

SPECIES RICHNESS AND HABITAT PREFERENCE OF LARGE VERTEBRATES IN THE  
CENTRAL SURINAME NATURE RESERVE

By

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To my parents, family and friends

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## TABLE OF CONTENTS

	<u>page</u>
ACKNOWLEDGMENTS .....	4
LIST OF TABLES .....	7
LIST OF FIGURES .....	8
ABSTRACT .....	9
CHAPTER	
1 INTRODUCTION .....	11
2 MATERIALS AND METHODS .....	15
Site Description .....	15
Data Collection .....	17
Analyses .....	20
3 RESULTS .....	22
Species Richness .....	22
Plant Phenology .....	22
Predictors of Species Richness .....	24
Line –Transect .....	24
Temperature and rainfall .....	24
Leaf cover .....	25
Fruiting and flowering .....	25
Opportunistic Sightings .....	25
Temperature and rainfall .....	25
Leaf cover .....	26
Fruiting and flowering .....	26
Pooled Data .....	26
Temperature and rainfall .....	26
Leaf cover .....	26
Fruiting and flowering .....	27
Habitat Preference .....	27
Detectibility .....	28
4 DISCUSSION .....	34
Assessing Consistency of Survey Protocols with the Assumptions of Line-transect Methods .....	35
Species Richness .....	36
Predictors of Species Richness .....	37

Habitat Preference .....	40
Detectability .....	42
Conclusions.....	45
APPENDIX.....	46
LIST OF REFERENCES .....	49
BIOGRAPHICAL SKETCH .....	54

## LIST OF TABLES

<u>Table</u>	<u>page</u>
1-1. Factors hypothesized to influence species richness, interpreted from Currie (1999).....	12
2-1. Characteristics of habitat types for line transect census in Raleighvallen, Central Suriname Nature Reserve, Suriname .....	20
2-2. Characteristics of habitat used in opportunistic sightings census in Raleighvallen, Central Suriname Nature Reserve, Suriname .....	20
3-1. Rare species seen by sampling method in Raleighvallen, during 2000-2005 .....	24
3-2. Predictors of species richness based on p-values from line-transect data .....	25
3-3. Predictors of species richness based on p-values from opportunistic sightings data .....	26
3-4. Predictors of species richness based on p-values from pooled data .....	27
3-5. Observed and expected encounters in habitat types, $\chi^2$ , and adjusted residuals for primate species (indicated by initials of Latin name) using both sampling methods .....	29
3-6. Observed and expected encounters in habitat types, $\chi^2$ , and adjusted residuals for terrestrial mammal species (indicated by initials of Latin name) using both sampling.....	30
3-7. Observed and expected encounters in habitat types, $\chi^2$ , and adjusted residuals for birds and arboreal mammal species (indicated by initials of Latin name) using both.....	31
3-8. Number of species encounters in the bamboo habitat .....	32
3-9. Detectability of species from line-transect data .....	33
4-1. Overall predictors of species richness using line-transect, opportunistic sightings, and pooled data .....	34
4-2. Adjusted residuals results on which species appeared more or less than expected in habitat types by sampling method.....	34

## LIST OF FIGURES

<u>Figure</u>	<u>page</u>
2-1. Map of Suriname, highlighting Central Suriname Nature Reserve.....	16
2-2. Average rainfall and temperature in Raleighvallen during 2000-2005. ....	16
2-3. Map (a) line-transect labeled as Voltzberg trail (7km) and map (b) opportunistic sighting area (3km <sup>2</sup> ) with first 3km of line-transect highlighted in Raleighvallen.....	18
3-1. Species accumulation curves using two sampling methods in Raleighvallen, 2000-2005. ...	23
3-2. Average number of trees fruiting and flowering in Raleighvallen during 2000-2005. ....	23

Abstract of Thesis Presented to the Graduate School  
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Two important concepts for understanding community diversity are species richness and habitat preference. These concepts are also of great utility in assessing the effects of human disturbance on biodiversity, management and for making environmental policy decisions. The Central Suriname Nature Reserve, a world heritage biodiversity site, is a prime location for collecting baseline data on large vertebrates. The reserve has had no significant hunting, mining or timber harvest in over a century and scant data have been collected since the 1970s. I provide the first estimates of predictors of species richness and habitat preference available for large vertebrates. These evaluations are based on five years of continuous study by the Monkey-field crew from 1,666 km of a line-transect census, 70.5 km of a phenological survey, and 747 walks/days of opportunistic sightings. Numbers of fruiting and flowering trees, rainfall, temperature, and leaf cover were used as predictors of species richness. Habitat preference is based on observed and expected encounters of species in the three habitat types (plateau, liana, and swamp).

The analysis shows that the strongest predictor of species richness is plant productivity followed by temperature and rainfall. Our data suggest that habitat preference of large vertebrates is influenced by predator avoidance, interspecies interactions, both positive and

negative, and food availability. The particulars of the data set are site specific, but likely critical baseline data for other sites in Suriname and in the Guiana Plateau geographic region. The general patterns and methodologies presented here can be used as models for other research.

## CHAPTER 1 INTRODUCTION

Two important concepts for understanding community diversity are species richness and habitat preference. These concepts are also of great utility in assessing the effects of human disturbance on biodiversity, management and for making environmental policy decisions. Most conservation planning involving the selection of reserves is based on one or a few species (Simberloff 1988); often the most charismatic and/or those species considered umbrella, flagship, or keystone are used (Caro & O'Doherty 1999). Reserve networks selected in this way may be ineffective for the conservation of other, non-target species (Gatson & Rodrigues 2001). Species richness or habitat preference become obvious tools for overcoming this problem when considering conservation management plans, assessing the effects of human disturbance on biodiversity and for making environmental policy decisions. In this study we define species richness as the number of distinct species present in our study area.

Many hypotheses have been proposed for why certain areas have more species than others (Table 1-1 provided by Currie 1991). The energy hypothesis as proposed by Hutchinson (1959) states that the abundance of terrestrial organisms, as a whole, must be limited by their supply of energy. The energy available to animals consists of the production of food items that can be included in the diet of the group in question (Wright 1983). Hawkins *et al.* (2003) divides the energy hypothesis into the productivity and ambient-energy hypothesis.

The productivity hypothesis states that the level of diverse resource biomass in an ecosystem limits animal species richness. Productivity is defined as the net primary productivity of plants or the secondary productivity of consumers (Connell & Orias 1964). Ambient-energy hypothesis proposes that the animal species richness of a region is directly controlled by the total average energy available. We are going to test these hypothesis respectively using measures of

energy closely related to the level of primary production in a region, annual rainfall, leaf cover, average temperature and number of trees fruiting and flowering.

Table 1-1. Factors hypothesized to influence species richness, interpreted from Currie (1999)

Factor	Rationale
1. Climate	Mild conditions allow more species
2. Climatic variability	Constancy permits specialization
3. Habitat heterogeneity	Biologically or physically complex habitats provide more niches Prolonged time permits more complete colonization and evolution of new species
4. History	
5. Energy	Partitioning of energy among species limits richness
6. Competition	a. Competition favors reduced niche breadth b. Competitive exclusion eliminates species
7. Predation	Predation maintains unexploited niche breadth
8. Disturbance	Moderate disturbance hinders competitive exclusion

Line transects have been extensively used throughout forested tropics as a means of calculating relative abundance, density estimates, and species richness of a wide variety of vertebrates (Bennett *et al.* 2001, Thomas 1991, Rahbek & Graves 2001). A sampling effort which yields at least 40 and preferably 60-80 encounters for a given target species has been recommended (Burnham *et al.* 1980). However, useful comparisons between areas and/or habitats have been possible with fewer encounters. Our study advocates the combining of line-transect and opportunistic sightings methods because it increases the rate and size of an area that can be effectively surveyed.

When describing an area using either line-transect or opportunistic sightings the detection probability of species must be taken into account. Detection probability is defined as the probability that a member of the species of interest is included in the count at the given time or location (MacKenzie & Kendall 2002). Failure to detect species when they are present at a site is not uncommon in field surveys (Gu & Swihart 2004). The vast majority of wildlife-habitat

models that use presence-absence as a response variable have assumed that if a species occurs at a site, it will be detected. This assumption has the effect of equating detection probability to one.

The Guiana Shield is a Precambrian eroded base, sweeping from the Orinoco Delta in Venezuela to the Amazon Delta, beyond Amapa, in Brazil (de Granville 1988). The vegetation of the Guiana Plateau is comprised primarily of variants of tropical forests (de Granville 1988) resulting in high levels of plant endemism that characterize the forests of the Guiana Shield (Lehman 2000).

Vertebrate frugivores are the dominant group of large animals in tropical forests (Haugaasen & Peres 2007). Information on the large vertebrates of Suriname is scant. Walsh and Gannon (1967) were some of the first to describe the large vertebrates in Suriname. They described the mammals that were rescued and/or recovered from a flooding of the large lowland area during the construction of the Afobaka Dam. Studies on deer (Branan *et al.* 1985) and primate (Norconk *et al.* 2003) species have also been collected in Suriname. The primates of Raleighvallen, the location of our study, have been the subject of only a few reports ( Mittermeier 1976, Mittermeier & van Roosmalen 1976, Fleagle & Mittermeier 1980, Fleagle *et al.* 1981, van Roosmalen *et al.* 1988, and Baal *et al.* 1988), most of which were derived from a single survey (March 1976- February 1977). The other large vertebrates within Raleighvallen have been ignored.

In 2000, The Central Suriname Nature Reserve (CSNR) incorporated smaller preserves to protect 1.6 million ha of tropical forest in west central Suriname and the upper watershed of the Coppename River. Raleighvallen is approximately 78,000 ha and is located in the northern part of the reserve on the Coppename piedmont. The reserves flora and fauna are virtually undisturbed, and includes a full component of predators, including felids, raptors and snakes. No

significant hunting, mining, or timber harvest has occurred in more than a century. Information on species richness in an undisturbed tropical forest can act as a useful model when trying to protect areas similar to Raleighvallen in the Guianan Shield. The data can also be used for comparisons with disturbed forests, mainly to see how disturbance changes species richness levels or habitat preferences.

The principal aims of this study are to determine species richness levels, what predicts species richness in Raleighvallen, and to quantify patterns of differential habitat use among these species. The specific aspects of habitat use examined are “forest type”. Three distinct floristic associations are recognized: plateau, liana, and swamp. Census data also provide the baseline for more detailed socioecological and behavioral studies (Butynski 1990, Struhsaker 1975) essential for effective long term management of the site.

## CHAPTER 2 MATERIALS AND METHODS

### Site Description

Available data are from five years of continuous line-transect and opportunistic sightings sampling, collected at a well established study site in the Central Suriname Nature Reserve, Raleighvallen, Suriname. The site encompasses ~ 3 km<sup>2</sup> and is bounded on the northern and western aspects by the eastern bank of the Coppename River. Raleighvallen is part of the larger Central Suriname Nature Reserve (4 71 N, 56 21 W; 30 m altitude) consisting of 1.6 million ha of primary tropical forest (Figure 2-1). We have classified the forest structure of our field site into four distinct habitats and ranked them by physical complexity (Boinski *et al.* in prep):

1) Plateau forest: Not affected by seasonal flooding of the rivers, usually possible to distinguish three to four stories (the highest being up to 60 m), lianas are not individually abundant and plateau forest has more fruit and flower producing tree species.

2) Liana forest: Does not usually exceed 20 m in height, richer in lianas than plateau forest and has fewer Boegroe maka palms, tall trees with a wide circumference do occur but are widely separated, space between trees is filled with dense tangles of lianas and vines, and liana tangle itself rarely exceeds 10-15 m in height.

3. Swamp forest: Soil stays moist to wet throughout the year, lianas and epiphytes are not common, but stilt root trees (*Euterpe oleraceae*) are.

4) Bamboo patches: continuous, dense, homogenous patches of bamboo (*Guadua latifolia*).

Annual average rainfall in Suriname is 2200 mm, average temperature is 27°C; with a short rainy season in December-January, long wet season in March-August, and a dry season in September-November (Baal et al. 1988).

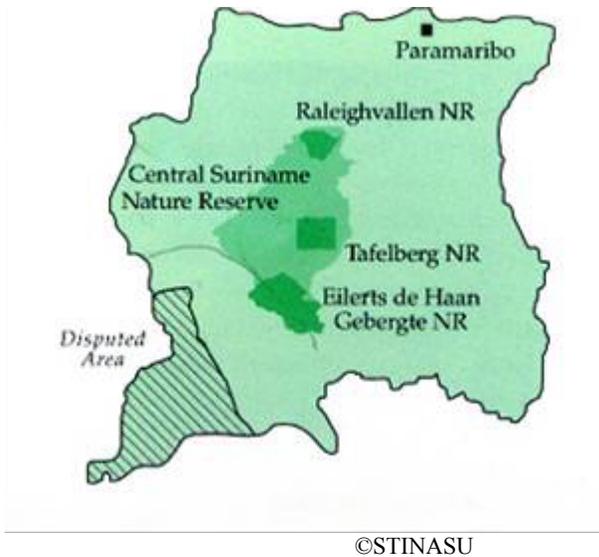


Figure 2-1. Map of Suriname, highlighting Central Suriname Nature Reserve

Rainfall at the Monkey-Forest field camp in Raleighvallen, between 2000 and 2005 averaged 1967mm, and the minor dry and wet seasons exhibit marked variation in cumulative rainfall, onset, end and duration. We see a short rainy season in December-January, a short dry season February-March, a long wet season April-July and a long dry season August-November. Minimum and maximum temperatures at the Monkey-Forest field camp are noted daily at 18:00 h local time and averaged 23.7-28.9, °C (Figure 2-2).

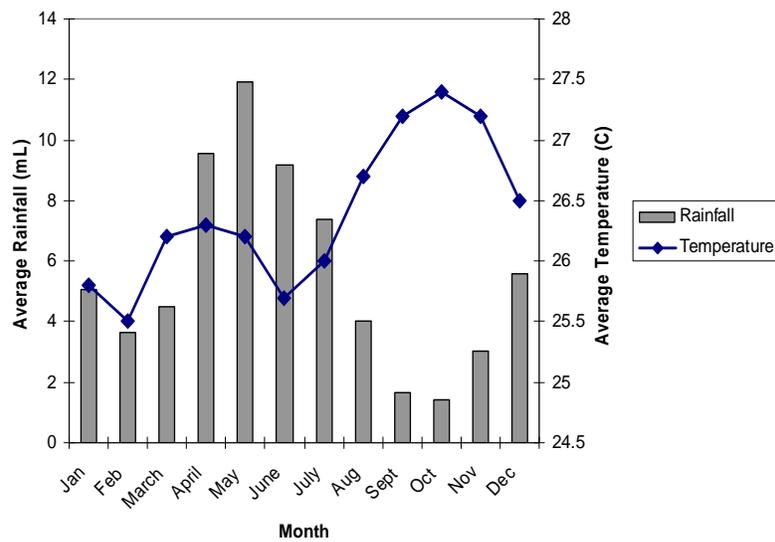


Figure 2-2. Average rainfall and temperature in Raleighvallen during 2000-2005.

## Data Collection

We collected census data using a double-observer dependent line-transect method. The double observer method is when two observers walk a line-transect in a single file keeping no more than 3m between them. The second observer notes any observations that the first observer missed. The roles are then reversed for the return trip on the line-transect. An existing pathway that runs North to South for 7 km (approximately 1 m wide) makes up our line-transect (Figure 2-3a). This path is maintained and guarded by the Suriname Nature Conservation agency (STIANSU). The trail is also used by tourists to reach the Voltzberg-Inselberg, a 240m dome shaped granite inselberg. Kauffman (2008) found that 1,300 tourists used the trail during 2006, which she believes is much higher than previous years. Because the trail is maintained the usual 1 m visibility on each side of the transect was expanded to 2 m. Observers walked the census line beginning at 0600-0730 h at an average speed of about 1 km h<sup>-1</sup>, recording all sightings of large vertebrates (>250g). The number of censuses conducted per month ranged from 2 to 7, with an average of 3.9 per month. The line-transect was not done during rainy weather because this would affect the intrinsic detectability of different species. Census data collected during October 2000-September 2005 resulted in 238 walks (1,666km) with 1,182 animal sightings along the single 7km transect.

For each animal sighting we recorded time, species, estimated number of individuals, how observed or detected (audio or visual cues), perpendicular distance, grid location along the line-transect, predator avoidance behavior, habitat type, duration of observation and/or why observation ended. Observers were trained by experienced field assistants. Transect markers are 50m-150m apart rather than being equidistant. Examples of transect markers are: streams, boulders, unique trees, and other distinctive points in the landscape. For this study only the first



searched for *Cebus apella* troops, visited the harpy eagle nest site, hiked around on their days off, and whenever they were in the forest and not following a monkey troop. Sightings were recorded from November 2000-September 2005. A total of 747 walks/days had recordings that resulted in 1,640 large vertebrate sightings. When a sighting occurred, species, number of individuals seen, habitat type, and location were recorded. Table 2-2 shows the available habitat that was surveyed and how much of the habitat had sightings.

Phenological data was obtained at monthly intervals during the last week of every month; from October 2000 through September 2005 resulting in 47 survey walks (70.5km). The survey was conducted on 1.5 km network of trails established to haphazardly cross through the four habitat zones within the monkey-forest field site (3km<sup>2</sup>). A set of trees with a diameter at breast height (DBH) of greater than 20 cm and within 1 m of each side of the trail were aluminum-tagged, mapped and identified beginning in May 1998 by local tree spotters and botanists. Due to tree falls, tree deaths and the addition of new trees the number of trees in the survey ranged from 135-229 with an average of 175 trees. Liana and plateau forest combined represented more than 90% of the phenological survey area.

Presence and absence of ground fruit, mature and immature, overall fruit cover, mature and immature, flowers, flower buds, leaf cover, and presence of rotten or processed fruits were recorded using a scale of 1-4, 4 being 75-100%, 1 being 0- 25%,. Trees were scored as flowering or fruiting if flowers/fruits were visible in at least 25% of the crown.

Table 2-1. Characteristics of habitat types for line transect census in Raleighvallen, Central Suriname Nature Reserve, Suriname

Habitat	Total quadrants on transect	Percent of total area	Total sightings	Number of species encountered
Plateau	41	23	454	19
Liana	116	66	696	19
Swamp	19	11	33	12

Table 2-2. Characteristics of habitat used in opportunistic sightings census in Raleighvallen, Central Suriname Nature Reserve, Suriname

Habitat	Total quadrants in study site	Quadrants with sightings	Percent of total area	Total sightings	Number of species encountered
Plateau	401	199	49.6	1007	32
Liana	174	100	57.5	482	28
Swamp	20	14	70	157	22
Bamboo	40	21	52.5	86	18

### Analyses

Total species richness in the reserve was determined as number of distinct species seen over time using both line-transect and opportunistic sightings. Species were combined into 4 distinct groups: Primates (includes all primate species), Rodents (*Myroctca exilis* and *Dasyprocta punctata*), Birds (*Psophia crepitans*, *Crax alector* and *Harpia harpyja*), and Other Mammals (includes carnivores, ungulates, and sciuridae). Other bird species (guans and tinamous) were encountered but could not be reliably identified and were removed from the data set. Species were also divided into arboreal and terrestrial groups. Regression models were used to test which variables were the best predictor of species richness. The explanatory variables used are total trees fruiting (trees having both mature and immature fruit present) and flowering (mature flowers and flower buds), temperature, rainfall, and leaf cover. Chi squared test compared the distribution of species among vertebrate groups (primates, terrestrial mammals, and arboreal mammals and birds) and different habitat types assuming no selection, i.e., proportional to the availability of habitat types within the study site and along the transect route.

The adjusted residual equation was used to test if there was significant preference towards or against habitat types:

$$(O_{ij} - E_{ij}) / [E_{ij} (1-O_{i.})(1-O_{.j})]$$

where

$X_{xx}$  means X subscripted with xx

and

$O_{ij}$  is the observed value in the ith row, jth column

$E_{ij}$  is the expected value of the cell in the ith row, jth column

$O_{i.}$  is the observed row total for the ith row

$O_{.j}$  is the observed column total for the jth column

Species detectability was calculated using DISTANCE program version 5.0 (Thomas et al. 2006). Data input into the program consisted of estimates of cluster size, perpendicular distance, line-transect length, observer, and habitat type. The program is designed to determine the best fit probability of detection function based on the estimated perpendicular distances by generating a key function and a series expansion. The best-fit model is based on the smallest Akaike's Information Criterion (AIC) value (Buckland et al. 1993).

## CHAPTER 3 RESULTS

### **Species Richness**

A total of 1,182 animal sightings were recorded from line-transect data collected from October 2000 through September 2005. Twenty-one species were seen with one additional new species being encountered every year after 2002. The use of opportunistic sightings resulted in 1,640 animal sightings with a total of thirty-four species seen. An accumulation curve of richness is shown in Figure 3-1.

The five most commonly sighted species using the line transect method are *Cebus apella*, *Dasyprocta punctata*, *Ateles paniscus*, *Saguinas midas*, and *Saimiri sciureus*. These species accounted for 854 (72%) of the 1,182 sightings. The opportunistic sighting method has *Dasyprocta punctata*, *Alouatta seniculus*, *Psophia crepitans*, *Myroctoa exilis* and *Cebus apella* as the most sighted species accounting for 917 (55%) of the 1,640 sightings. The seven most commonly sighted species in order of frequency using pooled data are *Dasyprocta punctata*, *Cebus apella*, *Alouatta seniculus*, *Saguinas midas*, *Ateles paniscus*, *Crax alector*, and *Psophia crepitans*. These species accounted for 1,989 (70%) of the 2,829 pooled sightings. Many rare species were encountered but their low encounter rates prohibited any analysis (Table 3-1).

### **Plant Phenology**

The 135-229 phenology trees monitored included 41 families and 72 genera. The most abundant families are Areaceae, Mimosaceae, Cecropiaceae, Strelitziaceae, Sapotaceae, Burseraceae, Apocynaceae, Lecythidaceae, Meliaceae, and Tiliaceae. The emergence of fruits commenced during the start of the long dry season (August-November), with fruiting peaking in October. Flowers and flower buds began to appear

in December at the start of the short wet season. Flowers peaked in March, the end of the short wet season (Figure 3-2).

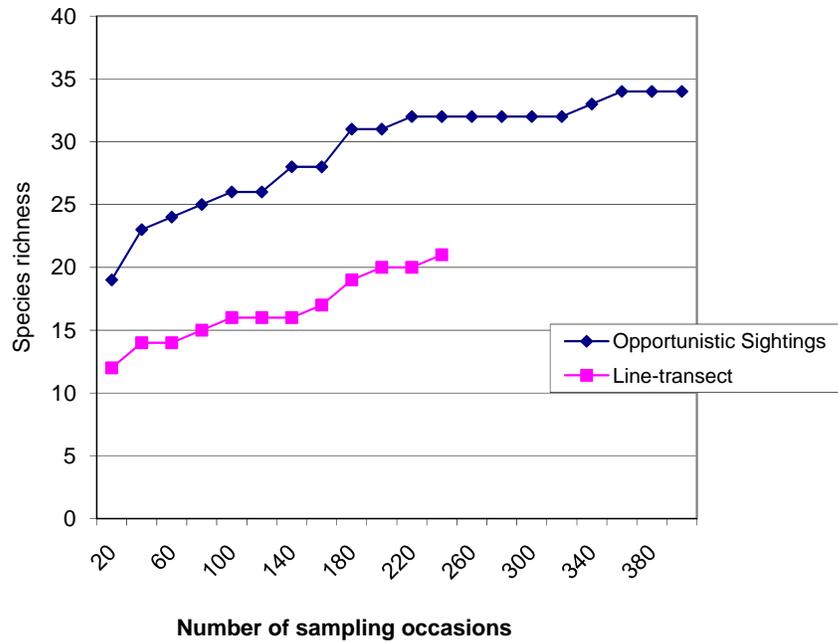


Figure 3-1. Species accumulation curves using two sampling methods in Raleighvallen, 2000-2005.

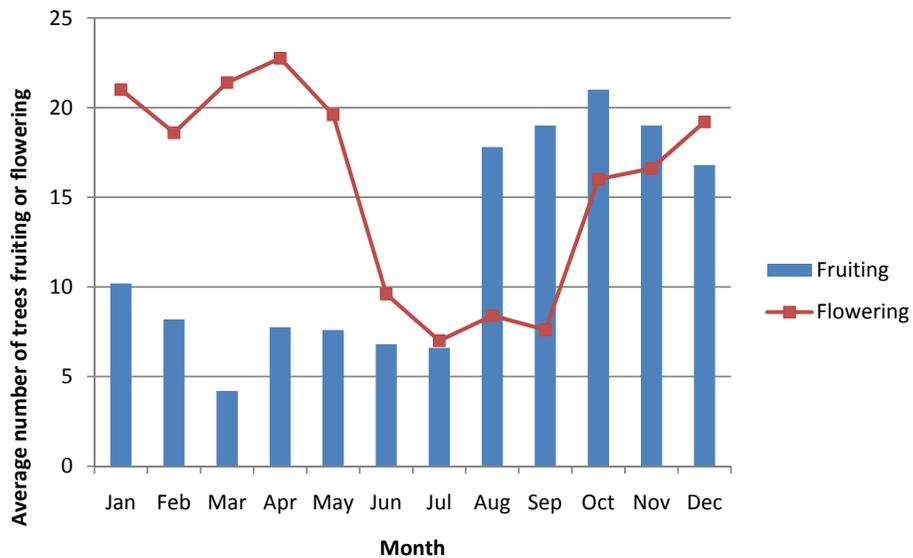


Figure 3-2. Average number of trees fruiting and flowering in Raleighvallen during 2000-2005.

Table 3-1. Rare species seen by sampling method in Raleighvallen, during 2000-2005

Species	Line-transect	Opportunistic sightings
<i>Cyclopes didactylus</i>	0	1
<i>Speothos venaticus</i>	0	2
<i>Felis wiedii</i>	0	2
<i>Myrmecophaga tridactyla</i>	0	3
<i>Potos flavus</i>	0	3
<i>Hydrochaeris hydrochaeris</i>	0	4
<i>Didelphi marsupialis</i>	0	4
<i>Nausa nausa</i>	0	4
<i>Felis yagouroundi</i>	0	4
<i>Felis pardalis</i>	0	7
<i>Dasypus novemcinctus</i>	0	19
<i>Bradypus tridactylus</i>	1	3
<i>Panthera onca</i>	1	5
<i>Cebus olivaceus</i>	1	15
<i>Tapirus terrestris</i>	3	31
<i>Eira barbara</i>	5	38

### Predictors of Species Richness

Data were analyzed by sampling method and by pooling both data sets. The count per unit effort (CPUE) is species seen divided by total walks. This value was then modeled against: average rainfall and temperature from 2000-2005, average leaf cover (based on the 1-4 scale, 4 =75-100% cover, 1 =0-25% cover) from the phenological surveys, and total trees fruiting and flowering divided by total phenological survey walks.

#### Line –Transect (Table 3-2)

##### Temperature and rainfall

Temperature ( $p=0.0545$ ) and rainfall ( $p=0.4215$ ) have no significant predicative value on species richness.

## Leaf cover

Leaf cover ( $p=0.9569$ ) had no significance in predicative value with encounter of species guilds (primate, rodents, birds, or other mammal) or by forest level (arboreal or terrestrial) groups.

## Fruiting and flowering

Fruiting ( $p=0.0333$ ) had predictive power on species richness but when tested against species guild and forest level no significance was detected. Flowering ( $p=0.1922$ ) has no significant predictive power on species richness.

Table 3-2. Predictors of species richness based on p-values from line-transect data

	Temperature	Rainfall	Leaf cover	Fruiting	Flowering
All Species	0.0545	0.4215	0.9569	<u>0.0333</u>	0.1922
Guilds					
Primate	0.2287	0.6021	0.7037	0.1280	0.1528
Rodent	0.0970	0.0916	0.8636	0.1241	0.9779
Bird	0.1185	0.3365	0.7675	0.1116	0.2575
Other Mammals	0.9041	0.8179	0.4050	0.9610	0.7146
Forest Level					
Arboreal	0.1847	0.9445	0.8237	0.1323	0.1030
Terrestrial	0.1276	0.1276	0.9261	0.8690	0.7105

## Opportunistic Sightings (Table 3-3)

### Temperature and rainfall

Temperature ( $p=0.0123$ ) has a predictive value on determining species richness. The other mammal ( $p=0.0072$ ) guild and terrestrial ( $p=0.0288$ ) group are most affected by temperature. Rainfall ( $p=0.3317$ ) fails to have any predictive value.

### Leaf cover

Leaf cover ( $p=0.0271$ ) is shown to be significantly predictive with the opportunistic sightings data. When species are divided into guilds and forest level groups no significance is found.

### Fruiting and flowering

The opportunistic data shows fruiting ( $p=0.0004$ ) has significance with the other mammal ( $p=0.0024$ ) guild and arboreal ( $p=0.0459$ ) and terrestrial ( $p=0.0041$ ) groups. Flowering ( $p<0.0001$ ) shows significance with the primates ( $p<0.0001$ ) and bird ( $p=0.0314$ ) guilds. Forest level analysis reveals flowering only has significance with arboreal ( $p<0.0001$ ) species.

Table 3-3. Predictors of species richness based on p-values from opportunistic sightings data

	Temperature	Rainfall	Leaf cover	Fruiting	Flowering
All Species	<u>0.0123</u>	0.3317	<u>0.0271</u>	<u>0.0004</u>	<u>&lt;0.0001</u>
Guilds					
Primate	0.2443	0.7527	0.5010	0.1365	<u>&lt;0.0001</u>
Rodent	0.3499	0.5335	0.6161	0.1935	0.2470
Bird	0.5424	0.6727	0.0936	0.4073	<u>0.0314</u>
Other mammals	<u>0.0072</u>	0.2970	0.2032	<u>0.0024</u>	0.7254
Forest Level					
Arboreal	0.1954	0.9076	0.1972	<u>0.0459</u>	<u>&lt;0.0001</u>
Terrestrial	<u>0.0288</u>	0.1367	0.0724	<u>0.0041</u>	0.1779

### Pooled Data (Table 3-4)

#### Temperature and rainfall

Temperature ( $p=0.0280$ ) has predictive value on terrestrial species ( $p=0.0085$ ).  
Rainfall ( $p=0.1624$ ) has a predicative value on terrestrial species ( $p=0.0334$ ).

#### Leaf cover

Leaf cover ( $p=0.0929$ ) is not significant with guilds or forest level groups.

## Fruiting and flowering

Fruiting ( $p < .0001$ ) has a significant predictive value on arboreal ( $p = 0.0009$ ) and terrestrial ( $p = 0.0018$ ) species. The primate ( $p = 0.0001$ ) and bird ( $p = 0.0014$ ) guilds are also influenced by fruiting. Flowering ( $p = 0.0623$ ) has predictive value on arboreal ( $p = 0.0281$ ) species and the primate ( $p = 0.0070$ ) and bird ( $p = 0.0022$ ) guilds.

Table 3-4. Predictors of species richness based on p-values from pooled data

	Temperature	Rainfall	Leaf cover	Fruiting	Flowering
All Species	<u>0.028</u>	0.1624	0.0929	<u>&lt;0.0001</u>	0.0623
Guilds					
Primate	0.2832	0.2601	0.7001	<u>0.0001</u>	<u>0.007</u>
Rodent	0.0925	0.1964	0.1432	0.0815	0.5405
Bird	0.4801	0.7665	0.1195	<u>0.0014</u>	<u>0.0022</u>
Other Mammals	0.0598	0.2485	0.2595	0.2269	0.1463
Forest Level					
Arboreal	0.3922	0.7644	0.2563	<u>0.0009</u>	<u>0.0281</u>
Terrestrial	<u>0.0085</u>	<u>0.0334</u>	0.1334	<u>0.0018</u>	0.8117

## Habitat Preference

An association between habitat and species is seen with the line-transect data ( $DF=28$ ,  $\chi^2 = 94.513$ ,  $p < 0.0001$ ) and the opportunistic sightings ( $DF=34$ ,  $C = 103.743$ ,  $p < 0.0001$ ). Table 3-5, Table 3-6, and Table 3-7 shows all  $\chi^2$  and adjusted residuals  $((O_{ij} - E_{ij}) / [E_{ij} (1 - O_{i.})(1 - O_{.j})])$  values between species and habitat type. *Alouatta seniculus*, *Ateles paniscus*, and *myroocta exilis* are seen more than expected in plateau habitat while *Cebus apella*, *Crax alector*, and *Psophia crepitans* are seen less than expected. *Cebus apella* and *Crax alector* are seen more than expected and *Alouatta seniculus*, *Ateles paniscus*, and *myroocta exilis* are seen less than expected in liana habitat. *Alouatta seniculus* is seen more than expected and *cebus apella* and *myroocta*

*exilis* are seen less than expected in the swamp habitat. The bamboo habitat had 86 sightings but due to low sample size no statistical analysis was done (Table 3-8).

### **Detectability**

Table 3-9 displays the results from the detectability analysis. *Alouatta seniculus*, *Cebus apella*, and *Pithecia pithecia* have the highest detection rates and *Myrocyta exilis*, *Psophia crepitans* and *Dasyprocta punctata* have the lowest detection rates.

Table 3-5. Observed and expected encounters in habitat types,  $\chi^2$ , and adjusted residuals for primate species (indicated by initials of Latin name) using both sampling methods from census data collected in Raleighvallen, Central Suriname Nature Reserve, Suriname

Habitat	Line Transect							Opportunistic Sightings					
	C.s. <sup>a</sup>	C.a. <sup>b</sup>	A.s. <sup>c</sup>	S.s. <sup>d</sup>	A.p. <sup>e</sup>	S.m. <sup>f</sup>	P.p. <sup>g</sup>	C.s.	C.a.	A.s.	A.p.	S.m.	P.p.
	11	82	31	33	91	43	7	23	79	101	24	80	24
	6	103	21	43	53	49	6	18	91	96	15	75	28
	2.41	4.55	4.65	2.66	27.2	0.77	0	0.9	1.6	0.3	4.2	1.1	0.7
Plateau	1.64	<u>-2.6*</u>	<u>2.3+</u>	-1.6	<u>6.3+</u>	-0.9	0.43	1.2	-1.3	0.6	<u>2.3+</u>	-1	-1
	6	179	24	79	46	80	10	6	65	32	2	25	18
	10.5	158	33	67	81	75	10	9	44	46	7	17	13
	1.98	2.55	2.71	2.12	15.3	0.29	0.03	1.1	9.8	4.5	4.2	3.7	1.3
Liana	-1.5	<u>2.2+</u>	-1.7	1.6	<u>-4.3*</u>	0.65	-0.2	-1	<u>3.5+</u>	<u>-2.2*</u>	<u>-1.9*</u>	<u>2</u>	1.4
	1	9	1	2	1	5	1	2	6	25	0	4	5
Swamp	0.49	7	1	3	3	3	0.49	3	16	15	2	5	4
	0.51	0.34	0.2	0.4	2.05	0.62	0.51	0.3	5.1	6	2.5	0.5	0
	1	1	-0.4	-0.6	-1.5	0.93	0.98	-1	<u>-2.2*</u>	<u>2.9+</u>	-1.4	-0.4	0.5
Total	18	270	57	114	138	128	18	31	150	158	26	58	47

Note. + = species seen more than expected, \* = species seen less than expected based on adjusted residuals.

<sup>a</sup>*Chiropotes satanus*

<sup>b</sup>*Cebus apella*

<sup>c</sup>*Alouatta seniculus*

<sup>d</sup>*Saimiri sciureus*

<sup>e</sup>*Ateles paniscus*

<sup>f</sup>*Saguinas midas*

<sup>g</sup>*Pithecia pithecia*

Table 3-6. Observed and expected encounters in habitat types,  $\chi^2$ , and adjusted residuals for terrestrial mammal species (indicated by initials of Latin name) using both sampling methods from census data collected in Raleighvallen, Central Suriname Nature Reserve, Suriname

Habitat	Line Transect					Opportunistic Sightings					
	M.e. <sup>a</sup>	D.p. <sup>b</sup>	T.t. <sup>c</sup>	T.p. <sup>d</sup>	M.a. <sup>e</sup>	M.e.	D.p.	T.t.	T.p.	M.a.	T.te. <sup>f</sup>
	21	75	3	3	9	75	298	23	28	33	22
	15	78	3	3	6	55	301	20	24	38	18
Plateau	2.06	0.14	0.06	0.06	1.32	7	0	0.26	0.4	0.7	0.52
	<u>15.4</u>	-0.4	-0.2	-0.2	1.1	<u>2.9</u>	-0.8	0.68	0.8	-0.8	0.96
	19	120	6	6	7	15	143	10	10	22	8
	23	120	5	5	9	26	146	10	12	18	9
Liana	0.87	0	0.09	0.09	0.61	5.2	0.1	0	0.4	0.6	0.13
	-1	0	0.36	0.36	-0.8	<u>-2.2</u>	-0.3	0	-0.5	1	-0.3
	0	9	0	0	0	1	55	1	3	8	1
	1	5.5	0.24	0.24	0.43	8	48	3	3	6	3
Swamp	1.09	2.06	0.24	0.24	0.43	7	0.9	1.61	0.2	0.6	1.35
	-1	2	-0.45	-0.5	-0.6	<u>-2.5</u>	1.5	-1.1	0	0.9	-1.1
Total	40	204	9	9	16	90	496	34	41	63	31

Note. + = species seen more than expected, \*=species seen less than expected based on adjusted residuals.

<sup>a</sup>*Myroctoa exilis*

<sup>b</sup>*Dasyprocta punctata*

<sup>c</sup>*Tayassu tajacu*

<sup>d</sup>*Tayassu peccary*

<sup>e</sup>*Masama americana*

<sup>f</sup>*Tapirus terrestris*

Table 3-7. Observed and expected encounters in habitat types,  $\chi^2$ , and adjusted residuals for birds and arboreal mammal species (indicated by initials of Latin name) using both sampling methods from census data collected in Raleighvallen, Central Suriname Nature Reserve, Suriname

Habitat	Line Transect			Opportunistic Sightings					
	C.a. <sup>a</sup>	P.c. <sup>b</sup>	T.t. <sup>c</sup>	C.a.	H.h. <sup>d</sup>	P.c.	S.a. <sup>e</sup>	T.t.	E.b. <sup>f</sup>
Plateau	20	16	2	45	27	54	31	15	23
	30	21	3	46	23	54	36	24	22
	3.75	1.58	0.4	0.1	0.65	0.009	0.82	4	0
	<u>-2</u> *	-1.8	-0.5	-0.2	0.85	0	-0.8	-1.8	0.2
	59	40	5	20	10	26	23	18	9
Liana	47	33	4	22	11	26	17	12	10
	3.02	1.24	0	0.3	0.12	0.009	1.6	2.9	0.3
	<u>1.9</u> <sup>+</sup>	0.66	0.5	-0.4	-1.9	0	1.5	1.7	-0.3
	1	1	1	12	1	10	6	8	5
	2	1	0.2	7	3	8	5	3	3
Swamp	0.65	0.2	2.8	2.7	1.97	0.17	0	4	0.5
	-0.8	-0.59	1.9	2	-1.2	0.75	0.46	3	1.1
Total	80	57	8	77	38	90	60	41	37

Note. Note. + = species seen more than expected, \*=species seen less than expected based on adjusted residuals.

<sup>a</sup>*Crax alector*

<sup>b</sup>*Psophia crepitans*

<sup>c</sup>*Tamandua tetradactyla*

<sup>d</sup>*Harpia harpyja*

<sup>e</sup>*Sciurus aestuans*

<sup>f</sup>*Eira barbara*

Table 3-8. Number of species encounters in the bamboo habitat

Species	Number of encounters
<i>Dasyprocta punctata</i>	37
<i>Crax alector</i>	14
<i>Cyclopes didactylus</i>	4
<i>Mazama americana</i>	4
<i>Sciurus aestuans</i>	4
<i>Tamandua tetradactyla</i>	4
<i>Psophia crepitans</i>	3
<i>Tayassu tajacu</i>	3
<i>Cebus apella</i>	2
<i>Dasypus novemcinctus</i>	2
<i>Nausa nausa</i>	2
<i>Eira barbara</i>	1
<i>Felis pardalis</i>	1
<i>Harpia harpyja</i>	1
<i>Myroctca exilis</i>	1
<i>Panthera onca</i>	1
<i>Saguinas midas</i>	1
<i>Saimiri sciureus</i>	1
Total	86

Table 3-9. Detectability of species from line-transect data

Species	Number of observations	Key function	Adjustment	AIC	Detectability
<i>Myorocta exilis</i>	38	Hazard-Rate	Cosine	148.26	94.5
<i>Dasyprocta punctata</i>	99	Hazard-Rate	Cosine	825.5	84.0
<i>Tayassu tajacu</i>	20	Hazard-Rate	Cosine	116.81	69.0
<i>Tayssu peccary</i>	20	Hazard-Rate	Cosine	116.81	69.0
<i>Psophia crepitans</i>	58	Hazard-Rate	Cosine	252.26	86.7
<i>Crax alector</i>	77	Hazard-Rate	Cosine	322.66	79.3
<i>Saguinas midas</i>	123	Uniform	Cosine	721.4	31.9
<i>Saimiri sciureus</i>	90	Hazard-Rate	Cosine	512.79	72.8
<i>Cebus apella</i>	192	Hazard-Rate	Cosine	1147.83	16.5
<i>Pithecia pithecia</i>	18	Uniform	Cosine	106.54	24.2
<i>Chiropotes satanus</i>	11	Uniform	Cosine	65.91	72.9
<i>Alouatta seniculus</i>	54	Uniform	Cosine	370.81	13.2
<i>Ateles paniscus</i>	131	Half-Normal	Cosine	872.17	39.2

CHAPTER 4  
DISCUSSION

We were able to identify key variables in large vertebrate species richness (Table 4-1) and determined that various species show habitat preference (Table S4-2) in Raleighvallen, Suriname. Raleighvallen is so little disturbed and has high habitat heterogeneity that the baseline data collected with the combination of line-transect and opportunistic sightings methods provides taxon information of what should theoretically be seen throughout Suriname.

Table 4-1. Overall predictors of species richness using line-transect, opportunistic sightings, and pooled data

Variable	Prediction
Temperature	Predicts terrestrial species & other mammals sightings
Rainfall	Weakly predicts terrestrial detectability
Leaf cover	Does not influence guild or forest level vertebrate sightings
Fruiting	Predicts arboreal, terrestrial, primate, bird and other mammal sightings
Flowering	Predicts arboreal, primate and bird encounters

Table 4-2. Adjusted residuals results on which species appeared more or less than expected in habitat types by sampling method

		<u>Line-Transect</u>					
		<u>More than expected</u>			<u>Less than expected</u>		
		Plateau	Liana	Swamp	Plateau	Liana	Swamp
<i>A. seniculus</i>			<i>C. apella</i>		<i>C. apella</i>	<i>A. paniscus</i>	
<i>A. paniscus</i>			<i>C. alector</i>		<i>C. alector</i>		
<i>M. exilis</i>							
		<u>Opportunistic Sightings</u>					
		<u>More than expected</u>			<u>Less than expected</u>		
		Plateau	Liana	Swamp	Plateau	Liana	Swamp
<i>A. paniscus</i>			<i>C. apella</i>	<i>A. seniculus</i>		<i>A. seniculus</i>	<i>C. apella</i>
<i>M. exilis</i>			<i>S. midas</i>			<i>A. paniscus</i>	<i>M. exilis</i>
						<i>M. exilis</i>	

## **Assessing Consistency of Survey Protocols with the Assumptions of Line-transect Methods**

The basic assumptions underlying density and detection estimation from line-transect sampling are (following Peres 1999): (1) all animals on the transect line must be detected; (2) animals are detected at their initial location, prior to any movement in response to the observer and the animal is not counted twice; (3) animals of target species move slowly relative to the speed of the observer; (4) distances from the transect are measured accurately; (5) detections are independent event.

Our line-transect is a pre-existing trail that is maintained by the local park agency STINASU. The trail is the only access to the Voltzberg-Inselberg which is a tourist attraction. Less than 200 tourists per month used the trail in 2006 and Kauffman (2008) determined that the presence of tourists does not negatively affect the presence of primates along the path. We therefore felt confident that the tourist traffic would not influence our detectability of species sighting data. The trails maintenance and a visual field of 2m on each side of the line-transect paired with the negligible impact of tourist presence we feel that we did not introduce any violation of assumption (1).

If animals respond to the presence of the observer before being detected, sighting distances may be biased (assumption (2)). Because animals usually respond by fleeing, violation of assumption (2) usually causes sighting distances to be biased towards larger values. Our line-transect allowed for relatively quiet movement by observers; data was usually collected on the first animal detected and occurred before animals gave alarm calls, indicating the detection of the observer. The presence of tourists could increase species habituation, which in turn would decrease the flee response and increase the probability that animals are only counted once and at their initial location. Kauffman (2008) reports that all primate species in Raleighvallen fled and alarm called less the more habituated the troop.

Having the observers move slowly decreases the chance of violating assumption (3). The double-observer dependent sampling method does violate assumption (5) in that detections are not independent events. The lack of data heaping (the observed rounding of detection distances to set numbers, i.e. 5, 10, 15 etc.) seen in our data reflects that assumption (4) was not violated.

To determine the detection probability of various species from the line-transect data we used DISTANCE software. This software is used to estimate abundance and as a result it also computes the detection probabilities. A single line-transect is not sufficient to calculate accurate abundance estimates so we only report the detection probabilities. The detectability of species is used as a descriptive tool to explain our outcomes of species richness based on presence/absence data.

### **Species Richness**

Numerous methods have been proposed for estimating species richness in a community (Palmer 1990). Our use of presence/absence data collected from the line-transect and opportunistic sightings data revealed that the opportunistic sighting method attained a greater number of species primarily due to its higher levels of effort (Fig. 3-1). Gotelli and Colwell (2001) state that raw species richness counts or higher taxon counts can be validly compared only when taxon accumulation curves have reached an asymptote. A species accumulation curve is a plot of the cumulative number of species discovered within a defined area, as a function of some measure of the effort expended to find them (Colwell & Coddington 1994). The opportunistic sightings reached an asymptote after 380 sampling occasions and if given the same amount of effort it is assumed that the line-transect should also reach an asymptote as the two areas surveyed should have the same levels of species overlap.

The greater level of species richness determined by the opportunistic sightings may be a result of the detection of shy and elusive species being seen in areas that had less human

disturbance; probably due to the use of less frequently traveled paths. Time of day might be a contributing factor to the disparity of species richness between the two methods. The line-transect was completed by early afternoon but opportunistic sightings occurred until dusk, increasing the odds of encountering nocturnal species beginning their nightly activities (the opportunistic sightings encountered two species that are nocturnal).

Many species defend territories and this could limit the number of individuals in an area that can be encountered. The line-transect may have been part of a range for only one felid or canid; whereas, the opportunistic sightings may have covered multiple individuals territories increasing the likelihood of an encounter. The opportunistic sightings also covered a 3km<sup>2</sup> site while the single line-transect was only 7km x 2m in length. The effort of sampling is also a factor, with 747 days/walks being conducted versus 238 on the line-transect.

Recommendations for conservation depend on the information of interest. If levels of species richness are the primary concern than the use of opportunistic sightings are best suited for low budgets and limited time. If abundance estimates and species richness are the goal than the use of multiple line-transects and increased sampling effort are recommended.

### **Predictors of Species Richness**

Species richness is undoubtedly influenced by many factors. There is evidence (reviewed by Begeon *et al.* 1990) that most of the process listed in Table 1-1 influence species richness, at least locally under some circumstances. In this study we looked at the proximate mechanisms (climate (rainfall and temperature), leaf cover, and plant productivity) as possible predictors of species richness.

It has been argued that regions with more stable conditions permit more species. Currie (1991) believes that one can reject the hypothesis that annual variability of climate *per se* has any important effect on richness. Currie (1991) found that terrestrial vertebrate richness was closely

related to potential evapotranspiration (PET), temperature, and solar radiation. Other studies found that a correlation between animal richness and environment were linked with temperature, sunshine, and solar radiation (Schall & Pinka 1978, Turner *et al.* 1987).

Using temperature as a proximate mechanism for species richness in Raleighvallen we found that it had a predictive value with the opportunistic sightings ( $p=0.0123$ ) and the pooled data ( $p=0.0280$ ) but not on the line-transect data ( $p=0.0545$ ). Terrestrial vertebrates ( $p=0.0288$ ) and the other mammal guild ( $p=0.0072$ ) (Table 3-3) were affected by temperature with the opportunistic data but only the terrestrial ( $p=0.0085$ ) guild had significance with the pooled data. The pooled data set found that rainfall ( $p=0.1624$ ) also has a significant predictive value for terrestrial vertebrates ( $p=0.0334$ ) (Table 3-4). The lack of predictive value with the transect data could be a result of small sample size, yet even when the data was pooled it did not have increased predicative value on guilds and forest level groups. This could indicate that key species that are influenced by temperature are missing from the line-transect data.

The ambient-energy hypothesis states that endotherms usually maintain themselves at a higher temperature than the environment, a higher ambient temperature promotes faster growth of individuals and populations; and the higher biomass will, in turn, promote greater species richness (Turner *et al.* 1996). Our data from Raleighvallen shows that increases in temperature lead to behavioral changes, such as increased activity, which increases the number of species encountered.

Leaf cover is used as a proxy for canopy cover in this study. We hypothesized that an increase in leaf cover would increase the sightings of all species. Arboreal species should have a higher encounter frequency due to the ability to potentially move more freely in the understory and terrestrial species should also travel more because of total coverage.

Leaf cover is shown to have predictive value with the opportunistic sightings ( $p=0.0271$ ) data but when species were divided by guilds and forest level no predictive value was detected. The results could indicate that the division of species by guilds and forest level is not detailed enough to determine which animals are most sensitive to leaf cover.

The species energy hypothesis proposes that species richness is limited by the total or average amount of energy entering into an ecosystem. A sub-area of this hypothesis is the productivity hypothesis. The productivity hypothesis states that the level of resource production in an ecosystem limits animal species richness. South American mammals support the productivity version of the species-energy hypothesis (Ruggiero & Kitzberger 2004). Using number of trees fruiting and flowering as a mode of ecosystem production we found that fruiting and flowering could be used as an effective predictor of species richness. Fruiting was seen to be significant with the arboreal and terrestrial forest level groups in the opportunistic sightings and pooled data sets. The opportunistic sightings data showed that fruiting influenced the other mammal ( $p=0.0024$ ) guild. Fruiting was also shown to influence the primate ( $p=0.0001$ ) and bird ( $p=0.0014$ ) guilds using the pooled data set. Our results corroborate Mittermeier and van Roosmalen (1981) findings that fruit makes up the majority of plant material consumed by the primate species in Raleighvallen; and therefore, their detection might be related to increases in food availability. The other mammal guild is made up of insectivores, carnivores, and frugivores. The other mammal and bird guilds species richness in Raleighvallen is predictive because the frugivorous species are reliant on the fruits and the carnivores increased hunting on more active prey species is also dependent on the fruits.

Flowering influenced the primate, bird, and arboreal groups using the opportunistic sightings and pooled data sets. The influence of flowers on the primate, bird and arboreal groups

makes intuitive sense as these are the only animals that are able to reach the flowers in the canopy.

### **Habitat Preference**

The two different sampling methods reveal pertinent information about which habitats the species prefer. Species will have different reasons for preferring one habitat over another and our data shows that certain species were observed in habitats more and less than would be expected (Table 3-5, Table 3-6, Table 3-7). The distinction in habitat preference could be a result of different evolutionary and ecological factors.

It was found that *Cebus apella* and *Crax alector* were encountered more than expected in liana habitat and less than expected in the plateau habitat. *Alouatta seniculus*, *Ateles paniscus*, and *Myorocta exilis* were found more than expected in the plateau and less in the liana habitat. *A. seniculus* was also seen more than expected in the swamp habitat. Although, our data did not find a preference of habitat type by *Saimiri sciureus*, Mittermeier and van Roosmalen (1981) and Frechette (2007) found that they were observed in liana more than any other habitat type.

Possible explanations for *C. apella* and *S. sciureus* preference for the liana habitat could be predator avoidance and interspecies association. Predation risk is a strong selective force that affects many aspects of animal behavior as well as having important repercussions on prey morphology and life history (Sih 1987, Lima & Dill 1990, Lima 1998, Stanford 2002). Lima and Dill (1990) argue that predation risk influences what, when and where to eat, which means that animal behavior is closely tied to predator behavior as well as local ecology. The liana habitat offers the greatest amount of cover and protection against ambush aerial predators, such as the harpy eagle (*Harpia harpyja*). Frechette (2007) found that *S. sciureus* had a strong interspecies association with *C. apella*. These mixed-species groups may deter predators because predators may be less inclined to attack a larger group of animals (Fitzgibbon 1990). The formation of

mixed-species groups ‘dilutes’ the predation risk to an individual because of the increase in group size. The increase in group size also increases combined vigilance, which in turn can allow individuals more time to forage and conduct social behavior.

Mittermeier and van Roosmalen (1981) found that *S. sciureus* had a high level of association with *C. apella* because it is a highly manipulative forager. *C. apella* regularly break branches, rips off bark and tears through leaf debris creating an increase of flushed insects accessible to *S. sciureus*. It is a common for *C. apella* to forage on hard husked fruits and then observe *S. sciureus* foraging on the remains. This association not only helps with predator avoidance but it also increases the nutritional variety in the *S. sciureus* diet.

*Crax alector* is a poorly studied species in the tropics. It is believed that they play an important role in the dispersal of seeds (Strahl & Grajal 1991). Borges (1999) found that *C. alector* was most abundant in the secondary forests of Brazil. We believe that the more than expected presence of *C. alector* in the liana habitat is most likely due to an association with *C. apella* and the acquisition of fallen fruits.

The more than expected presence of *Ateles paniscus* and *Alouatta seniculus* in plateau habitat matches the findings of Sussman and Phillips-Conroy (1995). This could be related to interspecies avoidance and food availability. *A. paniscus* and *A. seniculus* have the largest body size of the primates in Suriname. This large body size makes adults and juveniles unsuitable prey items for the aerial predators negating the need for high amounts of foliage cover. Mittermeier and van Roosmalen (1981) found that *A. paniscus* and *A. seniculus* were the most dependent on plateau forest for food causing them to prefer the plateau habitat for nutritional requirements. These two primates were encountered less than expected in the liana habitat because they might have been avoiding an association with *Cebus apella*. *C. apella* has been observed displaying

aggressive behaviors, throwing sticks, pulling tails, and shaking branches, towards both of these species causing them to leave the area (personal observation). The antagonistic behavior of *C. apella* and low levels of fruit options in the liana habitat could be another reason for these species preference of plateau habitat.

Dubost and Henry (2006) determined that *Myroctea exilis* stomach contents were composed mainly of plateau forest fruits. Our observation of their more than expected presence in the plateau habitat could be a result of their diet.

*Alouatta seniculus* was observed more than expected in the swamp habitat. The swamp has a higher abundance of *Euterpe Oleracea* and *Socrata exorhiza* which *A. seniculus* has been observed eating. The abundance of food and lack of competition with other species could be enough incentive for their preference of this habitat type or maybe they are being pushed into this suboptimal habitat by the other primate species. We have witnessed successful harpy eagle predation on *A. seniculus* infants when in the swamp habitat. Therefore, the risk of infant predation does not appear to outweigh the other benefits associated with this habitat.

### **Detectability**

One of the key components of using line-transect data is the observers ability to detect target species. Our study implemented the double-observer dependent method to insure that new field assistants were equally proficient at their detection and identification skills. The majority of the field assistants had never worked in the neotropics; and for many of them this was their first time performing line-transect surveys. The double-observer method allowed for the inexperienced assistants to be trained on animal identification by an experienced team member. The inexperienced assistants were also paired with an experienced team member so that search images and acoustic cues, such as alarm-calls, patterns of branch crashes and other escape maneuver information was properly transmitted.

Detectability of species along the line-transect was analyzed using DISTANCE 5.0 software. A sample size minimum of 40 encounters is required to get more accurate estimates. Our sample sizes ranged from 11-192 encounters. Table 3-9 shows our probability of detection for the various species tested. Although there was insufficient line-transect sample sizes we still ran the detectability tests. The greatest detection probability was with *Cebus apella* and *Alouatta seniculus*. Our lowest detection probability was with *Myroctea exilis* and *Psophia cerpitans*.

Regardless of sampling method, observers will detect some species more easily than others. Gu and Swihart (2004) believe that failures to detect a species at occupied sites can lead to poorly formulated habitat models and thus to erroneous predictions of a species' response to habitat change.

Species that are less easily detected tend to live in small and/or more closely aggregated social groups, frequent tangles of liana or dense understory vegetation, and make relatively little noise (Whitesides *et al.* 1988). Innate animal behavior, habituation, and habitat type could be three of the contributing factors for our low detection probabilities. An increase in group size increases detection (Quinn 1981, Freese *et al.* 1982) and solitary animals are therefore harder to detect. A prime example from our data is *Bradypus tridactylus*, the three-toed sloth. It was primarily observed in the plateau habitat and is a slow moving, well camouflaged, and quiet animal. These behaviors make it very easy for observers to miss it. A study by Montgomery and Sunquist (1973), on Barro Colorado Island, found that the three-toed sloth may reach a density of 7.6 animals per hectare. In spite of its high density, the animal was so cryptic that it was rarely seen and impossible to census (Eisenberg & Thorington 1973). We had only four sloth encounters during the five years of survey but we know from observations and collection of kill

residue from the local harpy eagle nest site that three-toed sloths are very abundant (Boinski, personal communication).

Species that flee loudly will often be detected over species that remain silent and motionless. Mild levels of habituation might increase detection due to the animals lack of flee response. *C. apella* and *A. seniculus* often paid little to no attention to the observers and did not flee as the observers approached. Habitat type can either help or hinder species detection. The plateau habitat had the highest counts of animal encounters and the best overall visibility. I think that in Raleighvallen's case animal behavior and habituation is a greater factor in detectability than habitat type.

Future work should include the addition of more line-transects, evaluating elevation and distance from water as potential predictors of species richness, and creating a phenological survey along the line-transect trail to gain a more well rounded picture of what is happening in the forest. In this study all fruit was pooled together, it would be interesting to see the influences of mature versus immature fruits on species detectability. Robinson and Redford (1986) proposed that the amount of potentially available energy depends on the availability of appropriate resources and which resources are appropriate depends on the animal's diet. Recording what the animals were eating and what trees they were in or near when detected would also be valuable information. Determining tree species richness in Raleighvallen is also an important step. Andrews and O'Brien (1999) found that variability in the plant species richness alone accounted for 75% of the variability in mammal species richness. Tying both of these other works together could disentangle the ambiguity in the relationship between mammal species richness and productivity, as it might increase or decline with increased habitat productivity

(Rosenzweig 1997). Looking at specific trees and trying to determine which tree species have a greater influence on the community structure would also be beneficial information.

### **Conclusions**

Climate and plant productivity were found to be the proximate mechanisms that influenced species richness in Raleighvallen. Habitat preference could be influenced by predator avoidance, interspecies association or avoidance, and food availability. The detection of species is thought to be a result of levels of innate animal behaviors, habituation, and habitat type.

APPENDIX

Species encountered, frequency of encounters, trophic guild, and use of forest level of pooled data censused at Raleighvallen, Central Suriname Nature Reserve, Suriname. Species encountered are expressed as total number of sightings per census walked and species frequency of encounter is total sightings/total sampling effort. Species are listed within orders and families according to their body size.

Species	English name	Individuals encountered (pooled)			Frequency of encounter	Guild <sup>a</sup>	Forest level <sup>b</sup>
		Plateau	Liana	Swamp			
MAMMALS							
Primates							
Callitrichidae							
<i>Saguinus midas</i>	Golden-hand tamarin	72	105	9	19%	Fr/In	A
Cebidae							
<i>Saimiri sciureus</i>	Squirrel monkey	37	80	3	12%	Fr/In	A
<i>Cebus apella</i>	Brown capuchin	116	224	14	36%	Fr/Sp/In/Vp	A
<i>Cebus olivaceus</i>	Weeper capuchin	6	1	0	1%	Fr/Sp/In/Vp	A
<i>Pithecia pithecia</i>	White-face sakis	31	28	10	7%	Sp/Fr	A
<i>Chiropotes satanus</i>	Bearded sakis	34	12	3	5%	Sp/Fr	A
<i>Alouatta seniculus</i>	Red howler monkey	66	69	6	14%	Fo/Fr	A
<i>Ateles paniscus</i>	Spider monkey	115	48	1	17%	Fr	A
Total primates		477	567	46			
Xenarthra							
Myrmecophagidae							
<i>Cyclopes didactylus</i>	Silky anteater	1	3	0	0%	A/In	A
<i>Tamandua tetradactyla</i>	Southern tamandua	17	23	9	5%	A/In	A
<i>Myrmecophaga</i>							
<i>tridactyla</i>	Giant anteater	1	1	1	0%	A/In	T
Dasypodidae							
<i>Dasypus novemcinctus</i>	9-banded armadillo	14	2	0	2%	A/In	T
Bradypodidae							
<i>Bradypus tridactylus</i>	3-toed sloth	3	1	0	0%	Fo	A

Species	English name	Individuals encountered (pooled)			Frequency of encounter	Guild <sup>a</sup>	Forest level <sup>b</sup>
		Plateau	Liana	Swamp			
Rodentia							
Sciuridae							
<i>Sciurus aestuans</i>	Guianan squirrel	33	28	6	7%	Sp/Fr	A
Dasyproctidae							
<i>Myroctoa exilis</i>	Red acouchy	95	34	1	13%	Sp/Fr	T
<i>Dasyprocta punctata</i>	Red rumped agouti	372	263	64	71%	Sp/Fr	T
Hydrochaeridae							
<i>Hydrochaeris hydrochaeris</i>	Capybara	4	0	0	0%	Fo/Fr	T
Carnivoria							
Procyonidae							
<i>Nausa nasua</i>	Coati	2	0	0	0%	In/Vp/Fr	SA
Mustelidae							
<i>Eira barbara</i>	Tayra	26	11	5	4%	Fr/In/Vp	SA
<i>Pteronura brasiliensis</i>	Giant otter	30	3	0	3%		
Felidae							T
<i>Leopardus wiedii</i>	Margay	0	2	0	0%	Vp	T
<i>Leopardus pardalis</i>	Ocelot	5	0	1	1%	Vp	T
<i>Felis yagouroundi</i>	Jaguarundi	2	2	0	0%	Vp	T
<i>Panthera onca</i>	Jaguar	0	5	0	1%	Vp	T
Canidae							
<i>Speothos venaticus</i>	Bush dog	2	0	0	0%	Vp	
Procyonidae							
<i>Potos Flavus</i>	Kinkajou	3	1	1	1%	Ne/Fr	A

Species	English name	Individuals encountered (pooled)			Frequency of encounter	Guild <sup>a</sup>	Forest level <sup>b</sup>
		Plateau	Liana	Swamp			
Ungulates							
Perissodactyla							
Tapiridae						Fr/Fo	
<i>Tapirus</i>							
<i>terrestris</i>	Tapir	22	10	2	3%		
Artiodactyla							
Tayassuidae							
<i>Pecari tajacu</i>	Collard peccary	26	16	1	4%	Fr/Sp/In	
<i>Tayassu pecari</i>	White-lipped peccary	31	16	3	5%	Sp/Fr/In	
Cervidae							
<i>Mazama americana</i>	Red brocket deer	42	29	8	8%	Fr/Fo	
Total other mammals		719	440	100			
BIRDS							
Cracidae							
<i>Crax alector</i>	Black currasow	65	75	13	16%	Fr/Sp	
Psophiidae							
<i>Psophia crepitans</i>	Grey-winged trumpeter	70	66	11	15%	Fr/In	
Accipitridae							
<i>Harpia harpyja</i>	Harpy eagle	27	10	1	4%	Vp	
Total birds		162	151	25			
Total		1370	1168	81			

<sup>a</sup> Fr = frugivore, Fo = folivore, Sp = seed predator, Ne = nectivore, A = anteater, In = insectivore, Vp = vertebrate predator

<sup>b</sup> A = arboreal, T = terrestrial, SA = semi-arboreal (scansorial)

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## BIOGRAPHICAL SKETCH

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