover, move away, grunt softly, or stop howling abruptly
3 (Intense Physical or Vocal Response)	Flee, exaggerated grunt, bark, roar, or defecate
4 (Combined Response)	Two or more responses of at least Rank 2 to the same disturbance

I also assigned rankings to the different types of human disturbance, basing the decision primarily on noise level. Monkeys in both the non-tourist area and the tourist area responded occasionally to my presence, and since I always tried to remain quiet and generally out of sight of the monkeys, I assigned my presence a rank of 1. Therefore, every scan I recorded in both areas had at least a human disturbance of rank 1- me. I assigned a ranking of 2 to quiet disturbances including tourists walking by, low volume music, voices, the water pump, etc., as well as background and distant noises such as airplanes, far off machinery, and the like. I assigned a ranking of 3 to louder disturbances

including cars, trucks, buses, honking, and any rank 2 disturbances that I labeled as "loud." Due to the fact that monkeys in the non-tourist area were unlikely to experience a great number of disturbances, I occasionally tried to disturb them to study their reactions. My occasional disturbances, such as shouting or whistling, were restricted to rank 2 disturbances because it would have been difficult for me to drive by the monkeys in a vehicle while watching their reactions.

As expected, the frequencies of disturbance levels were significantly associated with area (Rao-Scott Adjusted χ^2 test for all disturbance ranks: $\chi^2 =$ 476.09, $df = 2$, $P < 0.0001$; disturbance rank 1: $\chi^2 = 2514.13$, $df = 1$, $P < 0.0001$; disturbance rank 2: $\chi^2 = 140.81$, $df = 1$, $P < 0.0001$; and disturbance rank 3: $\chi^2 =$ 164.09, $df = 1$, $P < 0.0001$). In general, monkeys in the tourist area experienced many more disturbances of Rank 2 and 3, than monkeys in the non-tourist area (Table 4.21). Additionally, my presence was a greater proportion of disturbances in the non-tourist area, whereas in the tourist area, my presence was of equal proportion to disturbances of Rank 2.

Table 4.21: Human Disturbances by Rank and Area

Disturbance	NT % (# Scans)	Tour % (# Scans)
Rank 1	84.93 (3174)	44.80 (3337)
Rank 2	13.65 (510)	45.86 (3416)
Rank 3	1.42 (53)	9.33 (695)

To determine the relative impact of the different human activities on the behavior of the monkeys, I tallied all disturbances by rank. Often, especially in the tourist area, a single scan encompassed more than one disturbance, often of more than one rank. I did not look at disturbances per scan, but instead all disturbances encountered by the monkeys, and all reactions to them or lack thereof. For this reason, there were actually more total disturbances (including me) than there were scans. Additionally, sometimes one disturbance prompted more than one response from the monkeys, often of more than one ranking. To conduct statistical analyses, I needed to combine these responses so that each

disturbance prompted only one response from each monkey. When the two responses were mild, such as a rank 1 response combined with a rank 2 response, I considered the final response to be of a rank 2 for purposes of analysis. When responses were more intense, such as a rank 2 response with a rank 3, or two rank 3 responses together, I assigned the final response a rank of 4. Due to the limited occasions of rank 4 responses, and the inability to complete χ^2 analyses for these limited responses, I had to devalue rank 4 responses for the purposes of analysis. For this reason, my results were conservative as far as level of response in many cases (i.e. multiple intense responses to a single disturbance were analyzed as single intense responses, thus minimizing the magnitude of response). I was able to look at rank 4 responses in certain circumstances, such as in response to me, and these analyses will follow shortly.

I was able to calculate the percentages of disturbances of each type that prompted a response of some kind in one or more monkeys. I totaled all disturbances per study area, and also kept the tallies separate for adult females and adult males in each area to investigate whether monkeys in either area or of either sex responded more often or with higher magnitude to disturbances than the other (Table 4.22). The percentages reflect the number of scans in which a monkey reacted to a disturbance out of the total number of scans in which a disturbance was experienced by the monkeys. The numbers of disturbances reacted to/total disturbances are listed below the percentages. Often I was not certain whether an animal was looking towards a disturbance, or just looking around. I also was not always certain whether the human disturbance was the catalyst for the resulting behavioral response. However, for the purpose of painting the broadest picture of human disturbance in both areas of the park, all known or assumed responses were included in this analysis.

**Table 4.22: Frequency of Monkey Reactions to Human Disturbance
by Area, Sex, and Disturbance Rank**

Disturb.	Non-T Female	Tour Female	Non-T Male	Tour Male	Non-T Average	Tour Average
Rank 1 (me)	6.57% 102/1552	2.72% 45/1657	8.69% 141/1622	2.98% 50/1680	7.66% 243/3174	2.85% 95/3337
Rank 2	8.43% 21/249	1.77% 30/1692	11.49% 30/261	2.84% 49/1724	10.00% 51/510	2.81% 79/3416
Rank 3	17.39% 4/23	4.65% 16/344	40.00% 12/30	8.26% 29/351	30.19% 16/53	6.47% 45/695

Clearly, based on scan percentages, non-tourist area monkeys, of both sexes, responded much more often to human disturbances of all rankings than did the monkeys in the tourist area. Monkeys in both areas responded about the same percent of the time to my presence as to a human disturbance of rank 2. Disturbances of rank 3 in both areas prompted at least twice the frequency of responses, than did disturbances of rank 1 and 2. This was probably due to the fact that rank 3 disturbances were louder and more intrusive.

As mentioned above with the behavioral scans, not all disturbance scans were statistically independent (for example a plane that flew overhead for 10 minutes or a generator that was turned on for a half hour). For this reason I clustered the observations by locale, date, and group per day as with the behavioral observations above. I then conducted Rao-Scott Adjusted χ^2 analyses to take into account this clustering. I found that monkeys in the non-tourist and tourist areas responded differently to human disturbances, regardless of sex and level of disturbance. Monkeys in the non-tourist area consistently responded to disturbances more often and with a higher magnitude of response compared to monkeys in the tourist area (Table 4.23 for females, Table 4.24 for males). Due to the complexity of the data, analyses of monkey responses to different levels of disturbance were conducted separately by sex and disturbance level. All tests conducted were Rao-Scott Adjusted χ^2 analyses (Table 4.25).

Table 4.23: Female Responses to Human Disturbance by Disturbance Level and Area

Non-Tour	Resp.	% (# Scans)	Tour	Resp.	% (# Scans)
Disturb. 1	0	93.43 (1450)	Disturb. 1	0	97.28 (1612)
	1	4.51 (70)		1	1.93 (32)
	2	1.42 (22)		2	0.54 (9)
	3	0.64 (10)		3	0.24 (4)
Disturb. 2	0	91.57 (228)	Disturb. 2	0	98.23 (1662)
	1	6.02 (15)		1	0.89 (15)
	2	2.01 (5)		2	0.65 (11)
	3	0.40 (1)		3	0.24 (4)
Disturb. 3	0	82.61 (19)	Disturb. 3	0	95.35 (328)
	1	8.70 (2)		1	0.87 (3)
	2	4.35 (1)		2	1.74 (6)
	3	4.35 (1)		3	2.03 (7)

Table 4.24: Male Responses to Human Disturbance by Disturbance Level and Area

Non-Tour	Resp.	% (# Scans)	Tour	Resp.	% (# Scans)
Disturb. 1	0	91.31 (1481)	Disturb. 1	0	97.02 (1630)
	1	4.07 (66)		1	1.90 (32)
	2	3.39 (55)		2	0.65 (11)
	3	1.23 (20)		3	0.42 (7)
Disturb. 2	0	88.51 (231)	Disturb. 2	0	97.16 (1675)
	1	7.28 (19)		1	1.80 (31)
	2	2.30 (6)		2	0.70 (12)
	3	1.92 (5)		3	0.35 (6)
Disturb. 3	0	60.00 (18)	Disturb. 3	0	91.74 (322)
	1	16.67 (5)		1	2.56 (9)
	2	10.00 (3)		2	2.85 (10)
	3	13.33 (4)		3	2.85 (10)

Table 4.25: Rao-Scott Adjusted χ^2 Analyses of Area Differences in Monkey Response to Human Disturbance by Sex and Disturbance Level

NT vs. T Female	Disturbance	χ^2 (*df*)	*P*
	1	10.16 (3)	**0.02**
	2	23.87 (3)	**<0.0001**
	3	8.63 (3)	**0.03**
NT vs. T Male	Disturbance	χ^2 (*df*)	*P*
	1	19.28 (3)	**0.0002**
	2	19.91 (3)	**0.0002**
	3	17.37 (3)	**0.0006**

I looked as well at sex differences in response to human disturbance. I found mixed results between the areas (Table 4.26 for the non-tourist area, Table 4.27 for the tourist area). In the non-tourist area, males responded more often

and with a higher magnitude of response to disturbance rank 1 (me) than did females. Males and females in the non-tourist area, however, did not respond differently to disturbances of rank 2 or 3. In the tourist area, I found the opposite result; males and females did not respond differently to me, but they did respond differently to disturbances of rank 2 and 3. For both these categories of disturbance, males in the tourist area responded more often and with a higher magnitude of response than did females. Again, analyses of monkey responses to different levels of disturbance were conducted separately by area and disturbance level. All tests conducted were Rao-Scott Adjusted χ^2 analyses (Table 4.28).

Table 4.26: Non-Tourist Area Monkey Responses to Human Disturbance by Disturbance Level and Sex

Females	Resp.	% (# Scans)	Males	Resp.	% (# Scans)
Disturb. 1	**0**	**93.43 (1450)**	**Disturb. 1**	**0**	**91.31 (1481)**
	1	**4.51 (70)**		**1**	**4.07 (66)**
	2	**1.42 (22)**		**2**	**3.39 (55)**
	3	**0.64 (10)**		**3**	**1.23 (20)**
Disturb. 2	**0**	91.57 (228)	**Disturb. 2**	**0**	88.51 (231)
	1	6.02 (15)		**1**	7.28 (19)
	2	2.01 (5)		**2**	2.30 (6)
	3	0.40 (1)		**3**	1.92 (5)
Disturb. 3	**0**	82.61 (19)	**Disturb. 3**	**0**	60.00 (18)
	1	8.70 (2)		**1**	16.67 (5)
	2	4.35 (1)		**2**	10.00 (3)
	3	4.35 (1)		**3**	13.33 (4)

Table 4.27: Tourist Area Monkey Responses to Human Disturbance by Disturbance Level and Sex

Females	Resp.	% (# Scans)	Males	Resp.	% (# Scans)
Disturb. 1	0	97.28 (1612)	Disturb. 1	0	97.02 (1630)
	1	1.93 (32)		1	1.90 (32)
	2	0.54 (9)		2	0.65 (11)
	3	0.24 (4)		3	0.42 (7)
Disturb. 2	0	98.23 (1662)	Disturb. 2	0	97.16 (1675)
	1	0.89 (15)		1	1.80 (31)
	2	0.65 (11)		2	0.70 (12)
	3	0.24 (4)		3	0.35 (6)
Disturb. 3	0	95.35 (328)	Disturb. 3	0	91.74 (322)
	1	0.87 (3)		1	2.56 (9)
	2	1.74 (6)		2	2.85 (10)
	3	2.03 (7)		3	2.85 (10)

Table 4.28: Rao-Scott Adjusted χ^2 Analyses of Sex Differences in Monkey Response to Human Disturbance by Area and Disturbance Level

NT Female vs. Male	Disturbance	χ^2 (*df*)	P
	1	14.08 (3)	**0.0028**
	2	2.59 (3)	0.46
	3	5.46 (3)	0.14
T Female vs. Male	Disturbance	χ^2 (*df*)	P
	1	1.34 (3)	0.72
	2	14.74 (3)	**0.0021**
	3	10.56 (3)	**0.01**

I also looked at whether or not monkeys responded more often to the onset of a disturbance, as opposed to subsequent scans in which the monkeys could habituate to the prolonged noise. For example, I coded the first scan of my

arrival with a group as "initial," and the rest of the scans while I was still present with the group as "non-initial." I then looked at whether monkeys responded differently to initial disturbances depending on whether they were non-tourist or tourist area monkeys, or female or male monkeys. I found a significant association between likelihood of response, initial status, and area. In all analyses, non-tourist area monkeys responded more often and with a higher magnitude of response to disturbances than did tourist area monkeys (Table 4.29 for females, Table 4.30 for males). Analyses of monkey responses to initial and non-initial disturbances were conducted separately for each sex; all tests conducted were Rao-Scott Adjusted χ^2 analyses (Table 4.31).

Table 4.29: Female Responses to Human Disturbance by Initial Status and Area

Non-Tour	Resp.	% (# Scans)	Tour	Resp.	% (# Scans)
Initial	0	77.90 (141)	Initial	0	94.87 (776)
	1	12.15 (22)		1	1.71 (14)
	2	6.08 (11)		2	2.08 (17)
	3	3.87 (7)		3	1.34 (11)
Non-Initial	0	94.70 (1556)	Non-Initial	0	98.30 (2826)
	1	3.96 (65)		1	1.25 (36)
	2	1.03 (17)		2	0.31 (9)
	3	0.30 (5)		3	0.14 (4)

Table 4.30: Male Responses to Human Disturbance by Initial Status and Area

Non-Tour	Resp.	% (# Scans)	Tour	Resp.	% (# Scans)
Initial	0	73.36 (157)	Initial	0	92.36 (786)
	1	13.08 (28)		1	3.41 (29)
	2	7.94 (17)		2	2.59 (22)
	3	5.61 (12)		3	1.65 (14)
Non-Initial	0	92.58 (1573)	Non-Initial	0	97.83 (2841)
	1	3.65 (62)		1	1.48 (43)
	2	2.77 (47)		2	0.38 (11)
	3	1.00 (17)		3	0.31 (9)

Table 4.31: Rao-Scott Adjusted χ^2 Analyses of Area Differences in Monkey Response to Disturbance by Sex and Initial Status

NT vs. T Female	Initial	χ^2 (*df*)	*P*
	Yes	59.70 (3)	<0.0001
	No	18.46 (3)	0.0004
NT vs. T Male	Initial	χ^2 (*df*)	*P*
	Yes	50.59 (3)	<0.0001
	No	39.06 (3)	<0.0001

I found varied results when I analyzed response differences to initial versus non-initial disturbances between the sexes in the non-tourist and tourist areas (Table 4.32 for the non-tourist area, Table 4.33 for the tourist area). In the non-tourist area I found no association between response to initial disturbances and sex, but a significant association between response to non-initial disturbances and sex (Table 4.34). Non-tourist area males responded more often and with a higher magnitude of response than females to non-initial disturbances, except for rank 1 responses which females employed more often than males to non-initial disturbances. In the tourist area I found a significant association between response to initial disturbances and sex, but no association between

response to non-initial disturbances and sex (Table 4.34). Tourist area males responded more often and with a higher magnitude of response than females to initial disturbances.

Table 4.32: Non-Tourist Area Monkey Responses to Human Disturbance by Initial Status and Sex

Females	Resp.	% (# Scans)	Males	Resp.	% (# Scans)
Initial	0	77.90 (141)	Initial	0	73.36 (157)
	1	12.15 (22)		1	13.08 (28)
	2	6.08 (11)		2	7.94 (17)
	3	3.87 (7)		3	5.61 (12)
Non-Initial	0	**94.70 (1556)**	Non-Initial	0	**92.58 (1573)**
	1	**3.96 (65)**		1	**3.65 (62)**
	2	**1.03 (17)**		2	**2.77 (47)**
	3	**0.30 (5)**		3	**1.00 (17)**

Table 4.33: Tourist Area Monkey Responses to Human Disturbance by Initial Status and Sex

Females	Resp.	% (# Scans)	Males	Resp.	% (# Scans)
Initial	0	**94.87 (776)**	Initial	0	**92.36 (786)**
	1	**1.71 (14)**		1	**3.41 (29)**
	2	**2.08 (17)**		2	**2.59 (22)**
	3	**1.34 (11)**		3	**1.65 (14)**
Non-Initial	0	98.30 (2826)	Non-Initial	0	97.83 (2841)
	1	1.25 (36)		1	1.48 (43)
	2	0.31 (9)		2	0.38 (11)
	3	0.14 (4)		3	0.31 (9)

Table 4.34: Rao-Scott Adjusted χ^2 Analyses of Sex Differences in Monkey Response to Disturbance by Area and Initial Status

NT Female vs. Male	Initial	χ^2 (*df*)	*P*
	Yes	2.18 (3)	0.54
	No	14.21 (3)	**0.0026**
T Female vs. Male	Initial	χ^2 (*df*)	*P*
	Yes	14.34 (3)	**0.0025**
	No	3.78 (3)	0.29

The final analysis I conducted regarding initial disturbances was testing whether monkeys within each area responded more often to initial versus non-initial disturbances. I found that in both areas, monkeys, regardless of sex, responded more often and with a higher magnitude of response to initial disturbances versus non-initial disturbances (Table 4.35) (Rao-Scott Adjusted χ^2 test for the non-tourist area: $\chi^2 = 99.06$, *df* = 3, $P < 0.0001$; tourist area: $\chi^2 = 62.67$, *df* = 3, $P < 0.0001$).

Table 4.35: Responses to Human Disturbance by Area and Initial Status

Initial	Resp.	% (# Scans)	Non-Initial	Resp.	% (# Scans)
Non-Tourist	0	75.44 (298)	**Non-Tourist**	0	93.63 (3129)
	1	12.66 (50)		1	3.80 (127)
	2	7.09 (28)		2	1.92 (64)
	3	4.81 (19)		3	0.66 (22)
Tourist	0	93.59 (1562)	**Tourist**	0	98.06 (5667)
	1	2.58 (43)		1	1.37 (79)
	2	2.34 (39)		2	0.35 (20)
	3	1.50 (25)		3	0.23 (13)

Rank 4 responses were combined rank 2 and 3 responses to a single disturbance. The only disturbance that resulted in a rank 4 response from both

females and males in both areas was me (disturbance rank 1). Therefore, I could only statistically analyze rank 4 responses in regards to my presence. I found that both females and males in the non-tourist area responded to my presence more often and with a higher magnitude of response, including more rank 4 responses, than monkeys in the tourist area (Table 4.36) (Rao-Scott Adjusted χ^2 test for non-tourist versus tourist area females: χ^2 = 12.08, df = 4, P = 0.02; for non-tourist versus tourist area males: χ^2 = 21.22, df = 4, P = 0.0003). These results are consistent with the differences seen above in frequency and magnitude of response between areas when rank 4 disturbances were not taken into account (Tables 4.23 and 4.24 above).

Table 4.36: Monkey Responses to My Presence by Sex and Area

Non-Tour	Resp.	% (# Scans)	Tour	Resp.	% (# Scans)
Females	0	93.43 (1450)	Females	0	97.28 (1612)
	1	4.51 (70)		1	1.93 (32)
	2	1.42 (22)		2	0.54 (9)
	3	0.39 (6)		3	0.18 (3)
	4	0.26 (4)		4	0.06 (1)
Males	0	91.31 (1481)	Males	0	97.02 (1630)
	1	4.07 (66)		1	1.90 (32)
	2	3.39 (55)		2	0.65 (11)
	3	0.62 (10)		3	0.24 (4)
	4	0.62 (10)		4	0.18 (3)

I also found a significant association between response to my presence and sex in the non-tourist area when rank 4 responses were taken into account, but no association in the tourist area (Table 4.37) (Rao-Scott Adjusted χ^2 test for non-tourist area females versus males: χ^2 = 14.62, df = 4, P = 0.0056; for tourist area females versus males: χ^2 = 1.72, df = 4, P = 0.79). Males in the non-tourist area responded more often and with a higher magnitude of response, including

more rank 4 responses, than females to my presence, except for rank 1 responses which females employed more often than males to my presence. These results are consistent with the sex differences in response to my presence as seen above when rank 4 responses were not taken into account.

Table 4.37: Monkey Responses to My Presence by Area and Sex

Females	Resp.	% (# Scans)	Males	Resp.	% (# Scans)
Non-Tour	**0**	**93.43 (1450)**	**Non-Tour**	**0**	**91.31 (1481)**
	1	**4.51 (70)**		**1**	**4.07 (66)**
	2	**1.42 (22)**		**2**	**3.39 (55)**
	3	**0.39 (6)**		**3**	**0.62 (10)**
	4	**0.26 (4)**		**4**	**0.62 (10)**
Tour	**0**	97.28 (1612)	**Tour**	**0**	97.02 (1630)
	1	1.93 (32)		**1**	1.90 (32)
	2	0.54 (9)		**2**	0.65 (11)
	3	0.18 (3)		**3**	0.24 (4)
	4	0.06 (1)		**4**	0.18 (3)

I also investigated whether tourist, weather, or fruit seasons had any impact on the monkeys' likelihood of responding to human disturbance (see also the ordinal logistic model below). I found no association between response patterns and tourist or weather seasons in either area, or fruit season in the non-tourist area, but I found an association in the tourist area between likelihood of response and fruit season, regardless of sex or disturbance rank (Table 4.38). Tourist area monkeys responded more often and with a higher magnitude of response during the high fruit season. Whether the increase in responses during the high fruit season was actually related to the presence of fruit or not is debatable; however, with more access to high-energy fruit, monkeys in the tourist area would have had more energy to increase their responses to human disturbance.

Table 4.38: Rao-Scott Adjusted χ^2 Analyses of Seasonal Influence on Monkey Response to Human Disturbance

Non-Tourist Area	χ^2 (*df*)	*P*
Tourist Season	1.34 (3)	0.72
Weather Season	2.98 (3)	0.40
Fruit Season	3.25 (3)	0.35
Tourist Area		
Tourist Season	2.53 (3)	0.47
Weather Season	2.96 (3)	0.40
Fruit Season	13.97 (3)	**0.0029**

I investigated whether disturbance rank itself influenced the monkeys' responses (i.e., whether the response fit the disturbance). I found that responses were significantly associated with disturbance rank, regardless of area or sex (Table 4.39) (Rao-Scott Adjusted χ^2 test: $\chi^2 = 31.91$, $df = 6$, $P < 0.0001$). Overall, the monkeys responded more often and with a higher magnitude of response, except for response 1, to disturbances of rank 3 versus 1, indicating they were more affected by rank 3 disturbances than by my presence (rank 1 disturbance). The pattern of response to disturbances of rank 2 was not the same; rank 2 disturbances evoked fewer and lower magnitude responses than either disturbance 1 or 3.

Table 4.39: Overall Monkey Response by Disturbance Rank

Response	Disturb. Rank 1 % (# Scans)	Disturb. Rank 2 % (# Scans)	Disturb. Rank 3 % (# Scans)
Rank 0	94.81 (6173)	96.69 (3796)	91.84 (687)
Rank 1	3.07 (200)	2.04 (80)	2.54 (19)
Rank 2	1.49 (97)	0.87 (34)	2.67 (20)
Rank 3	0.35 (23)	0.33 (13)	2.41 (18)
Rank 4	0.28 (18)	0.08 (3)	0.53 (4)

Finally, I created an ordinal logistic model, with GEE (Generalized Estimating Equations allowing for correlation among observations of monkeys in the same group (Diggle et al. 2002)) to assess the influence of each predictor (tourist, weather, and fruiting seasons, sex, disturbance rank, area, and initial status) on the level of monkey response to human disturbance. I found that sex, area, and initial status had significant influences on monkey response, but tourist, weather, and fruiting seasons, and disturbance rank did not have a significant influence (Table 4.40).

Table 4.40: Ordinal Logistic Model of Predictors of Monkey Response to Human Disturbance

Predictor	Parameter Estimate	Standard Error	95% Confidence Limits		Z	*P*
Tourist (Low)	0.1256	0.3005	-0.4634	0.7146	0.42	0.6759
Weather (Rainy)	0.3370	0.2395	-0.1325	0.8065	1.41	0.1594
Fruit (Low)	-0.1811	0.2602	-0.6910	0.3288	-0.70	0.4864
Sex (Male)	0.3408	0.0980	0.1487	0.5330	3.48	**0.0005**
Disturb. 2	-0.4695	0.2553	-0.9698	0.0308	-1.84	0.0659
Disturb. 3	-0.0262	0.3288	-0.6707	0.6183	-0.08	0.9365
Area (Tour)	-1.1930	0.3049	-1.7906	-0.5954	-3.91	**<0.0001**
Initial (Yes)	1.5551	0.1695	1.2229	1.8874	9.17	**<0.0001**

D. Discussion and Conclusions

Monkeys in the non-tourist area spent more time stationary and less time foraging and traveling, on average, than monkeys in the tourist area. These differences may have been due in part to the fact that park personnel and tourists often alerted me to the presence of howlers in the tourist area, even when I was not actively searching for the monkeys. On all of these occasions, the monkeys

were active which caught the attention of the observers; thus by recording the behaviors of the monkeys at these times, I may have biased the data toward higher levels of activity in the tourist area monkeys. I may also have inadvertently increased the results for the percentage of time spent foraging in the tourist area due to a few occasions in which I had chance encounters with monkeys foraging. These instances occurred when I was on my way back to camp after a day spent in the non-tourist area, and because I was headed home, I did not remain with the monkeys beyond the time necessary for ten scans or so, thus increasing my recordings of foraging scans without the behaviors exhibited before or after the foraging bout. I searched my data for these occasions and removed 58 foraging scans, along with 11 associated scans (9 of which were "locomote"), for a total of 69 "opportunistic scans" removed from the tourist area data before analysis. The above percentages reflect the final data set after the observations were removed. I also was more likely to follow troops in the tourist areas because there was less of a chance I would get lost, which may have biased the data against locomotion in the non-tourist area. On the other hand, due to the fact that the tourist area monkeys lived in my backyard, I was able to find them earlier in the morning and stay with them until later in the evening, in general, than monkeys in the non-tourist area. Because the monkeys were the least active in the earliest and latest times of the day, I expected my observation schedule to have resulted in more scans of stationary behavior in the tourist area than the non-tourist area. Indeed, from the hours of 06.00 until 08.00, and 18.00 until 19.00, I logged 88 scans of stationary behavior in the non-tourist area (2.67% of all non-tourist area scans), and 345 scans in the tourist area (8.58% of all tourist area scans), almost four times as many.

It is unlikely that the differences in behavioral patterns seen between the non-tourist and tourist area monkeys were due solely to biases in data collection, especially because I tried to control for this bias by removing many opportunistic "active" scans, and I expected a bias, if any, towards more resting in the tourist area, as mentioned above. In looking at the analyses of the ecological factors that may have influenced monkey behavior, I found a few aspects that may shed

light on the issue. First, although there was a minimal difference in average weekly temperatures between the non-tourist and tourist areas (approximately 0.5 ºC), it was a statistically significant difference and one worth looking into. If in fact the tourist area was hotter on average than the non-tourist area, my predictions as far as monkey behavior in the tourist area would be thus: more often stationary to rest during the hottest part of the day and because it would be too hot to move, less time spent foraging due to a slower metabolism during high temperatures and less of a need for dietary energy to heat their own bodies, and less time spent traveling due to it being too hot to move and the monkeys having less energy because they were not foraging enough to support a lot of movement. This is the exact opposite of what I found in the tourist area.

Second, the percentages of monitored phenology trees bearing food items for the monkeys were lower in the tourist area than in the non-tourist area. These differences were not statistically significant, but they were consistent. It is possible that the monitored trees were poorly chosen and did not reflect actual food availability in the tourist area. It is also possible that the tourist area monkeys did indeed need to travel further between food trees because fewer trees along the way provided food. This idea is supported by the fact that monkeys in the tourist area seemed to have been less influenced by fruit fluctuations than monkeys in the non-tourist area. Across weather and fruit seasons, non-tourist area monkeys varied their food choices to a greater degree than did the tourist area monkeys. This was especially true of fruit, as the non-tourist area monkeys foraged significantly less on fruit and more on leaves and flowers when fruit was less available. In contrast, monkeys in the tourist area did not forage on significantly different proportions of fruit in different weather or fruit seasons; they were able to maintain high levels of fruit in their diet regardless of availability. This scenario supports the findings that tourist area monkeys were less often stationary, traveled more, and foraged more. They would have had to travel farther to maintain a consistent diet of fruit, would have foraged more to maintain the energy to travel, and would not have had time to rest as much due to the increase in foraging and travel. Alternatively, though the lower percentages

of phenology trees bearing food per phenology period in the tourist area compared to the non-tourist area might lead to the assumption that the trees with food in the tourist area were more spread apart, thus requiring the monkeys to travel further between them, this was not necessarily the case. Even though the phenology transects in both areas covered a little more than eight kilometers of trails, those trails in the tourist area were more compact, and thus the phenology trees were more closely spaced providing food sources a short distance apart. This means that even if a higher percentage of trees were not providing fruit, the monkeys did not have far to go to reach the next phenology tree that did have fruit.

Third, although I found no difference in average food biomass available per phenology period between the non-tourist and tourist areas, I did find that the average food biomass available per tree was higher in the monitored trees of the tourist area than in the non-tourist area per phenology period (paired t test: $t = -3.50$, $df = 27$, $P = 0.0016$). This implies that the average monitored food tree in the tourist area was larger (carried more food), and/or had fruit versus leaves (better and weightier food), and thus had more food than the average non-tourist area tree. According to the phenology monitoring, the same actual food biomass was available between areas per phenology period, but fewer trees in the tourist area provided more food. This also accounts for the slightly lower percentages of monitored trees bearing food items per phenology period in the tourist area. Additionally, a fruit-bearing tree had a higher food biomass measurement than a similarly-sized tree bearing only leaves. In fact, the average dbh of food biomass trees did not differ between areas (independent samples t test: $t = 0.31$, $df = 264$, $P = 0.76$), meaning more monitored trees in the tourist area had fruit or fruit with flowers or leaves compared to trees in the non-tourist area. If each tree had more or better food, monkeys in the tourist area would have been able to linger and get their fill, rather than move on after only a short time. High quantities of fruit per tree could also explain why tourist area monkeys were able to maintain a consistent diet of fruit during the year. This scenario leads to opposite predictions for behavioral patterns than what was predicted immediately above: less travel

because there was plenty of food at one source, less foraging because they would not need energy for travel and because they would be eating higher-energy fruit rather than lower-quality leaves, and more time spent stationary digesting their large meals. This contradicts what I found in the tourist area.

Finally, tourist presence could have been the motivation for the behavioral patterns seen in the tourist area monkeys. Tourist presence can be annoying to the monkeys at the very least. During the year of observations, I witnessed tourists yelling and pointing at monkeys, shaking branches, and attempting to howl, among other things. Additionally, human activities related to tourism, such as running the generator or water pump, or driving a bus or tractor, can also be disruptive. The tourist area monkeys may have become habituated to these disturbances (see below), but they may also have altered their behavior to minimize their impact. Tourist area monkeys in general spent less time stationary and more time traveling and foraging than did monkeys in the non-tourist area. They may have been trying to avoid the antics of the tourists to some extent by keeping on the move or retreating to the forest interior where tourists did not go. To quantify the possibility that tourists interrupted monkey behaviors, I looked at behavior bout durations. I found that tourist area monkeys had shorter overall bout lengths of foraging, resting, and sitting, when compared to non-tourist area monkeys. This may indicate that the monkeys there were changing locations and behaviors more frequently in order to avoid the presence of humans. Tourists may have frequently interrupted the activities of the monkeys in the tourist area, thus resulting in shorter bout durations, and altered behavioral profiles in general.

I additionally investigated whether the differences in behavioral patterns seen between the tourist and non-tourist area monkeys were maintained during the different weather and fruit seasons. Seasonal change clearly played a role in the behavior and feeding patterns of the monkeys, but I wanted to know if seasonal influence overshadowed actual behavioral differences due to tourism. I found that the behavioral differences between areas were consistent no matter what the season (i.e. behavior was consistently and significantly associated with area). Non-tourist area monkeys rested more and foraged and traveled less than

tourist area monkeys regardless of season. The single exception to this conclusion regarded foraging differences during the high fruit season. Though it was not significant, the trend of non-tourist area monkeys foraging less than tourist area monkeys was still evident during the high fruit season. Seasonal changes affected monkey behavior in general, but the influence of seasonal change on the behavioral differences seen between the non-tourist and tourist areas was minimal. This lends further support to the conclusion that tourism influences behavior in red howler monkeys.

Monkey behaviors were not found to be significantly different by locale, leading me to conclude that a continuum of behavioral pattern changes among monkeys with differing levels of human contact did not exist. Scan sample sizes varied among locales as well, and some locales probably were not observed often enough to present a complete picture of monkey behavioral patterns. I designated locales somewhat arbitrarily as well, which may account for the lack of differences in monkey behaviors among them.

I found differences in behavioral patterns between the sexes. In general, females remained stationary and vocalized less than males and foraged more. Some of the differences in behavior patterns are likely due to differences in calling behavior and my willingness to assign a vocalization to an adult male, but reluctance to assign one to an adult female unless I could see her. Males initiate and participate in most, if not all, of the group's vocalizations (Kitchen 2004, Wich and Nunn 2002, Chiarello 1995, Drubbel 1993, Sekulic 1982b). However, even when removing the behavior category "vocalize" from my analysis, I still found a significant difference in behavior patterns overall between males and females (Rao-Scott Adjusted χ^2 test: $\chi^2 = 22.91$, $df = 4$, $P = 0.0001$). Females also rested less and foraged more than males. My general sense of this difference is that dependent offspring played a role in the female behavioral patterns. Males seemed to have had less interaction with subadults in general and tended to eat their fill and go promptly to sleep. Females on the other hand, foraged longer than males, attended to their offspring, or were woken up by them during a nap, and therefore rested less. Females presumably would have had a higher dietary

energy need than males if they were pregnant or lactating, and thus would have traded resting time for foraging time.

Although overall ecological conditions did not differ between the non-tourist and tourist areas, I thought it important to investigate whether monkeys in each area responded to changing conditions in weather patterns and fruit availability over the course of the year. Presumably, weather and fruit seasons were similar in the two areas, thus providing the same influences on monkey behavior and food types eaten, however, the monkeys may not have responded to these influences in the same way in each area. I wanted to determine whether the non-tourist and tourist area monkeys responded to these fluctuations, thus exhibiting different coping mechanisms. In addition to weather and fruit seasons, I also looked at high and low tourist seasons to see if not only tourist presence in space affected the monkeys (non-tourist versus tourist area), but also tourist presence in time (high versus low tourist season). It is with tourism that I will begin the discussion of seasons.

Tourist seasons influenced behavior in both the tourist area and the non-tourist area, though the difference was not significant in the non-tourist area. Monkeys in both areas spent less time locomoting during the high tourist season. The possible explanation for this is that the monkeys remained still or "froze" around humans. The increase in tourism for a few months of the year may have been drastic enough that the monkeys responded by stopping all activity and waiting for the people to move on and leave them alone, a kind of "deer in the headlights" response. Alternatively, although the high tourist season would have been characterized by an increase in noises and disruptions, it would have been a more consistent noise than that of the low tourist season. In general, there would have been a constant presence of people, vehicles, music, etc. During the low tourist season, human disturbances would have possibly been more isolated, more startling, and more difficult to tune out, but during the high tourist season, human disturbances would have been more constant, even until the late hours of the night, and the monkeys may have been better able to ignore them. This would imply the opposite result than that mentioned above; monkeys would be

less likely to freeze around humans if the situation was characterized by a constant din, rather than isolated startling disturbances. An additional explanation for the reduced monkey locomotion during the high tourist season, is the fact that the high tourist season coincided with the long dry season, during which, monkeys in both areas were likely to move less. Presumably this was due to the need to minimize heat production through movement during the hottest times of the year, and could further explain the result seen during the high tourist season.

Weather seasons also influenced monkey behavior in both areas, though the differences were only significant in the tourist area. Monkeys in the tourist area spent less time locomoting and more time stationary during the dry seasons than during the wet seasons. Likewise, monkeys in the non-tourist area spent slightly more time stationary. In general, the trend in both areas, as seen in the analysis of seasonal differences overall, was that the monkeys spent more time stationary and less time locomoting and foraging during the dry season. This pattern has also been found during the dry season for red howlers in Venezuela (Sekulic 1982a). This could have been due to the weather itself, where hot and dry conditions lead monkeys to sit and rest rather than move and generate body heat. It could also be due to food availability and the fact that fruit was less available during the dry seasons in general. Monkeys in both areas during the dry seasons would have had little access to high-energy fruit and therefore would have minimized energy expenditure while resting to digest a diet of leaves and flowers. There was also less time spent foraging in both areas during the dry season, though neither difference was significant. With less movement and more time stationary, and with less fruit available leaving low-quality leaves as the only dietary option, it makes sense that the monkeys would have spent a little less time foraging.

Fruit seasons affected behavior patterns as well. Again, the differences in behavioral categories seen in the tourist area were significant, but they were not significant in the non-tourist area. Overall, monkeys in both areas spent less time stationary and more time locomoting during the high fruit season. This result complements that which was found for behaviors in the two weather seasons.

During the dry season, monkeys spent more time resting and less time traveling; fruit availability was low. Monkeys had less quick dietary energy, and more of a need to remain stationary to digest their diet of leaves. During the rainy season, monkeys in contrast were more active and less stationary; fruit availability was generally higher during times of rain. Monkeys had the energy to travel and the need to find patchy fruit trees across far distances.

Perhaps the most striking difference in behavioral patterns in response to tourist, weather, and fruit seasons between the two areas was the difference in statistical significance. Tourist area monkeys were shown to alter their behaviors to a greater extent in response to seasonal fluctuations than monkeys in the non-tourist area. Although the same behavioral trends were seen in the non-tourist area, they were not significant. This led me to conclude that the tourist area monkeys were more flexible in their behavioral responses to changing environmental conditions than were the non-tourist area monkeys. The behavioral pattern differences in the tourist area were altered significantly in all three seasonal comparisons, whereas the non-tourist behavioral patterns were not altered significantly in any of the three seasons. Perhaps the presence of tourists and the history of logging, construction, vehicles, and noises, has led the tourist area monkeys to alter their behaviors more readily in response to changing conditions than the non-tourist area monkeys who live in an area in which the habitat have not changed or been disrupted much in the past. The two behaviors that were altered consistently in the tourist area were remaining resting and moving. Monkeys there were able to choose between more rest and more travel in order to find preferred foods, deal with hot, dry conditions, and possibly most importantly, avoid disruptive tourists and tourist noises.

In all of the behavioral analyses discussed above, in each area, time spent foraging did not differ across any of the different seasons. Clearly foraging is an important behavior and should not vary considerably from week to week or season to season. The monkeys in each area spent about the same proportion of their time foraging year-round, though the tourist area monkeys spent more time foraging than the non-tourist area monkeys in general. Within the context of

foraging, I looked at whether food types eaten differed among various conditions, including areas, sexes, and seasons. I found no differences in food types eaten between areas, indicating that in general, monkeys in each area ate the same proportions of leaves, fruit, and flowers year-round.

There was no difference in plant parts eaten between the sexes in either area; thus males and females consumed the same proportions of leaves, fruit, and flowers during the year of observations. This makes sense given that troops of monkeys tended to forage together in the same tree before moving as a group to the next food tree. Occasionally, one or more members of a group ate leaves along the way to a new food tree, but this did not necessarily differ by sex. So, although females in both areas foraged more than males on average, they did not consume significantly different proportions of plant parts.

Tourist season seems to have had an effect on food types eaten in both areas, though only the non-tourist area was significant. Monkeys in both areas ate more leaves and less fruit during the high tourist season. Part of the reason for this lies in the fact that the high tourist season coincides with the low fruit season, leading monkeys in both areas to rely on leaves more than fruit during the high tourist season. The extreme difference found in the non-tourist area probably also has something to do with the fact that non-tourist area monkeys seemed more susceptible to changes in food availability than tourist area monkeys did in general (see the discussion of weather and fruit seasons below). Additionally, and perhaps most importantly, the extreme skew found in the non-tourist area in foods eaten by tourist season probably had a lot to do with my extremely small sample of foraging scans during the high tourist season. The high tourist season was a very short period of time, and it was difficult to observe foraging in general. During the high tourist season, I only observed foraging on 10 days in the non-tourist area, compared to 12 in the tourist area. This represented only 84 foraging observations in the non-tourist area, but 234 in the tourist area. The tourist area observations therefore were most likely a more accurate and realistic assessment of foods eaten during the high tourist season, while in the non-tourist area, small sample sizes precluded a realistic

assessment. The extreme skew of non-tourist area may also have accounted for the significant difference in food types eaten by tourist season overall as well.

Weather seasons had an effect on food types eaten in both areas as well, which was significant in the non-tourist area and partly significant in the tourist area. In both areas, monkeys ate more flowers (significant in both areas), and less fruit (significant only in the non-tourist area) during the dry season. This clearly had to do with food availability as fruit was less abundant during the dry season. Overall, the monkeys were eating food types based on what was seasonally available, in this case, less fruit and more flowers during the dry season. Monkeys in the non-tourist area, however, may have been subject to this availability more so than monkeys in the tourist area.

Fruit seasons obviously had an effect of the food types eaten by monkeys in both areas. In the non-tourist area, fruit and leaf percentages were significantly different between the high and low fruit seasons, while in the tourist area, flower percentages were significantly different. The actual differences in percentages of food types eaten between seasons were greater in the non-tourist area than in the tourist area, indicating that non-tourist area monkeys altered food preferences to a greater degree between the high and low fruit seasons than did the tourist area monkeys. While monkeys in both areas were certainly affected by food availability, and made food choices based on what was seasonally available, it may have been the case that monkeys in the non-tourist area were more susceptible to seasonal changes in food availability; hence the greater difference there than in the tourist area in percentage of time spent foraging on the three main plant parts, leaves, fruit, and flowers.

I also briefly described some of the vocalization patterns of the monkeys. I was interested in howling, but as this was not the focus of my study, I did not collect systematic data needed for detailed analyses. Despite that, I did conduct two analyses, regarding duration and timing of vocalizations. I did not find a difference in howl durations between the non-tourist and tourist areas, though I predicted that howls in the tourist area would be shorter on average due to interruption by noisy humans. This turned out not to be the case, and in fact the

durations were longer in the tourist area, which may actually reflect the need to call longer in order for the call to be heard over the noises of tourists. Therefore, though the result was not significant, tourism may have had an effect on call duration due to the sheer noisiness of the tourist area. As far as timing of howls, I found that the non-tourist area monkeys roared more per hour on average than did the tourist area monkeys, but that there was no difference between hourly bark tallies. The greater number of roars per hour in the non-tourist area may have been due to the greater number of roars observed overall in that area due to its expansive nature and the ease with which I could hear roars since the sound was not competing with the tractor motor, music, or some other tourist area distraction. I did not have enough systematic information about the calling behavior of the monkeys to investigate whether there was a connection between the longer, but less frequent howls in the tourist area. Perhaps monkeys there focused on quality rather than quantity. I would like to also investigate seasonal patterns and tourism effects in more detail in future studies. With a more rigorous data collection method, I will be able to do so.

In the behavioral analyses discussed above, it was the tourist area monkeys that altered their behavioral patterns in response to seasonal fluctuations. I argued that this was due in part to their need to alter their behaviors due to tourist presence, and that once they had the pattern of behavioral alteration for one stimulus, tourism, they could continue with the same alterations due to other stimuli, namely weather seasons and fruit availability. By increasing travel and minimizing rest, tourist area monkeys were able to search out the fruit they desired, even in the face of lower fruit availability, which explains why the proportion of fruit in their diet did not differ significantly between weather or fruit seasons. Non-tourist area monkeys on the other hand, did not alter their behavioral patterns significantly in response to changing seasons. In contrast, they altered their food items eaten in response to fluctuations in natural availability of fruit versus leaves and flowers. Non-tourist area monkeys have not had the kinds of habitat alteration, noise disturbance, or air pollution that monkeys in the tourist area have had to deal with. They still live out of the reach

of most human activities. Therefore, I conclude that they are more susceptible to natural seasonal cycles than monkeys in the tourist area due to their minimal need to respond to artificial cycles imposed on them by tourism.

The monkeys in the tourist area appear to have become habituated to tourist presence. It stands to reason that tourism had a greater impact on the daily lives of monkeys in the tourist area compared to monkeys in the non-tourist area. That was the definition of the two areas; and the tourist area experienced more frequent human disturbances and disturbances of a higher magnitude than did the non-tourist area. Tourist area monkeys responded less often and with a lower magnitude of response to human disturbances of all ranks. Non-tourist monkeys responded more often and with a higher magnitude of response, including more rank 4 responses, to infrequent human disturbances, including my presence, to which they did not have a chance to become habituated. However, the conclusion that tourist area monkeys were habituated and non-tourist area monkeys were not is not the only conclusion to be taken from this. Whereas tourist area monkeys responded less to noises and to my presence, they may have been altering their behavioral patterns to avoid or minimize the disturbance caused by the constant tourist presence. Tourist area monkeys traveled less during the high tourist season. They may have learned that by remaining still, tourists become bored with watching them and shouting at them, and are more likely to move on, leaving the monkeys in peace. During the entire year, of which most was during the low tourist season, tourist area monkeys spent less time stationary and more time traveling than monkeys in the non-tourist area. This may have been a way to move out of the view of tourists who tend not to follow monkeys into the forest. More movement could mean more avoidance of the tourists themselves, or avoidance of disturbing noises such as the generators or water pump, which were very loud and possibly disruptive to the monkeys. More travel also meant using more energy, which may have accounted for the significant increase in time spent foraging by monkeys in the tourist area versus the non-tourist area.

Within the framework of habituation, other conclusions can be made. Namely, males in both areas responded more often and with a higher magnitude of response, including more rank 4 responses, almost across the board for all disturbances, except to my presence, but including initial versus non-initial disturbances when compared to females (though not all comparisons were significant). Why would males react more to human disturbance? Perhaps they viewed human disturbances as a kind of attack on their group, such as they would encounter from an extragroup male or from a predator. Perhaps they were more vigilant to these attacks or disturbances in general because they were looking out for their females and offspring. I would have thought that females would respond more to disturbance because they have more to lose than males from attacks on their offspring. Maybe females were too busy foraging to care for their young. Males also exhibited stronger responses, including more rank 4 responses than females; again demonstrating that they were willing to go beyond vigilance behavior to actual deterrence of an outside threat.

Non-tourist area monkeys responded more often and with a higher magnitude of response to both initial and non-initial disturbances than did tourist area monkeys. Additionally, monkeys in both areas responded more often and with a higher magnitude of response to initial versus non-initial disturbances. The monkeys appeared to have been startled by many of the human disturbances they experienced and were more likely to respond at the onset of a disturbance than several minutes later. That does not mean that the monkeys did not respond to disturbances at all after their onset, and monkeys did still look towards noises or move away from a disturbance after it had been present for a few minutes. In regards to my presence, certain especially skittish troops often responded to my approach (an initial disturbance), but failed to settle down and responded even minutes later by moving for cover, even after I had been standing near them for several minutes. This of course happened more often in the non-tourist area than in the tourist area due to the lack of habituation to disturbance in general in non-tourist area monkeys.

Tourist, weather, and fruit season effects on the likelihood of monkey response to human disturbance were minimal. The one exception was in the tourist area, where monkeys were more likely to respond to human disturbance during the high fruit season. For monkeys who showed only minimal response levels during the rest of the year, it is interesting that they responded more when more high energy fruit was available. On the one hand, they would have had more energy to exhibit a higher response to human disturbance; on the other hand, they may have considered fruit patches to be worth defending from attack, regardless of whether the "attack" came from conspecifics or humans. Tourist area monkeys may have been responding to human presence more during the high fruit season as far as looking, grunting, or howling at possible usurpers of their fruit patch.

Another possible influence on monkey responses to human disturbance was the rank of the disturbance itself. I therefore investigated whether the frequency and magnitude of response fit the severity of disturbance. I found a significant difference among disturbance ranks and monkey responses, regardless of area or sex. A couple of interesting patterns also emerged from this analysis. First, although the pattern of response was what would be expected between disturbances of rank 1 and 3, meaning in general, the higher level of disturbance evoked a higher frequency and magnitude of response from the monkeys than the lower level of disturbance, the pattern of response to disturbances of rank 2 did not follow the same pattern. Rank 2 disturbances evoked fewer and lower magnitude responses than either disturbance 1 or 3. Perhaps I did not assign disturbances correctly by rank, or perhaps people talking or planes overhead (examples of rank 2 disturbances) were the types of disturbances to which the monkeys were already habituated, but my presence (rank 1 disturbance) was a novelty worth responding to. The latter idea is supported by the second interesting pattern: that the highest frequency of rank 1 response overall was in response to my presence. My presence was apparently more of a disturbance to monkeys in both areas because of its newness, and

was a disturbance at least worth looking at, than more common disturbances to which I had assigned higher ranks.

My final investigation into the influences on the likelihood for monkey responses to human disturbance was the creation of an ordinal logistic model. With it I assessed the influence of several predictors (tourist, weather and fruiting seasons, sex, disturbance rank, area, and initial status) on the likelihood of monkey response to human disturbance. When all predictors were taken together, only sex, area, and initial status had significant influences on monkey response; tourist, weather, and fruiting seasons, and disturbance rank did not have a significant influence. As I found in previous statistical analyses, males had higher responses than females, monkeys in the non-tourist area had higher responses than monkeys in the tourist area, and monkeys had higher responses to initial disturbances than to non-initial. Consistent with previous analyses, tourist, weather, and fruiting seasons, and disturbance level, however, did not strongly influence monkey response to human disturbance.

In conclusion, monkeys in both areas responded behaviorally to tourist presence. Tourist area monkeys responded over the long term by altering common behavioral patterns, and non-tourist area monkeys responded over the short term to individual human disturbances. Tourist area monkeys coped with tourist presence by altering their behaviors to minimize contact or disturbance by humans. Non-tourist area monkeys have had less exposure to tourists and thus have not become habituated to tourist presence. They instead respond more often to individual disturbances. Seasonal fluctuations also played a role in the behavioral and feeding patterns of monkeys in both areas. Additionally, despite the obvious habituation to human disturbance exhibited by monkeys in the tourist area, other interesting conclusions have been made regarding sex differences in frequency and magnitude of response, and regarding my presence and its response-evoking effect. As far as behavioral alterations due to tourism, monkeys in the tourist area appear to have been coping with the presence of human activities. Although they may have been altering their behavioral patterns in response to tourist presence, they appeared not to be suffering behaviorally,

and they appeared to be relatively undisturbed by day-to-day interruptions such as talking and loud music. This general monkey ability to remain flexible and adaptable in the face of habitat change or disturbance (in this case through tourism) mirrors that found in other populations of howlers, and at other sites (Clarke et al. 2002b, Horwich 1998, de Thoisy and Richard-Hansen 1996). Howlers as a genus remain flexible and adaptable creatures. The next chapter investigates the influence of tourist presence on monkey health.

Chapter V

Health Responses to Tourist Presence

A. Introduction

To monitor the health of the monkeys in the study areas, I made observations on the overall health of the individuals, taking into account bot flies on the body and injuries or scars, and I collected and analyzed urine and fecal samples. Often studies of parasites in wild nonhuman primates are short-term, opportunistic, and include small samples (for example: Kalema-Zikusoka et al. 2005, Muehlenbein 2005, Phillips et al. 2004, Karere and Munene 2002, de Thoisy et al. 2001, Fandeur et al. 2000, Kahre 1999, Karesh et al. 1998, Müller-Graf et al. 1996). In order to take into account seasonal fluctuations in tourist presence, weather patterns, and food availability, I collected fecal samples from monkeys throughout the whole year, though I typically was not able to identify the individual from which the sample came, or samples of particular individuals. Because red howlers at Brownsberg defecated and urinated as a group, most fecal and urine samples were mixed when they fell to the ground. Only occasionally was I able to identify the fecal sample of a specific individual on the ground. This usually happened when a single individual defecated from a different tree, or at a different time than the rest of the group. Most often however, entire groups of red howlers defecated from a single branch while all monkeys were lined up in a row. Sometimes, one to three individuals defecated from a single branch and then moved away and a couple others took their places, resulting in a single pile of mixed samples on the forest floor below the branch. Most studies of the intestinal parasites of free-ranging primate have occurred at sites in which fecal samples have been attributed to known

individuals (for example: Eckert et al. 2006, Vitazkova and Wade 2006, Weyher et al. 2006, Krief et al. 2005, Muehlenbein et al. 2003, Murray et al. 2000, Müller-Graf et al. 1996, Stoner 1996, Hausfater and Watson 1976), individuals captured for health assessment and thus distinct (de Thoisy et al. 2001, de Thoisy et al. 2000, Karesh et al. 1998, Muriuki et al. 1998), or individuals identified by age/sex class (Phillips et al. 2004). A few studies, however, reported parasite data at the group or species level (Kalema-Zikusoka et al. 2005, Hahn et al. 2003, Lilly et al. 2002, McGrew et al. 1989, Appleton et al. 1986), and it is these studies from which I modeled my parasite analysis. Many of these studies collected samples anonymously while trying to maintain random sampling; that is what I did with my sample collection.

B. Overall Health

Whenever possible, I made observations regarding the overall health status of individual monkeys and/or troops. Often monkeys were not in view for more than a few minutes, or stayed in one position for the entire time of observation, and I was only able to see one side or the backside of the monkey. During these occasions, I was not able to determine whether or not the individual had scars, bots, or injuries. When possible, I did note these observations as well as the presence of wounds, excessive scratching (signifying ectoparasites or skin irritation), patchy fur, and the like. I quantified all notations that I made of health status, both for numbers of individuals affected out of the total number of individuals in the group, and numbers of groups containing affected individuals out of the total number of groups studied. I also eliminated repeated observations of the same individual for conditions that would not change over a certain period of time and thus were not independent. For example, I eliminated two observations of a male with a patch of fur missing that were within two weeks of my first noticing the condition. Presumably, the same male had the same patchy fur for those two weeks, and thus the subsequent sightings were not independent from the first sighting.

1. Poor Health

Indicators of poor health, such as scars, wounds, or patchy fur, were more common in monkeys and groups in the tourist area than in the non-tourist area. Over the year of observations, I noted poor health conditions in 7 individuals from 5 groups in the non-tourist area, and 19 individuals from 6 groups in the tourist area. Out of approximately 18 groups studied in the non-tourist area, 5 groups with individuals that had indicators of poor health constituted 27.78% of all studied groups. Seven individuals from these affected groups constituted 28.00% of all individuals in those groups. Comparatively, 6 groups in the tourist area constituted 46.15% of the approximately 13 groups studied, and 59.38% of the total individuals in those groups were afflicted with indicators of poor health. Using an approximate number of total individuals studied in both areas (~92 individuals from 18 groups, and ~70 individuals from 13 groups in the non-tourist and tourist areas, respectively), 7.61% of all non-tourist area monkeys and 27.14% of all tourist area monkeys exhibited signs of poor health. Thus, a higher proportion of tourist area groups, and a higher proportion of individuals both from those groups, and overall in the tourist area, were afflicted with indicators of poor health compared to those in the non-tourist area (Table 5.1). The number of groups with individuals having indicators of bad health was not significantly associated with area (Fisher's Exact test: $P = 0.45$), but the numbers of affected individuals were significantly associated with area (Fisher's Exact test for proportion of individuals affected out of all individuals in affected groups: $P = 0.03$; and proportion of individuals overall: $P = 0.0010$). In general, monkeys in the tourist area had more indicators of poor health than monkeys in the non-tourist area. Due to the small samples, and the fact that I did not record lack of indicators of bad health consistently during the year, I was unable to statistically analyze the effects of tourist, weather, or fruit seasons on the likelihood of having an indicator of bad health.

Table 5.1: Poor Health Indicators by Area

	Non-Tourist	Tourist
No. Groups Affected	5 out of ~18	6 out of ~13
% Groups Affected	27.78%	46.15%
No. Individuals Affected out of Total in Affected Groups	**7 out of 25**	**19 out of 32**
% Individuals Affected out of Total in Affected Groups	**28.00%**	**59.38%**
No. Indiv. Affected out of Total Indiv.	**7 out of ~92**	**19 out of ~70**
% Indiv. Affected out of Total Indiv.	**7.61%**	**27.14%**

2. Bot Flies

Bot fly larvae, *Alouattamyia baeri*, infestations are common in howlers at Brownsberg and throughout the Neotropics, and howler monkeys seem to be especially susceptible to bot fly parasitism (Crockett 1998). Adult female bot flies deposit eggs on plant material likely to be contacted by howler monkeys. Eggs hatch following the appropriate stimulus (a quick increase in temperature and a higher carbon dioxide concentration), and enter the body through the nose and mouth. Larvae then migrate internally to sites on the neck and throat where they open larval pores for breathing (Milton 1996). Larvae remain under the skin of howlers for about six weeks, passing through three instars. When the third instar is completed, and the larva is about 2.4 centimeters by 1.5 centimeters in size, the larvae leave the warble and fall to the ground to enter the soil and pupate for over a month. Adult flies only live about five days and do not drink or eat. The entire life cycle lasts about thirteen weeks (ibid.).

Due to infrequent grooming, howlers are more susceptible to bot flies, and are less likely to remove bots once in the skin (Crockett 1998). However, grooming may not help prevent or treat a monkey's bot infestation, as first instar bot fly larvae are very small, and rapidly enter the bodies of their hosts, and once established in the skin, even humans with their dexterity and strength have a difficult time removing them (Milton 1996). I commonly found bot fly lesions on

the faces, throats, and shoulders of the monkeys I observed. Bot infections can be low (one larva per monkey) to high (more than six larvae per monkey), and occasionally greater than 12 larvae, and infections tend to peak during the rainy season (de Thoisy et al. 2001, Milton 1996). Howler monkeys develop a collagenous capsule (larval warble) to surround the larva, and exhibit an inflammatory response to the first instar stage. Howlers sometimes scratch third instar lesions drawing blood, and secondary infection is common in the larval capsule. Capsules remain open for several days after the larva leaves, often with a conspicuous discharge. The open capsule may attract screwworm flies, *Cochliomyia hominivorax*, the infestation of which usually results in septicemia or destruction of vital tissues (Milton 1996). The monkeys develop antibodies to both the first and third instar stages, which possibly limit larval numbers; only a small percentage of introduced larvae actually become established. Bot fly larval prevalence is strongly correlated with howler mortality, and immature individuals are affected most strongly, possibly because of their higher activity levels and energy requirements. High numbers of bot fly larvae are associated with reduced or absent fat reserves, indicating that nutritional stress may also play a role (Milton 1996).

During my observations of the monkeys, I noted the presence of all bot fly lesions observed, and their location on the bodies of the monkeys. As expected, bot lesions were most common on the faces and throats of the monkeys, with occasional bots on the back, belly, or chest. Fewer than six bot lesions at one time on one monkey represented a low infection, while six or more bot lesions on one monkey at one time represented a high infection (as per Milton 1996). The lowest number of lesions on a single infected individual was one, and many of the afflicted monkeys only had one bot; the highest number of lesions on a single individual was 12 on a juvenile male in the tourist area. Juvenile males appeared to be especially prone to heavy bot fly infections (personal observation). Mean numbers of bots per individual were not significantly different between the non-tourist and tourist areas (independent samples *t* test: $t = -0.51$, *df* $= 97$, *P* $= 0.61$) (Table 5.2).

Table 5.2: Number of Bot Fly Lesions per Individual by Area

	Mean No. Bots Per Indiv.	SD No. Bots Per Indiv.
Non-Tourist Area	2.52	1.79
Tourist Area	2.74	2.21

Occasionally, I was not certain that the lump I observed on a monkey's body was in fact a bot lesion. I included these uncertain numbers in my analysis, because the percent of uncertainty was similar between the two areas, with five out of 83 (6.0%) uncertain in the non-tourist area, and eleven out of 181 (6.1%) uncertain in the tourist area. The figures for "Total Number Lesions" (Table 5.3 below) are a best guess given my limitations in observing the monkeys. These numbers are conservative due to the fact that although I recorded all observations of bot lesions that I saw, I did not always get a full view of each monkey to determine with absolute certainty that bots were not present, or to count accurately the number of lesions on each body. I did however control for infection length, and eliminated redundant observations from my data for groups observed to be harboring bots on multiple occasions within the typical six-week incubation time of bot larvae in the body of a howler monkey. I identified distinct groups with reasonable confidence, and then reviewed the data to eliminate observations that could have been the same infection already recorded in a previous observation. I eliminated five observations from the non-tourist area data, and thirteen observations from the tourist area data, leaving only distinct groups harboring distinct infections through time. I could thus be assured that the counts of bot infestations were not artificially inflated due to the inclusion of redundant observations. I also used conservative counts of individuals infected over the year. If, for example, I observed an adult female in February with one bot lesion, then in April an adult male from the same group with a couple lesions, then in August an adult female with a bot lesion, I considered that to be two infected individuals from that group: an adult female and an adult male. Even if a group had two adult females, I could not tell them apart with several months in

between observations, so I considered the two subsequent observations of the females (or adult males or subadults) to be the same individual through time.

Comparisons by area of bot fly presence per group and individual revealed a general trend of higher infestations for monkeys in the tourist area. Over the year of observations, I noted the presence of bot lesions on 26 individuals from 11 groups in the non-tourist area and 33 individuals from 11 groups in the tourist area (Table 5.3). This constituted 61.11% and 84.62% of all groups studied in the non-tourist and tourist areas, respectively. Likewise, 44.07% and 54.10%, of individuals from the infected groups had bot lesions in the non-tourist and tourist areas, respectively. Additionally, out of all monkeys infected with at least one bot, 15.38% in the non-tourist area and 27.27% in the tourist area had high bot infections; the remaining monkeys all had low infections. Out of all monkeys studied in each area, approximately 28.26% of the non-tourist area monkeys and 48.57% of the tourist area monkeys were infected with bots. In sum, a higher proportion of tourist area groups, and a higher proportion of individuals both from those groups, and overall, were afflicted with bot lesions, and a higher proportion of infected individuals carried high infections in the tourist area than in the non-tourist area (Table 5.3). The number of groups with individuals having bot infections, the number of infected individuals out of total individuals in infected groups, and the number of infected individuals harboring low versus high bot infections were not significantly associated with area (Fisher's Exact test for proportion of groups infected: $P = 0.24$; for proportion of individuals infected out of all individuals in infected groups: $P = 0.28$; and for proportion of high and low infections: $P = 0.35$), but the number of individuals harboring bot larvae overall was significantly associated with area, with monkeys in the tourist area harboring more bot infections (Fisher's Exact test: $P = 0.02$).

Table 5.3: Bot Fly Infection by Area

	Non-Tourist Area	Tourist Area
Number Groups Infected	11 out of ~18	11 out of ~13
Percent Groups Infected	61.11%	84.62%
No. Individuals Infected out of Total in Infected Groups	26 out of 59	33 out of 61
% Individuals Infected out of Total in Infected Groups	44.07%	54.10%
Number Individuals Infected	**26 out of ~92**	**33 out of ~70**
Percent Individuals Infected	28.26%	47.14%
% Infected w/ High Infection	15.38% (4 indivs.)	27.27% (9 indivs.)
Total Number Lesions	83	181

Because I did not record lack of bot infections consistently during the year of data collection, I was unable to statistically analyze the effects of tourist, weather, or fruit seasons on the likelihood of having an indicator of bad health. However, I can summarize the infections by season for descriptive purposes. I predicted that bot infections would have been higher during the rainy season due to the need for eggs and larvae to remain viable and not dry out. I also predicted that infections would be more common during the low fruit season due to the potential lack of dietary energy for fighting bot infections. There were not enough bot infection observations during the high tourist season to make any real conclusions, though if tourism increased the stress levels of the monkeys, I would have expected higher infection rates during the high tourist season. In the non-tourist area, 18 out of 33 individuals harboring bot larvae (54.55%) (repeated infections counted individually) were observed during the rainy seasons, and 15 out of 33 individuals with bots (45.45%) were observed during the dry seasons. Likewise, in the tourist area, 43 out of 66 individuals with bot infections (65.15%) were observed during the rainy seasons, and 23 out of 66 (34.85%) were observed during the dry seasons. These observations support the prediction that bot infections occur at higher rates during the rainy seasons. However, the

incidences of high and low infections did not fit this pattern. In the non-tourist area, one out of four high infections (25.00%) occurred during the rainy seasons, and three out of four (75.00%) occurred during the dry seasons; in the tourist area, three out of ten high infections (30.00%) occurred during the rainy seasons, and seven out of ten (70.00%) occurred during the dry seasons. Basically, there were more high infections during the dry season but more infections in general during the rainy season. Perhaps some individuals were more susceptible to bot infections already and had flare-ups during the dry season. Perhaps tourist presence or fruit availability also played a role. Fruit availability seems to have had an effect in the non-tourist area, where 21 out of 33 infected individuals (63.64%), and all four of the high infections (100.00%) occurred during the low fruit season, but not as much in the tourist area, where only 26 out of 66 infected individuals (39.40%) but seven out of ten high infections (70.00%) were observed during the low fruit season. Perhaps food availability did not play a role, and random effects such as my ability to see bots, or my time spent in each area during the different seasons, could have had more of an effect.

3. Responses to Parasites

Everyday actions may help to lessen the annoyance and health risks of parasites. These actions include slapping, scratching, and flicking the tail over the body to prevent insects from feeding on the skin. A study of free-ranging mantled howler monkeys on Barro Colorado Island in the Republic of Panama illustrated that slapping at insects can be very energetically costly (Dudley and Milton 1990). Monkeys were found to use their hands, feet, and tails to slap at pests, though the hand was most common. A conservative estimate of limb slapping in that study was 1500 times per day, though the true number may be at least one-third higher. Energy estimates found this to represent an average of 4.6% of metabolism after basal metabolism is subtracted. Dudley and Milton (1990) suggest that this amount of activity may elevate metabolism significantly. Feeding patterns and food choices may in turn be affected in order to meet the minimum metabolic requirements of insect avoidance. I witnessed frequent hand slapping and tail flicking by red howlers in Suriname, as well as scratching for

several minutes at a time. The tail flick was used quite frequently to scatter hovering insects, sometimes as much as 20 times or more during a ten-minute period. Grooming also requires energy, but can help reduce the impact of ectoparasites on blood loss and skin irritation.

Ectoparasites such as ticks can also greatly affect behavior and health of primates. For example, tick infestations are an important cause of infant mortality in chacma baboons, *Papio ursinus*, in Namibia, sometimes causing more than 50% of infant deaths (Brain and Bohrmann 1992). Grooming is an obvious way to reduce tick numbers, though these baboons do not seem to take advantage of it, possibly due to the pain of tick removal and a dislike of the taste of ticks. The study troop also failed to avoid areas of highest tick populations and continued to reencounter the parasites (Brain and Bohrmann 1992). The red howlers act similarly to these baboons in that they do not groom often enough to get rid of ectoparasites.

Researchers in Venezuela inspected free-ranging red howler monkeys for ectoparasites and found nits and lice on them, which were confined to the beard (Sánchez-Villagra et al. 1998). Troops with higher rates of allogrooming had lower infestations of lice, and in an earlier survey, researchers found that individuals with the highest infestations were solitary or recently solitary. This implies that grooming partners are critical to the removal of ectoparasites. Allogrooming in white-handed gibbons of Thailand was found to serve a hygienic function as well (Reichard and Sommer 1994). Gibbons groomed upper body parts, such as the face and head, of others more often than lower body parts. Upper body parts were more likely to be infested with ectoparasites due to the habitually upright posture of the gibbons (ibid.). Likewise, Japanese macaques were more likely to groom each other's backs, outer arms, and outer legs, which were areas of the body with higher lice and louse egg infestations (Zamma 2002).

In Venezuela, allogrooming rates of red howlers varied considerably among groups (Sánchez-Villagra et al. 1998). This variation was attributed to many factors including group history, social tensions, and group demography.

Although allogrooming was found to have a hygienic function, it also served a social function. Grooming pairs were non-randomly associated, different age/sex classes varied in grooming rates, and the parts of the body receiving the most grooming attention were not always the parts with the highest ectoparasites counts (Sánchez-Villagra et al. 1998).

I recorded all occurrences of allogrooming during the year of behavioral observations, and witnessed 28 instances in the non-tourist area, and 24 in the tourist area. I was not able to determine grooming rates due to the many hours during which I observed monkeys that were partially or completely obscured; they could have been grooming each other and I would never have known. However, I was able to compare allogrooming durations between the non-tourist and tourist areas. There was no difference in allogrooming bout duration between areas (Table 5.4) (independent samples t test: t = -1.52, df = 50, P = 0.14). I saw clearly who was grooming whom on all 28 grooming bouts in the non-tourist area, but on only 18 of the 24 bouts in the tourist area. Using this subset of bouts, I compared who was grooming whom between areas (Table 5.5). I found that non-tourist area adult males (n = 13) were equally as likely as adult females (n = 14) to groom another individual, but females were more likely to groom other females (n = 2) or subadults (n = 4) than males were likely to groom other males (n = 0) or subadults (n = 1). In the tourist area, adult females were almost three times as likely to groom another individual (n = 13) as adult males and subadults combined (n = 5). Additionally, adult females in the tourist area almost equally groomed adult males (n = 4), other adult females (n = 5), and subadults (n = 4), whereas adult males more often groomed adult females (n = 3) than subadults (n = 1), and never groomed another male. The individual doing the grooming was not associated with area, nor was the individual receiving the grooming (Fisher's Exact test for groomer: P = 0.21; and for groomee: P = 0.68). Females were similar in their grooming behaviors by area, and so were males (Fisher's Exact test for female grooming behavior: P = 0.15; and male grooming behavior: P = 0.18). Grooming and being groomed did differ by sex, with females grooming

other females, males, and subadults, but males preferentially grooming females (Fisher's Exact test: $P = 0.0001$).

Table 5.4: Allogrooming Bout Duration (sec) by Area

	Allogrooming Bout Duration	
Area	Mean	SD
Non-tourist	77.39	60.85
Tourist	108.17	84.83

Table 5.5: Groomers and Groomees by Area

	Groomer			**Groomee**		
Area	**% AF**	**% AM**	**% Other**	**% AF**	**% AM**	**% Other**
Non-Tour	50.00	46.43	3.57	53.57	28.57	17.86
Tourist	72.22	22.22	5.56	44.44	27.78	27.78
Total	58.70	36.96	4.35	50.00	28.26	21.74

C. Urinalysis

Howlers typically urinate after waking in the morning, or following an afternoon nap. It was at these times that I collected samples from several individuals whenever possible. To collect and analyze urine immediately in the field, I pressed the collection dipstick (Chemstrip 10 UA, Roche Diagnostics Corporation) to the surface of urine-splashed vegetation underneath the monkeys until enough urine had saturated the reagent patches on the dipstick. Once moistened, the reagent patches produced a color-change reaction. After the appropriate time (up to two minutes for some tests), I analyzed the urine samples by reading the color-changed reagent patches directly from the dipstick. I assessed ten urine characteristics for each sample: specific gravity, pH, leukocytes, nitrite, protein, glucose, ketones, urobilinogen, bilirubin, and blood. The urinary dipsticks were those routinely used in medical laboratories to evaluate human health status (Figure 5.1). They can be used for health assessment of nonhuman primates due to similar physiology (Knott 1996). I

tested methods of urine collection during prior field seasons, and though I planned to collect urine from vegetation using disposable pipettes, and then drip the urine onto the reagent patches, this turned out to be impossible. Most of the urine excreted by the monkeys was absorbed quickly into the leaf litter, and I was left with only the splatters remaining on surrounding leaves and litter. Collection of urine would have been more sanitary, and fewer contaminants would have been introduced to the sample, had I used pipettes. For this reason, I occasionally tested my collection method with pure water, on the same types of leaves, to make certain that my results were not somehow due to contaminants, or chemicals from the leaves themselves. Every few weeks I tested the quality of readings in both the non-tourist and tourist areas, and these always came back negative for contaminants. Additionally, each dipstick includes a blank reagent patch as a compensation area, and I made note of discoloration on this patch when applicable.

Figure 5.1: Chemstrip 10 UA, Roche Diagnostics Corporation (shown next to bottle)

Each of the 10 tests has a range of possible results from 2 to 7 categories (Table 5.6). Additionally, I recorded the date, time of urination, time of collection,

method of collection, urine color, presence of any debris or feces, location, and age/sex class (adult male, adult female, juvenile, or infant), and group, if known.

Table 5.6: Chemstrip 10 UA Possible Results for each of the Ten Tests

Test							
SG	1.000	1.005	1.010	1.015	1.020	1.025	1.030
pH	5	6	7	8	9		
Leukocytes	neg.	trace	+	++			
Nitrite	neg.	pos.					
Protein	neg.	trace	+ 30	++ 100	+++ 500 mg/dL		
Glucose	norm.	50	100	250	500	1000 mg/dL	
Ketones	neg.	+ small	++ mod.	+++ large			
Urobilinogen	norm.	1	4	8	12 mg/dL		
Bilirubin	neg.	+	++	+++			
Blood	neg.	about 5-10	about 50	about 250 Ery/µL			

The 10 tests on the dipstick measured presence of disease, trauma, or infection in the study subjects. Specific gravity (SG) measures the density of urine and indicates the kidney's ability to re-absorb water and the hydration status of the monkey, while pH reflects the kidney's ability to regulate the acid-base balance of the body, and highly acidic urine may indicate infection (Knott 1996). Leukocytes in the urine signify a bacterial infection in the renal/genitourinary system, or indicate general inflammatory disorders, while nitrite in the urine demonstrates the presence of bacteria. Proteins in the urine

may indicate a breakdown of muscle, strenuous physical exertion, or systemic disease. Glucose in the urine demonstrates diabetes mellitus in humans, and ketones indicate excessive fat metabolism as a result of inadequate carbohydrate intake (ibid.). The presence of bilirubin (a degradation product of hemoglobin) in human urine indicates liver disease, while urobilinogen (a degradation product of bilirubin) occurs in the urine when liver cells are damaged. Blood in the urine may indicate disease or damage to the genitourinary tract, while hemoglobin may result from trauma or severe infection (Krief et al. 2005, Knott 1996). It should be noted that I did not collect information directly on the presence of bacteria or viruses, but if the general health of the monkey was affected, the various tests of the urinalysis could detect it. Conclusions could be made about health of the monkeys based on the amount of each substance that was found in the urine. Healthy individuals should not excrete significant levels of any of these substances (Roche Diagnostics Corporation, Chemstrip 10 UA, package insert).

As mentioned above, red howler monkeys urinate and defecate as a group from a single branch, or a few closely-spaced branches. Distinguishing one individual's urine from another's was therefore impossible, so I resorted to collecting samples from under the monkeys from a "group splash area." I spread out the samples I collected in order to maximize the likelihood that I was collecting urine from different individuals. I also collected a couple samples from each group when possible, even though the samples may have been from the same individual, or a mix of individuals. Before analysis, I reviewed the data and eliminated redundant samples (i.e. duplicate samples from the same group and urination event) from each urine collection. Even though I collected urine from different areas of the understory vegetation, I was not assured that urine from multiple individuals did not mix, and in most cases all samples collected from one group had the same measurements; this was most likely due to the mixing of urine, and the fact that the monkeys live together and would have the same dietary intake and exposure to diseases. Therefore, one representative sample per group per urination event was sufficient to denote the health status of the

group at that time, and I removed fifteen redundant samples from the non-tourist area data and twelve redundant samples from the tourist area data. Even though urine characteristics can change throughout the day, I was looking at broader patterns of health than would change from day to day, such as malnutrition, serious injury, breakdown of muscle, or infection. Therefore, I also eliminated any samples that were collected within a week of a previous sample for the same group (two from the non-tourist area and three from the tourist area), which in almost all cases also had the same measurements as the previous samples. That left me with 18 samples in the non-tourist area and 23 in the tourist area. I collected at least one sample from each of nine groups in both areas, collecting up to four samples per group throughout the year. I collected at least one sample in each area during each of the tourist, weather, and fruit seasons.

The results for nitrite, ketones, and bilirubin were all negative for all samples taken in both the non-tourist and tourist areas. Likewise, urobilin was normal, pH was 5, and there was no hemoglobin (a subset of the blood measurement) found in any of the samples. Because all of these values were the same for all samples, I eliminated them from further consideration. Additionally, only one sample from all samples collected was positive for leukocytes. This sample was from the non-tourist area and was also positive for blood. Because there was no sample positive for leukocytes in the tourist area, I did not think that a comparison of leukocyte presence by area would be instructive, and in fact, I found that there was no significant association between the presence of leukocytes and area (Fisher's Exact test: $P = 0.44$). Specific gravity, protein, glucose, and blood all had enough variability among samples that I could analyze them between sites using Fisher's Exact tests. None of the four urine measurements, including specific gravity, protein, glucose, and blood, were significantly associated with area (Fisher's Exact test for SG: $P = 0.49$; protein: $P = 0.13$; glucose: $P = 1.00$; and blood: $P = 1.00$). Although there was no difference between areas, the tourist area had more samples that had high specific gravity and high protein levels, and more samples that were positive for blood compared to the non-tourist area. These were not significant, and I did collect five more

samples in the tourist area than in the non-tourist area, which might have increased my chances of finding higher measurements there. I additionally investigated whether tourist, weather, or fruit seasons influenced urine characteristics by area and overall (labeled "both" in the table), and found very few significant influences (Table 5.7). The one possible significant influence on urine parameters was fruit season. There were more urine samples with higher protein values during the low fruit season in both the tourist area and overall (Table 5.7). High levels of urine protein may indicate a breakdown of muscle, strenuous physical exertion, or systemic disease. There was no real reason why monkeys in the tourist area would have been traumatized in this way, and during the low fruit season they actually got more rest and exerted themselves through travel less often than during the high fruit season. Perhaps the increased urine protein levels seen during the low season in the tourist area may have been due to the body's need to eliminate excess protein ingested through a diet of high-protein young leaves during the period of low fruit availability. Additionally, there were significantly more urine samples with high specific gravity measurements overall during the low fruit season. Again, this may have been related to a diet high in dry leaves and low in juicy fruits. Monkey urine may have been denser during the low fruit season because their bodies could spare little water to dilute it. The overall lack of a significant difference in urine parameters in response to seasonal change was probably partly due to small sample sizes of urine measurements, but mostly it was probably due to the fact that urine characteristics do not change drastically due to natural seasonal fluctuations, or for that matter, due to tourism.

Table 5.7: *P*-values for Fisher's Exact Tests of Seasonal Influence on Urine Measurements

	Tour. Seas.			Weath. Seas.			Fruit Seas.		
	NT	T	Both	NT	T	Both	NT	T	Both
SG	1.00	1.00	0.88	1.00	0.65	0.64	0.13	0.12	**0.02**
Prot.	0.91	0.48	0.42	0.94	0.90	0.98	0.13	**0.0003**	**0.0003**
Gluc.	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Blood	1.00	0.53	0.54	1.00	1.00	0.55	0.33	0.46	0.20

D. Fecal Analysis

In addition to collection and analysis of urine samples from the monkeys, I collected and analyzed fecal samples. Wild populations of howlers are known to harbor various intestinal parasites including, but not limited to, amoebas: *Entamoeba* spp.; protozoa: *Enteromonas* sp., *Giardia* sp., *Trichomonas* sp., *Toxoplasma* sp.; trematodes (flukes): *Controrchis biliophilus*; cestodes (tape worms): *Raillietina* sp.; and nematodes (round worms): *Strongyloides* sp., *Necator americanus*, *Ascaris* sp., *Trichostrongylus* sp., *Ancylostoma* sp., *Trypanoxyuris minutus*, among others (Eckert et al. 2006, Vitazkova and Wade 2006, de Thoisy et al. 2001, Stuart et al. 1998, Stuart et al. 1990). Evidence of these intestinal infections can be found in the form of cysts or eggs in the feces. Howler monkeys defecate upon waking in the morning or from a nap, at which times I collected specimens from several individuals. Additionally, I opportunistically collected samples found on the ground when these samples appeared to be less than 24 hours old. I looked for the prevalence of infection (number of samples infected per number of samples examined), and for each sample, the intensity of infection (number of parasites of a particular species in each host) for each area of my study, over the course of one year. Intestinal parasite prevalence in the wild can range from about 50% (Stuart et al. 1990) to 100% (Stoner 1996) but intensity is more variable. I also looked at species richness which is a measure of the number of unique parasite species recovered from an individual's fecal sample (Muehlenbein 2005).

I collected fecal samples directly from the ground or vegetation, minimizing contamination with urine, soil, or gravel. Upon collection, I recorded the date, time of defecation, time of collection, substrate from which the sample was collected: gravel, log, leaf litter, etc., consistency: diarrheic, soft/pasty, solid/well-formed, or dry/hard from constipation as per Krief et al. (2005), location, color, presence of pinworms, and age/sex class and group, if known. When I witnessed a defecation event, I was able to note the degree of overlap of fecal material. As mentioned above, red howler monkeys in Suriname tend to defecate as a group from a single branch or a few nearby branches, and identification of an individual monkey's fecal material is near impossible. Occasionally I got lucky and a single individual defecated at a time distinct from the rest of his or her group, or defecated from a separate tree under which I was able to collect a fecal sample and assign it to that particular individual's age/sex class. More often than not, however, all fecal material for a particular troop of howlers was mixed on the ground under the communal defecation branch. In that event, I collected up to 4 or 5 samples from the group, while attempting to take samples from spatially distinct piles of feces (i.e. piles with the most likelihood of being from different individuals). Sometimes, I happened upon relatively fresh fecal material lying in the road or just off the path, from which I collected a few samples. Of course, in this event, I was not able to determine which group or individuals left the samples, but I recorded the geographical locations of the samples, to narrow down the subjects that could have left them. Due to the overlapping nature of howler monkey fecal material and my collection of the material found opportunistically on the ground, it is highly probable that the same individual was sampled more than once. Before conducting analyses on the fecal material, I used information I recorded regarding number of individuals in each group and timing and location of defecations to summarize fecal analyses at the group level on at most an approximate six-week cycle (see below).

1. Pinworms

One of the parasitic nematodes commonly occurring in the digestive tract of the howler monkey, and easily found on fecal samples is the pinworm,

Trypanoxyuris minutus (Vitazkova and Wade 2006, Hugghins 1969, Pope 1966, personal observation) (Figure 5.2). Pinworms are a common problem in humans, especially children, and children may spread infection to their families (Roberts and Janovy Jr. 2000). Pinworms often cause no obvious negative effects, however, infection is uncomfortable and itchy, and the presence of large numbers of worms may be related to other health issues and/or an immune system unable to fight off the worm infection. Worms can cause damage to both the intestinal mucosa, resulting in inflammation and bacterial infection, and the perianal skin, where eggs cause itching, which, if indulged, can result in bleeding, infection, and discomfort (ibid.). Other symptoms have also been reported in human children, including nervousness, restlessness, loss of appetite, nausea, and vomiting. All pinworms I observed on the fecal samples of the monkeys were females, which measure on average 8 millimeters to 13 millimeters in length (males are only 1 mm to 4 mm long), and are easily identified by their long, pointed tails, from which they get their name (Roberts and Janovy Jr. 2000). Adult worms usually congregate at the end of the digestive tract, but they can wander around from the stomach to the anus. They attach themselves to the mucosa and feed on epithelial cells and bacteria. Females migrate to the outside of the anus to lay eggs, which stick to the perianal skin. The entire lifecycle of the pinworm is 15 to 43 days (ibid.). Infection in humans most often occurs when eggs are ingested, then hatch and mature by the time they reach the terminus of the digestive tract. Eggs can also hatch while on the perianal skin, and juvenile worms may wander into the anus and up to the intestine in a process called retroinfection (Roberts and Janovy Jr. 2000). Howler defecation patterns minimize contamination of food sources (see latrine observations below), and thus fecal-oral transmission; and the monkeys do not groom themselves or others often, and especially not in the perianal area, thus they probably do not remove eggs from the skin. For these reasons, I expect that retroinfection is the most common route of pinworm infection in howler monkeys. Eggs can also be wind dispersed, and they do remain viable in moist conditions for up to a week,

though it is unlikely that eggs dropped to the forest floor could be blown back up into the canopy.

Figure 5.2: Two Adult Female Pinworms on a Leaf (scale is mm)

I often found pinworms on the fecal material that I collected, or nearby on leaves or leaf litter. Usually, these worms were still alive and were moving around. I recorded the presence of pinworms for all samples collected, and I noted whether I found pinworms away from the fecal material. It should be noted that the lack of pinworms on fecal material does not mean a lack of a pinworm infection. The monkeys would not necessarily eliminate worms from their bodies even if they were positive for infection. That being said, the pinworms I found could still be compared between areas, but total infection rates were low estimates at best. I collected 181 fecal samples in the non-tourist area and 189 samples in the tourist area (Table 5.8). Of these, 25 samples (13.81%) in the non-tourist area and 33 samples (17.46%) in the tourist area had pinworms present on them at the time of collection. That is not to say that 25 and 33 individuals harbored pinworm infections, but because I tried to collect fecal material from distinct, if unidentifiable, individuals, the true numbers are not that far off. Admittedly, some of the samples on which I found pinworms may have been collected from the same individuals or groups harboring pinworm infections already recorded from previous samples. To eliminate this redundancy, I first eliminated superfluous group samples and left a single representative sample per

group per defecation event (5 samples eliminated from the non-tourist area and 6 from the tourist area). I then paired samples collected from similar locations, and thus most likely from the same groups or individuals. When samples taken from the same group/location were collected within six weeks of each other, the maximum lifecycle of the pinworm, I eliminated the second set of samples from my analysis. When samples taken from the same group/location were collected more than six weeks apart, I allowed these samples to be included as independent infections. Presumably, even though samples collected after a six-week delay may have been collected from previously sampled individuals and groups, pinworm presence would have resulted from a re-infection or new infection, and thus could be considered independent. I thus eliminated 3 more samples from the non-tourist area and 6 more from the tourist area. Seventeen independent infections remained in the non-tourist area and 20 remained in the tourist area (Table 5.8). To report the number of pinworms found on monkey fecal material for a single "infection period" per group, I added the total number of pinworms found on all samples taken for that group during the six-week period. The total number of pinworms observed in the non-tourist area was 38 and in the tourist area was 46. This equated to an average of 2.24 pinworms per group per infection period in the non-tourist area, and 2.30 in the tourist area (Table 5.8). Average infection was therefore not significantly different between areas (independent samples t test: t = -0.08, df = 35, P = 0.94).

Table 5.8: Pinworm Infection by Area

	Non-Tourist Area	Tourist Area
No. Fecal Samples Collected	181	189
No. Samples with Pinworms	24 (13.26%)	33 (17.46%)
No. Total Groups Studied	~18	~13
No. Groups Sampled	~15 (83.33%)	~11 (84.62%)
No. Sampled Grps. w/ Worms	10 (66.67%)	10 (90.91%)
No. Indep. Fecal Collections	45	40
No. Independent Infections	17 (37.78%)	20 (50.00%)
Pinworms per Indep. Infection	2.24	2.30
Ave. No. Collections per Group	3.00	3.64
Total No. Pinworms	38	46

I was unable to collect fecal material from all groups for which I also had observed behavior; however, I sampled the fecal material of 15 groups out of a total of approximately 18 groups in the non-tourist area (83.33%), and 11 of approximately 13 groups (84.62%) in the tourist area. Of the 15 sampled groups in the non-tourist area, 10 had pinworms (66.67%), and of the 11 sampled groups in the tourist area, 10 (90.91%) had pinworms (see Table 5.8 above). Even though a higher proportion of the sampled groups in the tourist area had pinworms when compared to the non-tourist area, this was not a significant difference (Fisher's Exact test: $P = 0.20$). I then went through all the collections of fecal material during the year and eliminated collections for the same group within about the six-week window already established for pinworm infection. What remained was a list of fecal collections per group, including the collections that were positive for pinworms, on at most an approximate six-week basis: 45 separate collections (including 17 or 37.78% that were positive for pinworms) in the non-tourist area and 40 (including 20 or 50.00% that were positive for pinworms) in the tourist area. I collected group fecal samples from one to eight times per group throughout the year, with an average of 3.00 collections per group in the non-tourist area, and 3.64 collections in the tourist area (see Table

5.8 above). I then looked at whether or not monkeys in the non-tourist area were more or less likely than monkeys in the tourist area to carry pinworms given a somewhat regular sampling of the feces for each group. I found no association between pinworm infection and area with this relatively consistent sampling of the groups (Fisher's Exact test: $P = 0.28$). In general, tourist area monkeys were infected at higher rates, and with higher numbers of pinworms on average than non-tourist area monkeys, but these differences were not statistically significant.

Using the 85 independent fecal collections throughout the year, I investigated whether tourist, weather or fruit seasons influenced the likelihood of a group having at least one member with a pinworm infection. None of the three seasons was significantly associated with pinworm infections either within areas or overall (labeled "both" in the table) (Table 5.9). Although the influence of the seasons on pinworm infection was not significant, there were more pinworm infections during both the rainy seasons and the low fruit season in both areas and overall. This may have been due in part to the moist environment providing a suitable environment for pinworms, and the lack of monkey ability to fight off a pinworm infection due to lower energy intake during the low fruit season.

Table 5.9: *P*-values for Fisher's Exact Tests of Seasonal Influence on Likelihood of Pinworm Infection

	Tour. Seas.			Weath. Seas.			Fruit Seas.		
	NT	**T**	**Both**	**NT**	**T**	**Both**	**NT**	**T**	**Both**
Infect	0.32	0.24	0.12	0.76	1.00	0.67	1.00	0.11	0.27

2. Ova and Parasites

I collected, stored, and analyzed fecal samples according to the merthiolate (thimerosal)-iodine-formalin (MIF) procedure (Meridian Bioscience, Inc.) (Figure 5.3). The MIF procedure is especially good for field surveys where samples can be collected within one hour of passage, though, as mentioned above, some of my samples were collected opportunistically when I encountered

them on the road or forest floor. I only collected samples that appeared to be fresh, but I do not know the exact age of all specimens. I collected approximately one gram of fresh fecal material and added it to the vial of MIF solution. Adequate mixing of sample and solution was critical, so I agitated the vials after the sample was sealed inside. I collected a total of 181 and 189 samples in the non-tourist and tourist areas, respectively. Before analyzing any of the samples, I selected six from each area to practice on. These samples were ones that I had deemed too old for collection but collected anyway, or ones that did not contain enough fecal material to make a full sample. Because I collected several samples from a single group defecation event, I also decided not to analyze all samples due to the redundant nature of parasite infections within "families" (Cheryl Westin personal communication). To confirm that the fecal material of all group individuals was in fact similar, I analyzed all the samples collected from six groups in each area. I did not know which sample was from which group or area while I analyzed them, but after completion of the twelve groups, I confirmed that, although I did not find many parasites, the other fecal artifacts were consistently similar among the samples. Therefore, I eliminated 11 redundant group specimens from the non-tourist area and 12 specimens from the tourist area. When conducting the fecal analyses, I only knew the specimen number and not the area from which the specimen came. In this way I prevented myself from biasing the results based on my expectations for each area. I analyzed 147 specimens in the non-tourist area and 157 in the tourist area, using the procedure described below.

Figure 5.3: MIF Bottle (photo by Meridian Diagnostics, Inc.)

Before analysis, the vials were allowed to sit undisturbed for at least one hour, after which the specimen formed three layers: a clear orange upper layer consisting of formalin, merthiolate, and water; a thick, pale orange or creamy yellow middle layer, one to two millimeters thick, which may trap some protozoa or helminth eggs; and a third layer of deeper-staining particulate matter in which eggs and protozoa could be found (Garcia and Bruckner 1993, Meridian Bioscience, Inc., MIF, package insert). With a disposable pipette, I made direct smears from both the middle and bottom layers. I placed a small amount of sample on a slide and covered it with a coverslip. I examined 40 high-dry (40x) fields for each coverslip, evenly spaced over the whole coverslip, noting presence of parasites when found. Both protozoa and helminth eggs should have been seen on this wet smear, though I fear that during storage of the specimens before analysis, much of the protozoan material may have degraded over time. I made two coverslips per fecal sample (one from each side of the vial), and reported specific species of parasite found as well as their life stage (egg, cyst, or larva). For 27 (14.92%) of the non-tourist area specimens and 22 (11.64%) of the

tourist area specimens I only analyzed one coverslip per sample. For these samples I looked at 50 high-dry fields and additionally conducted two low-power (10x) passes scanning for parasites. I prioritized my samples based on freshness, redundancy, and possibility of contamination, and analyzed the best samples first. I made several passes through the samples analyzing ones I had skipped previously, until I reached a point at which I was left with lower-quality samples. Some of these, such as the redundant group samples mentioned above, I chose not to analyze. Others were those for which I only analyzed one coverslip (described above). I therefore analyzed the most representative selection of the samples during the time available.

Identification of possible parasites in the fecal material proved to be a challenge. I did have help, both in the form of an assistant (Cheryl Westin) who had years of microbiological experience and some parasitological experience, and books and reference photos from several sources, both for parasites in general, and specific to howler monkeys (Roberts and Janovy Jr. 2000, Stuart et al. 1998, Stoner 1996, Garcia and Bruckner 1993, WHO 1991, Stuart et al. 1990, Toft 1986). Possible parasites were sketched and many were photographed to be later viewed by William Appleby of Metropolitan Medical Laboratory in Moline, Illinois. Bill confirmed that at least two species of worm and no species of protozoa were found in the fecal material, but he was hesitant to confirm species due to his inexperience with nonhuman primate parasitology. I am relatively confident about the identification of a Strongyle-type nematode egg (Figure 5.4). Eight of these eggs were found in the non-tourist area, and at least two were found in the tourist area. Without the presence of an adult nematode, definitive identification of the eggs is tentative at best, but howlers have been known to harbor hookworms, *Ancylostoma* spp., as well as two or more other species in the order Strongylida (see Stuart et al. 1998). The typical lifecycle of a strongyle nematode is direct, only involving one host (Roberts and Janovy Jr. 2000). The juveniles of some species need to come in contact with the skin, into which they burrow and begin their migration through the body of the host, arriving finally in the small intestine. Most human infections with the burrowing species, such as

Necator americanus, occur when the feet and hands come into contact with soil containing infective juveniles. In other species, infection can occur orally when infective juveniles are swallowed, and this, as opposed to soil contact, is what probably happened in the howler monkeys. Juveniles are very susceptible to desiccation; therefore, I predict that new infections are only possible during the rainy seasons. However, eggs are not produced immediately, and there can be a lag of up to five weeks or more before egg production (Roberts and Janovy Jr. 2000). Additionally, adult worms can live from five to fifteen years (ibid.), so they could be producing eggs for many years. Thus, I do not necessarily expect a peak in strongyle eggs in the feces of the monkeys during the rainy seasons. Adult worms feed on blood in the intestinal wall and symptoms of strongyle infection include abdominal pain, loss of appetite, hemorrhage, mild anemia, and the desire to eat soil (Roberts and Janovy Jr. 2000). There is minimal immune response to the presence of worms, and poor nutrition can also exacerbate symptoms.

Figure 5.4: Photomicrograph of an Embryonated Strongyle-Type Egg from a Non-Tourist Area Monkey

The second species of intestinal worm found in the howler monkey fecal samples was possibly from the order Oxyurida, of which the howler pinworm, *Trypanoxuris minutus*, is a member. I only had one photograph of a howler oxyurid to compare with my findings (Eckert et al. 2006), to which my specimens were similar. I therefore tentatively identified these eggs as a species of oxyurid, possibly the howler pinworm (Figure 5.5). In all but one sample in which I found these eggs, I also found adult pinworms on the same fecal sample. This further strengthened my confidence in my identification. However, digenean trematodes have been found in howlers, and the few photos I could find of these were not drastically different than that of Figure 5.5. Howlers have been reported as harboring a species of trematode called *Controrchis biliophilus* (Vitazkova and Wade 2006, Carmona et al. 2005), but I had difficulty finding a good egg photograph for comparison. That being said, I was hesitant to identify these eggs as a distinct species without support from a parasitologist familiar with howler monkey parasites, and felt a more conservative identification of a species already known to be carried by the monkeys was a better course of action. For those reasons, I tentatively identified the set of eggs that looked like that in Figure 5.5 as oxyurid eggs.

Figure 5.5: Photomicrograph of a Possible Oxyurid Egg from a Tourist Area Monkey

The third tentatively identified species of howler monkey parasite was *Schistosoma* sp., possibly *S. haematobium* (Figure 5.6). Only one egg of this species was found, and identification was tentative because I had no information that this species had been previously found in howlers, and because contact with contaminated water is the usual method of acquiring the parasite (Roberts and Janovy Jr. 2000). Since the monkeys rarely come to the ground to wade through freshwater ponds, the presence of this egg is a mystery. Additionally, *S. haematobium* is usually only found in Africa, but coincidentally the species exists in Suriname (ibid.). The egg pictured in Figure 5.6 is consistent with schistosome infection, but without more specimens, its identification remains tentative at best (Appleby personal communication).

Figure 5.6: Photomicrograph of a Possible *Schistosoma* sp. Egg from a Non-Tourist Area Monkey

As mentioned above, I collected 181 fecal samples in the non-tourist area, and 189 samples in the tourist area. I did not analyze all of the samples for parasites, but instead prioritized them according to freshness and group membership, and did not analyze samples that were of especially low quality, or were superfluous to an already thorough sampling of a group. I therefore analyzed 147 of the 181 samples (81.21%) in the non-tourist area, and 157 of the 189 samples (83.07%) in the tourist area. Of these, nine in the non-tourist area (6.12%), and eleven in the tourist area (7.01%) were positive for intestinal parasites (Table 5.10). The samples may have corresponded with particular individuals, with some individuals producing positive fecal specimens more than once throughout the year. The average number of parasite eggs per analyzed sample was 1.33 in the non-tourist area and 1.45 in the tourist area. This is not a true measure of infection intensity, because it does not exactly signify the number of adult worms inside the monkey (Gillespie 2006), however, more eggs passed in the feces can signify a higher number of adult worms living in the individual (Roberts and Janovy Jr. 2000). The number of eggs per sample on average was not different between areas (independent samples t test: $t = -0.26$, $df = 18$, $P = 0.79$). When looking at intestinal parasite infection rates at the group level, and when combining results from adult pinworm collections with fecal

analysis, I found that twelve of the 15 sampled groups (80.00%) in the non-tourist area had at least one individual that was positive for intestinal parasites. This was an increase by two groups that were previously reported as testing negative for pinworms, but upon analysis of the fecal samples turned out to be positive for a strongyle-type nematode. The tourist area still had the same infection rate of 90.91% of groups harboring intestinal parasites as reported above for pinworm infection, even when I included the fecal analysis results. The likelihood of a group having at least one individual with intestinal parasites did not differ between areas (Fisher's Exact test: $P = 0.61$). As mentioned previously for the pinworm analysis, I looked at only a subset of fecal collections that were representative of each group on an approximate six-week basis (at the most). For many groups, I collected fecal samples several times over the course of a few days or weeks. Clearly these would not have been independent as far as parasite infections due to the likelihood of expelling parasite eggs on sequential days during the entire infection period. Therefore, I considered only 45 fecal collections in the non-tourist area for analysis and 40 collections in the tourist area. Twenty-one out of 45 fecal collections (46.67%) in the non-tourist area were positive for at least one species of intestinal parasite, and 22 out of 40 collections (55.00%) in the tourist area were positive (Table 5.10). As stated above, the likelihood of collecting fecal material that was positive for pinworms, when the groups were sampled on a six-week cycle or more was not different by area (Fisher's Exact test: $P = 0.28$). Pinworm infections were common in the monkeys, but only five samples in the non-tourist area (23.81% of all infections) were positive for a strongyle-type nematode egg, or a *Schistosoma* sp. fluke egg, and two minimally were positive for a strongyle-type nematode egg in the tourist area (9.10% of all infections). Despite the differences between the two areas in percent of non-pinworm infections, the likelihood of finding fecal material that was positive for nematode or fluke infection did not vary by area, nor did likelihood of finding any of the three intestinal parasites (Fisher's Exact test for nematode/fluke infection: $P = 0.44$; and for all intestinal parasites: $P = 0.52$). Three species of parasite were found in fecal samples in the non-tourist area,

Schistosoma sp., pinworm, and stronglye-type nematode, but only two species were found in the tourist area, pinworm and strongyle-type nematode. Only one sample was positive for more than one species of parasite, given my conservative identification of eggs as pinworms rather than possibly a different species altogether, and that sample was from a non-tourist area monkey. The average number of species per infection was therefore 1.05 in the non-tourist area and 1.00 in the tourist area (Table 5.10). Granted, my conclusions about the fecal analysis were conservative as far as numbers of species per sample due to the difficulty of a non-specialist in identifying the parasites. Interestingly, although monkeys in the non-tourist area had lower percentages of infections and lower number of parasites overall, they may have had higher parasite richness both per individual and overall.

Table 5.10: Intestinal Parasite Infection by Area

	Non-Tourist	**Tourist**
No. Fecal Samples Collected	181	189
No. Samples Analyzed	147 (81.21%)	157 (83.07%)
No. Analyzed Samples w/ Parasites	9 (6.12%)	11 (7.01%)
Average No. Eggs per Sample	1.33	1.45
No. Total Groups Studied	~18	~13
No. Groups Sampled	~15 (83.33%)	~11 (84.62%)
No. Sampled Groups w/ Parasites	12 (80.00%)	10 (90.91%)
No. Indep. Fecal Collections	45	40
No. Independent Infections	21 (46.67%)	22 (55.00%)
Number Parasite Species Found	3	2
No. Non-Pinworm Infections	5 (23.81%)	2 (9.10%)
Ave. Species Richness per Infection	1.05	1.00
Total No. Parasites	50	62

I also investigated the influence of tourist, weather, and fruit seasons on the likelihood of parasite infection. I found that only fruit season was significantly

associated with parasite infection, both in the tourist area and overall (Table 5.11). There were more parasite infections during the low fruit season. This could have been due to energetic costs of a low-quality diet and the inability to fend off parasites. Tourist and weather seasons had no effect on parasite infections in either area or overall (labeled "both" in the table). Although the difference was not significant, there were actually more parasite infections during the dry seasons in both areas and overall, which may seem contradictory due to the need for moisture to keep parasites viable.

Table 5.11: *P*-values for Fisher's Exact Tests of Seasonal Influence on Likelihood of All Parasite Infections

	Tour. Seas.			Weath. Seas.			Fruit Seas.		
	NT	T	Both	NT	T	Both	NT	T	Both
Infect	0.50	0.25	0.20	0.24	0.76	0.28	0.53	**0.01**	**0.03**

E. Latrine Use (Mix of Behavior and Health)

The use of specific defecation sites, and the subsequent avoidance of areas with high fecal contamination, can be instrumental in reducing infection rates of intestinal parasites (Apio et al. 2006, Ezenwa 2004, Gunn and Irvine 2003, Freeland 1976), especially in animals such as red howlers, which could, if careless, defecate all over tomorrow's leafy lunch. Defecation of protozoan cysts or nematode eggs and larvae, from branches high in the trees onto the leaves of lower branches, could result in frequent fecal-oral reinfection in a folivorous primate. Also, repeated use of specific pathways through the tree canopies may lead to greater contamination (Stuart et al. 1990). Repeated use of one or more latrine sites would minimize exposure to a group's previously defecated feces, and care taken to avoid such should result in lower incidences of intestinal parasites.

Another way to avoid parasitic infection is to alter ranging patterns, and some primates may do this. One species that potentially does this is the grey-

cheeked mangabey. Mangabeys in the Ngogo Research Area, Kibale Forest, Uganda, have been observed to travel further during the dry season than in the wet season. Freeland (1980) proposed that this difference in travel patterns was due to the need to avoid exposure to fecal parasites. During the rainy season, fecal matter was washed from branches and leaves thus allowing the animals to travel the same pathways without re-infecting themselves from the group's recently deposited fecal matter. Mangabeys were not observed to attempt to avoid defecating on the branch on which they were sitting, and they did not avoid stepping in their own fecal matter or that of a conspecific. Perhaps avoiding the area was the only way of avoiding the parasites for these monkeys, though not stepping in feces seems the easier option. It did not appear that mangabeys altered their ranging patterns in response to food or water availability (Freeland 1980).

Yellow baboons, *Papio cynocephalus,* in the Amboseli National Park, Kenya, also appeared to alter their habitat use in response to parasite risk. These baboons alternated sleeping sites so as to minimize their exposure to intestinal parasites (Hausfater and Meade 1982, Hausfater and Meade 1978). Fecal matter accumulated under sleeping trees, which also provided a warm, moist environment suitable for the survival of the nematode parasites. It was important for the baboons to move from site to site every few days in order to avoid the accumulation of parasites under the tree. However, these baboons spent several hours feeding, resting and socializing on the ground under their sleeping tree when they first descended in the morning. Rather than moving from sleeping site to sleeping site to avoid buildup of dung underneath the tree, it seems a better strategy would be to not spend time directly under the sleeping tree each day. Sleeping trees such as the yellow acacia are important food sources, too, however, so baboons may need to spend time around them to forage (Hausfater and Meade 1982). It was observed that baboons stayed at one sleeping site only for one to two days before moving on, and returned after an average of 9.1 days. With this rotation, the baboons avoided the heaviest larval numbers under the tree. This cycle of rotation was found not to coincide with food

availability or predator avoidance, thus providing further support for the parasite avoidance hypothesis (ibid.).

Red howler monkeys also may utilize behavioral strategies to avoid parasite exposure, and this is what I will address in this final section. Even early observers of red howlers noted group urinations (Racenis 1952). Observations of mantled howlers in Costa Rica and red howlers in French Guiana also support this idea; troops of howlers were observed to defecate simultaneously in the same place producing large areas of clumped defecations (Wehncke et al. 2004, Julliot 1996b). Mantled howlers in Nicaragua were also observed to defecate from lower branches than those in which they foraged, indicating that they avoided soiling their food supply (Henry and Winkler 2001). Red howlers living on islands in Lago Guri, Venezuela, also used latrine sites- one centrally located latrine per small island (≤ 1ha) (Feeley 2005). Monkeys defecated in the latrines from mid-canopy while perched on vines spanning between trees. Latrines on these islands were in the same location for at least four years. Red howlers appear to choose particular defecation sites that have gaps in the canopy or a lack of underlying vegetation. Gilbert (1997) proposed that this behavior served to minimize the risk of contaminating arboreal pathways that would later be used by the monkeys, and vegetation that they would subsequently eat. Gilbert (1997) observed that after resting, the monkeys moved away from their sleeping site and looked down before defecating. Their fecal matter intercepted fewer leaves on its descent than was expected by chance and howlers were never observed to defecate on the branch on which they were sitting, unlike the mangabeys mentioned above. Those howlers also defecated at a lower height in the trees than used for normal foraging and travel, and many individuals defecated at the same time. This pattern of behavioral avoidance may account for the low level of parasitic infection found in this group of monkeys (Gilbert 1997). I found a similar pattern of latrine use by the red howlers at Brownsberg, characterized by repeated use of specific trees for group defecations over gaps in the canopy, and from lower heights in the trees than used for other activities. I also looked at

intestinal parasite infection to determine whether the latrine strategy was in fact working.

It is also worth noting that the red howler defecation patterns are different from other sympatric species in Suriname. While studying the red howlers, I also witnessed the defecation behavior of three golden-handed tamarins, *Saguinus midas*, one black spider monkey, *Ateles paniscus*, one brown capuchin, *Cebus apella*, and a group of Guianan saki monkeys, *Pithecia pithecia*. In the cases of all three tamarins, the capuchin monkey, and the spider monkey, I witnessed a single individual defecate a small amount of feces while traveling or foraging. I did not witness any of the other group members defecate, rather, they continued foraging and traveling. The exception was the spider monkey which was alone. My approach startled it and it displayed at me, vocalized, and threw branches before defecating. In the cases of the tamarins and the capuchin, the monkeys defecated such small amounts of feces that there was no soiling of vegetation under the branch used by the monkey, (though there was much vegetation to soil). The feces of the spider monkey did hit much of the understory, but it was low to the ground, and thus would not be eaten later. All observed defecation events took place in the middle or lower third of the canopy and all but one occurred in the periphery, additionally minimizing the vegetation that would have been contaminated. Also, these species do not consume many leaves, so both the defecation pattern (small amounts individually) and the diet (fruit and insects) support the idea that these monkeys do not need to use latrines in the way that the folivorous howlers do. I also collected fecal samples from one of the tamarins and the spider monkey. The specimen from the spider monkey was clean, but the tamarin's sample had a single possible whipworm egg, *Trichuris trichiura* (Figure 5.7). It would be unlikely though that the monkey would reinfect itself with whipworm at a later date because of the fact that the feces did not stick to the leaves over which the monkey may later walk. The case of the saki monkey defecation was similar to the behavior of the howlers. First two female sakis stood on a branch and urinated and defecated, then they moved away and a single male used the branch, and then when he moved away, a second male

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used the branch. All four monkeys used the same exact part of the branch, similar to what I often witnessed in the red howlers. One tree canopy intercepted the urine, which was not unusual for a howler latrine. The similarity between the behaviors of the sakis and the howlers was such that I would like to witness more saki defecations in the future, and possibly analyze the feces of the sakis to see if they are using latrines to avoid parasites, too.

Figure 5.7: Photomicrograph of a Possible *Trichuris trichiura* Egg from a Tamarin Monkey in the Non-Tourist Area
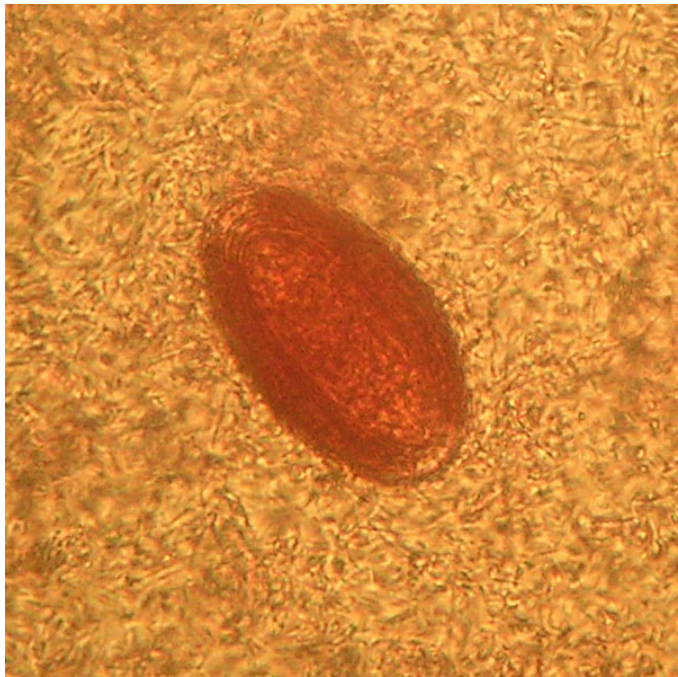
The excretory behaviors of several species of Neotropical monkey have been observed by other researchers in the wild. Black spider monkeys in Peru were observed to defecate while traveling and foraging during the day, as I found in one case in Suriname, but they also defecated from sleeping sites resulting in the accumulation of feces under the sleeping tree (Russo and Augspurger 2004). The authors, however, did not mention parasites, or possible latrine behavior in their study, and conclusions of this regard would necessitate further study. Capuchin monkey defecation behavior has also been studied. Capuchins typically produce small quantities of feces in scattered locations throughout the forest (*Cebus apella*: Vreedzaam personal communication and *C. capucinus*: Wehncke et al. 2003, Wehncke et al. 2004). Rarely does more than one

individual defecate simultaneously in space, which directly contrasts the behavior seen in howlers (Wehncke et al. 2004). A study of brown capuchin sleeping site preferences in Argentina also found that capuchins did not appear to choose sleeping sites as a parasite avoidance strategy (Di Bitetti et al. 2000). Brown capuchins used sleeping sites on consecutive days and used only a few sites repeatedly, which would have exposed them to defecated parasites from previous days. Di Bittetti et al. (2000) pointed out that capuchins rarely descended to the ground where most parasite eggs and larvae fell, therefore it may not have been critical to alter sleeping sites for parasite avoidance. Brown capuchins in Suriname do descend to the ground on a regular basis, however, their defecation habits (small amounts singly while traveling) preclude their repeated exposure to their own or their troop-mates' feces (Vreedzaam personal communication).

Tamarins also have unique defecation patterns, often characterized by the excretion of huge seeds surrounded by a minimal amount of fecal material. The sizes of tamarin-excreted seeds are often within the size range commonly eaten by chimpanzees and gorillas (Garber and Kitron 1997). These seeds may serve the purpose of mechanically dislodging and expelling parasites from the digestive tract. In particular, acanthocephalans, or spiny-headed worms, are a significant cause of discomfort, disease and even death in these monkeys. These intestinal worms bury their proboscis in the lining of the intestine, though the passage of a large seed may prevent them from attaching or scrape off attached worms. Garber and Kitron (1997) have not studied the actual effects of the seed ingestion on parasite loads, but a study of fecal output of worms would show if these tamarins are in fact successful at dislodging worms. Unfortunately, I was only able to witness one tamarin defecating, and collect one fecal sample from that individual. The sample I collected did not contain any large seeds, or any seeds at all for that matter.

In red howlers, studies in French Guiana have concluded that the slow gut passage rate (mean 20 hr 40 min) of red howlers resulted in a bimodal defecation rhythm, with peaks in defecations between 08.00 and 10.00, and

again from 14.00 to 15.00 (Julliot 1996a). Troops in French Guiana had thus 60-65% of defecations deposited under sleeping trees (Julliot 1997, Julliot 1996b). Red howlers in Suriname, however, exhibited a different pattern. There was a definite peak in defecation activity during the early morning hours with 37 out of 117 (31.62%) defecation events occurring before 08.00 hours. However, only 14 (11.97%) defecations occurred during the two hours between 08.00 and 10.00 (the peak defecation time observed in French Guiana), and there did not seem to be an afternoon peak. Instead, defecation events occurred during each hour of the day at a steady rate until ceasing around 18.00. Additionally, at Brownsberg Natuur Park, latrine trees were rarely sleeping trees, even though the monkeys tended to urinate and defecate upon waking in the morning and after a nap. A troop of Brownsberg howlers generally traveled out of its sleeping tree into an adjacent tree canopy (or a couple trees over) before stopping to defecate (personal observation). The monkeys often reused sleeping trees, as well as the paths to the latrine trees and the latrine trees themselves. Additionally, certain latrine trees were used for a period of weeks or months before the monkeys moved to other areas to establish new latrine sites (personal observation). Presumably this movement from latrine to latrine reflected the feeding patterns of the monkeys, and may map onto favorite fruit trees when they are in season. Several times when I witnessed the use of a "new" latrine site, I found evidence for past use in the form of old fecal residue still clinging to the understory vegetation.

1. Latrine Site Analysis

Monkey latrine behavior can be defined as the nonrandom selection of a defecation site such that feces accumulate over time (Irwin et al. 2004). Red howler latrines in Suriname are additionally characterized by their use by most of the individuals of a troop at one time for urination and defecation. Since howler monkeys remain in the trees to do so, a latrine site is actually composed of one or more trees (or lianas suspended between canopies) from which the troop members all urinate and defecate, as well as the corresponding patch of ground where the waste materials fall. The key aspect of red howler latrines is that the

majority of the troop urinates and defecates not only from the same tree or group of trees, but also at the same time. For the purposes of this study, a monkey "latrine" must exhibit both the temporal and spatial characteristics.

I began collecting latrine data halfway through my year of observations, which is why I only have latrine details for 71 events in both areas, but I collected fecal material from 149 defecations throughout the whole year. I collected data on various aspects of howler monkey latrines including date, time of day, location, whether or not I witnessed the event, what the monkeys were doing before the event if known, which part of the tree canopy was used, height in tree, species of tree if known, location of tree in relation to trail or road, whether it was a food tree or could have been a food tree, details about the pattern and extent of fecal matter on the ground, number of individuals using the latrine and how long the event lasted, number of fecal samples collected, and details of intervening branches or canopies that may have been hit by falling fecal matter and whether or not these could have been used as food sources. The latrine behavior that I witnessed included both the aspects of time and space to make them true latrines. Occasionally when monkeys defecated in response to an approaching group of conspecifics, their behavior may not have reflected latrine use, but because they defecated as a group, I included those observations in my analysis. Additionally, I often recorded latrine behavior to the best of my ability even when the monkeys were not around, and the event was not witnessed. By describing the pattern of fecal material on the ground and by looking directly up from the feces to the trees, it was usually possible to recreate the latrine behavior; however, it was not always possible to determine whether more than one individual used the latrine at one time (i.e. there was not a lot of feces on the ground to signify that multiple individuals had defecated there). I gave the monkeys the benefit of the doubt, though, because these cases occurred in a minimal number of observations (only once in each area). Therefore, I included all cases of witnessed and non-witnessed latrine behavior, including intergroup encounter events, in my analysis. Additionally, in many latrine events, multiple trees or multiple branches of the same tree were used by different individuals.

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These events were still considered latrines because the monkeys defecated at the same time, and the trees were always adjacent to each other or within ten meters apart. For purposes of analysis however, I considered these trees and branches to be distinct and independent because they each had their own details regarding height of the monkey, area of fecal material on the ground, and number and height of intervening branches or canopies. Therefore, observations of each tree or branch used as a latrine by at least one monkey were considered separate.

I was unable to determine conclusively many aspects of latrine behavior, such as time of day or what the monkeys were doing prior to the event, because I witnessed only 13 events out of 31 (41.94%) in the non-tourist area, and 17 out of 40 (42.5%) in the tourist area. Of the witnessed latrine events, only three in each area (20.00% of all witnessed latrines) occurred from trees in which monkeys had just slept or foraged. In two of those six cases, the individual defecating did not rest or forage in the tree, but other members of its group did, and in two other of the cases, I was not certain that an individual actually foraged from the latrine tree, but if it did, it foraged from a higher branch than that which was later used as a latrine. Therefore, the monkeys appeared to be non-randomly defecating from trees in which they had not rested or slept, or foraging above where they would later defecate. Also, as I mentioned above, the monkeys usually left their sleeping tree before defecating after a nap. Additionally, of all 102 latrine trees used overall, only 13 (12.75%) were known to be food trees, but aside from the cases mentioned above, the monkeys did not forage from them on the same day as they defecated from them. Thirty-five (34.31%) of the latrine trees were known food species, but the monkeys were not seen feeding in them, and 54 (52.94%) were unknown as to their food tree status. Even if more of the unknown trees were later discovered to be food trees, the monkeys usually did not forage from their food trees when they also defecated from them, therefore minimizing the likelihood that they were contaminating their immediate food source. Out of the 207 branches and trees below the latrine branch that intercepted the path of the feces, only 32 (15.46%) were large enough to possibly

have been food trees, but the monkeys were not seen foraging in any of them. The other 175 (84.54%) were either below or significantly below the 19 cm cutoff for howler food trees (see Chapter 3 above), and many of the intervening branches were merely low vegetation only 1 to 2 m off the ground.

I also analyzed quantitative measurements for all witnessed and non-witnessed latrines including monkey height in the tree, area of fecal material on the ground under the latrine branch, and numbers and heights of intervening branches and canopies on which fecal material may have fallen, thus contaminating the leaves. I compared monkey latrine heights to heights used for other behaviors including resting, foraging, sitting, and traveling, that I had recorded whenever possible during behavioral observations (n = 71). I made this comparison to investigate whether the monkeys avoided possibly soiled branches on which they had previously defecated by conducting other behaviors above the soiled branches. Finally, I selected control latrine branches to compare with the actual latrine branches regarding numbers and heights of intervening branches and canopies, to investigate whether the monkeys did indeed defecate over more open areas to further minimize soiling of branches with which they may later come in contact. I initially set out to compare the non-tourist and tourist areas for these measurements, along the same vein as my previous analyses. However, I did not expect the measurements to differ between areas, because I did not expect tourism to influence this particular behavior. Indeed, the only significant difference between areas for these measurements was monkey height in the latrine tree, with non-tourist area monkeys on average a couple meters higher than tourist area monkeys (Table 5.12) (independent samples t test: t = 2.14, df = 112, P = 0.03). I do not think this was due to tourist presence, and it was actually the opposite trend as what I would have expected had tourism been an influence. I might have expected tourist area monkeys to stay higher in the trees for all behaviors, including defecation, because they did not want to come close to humans on the ground. The tourist area latrines were actually lower in the trees than those of the non-tourist area monkeys, but this may have been due to other, random factors. The differences in latrine height between areas

also did not have an effect on the number of intervening branches between areas, which was perhaps a more important measurement than just tree height.

Table 5.12: Latrine Height, Monkey Height during Other Behaviors, and Control Latrine Height by Area

	Ht of Latrine		Other Behavior Ht		Control Latrine Ht	
Area	Mean	SD	Mean	SD	Mean	SD
Non-T	**20.00 m**	4.31 m	24.76 m	5.94 m	16.00 m	3.38 m
Tourist	**18.30 m**	4.14 m	23.89 m	6.73 m	14.60 m	3.22 m
Both	**19.07 m**	4.29 m	**24.30 m**	6.35 m	15.30 m	3.32 m

I then turned to summarizing all latrine data in both areas, in order to characterize the latrine behavior at Brownsberg Natuur Park (Table 5.13). I recorded whether monkeys preferred to use the central third of the tree branches (nearest to the trunk) for their latrine behavior, or the two outer thirds (left and right as I looked at the tree). I found that out of 114 latrine branches in both areas combined, the monkeys used the periphery of the tree on 96 of them (84.21%). This probably also aided in the minimization of fecal contamination of branches to be used later, as there are fewer thick, supportive branches in the periphery of a tree for the monkeys to travel over later. Additionally, monkeys were less likely to defecate from the top third of a tree (12 out of 114 branches or 10.53%) than either the middle third (68 out of 114 or 59.65%) or bottom third (37 out of 114 or 32.46%). The reluctance to defecate from the tops of the trees would also minimize the soiling of lower branches. I also looked at monkey height in the latrine trees to compare with heights used for other daily activities including resting, foraging, sitting, and traveling (see Table 5.12 above). I found that latrine heights were in fact lower than the heights observed for other behaviors (independent samples t test: $t = 6.68$, $df = 183$, $P < 0.0001$), thus monkeys may have been coming down to lower parts of the canopy to avoid soiling branches they would walk across and forage from in the future. I also looked at the area of

fecal matter on the ground as an estimate of how much vegetation in the trees would have been contaminated had it intercepted the path of the fecal material (Table 5.13). Finally, I examined the numbers and heights of intervening branches and canopies under the latrine branches (modified from Gilbert 1997). I often could see fecal material on these branches to confirm that they indeed were soiled. When I could not see fecal material on the leaves, I noted any branches directly below the latrine branch as potentially having been soiled. I tallied the numbers of intervening branches in the actual latrines above ten meters in height and below ten meters in height for comparison with the numbers of intervening branches in the control latrines. I searched for control latrines during a trip to Suriname after my year-long data collection, and mistakenly chose controls that were shorter on average than the previously observed actual latrines (see Table 5.12 above). I did not discover this error until returning home, but the effect on the comparison of intervening branches was minimal, and there was no effect on the comparison of intervening branches shorter than ten meters in height. In fact, with shorter control trees, I would expect any difference in numbers of intervening branches above ten meters in height to be greater in reality than my controls would be able illustrate. This was the case, as numbers of intervening branches both above and below ten meters were different between the actual and control latrines (Table 5.13) (independent samples t test for intervening branches greater than ten meters in height: $t = -2.25$, $df = 141$, $P = 0.03$; for branches less than ten meters in height: $t = -5.53$, $df = 141$, $P < 0.0001$). The monkeys did in fact defecate from branches with fewer intercepting leaves than would be expected by chance.

Table 5.13: Latrine and Control Latrine Measurements

	Mean	SD
Latrine Height (m)	19.07	4.29
Control Latrine Height (m)	15.30	3.32
Area of Fecal Material on Ground (m^2)	6.48	5.96
No. > 10 m Intervening Branches per Latrine	**0.75**	**0.82**
No. > 10 m Intervening Branches per Control	**1.17**	**1.15**
No. < 10 m Intervening Branches per Latrine	**1.08**	**0.90**
No. < 10 m Intervening Branches per Control	**2.03**	**0.56**

2. Health Aspects

In addition to investigating the manner in which red howlers in Suriname used latrines, I also collected fecal samples from the monkeys to determine whether latrine use as a parasite avoidance strategy was actually working. Based on the description of the latrine behavior above, I conclude that the monkey defecation patterns are consistent with parasite avoidance. Monkeys defecated from lower branches on the periphery of trees that were more likely to be above clearings than by chance. By engaging in other behaviors above the defecation heights and by minimizing soiled vegetation under the latrine branches, monkeys should be effectively avoiding reinfection of parasite larvae and eggs at later dates. To assess whether this strategy was working, I also collected fecal samples from the monkeys to check for intestinal parasites (see analyses above). While 22 out of 26 groups (84.62%) for which I collected fecal samples had at least one individual at one time during the year that had an intestinal parasite, most of these infections were pinworms, which for the most part result in asymptomatic infections (Roberts and Janovy Jr. 2000). Pinworms alone may not be enough of a selective force to result in the use of latrines. Additionally, pinworms can re-infect their original hosts without the monkey having to step in or eat any of its own fecal material. Pinworms may just be a fact of life for howlers that no defecation behavior can eliminate. On the other hand, a conservative estimate of 7 out of 26 groups (26.92%) had non-pinworm

infections. Perhaps this percentage is low enough to conclude that the latrine behavior was working. If I had more details about the defecation behavior of individuals, and could assign specific specimens to individuals, I might be able to investigate this possibility. However, I was not able to do that, but in future studies, I would like to focus on fewer groups, get to know the individuals in them, and hopefully collect samples for which I can identify their owner.

F. Discussion and Conclusions

The health aspects of this study turned out to be less informative than the behavioral aspects. Although a clear trend was seen between the two areas wherein the tourist area monkeys were consistently exhibiting signs of poorer health when compared to the non-tourist area, the differences were usually slight, and were not statistically significant. A higher percentage of groups studied, a higher percentage of individuals within those groups (statistically significant), and a higher percentage of individuals overall (statistically significant), exhibited wounds, scars, and other signs of poor health in the tourist area when compared with the non-tourist area. There could be several reasons for this higher incidence of poor health in the tourist area. High population density could play a role if monkeys in the tourist area were more crowded together and thus more frequently came into contact with and fought conspecific groups than non-tourist area monkeys. I did not measure population density specifically, but I did note intergroup encounters when witnessed. I never once witnessed actual physical contact between monkeys that resulted in injuries, but the occasional sighting of scars or wounds indicated to me that skirmishes did occur. Workers at the site witnessed one fight between neighboring groups in which a female was knocked out of the tree. She fell on some scrap metal and wood and subsequently died from her injuries. I was never told how she was actually pushed out of the tree, but possibly physical contact with another individual was the cause. This one instance occurred in the tourist area very near the restaurant. Dealing with the presence of tourists, and altering behavioral patterns in response, may have resulted in a situation where tourist area monkeys were experiencing low levels of stress at all times, which may have exacerbated

intergroup encounters, thus resulting in more frequent injuries. Tourist presence itself could have been an indirect cause of high population density in the tourist area. The cutting of trees for roads, parking areas, and buildings could have forced monkey groups into smaller areas, thus increasing their density.

Rates of wound infliction may have been the same between the tourist and non-tourist area monkeys, but the tourist area monkeys may have been slower to heal due to the stress imposed on them by the presence of tourists. Intergroup encounters may not have been the only cause of injuries; predator activities may have also left monkeys wounded. Potential howler predators, including tayras, and pumas, *Puma concolor*, have been sighted near the tourist facilities, so tourist area monkeys were not protected from predators by the presence of humans. Additionally, saki monkeys living very near the restaurant have been disappearing throughout June and July 2007, presumably due to predator attack (Norconk personal communication). The same predators responsible for saki disappearance could have attacked and wounded howlers in the same area. Stress caused by noise and air pollution of the tourists may have had the subtle impact of prolonging healing times for injuries that may have healed faster in the less-contacted non-tourist area monkeys. Longer healing times in the tourist area would have given me more opportunity to observe and record the presence of wounds there; I might have missed seeing wounds in the non-tourist area monkeys because they healed in between the times I was observing them. Health parameters in general were slightly poorer in the tourist area, compared to the non-tourist area, which may have been due generally to decreased immune defenses and healing capabilities caused by the presence of disruptive humans.

A higher percentage of groups studied, a higher percentage of individuals within those groups, and a higher percentage of individuals overall (statistically significant), exhibited bot lesions in the tourist area when compared with the non-tourist area. Additionally, monkeys in the tourist area had more bot lesions per individual, there were more infected individuals with high infections, and there were more total bots seen in the tourist area. Only a few of the comparisons by

area of indicators of poor health or bot infestation were significantly different, but in all cases, the tourist area was the area with the poorer health in regards to visible indicators of poor health including bot infestations. Possibly tourist presence increased the stress levels of the tourist area monkeys so that they were less able to heal from bot fly lesions than non-tourist area monkeys. Because I did not record all instances of the lack of indicators of poor health, or the lack of bot lesions, I could not use statistics to investigate whether seasonal changes influenced the likelihood of exhibiting signs of poor health. I did, however, summarize the numbers of bot infections by weather season and found that there were, in fact, more bot infections during the rainy seasons. This was as I predicted due to the need for a moist environment to keep eggs and larvae from drying out before they could infect their host. The incidences of high and low infections did not fit this pattern, however, as there were more high bot infections during the dry seasons in both areas. There were more infections in general during the rainy seasons, but more high infections during the dry seasons. This may have been due to the susceptibility of certain individuals to bot infections, which experienced flare-ups during the dry season. Tourist presence or fruit availability may have also influenced high versus low infection rate. I predicted that bot infections would be more common during the low fruit season due to the possibly reduced energy intake from a diet mostly of leaves, which may have hindered the monkey's ability to fight off bot infection. Fruit availability possibly had an effect in the non-tourist area, where all of the high infections and more of the infections in general occurred during the low fruit season. This was not the case in the tourist area, where more of the high infections did occur during the low fruit season, but less than half of the infections in general were observed during the low fruit season. Perhaps food availability did not play as strong a role in the tourist area as in the non-tourist area. As mentioned previously, the tourist area monkeys were less affected by seasonal fluctuations in fruit availability and continued to forage for fruit almost the same amount of time during the low fruit season as they did during the high fruit season (see Chapter 4 above). However, urine characteristics and intestinal parasites were influenced by fruit season, so

perhaps the lower incidence of bot infections during the low fruit season was only a coincidence, and in fact when looking at urine characteristics, fecal analyses, and bot infections together, the tourist area monkeys had poorer health during the low fruit season. Additionally, the results for bot infections during the fruit seasons may have been influenced by random factors such as my ability to see bots, or my time spent in each area during the different seasons. I did not report the incidences of bot infections by tourist season, because the high tourist season was so short that there were not enough observations of bot infections for comparison.

I also investigated the parasite avoidance behaviors of monkeys in both areas. I found that monkeys in both areas spend time each day swatting at flies with their hands, or flicking their tails over their bodies to discourage parasites from landing on them. This can be energetically costly (Dudley and Milton 1990), and though I did not investigate the possible energy costs of parasite deterrence behaviors, I would like to at a later date. I did investigate whether the grooming durations differed among monkeys in each area, and found that although there was no statistical difference in grooming duration, the tourist area monkeys groomed for longer periods of time on average than non-tourist area monkeys. There was also no difference in which individuals (adult female, adult male, or other) were doing the grooming or being groomed by area. However, there was a sex difference in grooming behavior, mainly because females were equal-opportunity groomers, while males tended to preferentially groom females. I suggest that both the social and hygienic functions of grooming played a role in this sex difference. While females wanted to curry favor with males, and possibly gain protection from them against other group or extragroup males (social function), they also wanted to maintain relationships with other females (social function) who may share in caring for their offspring, and they wanted to keep their offspring healthy by removing ectoparasites (hygienic function). On the other hand, males preferentially groomed females, presumably to establish relationships with them in order to gain access to them later when they were in estrous.

Grooming itself was an infrequent behavior. Interactions between group-mates constituted less than 0.5% of the activity patterns of monkeys in both the non-tourist and tourist areas (see Table 4.2 above). This behavioral category included grooming, fighting, and playing, so the proportion of time spent grooming or being groomed was even smaller. This lack of attention to grooming is not unique to this site; howlers of many species are infrequent groomers, though red howlers are more likely to groom than other species of howler (Sánchez-Villagra et al. 1998). In this study, grooming bout duration was found not to be significantly different between areas; however, the sample size of grooming bouts was small. Greater than 30 seconds separated the mean bout durations between the areas, but this was not significantly different. I would have wanted larger sample sizes for grooming bouts, but for this study, there was not much of a conclusion to be made from these data given the small samples sizes. Additionally, although the differences in groomers and groomees between areas are interesting, I feel that this also reflects small sample sizes, and in future studies, I would like to investigate grooming behavior and ectoparasites further.

For both the urine and fecal analyses, I was limited in my ability to identify individuals from whom I collected samples, and in my ability to identify samples that could be attributed to specific individuals. As described above, red howlers in Suriname defecate and urinate from latrines, which I defined as having both a temporal (all group members at the same time), and spatial (all group members from one or a few trees within ten meters apart) pattern. Due to the use of one or a few branches by all monkeys at the same time for defecation, it was nearly impossible to identify a specific individual's urine or feces. For that reason, I chose to report my results per group per urination or defecation event. Furthermore, I considered urine collections taken from the same group within a week of previous collections to be redundant and non-independent and therefore eliminated them from analysis. For the fecal collections, I used the length of a typical pinworm infection (six weeks) as my guide for non-independent collections, and eliminated from analysis samples collected from the same group within six weeks of previous collections. In this way, I was left with a set of urine

and fecal collections that could be considered statistically independent. Identification of independent groups was tentative, but I used geographic location, time, associated behavioral observations, and number of individuals to narrow down the possible groups. I erred on the side of caution with regards to identification, and was more likely to combine collections that could have been taken from separate groups, than separate collections, and thus consider them to be independent, which could have been taken from the same group. In this way, I may have combined samples that were from different groups, and thus could have had different susceptibilities to infection, but I chose to take that risk, rather than treat as independent collections that were actually not. That being said, I was very careful in my group assignments, and in only a small number of cases do I think I may have slightly compromised my data. In other words, I believe my error rate in assigning groups to urine and fecal collections was very low.

As for urine characteristics, comparisons between areas were not significantly different for presence of leukocytes, protein, glucose, blood, or for specific gravity. There were few samples collected, which may have had an effect on the lack of statistical significance, but also there was no consistent pattern between areas for poor health indicators as measured through urine characteristics. The one sample that was positive for leukocytes was from the non-tourist area, there were the same numbers of samples positive for glucose between areas, and there were more samples with higher specific gravity and protein, and more samples that were positive for blood in the tourist area. From these results, I might conclude that monkeys in the tourist area were slightly worse off as far as health compared to the monkeys in the non-tourist area, but that might be an artifact of random factors, more samples collected in the tourist area, or small sample sizes. In the future I would like to collect more samples from fewer groups to better investigate health patterns, as measured by urine characteristics.

I additionally investigated whether tourist, weather, or fruit seasons influenced urine characteristics within each area and overall. I found that fruit season seemed to have an effect on protein levels in the tourist area and overall,

and on specific gravity measurements overall. There were significantly more urine samples with higher protein values in both the tourist area and overall, and there were significantly more urine samples with higher specific gravity measurements overall during the low fruit season. High levels of urine protein may indicate a breakdown of muscle, strenuous physical exertion, or systemic disease. I did not witness any event that would lead me to think that trauma was the cause of the elevated urine protein, and monkeys actually rested more and exerted themselves through travel less during the low fruit season. Therefore, I would expect they would have little reason to have excess muscle breakdown or strenuous physical exertion. The possible explanation for elevated urine protein can however be dietary. Diet can influence protein levels in urine, and this has especially been seen in urine samples of people on high-protein, low-carbohydrate diets (Cheryl Westin personal communication). Perhaps the increased urine protein levels seen during the low fruit season in the tourist area may have been due to the increased ingestion of dietary protein in the form of young leaves during the period of low fruit availability. The monkey's bodies may have had trouble processing all the dietary protein and flushed the excess out in the urine. There were also significantly more urine samples with high specific gravity measurements overall during the low fruit season. Again, this may have been due to dietary patterns because the monkeys were eating more relatively dry leaves and fewer relatively wet fruits. Monkey urine may therefore have been denser during the low fruit season because their bodies could spare little water to dilute it. The overall lack of a significant influence of seasonal change on urine parameters was probably due in part to small sample sizes, but mostly it was probably due to the fact that urine characteristics do not change drastically due to natural seasonal fluctuations, or for that matter, due to tourism.

I next looked at fecal samples and investigated whether intestinal parasite infection differed between areas. I chose to look at pinworm infection separately from other intestinal parasites mainly due to the fact that I knew when I had found a pinworm on some fecal material. Adult pinworms were easy to identify, and I knew I could compare their presence between monkeys in the non-tourist and

tourist areas regardless of the outcome of my microscopic fecal analyses. As with the comparisons of poor health indicators and bot infections, I found a general, if insignificant, trend of more pinworms in the tourist area. Pinworms were found in a higher percentage of samples collected, a higher percentage of sampled groups, and a higher percentage of independent fecal collections in the tourist area when compared with the non-tourist area. Additionally, monkeys in the tourist area had a higher number of pinworms per infection and a higher number of pinworms collected overall, including eight worms collected from a single fecal sample. None of the comparisons for which I was able to conduct statistical analyses were significantly different by area. I also investigated seasonal influence on likelihood of at least one individual in a group having a pinworm infection and found that none of the three seasons had a significant influence on infections either within areas or overall. Although the influence of the seasons on pinworm infection was not significant, there were more pinworm infections during both the rainy seasons and the low fruit season in both areas and overall. This may have been due both to the abundant rain providing a moist environment suitable for pinworms, and to the lack of monkey ability to fight off a pinworm infection due to lower energy intake during the low fruit season.

I also analyzed 304 of the 370 fecal samples that I collected over a year of observation using the MIF preservation method (see details above). I analyzed all specimens using high-dry (40x) magnification, and recorded the presence of parasite eggs. Due to my inexperience, I had a difficult time identifying the parasite eggs, but I found the eggs of at least three possible different species of parasite in the fecal material: a strongyle-type nematode, an oxyurid nematode, and a schistosome fluke. The eggs that I identified as pinworms were the most questionable because I did not have good photographs of howler pinworm eggs for comparison. However, I know that they were some kind of parasitic worm egg, and it was just a conservative identification to call them pinworms, which the monkeys were already known to carry.

The presence of a strongyle-type nematode is not unusual, as they have been identified in howler monkey feces in previous studies (see Stuart et al. 1998

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for a review). Many of the strongylid nematodes enter a host by burrowing into the skin upon contact; they live in the soil and wait for a suitable host to come into contact with them. This seems an unlikely mode of infection for arboreal howlers, but there are some species of strongylid that are transmitted orally. The defecation patterns of the howlers (i.e. latrines) should preclude the transmission of fecal-oral parasites, but perhaps the latrines are not completely effective. The presence of a possible schistosome egg in howler monkey feces is somewhat unusual, especially because transmission of the parasite usually happens in freshwater ponds. I never saw the howlers on the ground, much less in a pond, though they do occasionally descend to the ground. *Schistosoma haematobium* is a parasite found in Suriname in humans, but its presence in monkeys is a bit baffling. However, the identification of the egg is tentative and without additional samples exhibiting this egg, it will be difficult to confirm its identification.

I compared intestinal parasite presence between areas, both with adult pinworms included and without. I found that there was no significant difference in infection levels between areas, and in fact, there was no consistent pattern of parasite infections between areas. The tourist area had a higher percentage of samples analyzed that were positive for parasites, a higher percentage of sampled groups with parasites, and a higher percentage of fecal collections that were positive for parasites. Additionally, the tourist area samples had more eggs per sample on average and more parasites overall compared to the non-tourist area. However, the non-tourist area had a higher percentage of fecal collections that were positive for non-pinworm infections, assuming the eggs I identified as pinworms were in fact pinworms. Additionally, the non-tourist area had one extra species of parasite that was not found in the tourist area, and one sample that was positive for two species of parasite, while in the tourist area, each sample only had one species. Therefore, the parasitic infections do not clearly follow area divisions. While there were more parasites in general and more groups and collections that were positive for parasites in the tourist area, thee was a higher diversity of parasites and more non-pinworm infections in the non-tourist area. It

is likely in this case that tourist presence and activity does not influence parasite presence in any meaningful way.

I also looked at seasonal influence on parasite infection, and found that again fruit season had a significant influence on the likelihood of parasite infection, both in the tourist area and overall. There were more parasite infections during the low fruit season, which may have been due to the fact that the monkeys were consuming a low-energy diet, and did not have spare energy to fend off parasites. Tourist and weather seasons had no effect on parasite infections either within areas or overall. Although the difference was not significant, there were more parasite infections during the dry seasons in both areas and overall, which contradicts the idea that parasites are more common in wet areas and during rainy seasons due to the need for moisture to keep parasites viable.

The final topic I addressed in this chapter was that of howler monkey latrines. This was sort of a pet project for me that I only took up halfway through my year of data collection. During the summer of 2004, I met with some students of Marilyn Norconk in Suriname and one of them, Tremaine Gregory, had just worked with a student at a field school in Nicaragua on latrines used by the mantled howler monkeys there. I realized that the behavior Tremie described was typical for red howlers in Suriname, so I decided to investigate latrine use in addition to my behavior and health studies. I also realized that having the fecal collections and intestinal parasite data to go along with the latrine behavior would be an added piece of the picture. I did not really expect this behavior to differ due to tourist presence or to seasonal fluctuations, though it would be interesting to look at seasonal patterns in the future, which might change due to parasite presence in the environment. I therefore kept to a description of the latrine behavior as well as a comparison of latrine trees to other control trees throughout the forest at Brownsberg. I found that the howler latrine behavior was consistent with parasite avoidance and that monkeys defecated from lower branches in the trees than those from which they conducted other behaviors, defecated from the periphery of trees, and preferentially defecated over clearings where less of their

fecal material would contaminate the leaves they may later eat. To determine whether the monkeys defecated over clearings, I compared the numbers and heights of intercepting branches under the latrine branch in actual latrine trees to those in control latrines. I mistakenly chose shorter control latrines on average than the actual latrines, which only affected my analysis slightly. I found that the actual latrines had fewer intercepting branches under them that were taller than ten meters in height and shorter than ten meters in height when compared with control latrines. These were significant differences, and because I chose short control latrines, the actual difference in number of intercepting branches taller than ten meters in height between latrine branches and non-latrine branches would be greater in reality than I was able to measure. If my control latrines had been on average three to four meters taller, similar to the actual latrine heights, I would have seen even more intervening branches above ten meters and thus the difference would have been greater. The monkeys also generally left the tree in which they were recently resting or foraging before defecating, thus maintaining contamination-free sleep and food trees. All of these details taken together suggest that the red howlers in Suriname avoided contaminating vegetation with which they would come in contact in the future.

I also looked at the area of fecal material on the ground under the latrine branch. I found a range from 0.25 to 24.00 square meters, and this fecal material could have covered the same area of leaves in the trees if the monkeys had not defecated over a clearing. In fact, in the cases where there was a larger area of fecal material on the ground, it was usually because one or more branches intercepted it on the way to the ground and caused it to splatter. The latrines with the most intercepting branches tended to have the largest area of fecal splatter on the ground, and obviously the most fecal matter on branches over which monkeys may in the future walk. The latrine behavior of howlers, when conducted over a clearing, allowing all fecal matter to accumulate in a small area on the ground, has implications for both seed dispersal and nutrient cycling. With a higher fecal "splash area" fecal material will be dispersed and may be harder for seed predator rodents to find. Seed in the feces will also be spread out more

and will have a better chance at germinating than seeds in a single clump on the ground. Nutrients in the fecal material will also be spread out rather than accumulated in one spot under a latrine branch. However, the more intervening branches serving to scatter fecal material, the more contaminated leaves with which the monkeys may come into contact in the future. So, the tradeoff may be between seed dispersal and efficient nutrient cycling and monkey health.

As far as the actual parasite loads and the possibility that latrine behavior was a strategy for parasite avoidance, the total intestinal parasite infection rates seem too high for the strategy to be working. I found that just over fifty percent of the 85 independent fecal collections were positive for intestinal parasites. On the one hand, this number could be much higher if the latrines were not working to reduce re-infection of intestinal parasites. On the other hand, the latrine behavior at times seemed so perfect as far as the monkeys defecating over totally open clearings from tree falls or on the road, that I would expect the intestinal parasite infection rate to be much lower than fifty percent. It is possible that pinworms specifically are just a fact of life for the monkeys, and since pinworm infection is usually only bothersome and not life-threatening, perhaps pinworms alone are not a strong enough selective force to result in latrine behavior. Additionally, it is possible to become re-infected with pinworms that hatch on the monkey's body and crawl back into the anus, meaning that the ingestion of contaminated vegetation is not a requirement for pinworm infection. For these two reasons, I focus on other intestinal parasites as the selective force for latrine behavior. Even if I assume that the eggs I identified as pinworms were not really pinworms, I found that only 17 out of 85 fecal collections (20.00%) were positive for intestinal parasites other than pinworms. If I consider that those eggs were really pinworms, the number of positive fecal collections drops to 7 out of 85 (8.24%). This definitely seems a low enough percentage of infections to conclude that latrine behavior is in fact working.

I also briefly compared the howler latrine behavior to the defecation behavior of other species in Suriname, and collected one fecal sample from a spider monkey and a tamarin for analysis. The fecal sample collections from

other species were not really meant as a comparison, since I only collected two. However, I was interested in seeing what I could find, and in fact, I found possibly an additional species of intestinal parasite, *Trichuris trichiura*, in the tamarin sample that I did not find in the howler samples. Capuchin monkeys, tamarins, and spider monkeys all generally defecate singly while traveling or foraging throughout their ranges. This contrasts with the howler pattern in which all members of a group defecate together in the same place. Interestingly, the one time I witnessed a defecation event by a group of saki monkeys, I saw the same pattern as that found in howlers. The sakis took turns defecating one after the other from the same branch.

In conclusion, for the most part health measurements did not differ significantly between monkeys in the non-tourist and tourist areas. There was a definite trend towards poorer health in general in the tourist area monkeys, but it was slight and not always consistent. The low fruit season also seems to have negatively affected the health of monkeys, especially in the tourist area. Perhaps fruit availability was the reason for poorer health in general in the tourist area, and not the presence of tourists. Perhaps tourist presence was the reason for poorer health in the tourist area and low fruit availability just exacerbated the situation. Because the differences were marginal, it may not be necessary to explain the difference. Additionally, more and better identified urine and fecal samples, and a more consistent tracking of health indicators would help identify true relationships between tourism, health, and fruit availability.

Chapter VI

Discussion and Conclusions

A. Summary of Results

I set out in this thesis to investigate the impact of tourism on the behavior and health of red howler monkeys in Suriname. The potential deleterious effects of tourism on primate populations are seldom investigated. My hypothesis for this project was that human tourism changes the behavior of, and has a detrimental effect on the health of wild red howler monkeys (*Alouatta seniculus*). I investigated whether monkeys living in areas of high tourist presence had different behavioral profiles and health status than monkeys living in areas with low tourist presence. I predicted that the behavioral patterns would be different and that health would be poorer in the tourist area due to the impact of human activities related to tourism. I also looked at the impact of the high tourist season on monkeys in both areas to see if there were behavioral or health changes during the year as tourist presence waxed and waned. Additionally, although I eliminated the confounds of forest structure, weather patterns and food availability from the relationship between tourism and monkey behavior and health, I looked at the seasonal patterns of weather and food availability to see whether the monkeys altered their behaviors or suffered from poor health during certain seasons of the year. In addition to daily activity patterns, I also looked at behavioral responses to specific human activities such as the playing of loud music, or the driving of vehicles near the monkeys, to see whether monkeys responded with fear, discomfort, or just curiosity at the presence of humans.

I found that the behavioral patterns of the non-tourist and tourist area monkeys did differ, with monkeys in the tourist area foraging and traveling more

and resting less than monkeys in the non-tourist area. These results may have been due to data collection bias, but it is likely that they reflect actual differences in monkey behaviors. Monkeys in the tourist area did travel more often and for longer durations than monkeys in the non-tourist area. They also foraged more frequently than non-tourist area monkeys, and perhaps as an opportunity cost of this increased travel and foraging, they rested less. I concluded that this was due to tourist presence and not ecological conditions; tourist presence forced the monkeys to change their behavioral patterns. Additionally, monkeys in the tourist area changed the amount of time that they spent traveling and resting in order to respond to high versus low tourist presence, dry and hot versus wet and cool conditions, and high versus low fruit availability. In contrast, monkeys in the non-tourist area did not respond significantly to seasonal fluctuations by altering their behavioral patterns. They did show the same trends in behavioral alterations as were seen in the tourist area, but not to the same extent. The non-tourist area monkeys may have been less flexible in their daily activity patterns, conducting their activities in the same proportions no matter what the season. With regards to food preferences, monkeys in the tourist area did not alter the food types that they consumed as food availability fluctuated, with the one exception of eating more flowers during the low fruit season. Activity patterns and food preferences went hand in hand. Tourist area monkeys altered their behaviors in response to seasonal change, rather than altering foods eaten, meaning that, they traveled further to find preferred foods like fruit, with resting as an opportunity cost of increased travel, and traveled less when fruit was more abundant and fruit trees were more closely spaced. The non-tourist area monkeys on the other hand significantly altered foods eaten in response to tourist, weather, and fruit seasons. They may not have been as flexible in their behavioral patterns, and could not choose to travel more or less to find fruit. Instead, they responded to seasonal changes by altering the food types that they ate, preferring to eat what they could find during their typical traveling and foraging schedules. Non-tourist area monkeys therefore were more impacted by seasonal fluctuations in food availability and altered their foods eaten in response to seasonal change, rather

than alter their fixed behavioral patterns. I think the tourist presence in each area (or the lack thereof) influenced the behavior of monkeys in both areas. Monkeys in the tourist area were disturbed by tourist presence and altered their behaviors to minimize this disturbance. By keeping on the move and resting only for short durations on average, they could get away from the noises and obnoxious behaviors of the tourists. Having already established the capacity for behavioral alteration in response to tourist presence, the tourist area monkeys could then easily alter their behavioral patterns in response to weather and fruit season fluctuations. The non-tourist area monkeys did not have the constant disturbance of tourist presence, so they did not need to alter their behavioral patterns to get away from tourists. They therefore did not have the capacity to alter their behaviors in response to weather or fruit season fluctuations, and found themselves subject to these fluctuations in their dietary choices. They did not seek out fruit when fruit was less available, they did not travel more in cool weather just because they could. Instead, they ate only what was available at the time, and kept to their established behavioral patterns. In essence, the non-tourist area monkeys were influenced by natural cycles living in a relatively undisturbed area of forest, whereas the tourist area monkeys were responding to tourists, which then affected their behaviors in general.

I also found differences in the non-tourist area and tourist area monkeys' responses to specific human disturbances. Monkeys in the non-tourist area, which were not constantly exposed to human disturbances, responded more often and with a higher magnitude of response than did tourist area monkeys for all disturbance levels. Tourist area monkeys were much less likely to respond to human disturbances, leading me to conclude that they were habituated to tourist activities. Perhaps by altering their behaviors they was able to avoid the most disruptive tourist disturbances, and the rest were just the noisy din in the background, which the monkeys were able to tune out. The non-tourist area monkeys did not alter their behavioral patterns in response to tourist presence because the tourist presence was not constant enough to necessitate behavioral alteration. However, when the occasional tourist or vehicle entered their vicinity,

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they responded with at least curiosity, and often with much stronger fear responses. The human disturbances encountered by monkeys in the non-tourist area were infrequent enough to be especially startling. The monkeys in both areas were also especially concerned about my presence, due to its novelty, though with a longer period of observation, they probably would have become habituated to my presence as well.

As far as the investigation into health differences between the non-tourist and tourist area monkeys, I found less of a conclusive pattern. I had quite a bit of trouble with the actual collection of the health data, which overshadowed the conclusions I could make regarding health. I struggled with trying to find statistically independent observations that I could reliably compare between areas, and as a result, my comparisons are not as powerful as they could have been. I also had difficulty identifying intestinal parasite eggs. Very few of the comparisons between areas were significantly different, but when they were, it was the tourist area monkeys exhibiting the poorer health conditions. The tourist area monkeys were in general slightly worse off than the non-tourist area monkeys for all the health measurements, with the possible exception of intestinal parasites. There were some minor seasonal fluctuations in health status as well, with the rainy and low fruit seasons influencing health for the negative, though there were slightly more intestinal infections during the dry seasons. I would be hesitant to attribute the slightly poorer health status of tourist area monkeys to tourist presence. However, the ecological conditions of the areas did not differ during the year, so it is possible that tourist presence did influence health status somewhat. The differences were slight, and perhaps the behavioral alterations exhibited by the tourist area monkeys were such that stress due to tourist presence and its subsequent effects on immune function were minimized and the monkeys were only slightly worse off than the non-tourist area monkeys who were not stressed regularly by tourist presence. Without further systematic studies of health parameters, in which individuals and groups are identified, it will be difficult to determine conclusively.

B. Discussion of Problems

If I could do this research project over again, I would do a couple things differently. Field research is a learning experience, and unfortunately, most of the lessons that need to be learned happen at the field site itself when the researcher is alone and out of touch with advisors and mentors back in the States. Also, despite careful planning, when the research actually commences, something always goes wrong. I would have liked to have identified individuals and groups for this project. I was trying to randomly sample the groups in both areas for observation, and figured that by observing different groups at different times of the day from week to week over the year of observations, I would paint the broadest picture of monkey behavior and health in Suriname. This worked out fine for the behavioral observations. The health measurements were a different story, and it would have been nice to have known which group's samples I was analyzing. That being said, I would not trade my experiences in this project even for a more rigorous scientific methodology. Because I did not limit myself to one group or a couple groups in each area, I constantly got to travel around looking for monkeys and seeing the full research site. I explored areas that I would not have been able to if I had only chosen one part of the park for my study. However, in the future, I would like to do a better job of getting to know the specific groups and individuals that I am studying.

I would like to have standardized my methods of behavioral observations a little better between the non-tourist and tourist areas. Because I lived in the tourist area, I had better luck finding the monkeys there, and also found them earlier and stayed with them later in the day. I attempted to find non-tourist area monkeys early in the morning, both by sleeping out in the non-tourist area, and by biking to the non-tourist area before the sun was up. No attempt on my part at finding the monkeys early in the morning seemed to work, especially when it was still dark out. The forest was too dense and the vegetation too thick to locate monkeys even when they were howling, even during the day. I know because I tried on many occasions. I also was more likely to opportunistically find tourist area monkeys on my days off and on the way back from the non-tourist area. I

should have ignored them because it was not my day to be studying them. I then would have had fewer short observation periods in the tourist area, which would have been more similar to the observation times of the non-tourist area. In the end, I eliminated some of the opportunistic behavioral observations so as not to bias my results towards foraging and travel. Next time I will stick to a more rigorous observations schedule to keep things equal between the two areas.

C. Discussion of Future Research Directions

I was very interested in my research project as I was conducting it, and especially now that I am writing about it, I am inspired to see in what other directions this first study will lead me. I would like to investigate the influence of tourism on health in a more standardized way, and with identified groups and individuals. In future studies, I will note indicators of both good and poor health, including presence or absence of bot infections, for each individual observed. A record of poor health indicators and bot infections through time would be useful in determining the true health status of the monkeys, as well as investigating the influences of seasonal cycles. I would be interested in the future in observing more red howler defecation events, and determining whether latrine use is typical behavior, and whether it is for the purpose of parasite avoidance. I would also like to look into the latrine behavior of other monkey species and see whether it helps them reduce intestinal parasite infections. I want to look into howling behavior in a more systematic way, and investigate seasonal influences on timing of roars and barks. I want to identify more feeding trees and look more at the ecological influences on feeding behavior. Finally, I would like to investigate the influence of the encroaching gold miners on forest health, and hopefully inspire the agencies charged with the protection of the Brownsberg Natuur Park to actually do something to protect it.

D. Summary of Conclusions and Recommendations for Park Managers

The findings of this project lead me to conclude that so far the tourist activities at the Brownsberg Natuur Park are not affecting the monkeys in a dangerous way. The monkeys are definitely affected by tourist presence, but because they are adaptable, they seem to be coping by altering their behaviors

in response to tourist presence. I fear that these altered behaviors may have a negative effect in the long term, however, because the monkeys in the tourist area are more active and are using more energy in travel than monkeys in the non-tourist area. They may suffer from malnutrition in the long run if they cannot continue to meet their energy needs in order to both avoid tourist activities and fight off parasite infections, with which they are certainly afflicted. For those reasons, I would recommend that tourism at Brownsberg not be allowed to increase drastically in the coming years. Tourism has been going on at Brownsberg for several decades now though, and perhaps the current state of the monkey behavioral patterns and health reflect a stasis that allows them to live relatively healthily and continue to reproduce and expand their numbers, rather than suffer at the individual, group, or population level due to tourist impact. I do not currently have observations of reproductive rates, though identification and monitoring of several groups or red howlers in the future would help to determine whether reproductive rates are comparable to sites without tourist presence.

The future of the Brownsberg Natuur Park at this time is unclear. The managers of the park are not effective at encouraging tourists to visit the park or discouraging miners from destroying it. On the one hand, increased tourist presence could further impact the monkeys, possibly harming them in the future. I would not say that the park runs at capacity in general, and I think more tourists could be allowed to visit the park without severe damage to the environment. A drastic increase in tourist numbers would be harmful, but the park has actually been experiencing a decline in visitors during the past two to three years, so a few more tourists should not be a problem. By continuing to allow tourists to visit, the managers of the park would be able to continue to run the site as a protected refuge, as long as the tourists' dollars were funneled back into the organization charged with its care. On the other hand, a decrease in tourist presence may allow the monkeys to return to a more natural behavioral pattern and would allow them to possibly improve their health due to the cessation of the stress caused by the tourist activities today. However, without tourists bringing in money to keep the park in operation, there would be no reason to stop the eventual

takeover by the gold miners, bauxite miners, or loggers. Specifically in the case of Brownsberg, the survival of the forest is dependent on the continued use by tourists. Until Surinamers, and especially employees of Stinasu, see the value of Brownsberg, both from a monetary and from a biodiversity standpoint, I fear for the future of the park and its inhabitants.

Appendix: Ethogram

Common Behaviors

Remain Stationary

Rest- sit still with no or minimal head or body movement

Sit, sit alert- transition between activities, not restful looking, looking around

Forage

Forage- search for, test ripeness of, chew, & otherwise eat some kind of food (often involved much movement throughout the tree canopy)

Locomote

Travel- leave one tree canopy and enter another, or move through several tree canopies along the way through the forest

Move- locomote within one tree canopy- common during foraging

Flee- travel quickly away from something- usually obviously frightened

Vocalize

Roar- long (~5 min), cyclic vocalization, usually started by an adult male's rumble

Bark- sudden, loud, frantic, and brief (10-30 sec) vocalization, often repeated several times in a row

Lawn mower grunts (exaggerated grunting)- a kind of ooo-gaahh sound like the repeated pulling on the starter-cord of a lawn mower

Rumble- a rolling vocalization in the throat

Grunt- brief staccato vocalization, could be quiet or quite loud, single or in a series

Eliminate Waste

Defecate, urinate- eliminate wastes from the body, most often while perched on a branch and not in motion

Interact with Others

Groom- visibly pick at fur and brush fingers through fur while looking intently at it

Fight- wrestle or otherwise physically engage while one or both individuals vocalize in a nervous manner

Play- wrestle, chase, tackle, etc., usually involving juveniles, sometimes exhibiting a "play-face"

Responses to Humans

These were considered possible responses to humans if they occurred immediately following a disturbance.

Rank 1 Responses (Mild Physical Response)

Look at me, look towards noise- look purposefully at me, turn head or gaze toward a sound

Shift position, sit alert after a disturbance- rotate the body or change posture, stop activity and sit at attention

Rank 2 Responses (Moderate Physical or Vocal Responses)

General nervous behavior, pacing- a combination of several possible behaviors including grunting, looking repeatedly, etc., just as you would expect from a nervous person, travel back and forth across a branch, approach an object or other monkey and retreat repeatedly, bounce up and down on one part of a branch

Join another monkey, retreat to cover, move away (not quickly)- move from original position to within one meter of another or multiple individuals or from an original exposed position to an out-of-sight perch deeper within the canopy (also observed as a response to rain), travel out of a tree and further away, not quickly enough to be labeled "flee," but in a direction away from a perceived human disturbance

Grunt softly- a quiet vocalization, repeated over one to several minutes, usually in association with other nervous behaviors such as pacing or looking to a noise

Stop howling abruptly- early cessation of a roar, often a response to loud tourists or vehicles approaching the monkeys

Rank 3 Responses (Intense Physical or Vocal Responses)

Flee- see common behaviors above, usually seen immediately after humans or vehicles approached a group of monkeys

Lawn mower grunting (exaggerated grunting)- see common behaviors above- It was generally impossible to determine conclusively that the grunting I heard was in response to a human disturbance; therefore assignment of this response was due to timing and proximity

Roar/bark- see common behaviors above- It was generally impossible to determine conclusively that the roar or bark that I heard was in response to a human disturbance; therefore assignment of this response was due to timing and proximity

Defecate- see common behaviors above- This was a common response to approaching conspecific groups; I also observed this response to my presence on three occasions

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