BEHAVIOR AND ECOLOGY OF NEOTROPICAL TREE SQUIRRELS IN
SEASONALLY FLOODED FORESTS IN THE PERUVIAN AMAZON

by

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TABLE OF CONTENTS

TABLE OF CONTENTS – *Continued*

TABLE OF CONTENTS – *Continued*

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES - *Continued*

ABSTRACT

Tree squirrels play an important role in the maintenance of forest ecosystems by functioning as seed and fungal spore dispersers, forest regenerators, and prey for forest predators. The highest species richness for tree squirrels occurs in tropical forests and these species are also the least studied. We conducted distance sampling to estimate population density, measured habitat variables to investigate forest characteristics that influence habitat selection and feeding site selection at three different scales, and conducted observations to obtain knowledge about activity pattern and behavior of Neotropical pygmy squirrels and Amazon red squirrels in the Peruvian Amazon. Density of Neotropical pygmy squirrels was 0.10 and 0.14 individuals/ha for 2009 and 2010. Activity peaked in early morning, squirrels were found mainly in the canopy but never on the ground, and frequency of behaviors differed by time and story level. Neotropical pygmy squirrels used mainly high and low restinga and areas that had more large trees. Squirrels also used species of trees disproportionately to availability. Neotropical pygmy squirrels seem to be associated with features related to mature forests. Amazon red squirrels use mainly high and low restinga and selected *Astrocaryum* and *Attalea* palm trees that were taller and larger as foraging sites compared to random locations. Amazon red squirrels used all vertical strata of the forest and the main behaviors observed were travel and forage. Behaviors were similar among time periods but differed in frequency by vertical strata. Although Amazon red squirrels used vegetation communities differently than their availability and selected for tree characteristics, they did not select for site characteristics and this is different from other tree squirrel species.

We also conducted surveys during a wet and a dry year to investigate and estimate diversity of diurnal mammals. We assessed the vertical strata of the forest to determine if diversity index varied by story level, and estimated alpha, beta, and gamma diversity. Overall mammal diversity did not differ between wet and dry years. Diversity index differed by story level between years, but was the highest in the canopy for both years. Alpha diversity was higher in the dry year, and gamma and beta diversity were higher in the wet year. Frequency of sightings of species was influenced by time of day and varied by story level. Protection of continuous, mature forests with large canopies has important conservation implications as these areas most likely protect the greatest diversity of mammals while also providing shelter and food for other taxa.

CHAPTER 1: INTRODUCTION

Rainforests represent a small percentage of the Earth's surface but support the highest biodiversity in the world (Wilson and Peter 1988, Myers 1988, Mittermeier et al. 1998), including the highest mammalian species richness and phylogenetic diversity (Schipper et al. 2008). Rainforests are also one the most threatened ecosystems (Myers 1988, Phillips 1997, Laurance 2004) mainly due to forest destruction, which results in changes in species composition, species interactions, ecosystem processes, and microclimate modifications (Newmark 1991, Terborgh 1992, Bierregaard et al. 1992, Hall et al. 1996, Benitez-Malvido 1998, Laurance 1998). Rainforest deforestation is also predicted to affect local and global climate, and concomitantly climate change is expected to have a great impact on rainforest ecosystems (Nobre et al. 1991, Laurance 1998, Laurance and Williamson 2002, Malhi et al. 2009). Conservation and management of rainforest ecosystems are important for the conservation of biodiversity within these ecosystems.

Tree squirrels (Rodentia: Sciuridae) are found on almost every continent and in many different ecosystems including rainforests (Koprowski and Nandini 2008; Thorington et al. 2012). The highest species richness of tree squirrels occurs in tropical forests and these species are also the least studied tree squirrels (Koprowski and Nandini 2008). The northern and southern Amazon red squirrel (*Sciurus igniventris*, *S. spadiceus*), and the Neotropical pygmy squirrel (*Sciurillus pusillus*) inhabit the Amazon Basin of Peru and are the most frequently sighted tree squirrel species (Emmons and Feer

1997, Thorington et al. 2012). The Neotropical pygmy squirrel is listed as data deficient and the northern and southern Amazon red squirrels are listed as species of least concern by the International Union for Conservation of Nature (IUCN; Amori et al. 2008), however, their population trends are unknown and their habitats are being destroyed rapidly.

Tree squirrels play an important role in the maintenance of forest ecosystems by functioning as seed and fungal spore dispersers, forest regenerators, and prey for forest predators (Kotter and Farentinos 1984, Gurnell 1987, Steele et al. 2004). Some species of tree squirrel are also recognized as indicators of forest condition because of their strict dependence upon mature forests for food, protection from predators, and nesting sites (Gurnell 1987, Bayne and Hobson 2000, Carey 2000, Koprowski 2005, Kremsater et al. 2003, Munch 1996), but a similar value in rainforests is unknown (Koprowski and Nandini 2008). Although tree squirrels have important impacts and implications in ecosystems, our knowledge of tree squirrels in the Neotropics is limited, with a dearth of information on natural history, behavior, and habitat use (Koprowski and Nandini 2008). Thus, a better understanding of these species is critical to assess how loss of tropical habitats will affect global biodiversity and ecosystem function. Herein, we provide the results from a study on habitat associations and use, ecology, and mammal diversity associated with 3 species of Neotropical tree squirrels in the Amazon Basin of Peru.

CHAPTER 2: PRESENT STUDY

The methods, results, and conclusions of this study are presented in the papers appended to this thesis. The following is a summary of the most important findings in this document.

In 2009 and 2010, we studied Neotropical pygmy squirrels with the objective to investigate characteristics of the forest that influence habitat selection at three different scales, and obtain knowledge about activity patterns and behavior. Density of Neotropical pygmy squirrels was 0.10 and 0.14 individuals/ha and the mean cluster size was 1.33 and 1.20 squirrels respectively for each year. Neotropical pygmy squirrels are diurnal and their activity peaked at 08:00 h, squirrels were found mainly in the canopy but never on the ground, and frequency of behaviors differed by time and story level. Neotropical pygmy squirrels are social with frequent vocalizations and co-nesting events. Neotropical pygmy squirrels used mainly high and low restinga, areas that had more large trees, and trees that were larger in DBH, taller, and had a larger live crown compared to random trees and areas of the forest. Neotropical pygmy squirrels did not use species of trees at random and seem to select for trees in the genus *Caryocar*, *Tachigali*, and *Eschweilera*. Neotropical pygmy squirrels are associated with features related to mature forests. This chapter is formatted for submission to the *Journal of Mammalogy*.

We also studied northern and southern Amazon red squirrels to evaluate habitat use, time budgets, feeding behavior, and characteristics of foraging sites. Because of the similar coloration patterns, melanistic forms, and body size, northern and southern

Amazon red squirrels are extremely difficult to distinguish in the field, and due to apparent similarities in life history we grouped both species. Amazon red squirrels used mainly high and low restinga and selected palm trees from the genus *Astrocaryum* and *Attalea* that were tall and large as feeding sites. Squirrels used all vertical strata of the forest and the main behaviors observed were travel and forage. Behaviors were similar among time periods but differed by vertical strata. Although squirrels selected certain vegetation communities and tree characteristics, they did not select for site characteristics, and this differs to other tree squirrel species. This chapter is formatted for submission to *Mammalia*.

Finally, we conducted surveys to determine the diurnal mammalian diversity in Neotropical tree squirrel habitat and if this diversity was influenced by flood and varied by story level. Mammal diversity index did not differ between wet and dry years, species richness was higher in the wet year, and evenness was low for both years. Diversity index differed by story level between years, but was the highest in the canopy for both years. Alpha diversity was higher in the dry year compared to the wet year, and gamma and beta diversity were higher in the wet year compared to the dry year. Frequency of sightings of species was influenced by time of day and varied by story level. Protection of continuous, mature forests with large canopies has important conservation implications as these areas most likely protect the greatest diversity of mammals while also providing shelter and food for other taxa. This chapter is formatted for submission to *Biotropica*.

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APPENDIX A: HOW DO NEOTROPICAL PYGMY SQUIRRELS (*Sciurillus pusillus*) USE A SEASONALLY FLOODED FOREST IN THE PERUVIAN AMAZON?
Paper was prepared to submit to a journal.

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ABSTRACT

Tree squirrels are important components of ecosystems but to understand how squirrels function and what their role is we must learn how squirrels select and use habitat. Tree squirrel species richness is highest in the tropics where the greatest number of data deficient species also occurs, and the Neotropical pygmy squirrel (*Sciurillus pusillus*) is one of these data deficient species. How do Neotropical pygmy squirrels select and use habitat in an igapó forest? In 2009 and 2010, we conducted distance sampling to estimate population density, measured vegetation variables to investigate forest characteristics that influence habitat selection at three different scales, and conducted observations to obtain knowledge about activity patterns and behavior of Neotropical pygmy squirrels in the Peruvian Amazon. Density of squirrels was 0.10 and 0.14 individuals/ha respectively for each year. Activity peaked at 08:00 h, squirrels were found mainly in the canopy but never on the ground, and frequency of behaviors differed by time and story level. Squirrels used mainly high and low restinga, areas that had more trees $\geq$ 30 and $\geq$ 40 cm DBH/ha, and trees that were larger in DBH, taller, and had a larger live crown compared to random trees and areas of the forest. Squirrels also used

species of trees different than their availability. Neotropical pygmy squirrels are associated with features related to mature forests.

INTRODUCTION

Although mammals occupy most of the earth's ecosystems, tropical rainforests support the highest mammalian species richness and phylogenetic diversity (Schipper et al. 2008). With such vast diversity, mammals fill niches that are highly interconnected and contribute to complex communities (Mares et al. 1986; Wells et al. 2004). Mammals play important roles in ecosystems by providing ecological services and driving dynamics and complexity of biological communities (Gessman and MacMahon 1984; Stoner et al. 2007; Terborgh 1988). Therefore, changes in mammal communities may have important consequences for the dynamics and function of rainforest ecosystems (Stoner et al. 2007).

Twenty five percent of mammal species are threatened with extinction, and this estimate does not include species that are categorized as data deficient by the International Union for Conservation of Nature (IUCN; Schipper et al. 2008). The highest number of threatened and data deficient mammals inhabit the tropics (Schipper et al. 2008). Although, the number of newly described mammal species is highest in the tropics (Patterson 2000; Schipper et al. 2008), natural history and ecology of most species is unknown. Many mammal species may face extinction due to habitat destruction in rainforests (Laurance 1998; Primack 2008) before we evaluate and understand the importance and role these species play in rainforest ecosystems.

Tree squirrels are a group of mammals found in almost every continent and in many ecosystems including rainforests (Koprowski and Nandini 2008; Thorington et al. 2012). The highest species richness for tree squirrels occurs in the tropics, as do the least studied tree squirrels (Koprowski and Nandini 2008). Many tropical tree squirrel species are data-deficient or species of least concern (Thorington et al. 2012); however, the tropics contain some of the most threatened ecosystems. Thus a better understanding of the little-known obligate species is critical to assess how loss of tropical habitats will affect global biodiversity and ecosystem functioning.

Tree squirrels play an important role in the maintenance of forest ecosystems by functioning as seed and fungal spore dispersers, forest regenerators, and prey for forest predators (Gurnell 1987; Kotter and Farentinos 1984; Steele et al. 2004). Some species of tree squirrel are also recognized as indicators of forest condition because of their strict dependence upon mature forests for food, protection from predators, and nesting sites (Gurnell 1987). Several studies in temperate forests of the United States and Europe support use of tree squirrels as indicator species of forest condition (Bayne and Hobson 2000; Carey 2000; Koprowski 2005; Kremsater et al. 2003; Munch 1996; Smith et al. 2005), but a similar value in rainforests is still unknown (Koprowski and Nandini 2008). Squirrels also provide anthropogenic services and in some cultures squirrels have an important economic value (Adeola 1992; Durojaye 2008; Steele and Koprowski 2001).

The Neotropical pygmy squirrel (*Sciurillus pusillus*) inhabits the Amazon basin of Peru, Colombia, Venezuela, Brazil, Guyana, Suriname, and French Guyana, and is the smallest squirrel in the western hemisphere (38 – 48g). Not surprisingly, this secretive

squirrel is listed as data deficient (Amori et al. 2008; Eisenberg and Redford 1999; Thorington et al. 2012). *S. pusillus* has a fragmented distribution, but the reason for this remains unknown (Emmons and Feer 1997), and may be attributed to insufficient data (Mercer and Roth 2003).

In 2009 and 2010, we conducted a study on *S. pusillus* in Amazonia, Peru, with the objective to investigate characteristics of the forest that influence habitat selection at three different scales, and obtain knowledge about activity pattern and behavior. Here we document selection of *S. pusillus* for certain vegetation communities as well as characteristics such as large trees that usually are indicative of mature forests.

MATERIALS AND METHODS

Study site.— Our study site was located in the Peruvian Amazon at the Amazon Research Center (ARC). The ARC is located within the Tamshiyacu - Tahuayo Reserve in northeastern Peruvian Amazon between the Tamshiyacu - Tahuayo and Yavarí Miri rivers in the state of Loreto, near the Brazilian border (4°39'S, 73°26'W). This 322,500-ha conservation area is a lowland, evergreen, and seasonally flooded forest that was created to protect it from overexploitation of natural resources by outside commercial interests, unregulated hunting, poaching, large-scale commercial fishing, fishing with explosives and chemicals, and large-scale logging (Newing and Bodmer 2003). The ARC is situated within igapó forest, a seasonally flooded forest with black water (Myster 2009). The major plant communities found within the study area included palm swamps (low-lying areas of poor drainage, low tree diversity, dominated by moriche palm, *Mauritia flexuosa*), bajial (forest that floods to a water level of 5-7 m, low tree diversity,

small trees, sparse understory vegetation), high restinga (unflooded forest, clay soils, high

tree diversity, large trees are common), and low restinga (forest that floods to a water

level of 2.5-5 m, low tree diversity; Kvist and Nebel 2001; Myster 2009; Prance 1979).

In 2009, the study site experienced above average total rainfall (3914 mm) and in

2010 a severe drought affected the area (21 % less than 2009: 3100 mm). In 2009, the

mean low was 23.3°C (± 0.05 *SE*, n = 346) and the mean high was 28.2°C (± 0.11 *SE*, n =

346). In 2010 the mean low was 23.2°C (± 0.07 *SE*, n = 365) and the mean high was

29.4°C (± 0.13 *SE*, n = 365).

Population Density.— During June and July of 2009 and 2010, we conducted

line-transect distance sampling (Buckland et al. 2001) to locate Neotropical pygmy

squirrels (hereafter *S. pusillus*) and to estimate density in the 400-ha ARC research grid.

The 2-km by 2-km research grid was initially created to study primates and was

completed at the beginning of 2009. The grid has 21 2-km line transects separated by

100-m intervals that run parallel northeast to southwest, with another set of 21 transects

offset by 90° that run northwest to southeast. Although *S. pusillus* are small, they are

very vocal and move conspicuously through the canopy, making distance sampling a

reliable method to estimate species density. Their vocalizations can be heard from long

distances but we decided to truncate our data in the field to 50-m from the transect line

because we were confident we were detecting every squirrel that was vocalizing up to 50-

m. Each year, we surveyed the entire 84-km grid system. We walked 2 entire transect

lines in a single day from 0600 until 1700 h. We measured perpendicular distance from

transect to *S. pusillus* locations with a range finder and recorded each location with a

handheld global positioning system (GPS; Garmin eTrex Legend Cx, Olathe Kansas USA – estimated accuracy 2-5m). We also recorded time of day, behavior (forage, travel, groom, vocalization, or agonistic interaction), story level [ground, understory (< 5 m; some cover and vegetation), midstory (5 – 15 m; minimal vegetation, mainly bare trunks from large trees), or canopy (> 15 m; usually very dense foliage); Monteiro Vieira and Monteiro-Filho 2003; Viveiros Grelle 2003], and forest type where *S. pusillus* were found (low restinga, high restinga, palm swamp, or bajial) for inclusion in behavioral and habitat use analysis.

To estimate density of *S. pusillus*, we used Program Distance (Version 6.0, Release 1). We developed 4 models including 4 key functions (half normal, hazard rate, negative exponential, and uniform), and used Akaike's information criterion (AIC) to select among competing models for each year (Burnham and Anderson 2002).

Behavioral Observations.— To learn more about *S. pusillus* activity patterns and feeding behavior, we used time of day (hour), behavior (discrete events: forage [searching for, processing, or consuming food], travel [movement through the forest using one or various story levels], groom , vocalization [any squirrel call], or social interaction [chase between individuals]), and story level (ground, understory, midstory, and canopy) where each *S. pusillus* was sighted from data collected through distance sampling as well as opportunistic observations. We worked in *S. pusillus* habitat each day from 0600 – 1700 h, therefore we believe that our observations capture an adequate sample of behaviors distributed across all time periods.

We used chi-square analyses to determine if frequency of sightings differed by hour, story level, and type of behavior. Because of the low frequency of sightings for certain behaviors, we used a log-likelihood ratio to determine if the frequency of behavior was the same at every hour or at every story level where *S. pusillus* were sighted.

Habitat use.—We evaluated vegetation at three different scales (landscape, forest, and focal tree) to determine what forest characteristics were most influential to *S. pusillus*. For the landscape level analysis, we used a digital map of vegetation community availability (palm swamps, bajial, high restinga, low restinga) in the research grid based on ground mapping surveys and plotted the squirrel locations that we obtained from distance sampling and opportunistic observations. We calculated the availability (%) of each vegetation community based on a digitized map of the research grid with ArcGIS 10.0 (Environmental Systems Research Institute, Inc., Redlands California, USA). We used a chi-square goodness-of-fit test to compare vegetation community availability to *S. pusillus* sightings in each vegetation community to determine if squirrels used any vegetation communities more frequently than their availability.

We used a standard center-point vegetation-sampling plot to permit comparison of characteristics of individual trees and sites where *S. pusillus* were observed to random sites (Litvaitis el at. 1996). To select the random sites, we used a random number generator to select trail intersections in the research grid and we then walked in a randomly determined direction and distance (0 - 50 m) from the intersection point. To quantify and describe forest characteristics of *S. pusillus* sightings and random locations, we used a 10-m radius plot (area = 0.03 ha) centered on the tree in which *S. pusillus* were

observed, or the tree located closest to a random location. For all trees ≥ 3 cm in diameter at breast height (DBH) we determined total number, species, condition (live or dead), and DBH, and used a spherical densitometer to estimate canopy cover (%) through the Strickler method (Edelman and Koprowski 2005; Smith and Mannan 1994; Strickler 1959). For physical characteristics of the individual tree, we recorded focal tree species, total height (m), live crown height (m), DBH, and condition (live or dead). We also recorded distance (m), species, and DBH of the tree closest to the focal tree.

We calculated Shannon-Wiener diversity indices, total basal area (m^2/ha), total number of trees/ha, number of live trees/ha, number of dead trees/ha, number of logs/ha, and number of trees ≥ 20 cm DBH/ha, ≥ 30 cm DBH/ha, and ≥ 40 cm DBH/ha within each circular plot. Although we attempted to identify all trees to species, we could only identify many trees to genus because of the difficulty identifying tree species in the Amazon (Gentry 1996; Vásquez Martínez 1997). We used the total number of trees in each genus documented across all random plots to calculate tree species availability (%). We use a chi-square goodness-of-fit test to compare tree species availability to the number of trees of each genus used by *S. pusillus*.

To meet assumptions of normality, we used log transformations for total number of trees, number of trees ≥ 20 cm DBH, basal area, DBH of focal tree, height of focal tree, size of live crown, DBH of nearest tree, and distance to nearest tree, we used square root transformation for number of trees ≥ 30 cm DBH, we used cube root for number of dead trees, and we used arcsine transformations for total canopy cover, canopy cover at center, canopy cover at 5 m from center, and canopy cover at 10 m from center (Ramsey

and Schafer 2002). We used 2-tailed t-tests (with a Bonferroni corrected α-value) to compare individual characteristics of squirrel location trees and forest structure with random trees and sites.

We chose an information-theoretic model selection approach (Burnham and Anderson 2002) to assess forest characteristics that were most important in predicting *S. pusillus* presence within the ARC forest. Because little is known about *S. pusillus* ecology (Koprowski and Nandini 2008), we used forest characteristics that are known to be important to other species of tree squirrels (Cudworth and Koprowski 2011; Halloran and Bekoff 1994; Merrick et al. 2007; Pereira and Itami 1991; Prather et al. 2006). We built a set of 13 candidate logistic regression models to determine characteristics of focal trees most important to *S. pusillus* presence, and another set of 19 candidate logistic regression models to determine characteristics of forest most important in predicting *S. pusillus* presence (Table 2). We used Akaike's Information Criterion (AIC) to rank and evaluate competing models. To reduce multicollinearity, we only included variables where correlation was low ($r < 0.70$). In instances of high correlation coefficients, we chose variables that accounted for the most variation (higher F-value) for inclusion in the models. For forest analysis, canopy cover at 5 and 10 m were highly correlated to total canopy cover (r = 0.727 and r = 0.942 respectively), and number of total trees/ha and number of live trees/ha were highly correlated with basal area/ha (r = 0.798 and r = 0.806 respectively), so we included only total canopy cover and basal area/ha. For focal tree analysis, the size of the live crown was highly correlated (r = 0.829) with height of tree, and was not included in any model. We report statistical results from transformed

parameters, but report means as untransformed values. We used JMP 10 (SAS Institute

INC., Cary, NC) to conduct all statistical analyses.

Our research protocol was authorized by Peruvian permit no. 0246-2010-AG-

DGFFS-DGEFFS from The Dirección General de Fauna y Flora Silvestre, was approved

by The University of Arizona Institutional Animal Care and Use Committee (IACUC

protocol 09-035), and conducted in accordance with the American Society of

Mammalogists guidelines (Sikes et al. 2011).

RESULTS

Population Density.—Density of *S. pusillus* in 2009 was 0.10 individuals/ha (95%

CI = 0.06 − 0.11) and the mean cluster size was 1.33 squirrels (95% CI = 1.15 − 1.52). In

2010, density was 0.14 squirrels/ha (95% CI = 0.10 − 0.22) and the mean cluster size was

1.20 squirrels (95% CI = 1.10 − 1.30). In 2009 and 2010, we sighted *S. pusillus* 53 and 79

times, respectively, during distance sampling. Because all models for *S. pusillus* density

estimation for each year had a ΔAIC < 4, we selected the top model based on having both

the lowest AIC value and the highest weight. The best model to estimate population

density for both years was a uniform key function with a cosine adjustment (2009: AIC =

311.37; Kolmogorov-Smirnov goodness-of-fit = 0.11, $P = 0.76$; 2010: AIC = 506.38;

Kolmogorov-Smirnov goodness-of-fit = 0.10, $P = 0.54$).

Behavioral Observations.—We observed *S. pusillus* 253 times over two years.

The frequency of sightings differed by hour of the day ($X^2 = 91.11$, $n = 253$, $P = < 0.001$).

More squirrels were sighted during the morning mainly between 0800 and 1200 h with a

peak activity at 0800 h (Figure 1). Squirrels used story levels differently ($X^2 = 391.81$, *n*

= 253, $P = < 0.001$). *S. pusillus* were sighted in the canopy 77.5%, in the midstory 15%,

and in the understory 7.5% of the time but were never sighted on the ground. The

frequency of each behavior differed ($X^2 = 108.96$, $n = 253$, $P = < 0.001$) among

vocalizations (36 % of time), forage (33.2 %), travel (20.2 %), social interaction (6.3 %),

and rest (4.3 %). Squirrels also vocalized while foraging, traveling, and interacting with

other squirrels, and if we reclassify those observations to vocalization, squirrels were

sighted vocalizing 95.7% of the time.

The frequency of *S. pusillus* behaviors differed among time periods ($X^2 = 71.315$,

$n = 253$, $P = 0.006$) as well as among story levels ($X^2 = 61.360$, $n = 253$, $P = < 0.001$). *S.*

pusillus vocalized and traveled frequently right after sunrise and before sunset (Figure 1).

Squirrels foraged, traveled, and interacted in all story levels except for the ground, and

vocalized and rested only in the midstory and canopy (Figure 2).

Habitat Use.—We successfully detected *S. pusillus* at 159 locations distributed

unequally across vegetation communities ($X^2 = 17.01$, $n = 159$, $P = < 0.001$). *S. pusillus*

used bajiales 0.4 and palm swamps 0.35 times less than their availability, but used high

restinga 1.6 and low restinga 1.3 times more than their availability (Figure 3).

We characterized the forest where *S. pusillus* were found at 54 sightings and 49

random locations. Univariate analyses revealed *S. pusillus* locations had 40 % more trees

that were ≥ 30 cm DBH ($t_{101} = -3.366$, $P = 0.001$) and 80 % more trees that were ≥ 40 cm

DBH/ha compared to random sites in the forest ($t_{101} = -3.515$, $P = < 0.001$; Table 1).

Total canopy cover, number of trees ≥ 30 cm DBH/ha, and number of trees ≥ 40 cm

DBH/ha were forest characteristics included in the top 4 performing logistic regression

candidate models (Table 2). When we consider the simplest top model: *S. pusillus* locations had 80% more trees that were $\geq$ 40 cm DBH/ha on average ($\beta = 0.02 \pm 0.01$, $\chi^2 = 8.44$, $P = 0.004$) and 1% more canopy cover on average ($\beta = 6.35 \pm 2.90$, $\chi^2 = 4.79$, $P = 0.029$; Table 2) compared to random sites of the forest.

At the scale of the focal tree, *S. pusillus* were located only in live trees (100%, $n = 54$) and used certain species of trees more than expected ($X^2 = 283.92$, $n = 54$, df = 17, $P < 0.001$; Table 3). Squirrels were found in almendra (*Caryocar*) 199 times more than expected, tangarana (*Tachigali*) 62 times more, and machimango (*Eschweilera*) 2.7 times more than expected (Table 3). Squirrels were located 28% of the time in tangarana trees, 13% in machimango, and 11% of the time in almendra.

S. pusillus were found in trees that were 3.7 times larger in DBH ($t_{101} = -13.292$, $P = < 0.001$), 2.3 times taller ($t_{101} = -11.246$, $P = < 0.001$), and had 2.3 times larger live crown ($t_{101} = -8.446$, $P = < 0.001$) than random trees in the forest (Table 1). Our top logistic regression model included DBH, height, and proportion of live crown of the focal tree (Table 2). Evaluation of our top candidate logistic regression model indicates *S. pusillus* selected trees that were on average 3.7 times larger in DBH ($\beta = 5.44 \pm 1.75$, $\chi^2 = 9.62$, $P = < 0.001$) with a 1% greater proportion of live crown ($\beta = -10.09 \pm 4.33$, $\chi^2 = 5.42$, $P = 0.020$) compared to random trees in the forest. Although height of focal tree was included in the top model, height of focal tree did not have strong explanatory value ($\beta = 2.49 \pm 1.95$, $\chi^2 = 1.63$, $P = 0.201$; Table 2).

DISCUSSION

Ours is the first study to estimate *S. pusillus* population density; however, when we compared densities of Neotropical pygmy squirrels with densities of other members of the family Sciuridae, Neotropical pygmy squirrel densities are similar to those of the southern Amazon red squirrel (*Sciurus spadiceus*) in Bolivia (0.12 individuals/ha; Peres 1999). Neotropical pygmy squirrel density at ARC is also higher than density estimates of southern Amazon red squirrels both in Brazil (0.02 individuals/ha; Gómez et al. 2003) and in our study area in Peru (0.01 individuals/ha; Jessen 2013) but low compared to densities of other tree squirrel species in the northern hemisphere (Gurnell 1983; Carraway and Verts 1994; Cudworth and Koprowski 2011; Jathanna et al. 2008; Koprowski 1994*a,b*; Nash and Seaman 1977; Pasch and Koprowski 2004).

Tree squirrel density can vary among populations and among years within a population, and is usually related to vegetation type and ultimately to the resources available within the habitat (Gurnell 1983). In 2009, density of *S. pusillus* was lower than in 2010. Although there was a large difference in total rainfall between these two years, we are uncertain about the underlying mechanism driving the apparent differences in density; however, one possible factor affecting abundance could be food availability. Neotropical pygmy squirrels feed on sap from trees (Emmons and Feer 1997; Heyman and Knogge 1997; Voss et al. 2001), therefore, estimates of sap flow would be necessary to evaluate food availability and determine the importance of sap to pygmy squirrel populations. Number of individuals observed together (cluster size) was similar for both years. Most *S. pusillus* encountered were solitary, but groups of 2 and 3 were

documented, similar to observations in other areas of the Amazon Basin in Peru

(Heymann and Knogge 1997). Other species of tree squirrels in the Amazon also forage

in groups (Eason 2010), but most species of tree squirrels in the northern hemisphere are

solitary and occasionally more than 2 individuals nest together (Koprowski 1996; Wells

& Giacalone 1985).

      S. pusillus at ARC are diurnal and have an active period of 11 hours per day.

Individuals were observed exiting and entering their nest at sunrise and sunset (Jessen et

al. In review), which marked the start and end of the active period. *S. pusillus* in our

study area had a bimodal activity pattern with 2 activity peaks; more squirrels were active

at 0800 and 1200 h. This activity pattern is similar to observations of other tree squirrel

species during the spring, summer and fall seasons in the northern hemisphere

(Koprowski and Corse 2005; Thompson 1977; Tonkin 1983; Wauters et al. 1992).

      S. pusillus used the 4 story levels in different proportions and appears to be a

canopy specialist in the winter months. Individuals were found in the canopy 77.5% of

the time, similar to observations in French Guyana (63.6%: Youlatos 2011), and at ARC

during diurnal mammal surveys (75%: Jessen 2013). However, squirrels were never

found on the forest floor compared to observations reported by Emmons and Feer (1997).

S. pusillus vocalized very frequently and also did so while they foraged, traveled, and

during social interactions. We documented co-nesting events and suggest the possibility

that *S. pusillus* are more social than other species of tree squirrels (Jessen et al. In review)

since communal nesting only rarely occurs in some species of tree squirrels in temperate

forests, most often between 2 individuals during cold weather (Edelman and Koprowski

2007; Halloran and Bekoff 1994; Koprowski 1996; Wells and Giacole 1985). Other tree squirrel species inhabiting the ARC do not vocalize often (Jessen 2013) except when found in groups (Eason 2010). Perhaps frequent vocalizations by *S. pusillus* potentially function to maintain contact in this species, similar to vocalizations and alarm calling by ground squirrels (Owings and Leger 1980; Thorington et al. 2012).

Foraging and traveling were also very common activities for *S. pusillus*, a pattern observed in other tree squirrels (Bertolino et al. 2004). Mexican fox squirrels (*Sciurus nayaritensis*) spend a similar amount of time foraging but more time resting (Koprowski and Corse 2005), and Eurasian red (*Sciurus vulgaris*) and eastern gray squirrels (*Sciurus carolinensis*) spend more time foraging and similar time resting (Erossy 1973; Gurnell 1987; Hampshire 1985; Tonkin 1983; Wauters et al. 1992) compared to *S. pusillus*. Although *S. pusillus* were observed traveling and foraging at different times of the day, traveling and vocalizing occurred most frequently soon after sunrise and before sunset. *S. pusillus* used the canopy, midstory, and understory to forage and travel, but they vocalized mainly from the canopy.

S. pusillus selected biotic and physical forest characteristics both at the plot and focal tree level, which is similar to other tree squirrel species (Lurz et al. 2000; Pereira and Itami 1991; Perkins and Conner 2004). Although the 4 different vegetation communities found in our study area are used, *S. pusillus* favored mainly high and low restinga, and only occasionally used bajiales and palm swamps. Restingas may be high quality habitat, whereas bajiales and palm swamps may be low quality habitat (Lanyon and Thompson 1986; Wolf and Batzli 2004). Restingas are composed of large trees from

the family Fabaceae and Lecythidaceae (Myster 2009). *S. pusillus* selected larger trees and trees from the genera *Tachigali* (Fabaceae family) and *Eschweilera* (Lecythidaceae family) more than available. *Tachigali* trees support tangarana ants (*Pseudomyrmex*; Gentry 1996), but we do not know if a relationship exists between Neotropical pygmy squirrels and tangarana ants. *Eschweilera* trees appear to be an important resource for squirrels and the fibers from the bark are used as nesting material (Jessen et al. In review). *Eschweilera* and *Caryocar* trees are also used by native human populations for timber, rope making, and artisan crafts (Vásquez Martínez 1997).

     S. pusillus in the Peruvian Amazon selected individual tree characteristics similar to squirrels in French Guyana (Youlatos 2011) and similar to other tree squirrels, to include trees that were tall, with a greater girth, and large crown size (Cudworth and Koprowski 2011; Edelman and Koprowski 2005; Gurnell 1987; Palmer et al. In press; Thorington et al. 2012). Larger trees with larger live crown may provide protection for tree squirrels against predators (Cudworth and Koprowski 2011; Edelman and Koprowski 2005), and this may be even more important for a small squirrel such as *S. pusillus*. Small tree squirrel species had been observed using larger trees more frequently than larger tree squirrel species (Samaras and Youlatos 2010). Also, larger and older trees are highly correlated with sap flow (Oguntunde et al. 2011), and sap is thought to be an important part of *S. pusillus* diet (Emmons and Feer 1997; Thorington et al. 2012).

     S. pusillus at ARC is associated with and selected for features related to mature forests. Old growth forests not only provide squirrels with resources necessary to live and reproduce, but are also home to a great diversity of mammal species (Jessen 2013), as

well as other vertebrates, invertebrates, and plants (Pitman et al. 2003). Because *S. pusillus* is associated with old growth forests, which is associated with a great diversity of species, and because these squirrels are easy to find, *S. pusillus* might serve as indicator species, but more studies are necessary. Conversely, if *S. pusillus* was a species of concern, protection of mature forests could be beneficial for conservation of the species. This study provides density estimates, habitat use, and habitat associations of a poorly studied Neotropical mammal, and shows the potential of the species as a conservation tool for mature forests and the great biodiversity found in these areas.

RESUMEN

La más alta riqueza de especies de ardillas arborícolas está en los trópicos; sin embargo el mayor número de especies en la categoría de datos deficientes también se

encuentra en los trópicos, los cuales están amenazados por la destrucción de su hábitat.

La ardilla Neotropical de Buffon (*Sciurillus pusillus*) es una de estas especies con datos

deficientes. En el 2009 y 2010, nosotros realizamos distance sampling para estimar la

densidad de la población, medimos propiedades de la vegetación para investigar las

características de bosque que influyen en la selección de hábitat a tres escalas diferentes y

realizamos observaciones para obtener conocimiento sobre el patrón de actividad y

comportamiento de la ardilla Neotropical de Buffon en la Amazonía del Perú. La

densidad de ardillas fue 0.10 and 0.14 individuos/ha respectivamente para cada año. La

actividad alcanzó su punto máximo a las 8:00 hr, las ardillas se encontraron

principalmente en el dosel, pero nunca en el suelo y la frecuencia de comportamientos

fue diferente de acuerdo al tiempo y nivel vertical en el bosque. Las ardillas utilizaron

principalmente las restingas altas y bajas, las áreas con más árboles ≥ 30 y ≥ 40 cm

DAP/ha y árboles con mayor DAP, más altos, y con una corona viva más grande,

comparado con árboles al y áreas del bosque al azar. Las ardillas también utilizaron

especies de árboles en diferente proporción a su disponibilidad. La ardilla Neotropical de

Buffon parece estar asociada con características relacionadas con los bosques maduros.

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TABLES AND FIGURES
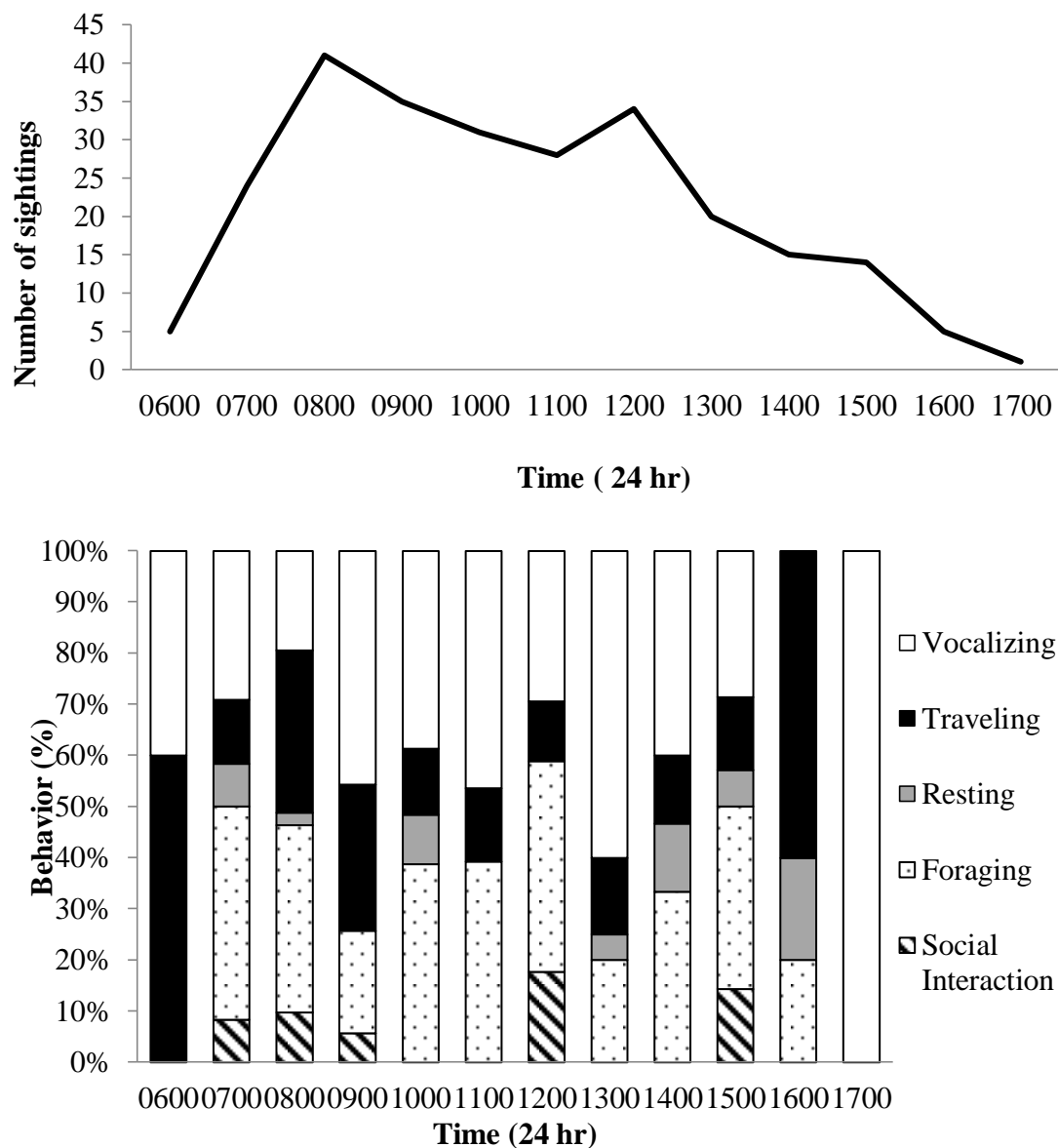
Figure 1: Distribution of sightings of Neotropical pygmy squirrels (*Sciurillus pusillus*) by time (top) and percentage of behaviors by time, from 0600 - 1700 hrs (bottom). Amazon Research Center in Tamshiyacu – Tahuayo Reserve, Loreto, Peru from June - July 2009 and 2010.
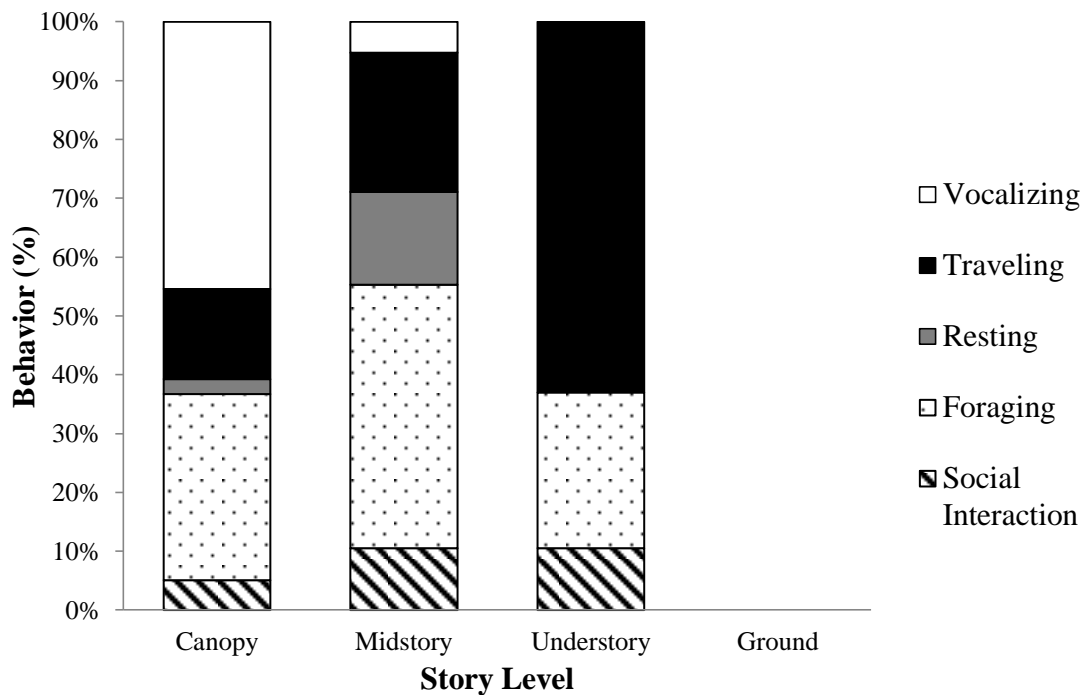
Figure 2: Percentage of Neotropical pygmy squirrel (*Sciurillus pusillus*) behaviors by story level (canopy, midstory, understory, and ground). Amazon Research Center in Tamshiyacu – Tahuayo Reserve, Loreto, Peru from June - July 2009 and 2010.
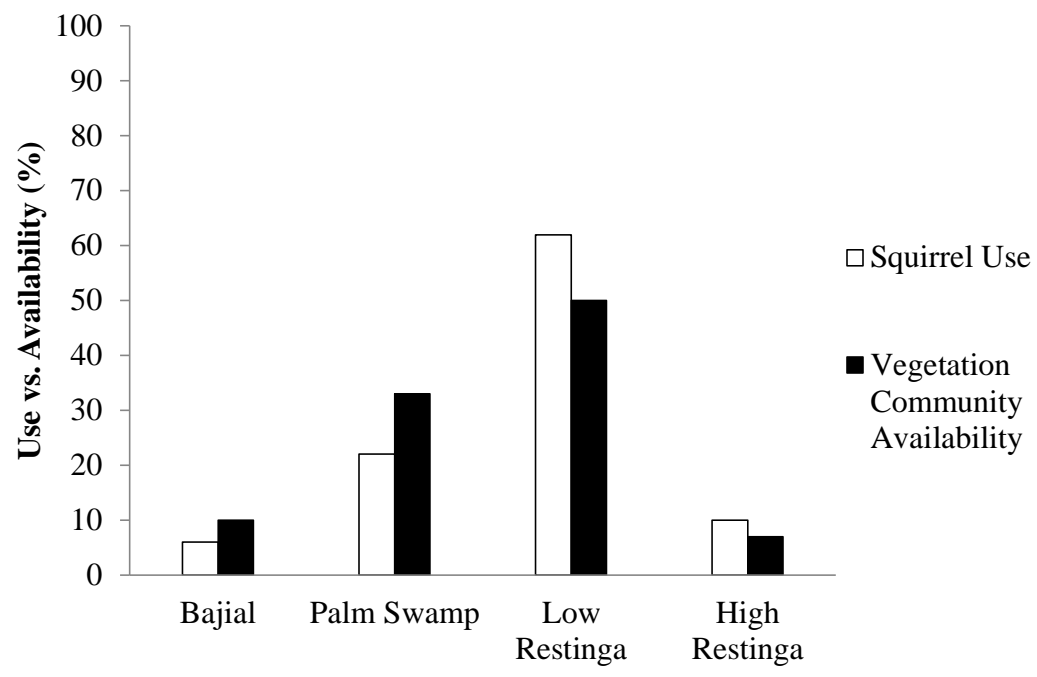
Figure 3: Vegetation type use vs. availability by Neotropical pygmy squirrels (*Sciurillus pusillus*). Amazon Research Center in Tamshiyacu – Tahuayo Reserve, Loreto, Peru from June - July 2009 and 2010.

Table 1: Forest and tree characteristics comparison ($\bar{x} \pm$ SE) at squirrel detection site (n = 54) and random sites (n = 49) for Neotropical pygmy squirrels (*Sciurillus pusillus*), Amazon Research Center in Tamshiyacu − Tahuayo Reserve, Loreto, Peru from June - July 2009 and 2010.

Characteristics of forest	Squirrel location	Random location
Total canopy cover (%)	98.2 ± 0.3	97.5 ± 0.2
Canopy cover at center (%)	98.7 ± 0.3	97.9 ± 0.4
Canopy cover at 5 m from center (%)	98.2 ± 0.3	97.5 ± 0.3
Canopy cover at 10 m from center (%)	98.0 ± 0.4	97.5 ± 0.3
Total trees (no./ha)	2380.2 ± 64.8	2438.8 ± 77.9
Live trees (no./ha)	2317.3 ± 64.1	2341.5 ± 75.2
Dead trees (no./ha)	65.4 ± 7.9	97.3 ± 11.7
Logs (no./ha)	32.1 ± 4.3	40.8 ± 6.5
Trees ≥ 20 cm DBH (no./ha)	247.5 ± 10.8	213.6 ± 11.2
Trees ≥ 30 cm DBH (no./ha)[a]	121.0 ± 7.7	85.0 ± 7.2
Trees ≥ 40 cm DBH (no./ha)[a]	57.4 ± 5.3	32.7 ± 4.5
Basal area (m^2/ha)	1363.4 ± 74.4	1220.7 ± 62.7
Shannon-Wiener diversity Index	1.68 ± 0.08	1.46 ± 0.07
Characteristics of trees	**Squirrel location**	**Random location**
DBH (cm)[b]	46.3 ± 2.8	12.4 ± 1.3
Height (m)[b]	29.1 ± 0.8	12.9 ± 1.1
Live crown size (m)[b]	11.1 ± 0.6	4.8 ± 0.6
Proportion of live crown	0.37 ± 0.01	0.34 ± 0.02
DBH of nearest tree (cm)	10.2 ± 1.5	8.6 ± 0.9
Distance to nearest tree (m)	0.68 ± 0.06	0.83 ± 0.10

[a] Indicates variables are different at α ≤ 0.004 (Bonferroni adjusted value for forest characteristic analysis) in 2-tailed *t*-test.

[b] Indicates variables are different at α ≤ 0.008 (Bonferroni adjusted value for focal tree characteristic analysis) in 2-tailed *t*-test.

Table 2: Model selection statistics and performance measures for models using logistic regression to explain differences between focal tree and forest site characteristics at squirrel and random locations for Neotropical pygmy squirrels (*Sciurillus pusillus*), Amazon Research Center in Tamshiyacu – Tahuayo Reserve, Loreto, Peru from June - July 2009 and 2010.

Forest Characteristics Models					
Model[a]	**K[b]**	**AIC[c]**	**ΔAIC[d]**	**w_i[e]**	**R^2**
Trees > 40, C.C., Trees > 40 X C.C.	3	129.78	0.00	0.256	0.15
C.C., Trees > 30, Trees > 30 X C.C.	3	130.69	0.92	0.162	0.14
Trees > 40, C.C.	2	131.26	1.48	0.122	0.12
C.C., Trees > 30, Trees > 40	3	131.69	1.91	0.098	0.14
C.C., Trees > 30, Trees > 40, Trees > 30 X C.C., Trees > 40 X C.C.	5	131.80	2.03	0.093	0.17
C.C., Trees > 30	2	132.09	2.31	0.080	0.12
Trees > 40, B.A., C.C.	3	133.42	3.64	0.041	0.12
Trees > 40, D.I., # dead trees	3	134.54	4.76	0.024	0.12
Trees > 40	1	134.58	4.80	0.023	0.08
Trees > 30, Trees > 40 cm	2	134.65	4.88	0.022	0.10
Trees > 40, D.I., # dead trees, # logs	4	135.76	5.99	0.013	0.12
Trees > 30	1	135.76	5.99	0.013	0.08
Trees > 40, B.A., D.I.	3	135.78	6.00	0.013	0.11
Trees > 30, Trees > 40 cm, B.A., D.I., C.C., # log, # dead trees	7	135.99	6.21	0.011	0.17
Trees > 30, Trees > 40, B.A., D.I	4	136.11	6.33	0.011	0.12
Trees > 40, B.A.	2	136.58	6.81	0.008	0.09
Trees > 30, Trees > 40, B.A.	3	136.78	7.00	0.008	0.10
C.C.	1	138.96	9.18	0.003	0.05
Null	0	144.59	14.81	0.000	0.00
Tree Characteristics Models					
Model[f]	**K[b]**	**AIC[c]**	**ΔAIC[d]**	**w_i[e]**	**R^2**
DBH, Height, P.C.	3	44.84	0.00	0.481	0.74
DBH, Height, P.C., DBH X Height	4	46.92	2.08	0.170	0.75
DBH	1	47.83	2.99	0.108	0.69
DBH, Height	2	48.89	4.05	0.063	0.70
DBH, Height, P.C., Distance, DBH N.T.	5	48.93	4.09	0.062	0.75
DBH, Height, DBH X Height	3	50.51	5.68	0.028	0.70
DBH, Height, DBH N.T.	3	50.69	5.85	0.026	0.70
DBH, Height, Distance	3	50.85	6.01	0.024	0.70

DBH, Height, P.C., Distance, DBH N.T., DBH X Height	6	51.06	6.23	0.021	0.75
DBH, Distance, DBH N.T.	3	51.64	6.80	0.016	0.70
Height, Distance, P.C.	3	62.72	17.88	6.3E-05	0.62
Height	1	64.08	19.24	3.2E-05	0.58
Null	0	144.59	99.75	0.000	0.00

[a] C.C. = total canopy cover (%), Trees $\geq$ 30 = trees $\geq$ 30 cm DBH (no./ha), Trees $\geq$ 40 = trees $\geq$ 40 cm DBH (no./ha), B.A. = basal area (m^2/ha), # logs = logs (no./ha), # dead trees = dead trees (no./ha), D.I. = Shannon/Wiener diversity.

[b] K = number of parameters.

[c] AIC = Akaike's Information Criterion values.

[d] ΔAIC = AIC relative to the most parsimonious model.

[e] w_i = AIC model weight.

[f] DBH = Diameter at Breast Height of focal tree (cm), Height = height of focal tree (m), P.C. = proportion of live crown of focal tree, Distance = distance of focal tree to nearest tree (m), DBH N.T. = Diameter at Breast Height of nearest tree (cm).

Table 3: Tree use (observed) by Neotropical pygmy squirrels and availability (expected)

in random sites on the Amazon Research Center in Tamshiyacu – Tahuayo Reserve,

Loreto, Peru from June - July 2009 and 2010.

Tree Genus	Observed	Expected
Buchenavia	1	0.045
Calophyllum	1	0.015
Caryocar	6	0.030
Copal	1	0.000
Eschweilera	7	2.636
Ficus	1	0.286
Hymenolobium	2	0.136
Inga	1	0.301
Licania	1	0.000
Marila	1	0.045
Parahancornia	1	0.030
Parkia	1	0.121
Perebea	2	0.030
Salacia	1	0.301
Tachigali	15	0.241
Vochysia	1	0.241
Xylopia	1	0.000
UNK Tree	10	31.556
Other	0	17.985

APPENDIX B: FEEDING BEHAVIOR AND ACTIVITY PATTERNS OF AMAZON RED SQUIRRELS

Paper was prepared to submit to a journal.

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Abstract

Foraging sites are important for the survival of animals. Individuals cue on characteristics of the forest that offer enough food resources and also provide safety. During June and July of 2009 and 2010, we studied northern and southern Amazon red squirrels (*Sciurus igniventris*, *S. spadiceus*) to determine what forest characteristics were associated with feeding sites. We examined habitat use at three levels: vegetation community, feeding site, and feeding sign tree. We measured site characteristics inside a 10-m radius circular plot, measured physical characteristics of the feeding sign tree, and measured the same variables at random locations for comparison. Because there is lack of knowledge about these squirrels, we also conducted focal observations to study their behavior. Squirrels use mainly high and low restinga and selected *Astrocaryum* and *Attalea* palm trees that were taller and larger compared to random locations. Squirrels used all vertical strata of the forest and the main behaviors observed were travel and forage. Behaviors occurred similarly across the day but differed by vertical strata. Although squirrels used vegetation communities different than available and selected for tree characteristics, site characteristics did not appear to be important in contrast with other tree squirrel species.

Introduction

Habitats must provide all of the qualities essential for reproduction and survival, including shelter from weather and predators, foraging sites, resources for nesting and feeding, and a place to reproduce and raise young (Benke et al. 1984, Lucherini et al. 1995, Fisher 2000, Dussault et al. 2005). When selecting habitat, individuals use a variety of cues to settle (Simonetti 1989, Tolimieri 1995, Doer et al. 2006). Availability of food and foraging sites are important cues for animal dispersal and settlement, and also serve as limiting factors that can affect population density (Gurnell 1983, Lurz et al. 1997, Thorson et al. 1998, Wauters et al. 2001). Animals may cue on food distribution and abundance, as well as particular characteristics of forest structure that offer protection from predators with routes of escape, or nearby refuge (Suhonen 1993, Lin and Batzli 2004, Hamel and Côté 2007).

Mammals can have positive and negative impacts on the biotic resources near nest and foraging sites, and may affect the structure and composition of plant communities (Danell et al. 1994, Gutiérrez et al. 1997, Olff and Ritchie 1998, Ickes et al. 2001). Mammal populations can be detrimental to vegetation communities (Kay 1997, Gill and Beardall 2001, Guldemond and Aarde 2010). Conversely, plants may rely exclusively on mammals to pollinate and disperse seeds to maintain gene flow and colonize new sites (Janson et al. 1981, Goldingay et al. 1991, Fleming and Sosa 1994, Jansen et al. 2012). Small mammals in particular perform important functions, such as dispersal and pollination, in a variety of ecosystems (Carpenter 1978, Goldingay et al. 1987, Jansen et al. 2012).

Tree squirrels are found on almost every continent (Koprowski and Nandini 2008, Thorington et al. 2012) and provide key ecosystem services, including seed dispersal and pollination (Miyaki 1987, Steele et al. 2004). In some cases, tree squirrels have even co-evolved with trees to fulfill these roles (Stapanian and Smith 1978, Benkman 1995). Although tree squirrels have important impacts and implications in ecosystems, our knowledge of tree squirrels in the Neotropics is limited, with a dearth of information on natural history, behavior, and habitat use (Koprowski and Nandini 2008).

Northern and southern Amazon red squirrels (*Sciurus igniventris*; Wagner 1842 and *S. spadiceus*; Olfers 1818) inhabit the Peruvian Amazon and are the most frequently sighted *Sciurus*. The two species are large-bodied (500 – 900 g) squirrels with a partially sympatric distribution and indistinguishable in the field (Emmons and Feer 1997, Eisenberg and Redford 1999, Gwinn et al. 2012). Both are considered solitary (Emmons and Feer 1997, Thorington et al. 2012, Youlatos 1999), but forage in groups ≤ 4 individuals (Eason 2010). Individuals feed on large palm nuts with thick and hard endocarps (Emmons 1984, Silvius 2002, Thorington et al. 2012), but little is known about their feeding behavior and characteristics of foraging sites. In temperate areas, where temperatures vary greatly across a day, tree squirrels often demonstrate a bimodal period of activity in summer, where the midday is often avoided, whereas in winter activity is unimodal (Thompson 1977, Tonkin 1983, Wauters et al. 1992, Koprowski and Corse 2005), however, activity patterns of tree squirrels in the tropics are relatively unknown (Koprowski and Nandini 2008).

In 2009 and 2010, we conducted a study to evaluate time budgets, feeding behavior, and characteristics of foraging sites of northern and southern Amazon red squirrels. Since Amazon red squirrels are diurnal, we tested the null hypothesis that squirrels would be sighted equally during daylight hours of the day. We predicted that squirrels would use the canopy levels of the forest more often because of its structural complexity that would allow for protection against predators. Finally, we tested the null hypothesis that squirrel feeding sites will be distributed in the four different vegetation types of our study area according to availability. Given our scant knowledge of the ecology of northern and southern Amazon red squirrels, we predicted that they will forage in palm trees (Emmons 1984, Silvius 2002) and squirrels will select areas with high canopy cover as seen in other tree squirrels (Pereira and Itami 1991, Koprowski 2005, Cudworth and Koprowski 2011, Palmer et al. In press).

Materials and methods

Study site

Our study site was located in the Peruvian Amazon at the Amazon Research Center (ARC). The ARC is located in Tamshiyacu - Tahuayo Reserve in northeastern Peruvian Amazon between the Tamshiyacu - Tahuayo and Yavarí Miri rivers in the state of Loreto, near the Brazilian border (4°39'S, 73°26'W). This 322,500-ha conservation area is a lowland, evergreen, and seasonally flooded forest that was created due to overexploitation of natural resources by outside commercial interests (Newing and Bodmer 2003). The main disturbances in the area were unregulated hunting, poaching,

large-scale commercial fishing, fishing with explosives and chemicals, and large-scale

logging (Newing and Bodmer 2003). The major plant communities found within the

study area included palm swamps (low-lying areas of poor drainage, low tree diversity,

dominated by moriche palm, *Mauritia flexuosa*), bajial (forest that floods to a water level

of 5-7 m, low tree diversity, small trees, sparse understory vegetation), high restinga

(unflooded forest, clay soils, high tree diversity, large trees are common), and low

restinga (forest that floods to a water level of 2.5-5 m, low tree diversity; Prance 1979,

Kvist and Nebel 2001, Myster 2009).

In 2009, the study site experienced above average rainfall and in 2010 a severe

drought affected the area. In 2009, the mean low was 23.3°C (± 0.05 *SE*, n = 346) and the

mean high was 28.2°C (± 0.11 *SE*, n = 346). In 2010 the mean low was 23.2°C (± 0.07

SE, n = 365) and the mean high was 29.4°C (± 0.13 *SE*, n = 365). Total rainfall was 21 %

greater (3914 mm) in the wet year of 2009 compared to the dry year of 2010 (3100 mm).

Behavioral Observations

During June and July of 2009 and 2010, we surveyed two areas at ARC that total

420-ha to locate northern and southern Amazon red squirrels as well as foraging sites.

Because of the similar coloration patterns, melanistic forms, and body size, northern and

southern Amazon red squirrels are extremely difficult to distinguish in the field (Emmons

and Feer 1997, Eisenberg and Redford 1999, Jessen et al. In press). Due to apparent

similarities in life history (Thorington et al. 2012), we decided to group both species to

study feeding behavior and activity patterns. From this point, we will refer to both species

collectively as Amazon red squirrels.

One of the areas surveyed was a 2-km by 2-km research grid, initially created to

study primates, and was completed at the beginning of 2009. The grid has 21 2-km line

transects separated by 100-m intervals that run parallel northeast to southwest, with

another set of 21 transects offset by 90° that run northwest to southeast. We also surveyed

an adjacent small area with 2 transects that were parallel to each other. Each year, we

surveyed a total of 85-km, walking 2 entire transect lines in a single day from 0600 until

1600 h. Our low frequency of sightings precluded a distance-sampling based analysis but

suggests that density is quite low (approximately 1.0 individual/km^2). We searched for

squirrels and squirrel feeding sign, and recorder coordinates (GPS; eTrex Vista GPS unit,

Garmin International Inc., Olathe, KS). For each squirrel encountered, we recorded time

of day (hour), initial behavior of the focal animal as a discrete event (forage [searching

for, processing, or consuming food], travel [movement through the forest using one or

various story levels], groom , vocalization [any squirrel call], or agonistic interaction

[chase between individuals]), and story level (ground, understory [< 5 m; some cover and

vegetation], midstory [5 – 15 m; minimal vegetation, mainly bare trunks from large

trees], and canopy [> 15 m; usually very dense foliage]). We analyzed these data to

determine patterns in squirrel behavior. We also conducted focal behavioral observations

(Altmann 1974) for every Amazon red squirrel that we encountered for as long as

possible. We timed each behavior performed by the focal animal, and once our presence

impacted behaviors of individuals, we ceased observations. We worked in Amazon red

squirrel habitat daily from 0600 – 1600 h, therefore we believe that our observations capture an adequate sample of behaviors across all time periods.

We used chi-square goodness-of-fit test analyses to determine if frequency of sightings differed by hour, story level, and type of behavior. Because of the low frequency of sightings, we used a log-likelihood ratio to determine if the frequency of behavior was the same at every hour or at every story level where an Amazon red squirrel was sighted.

Foraging sites

We evaluated vegetation at three different scales (landscape, site, and focal tree) and determined what forest characteristics were most influential to Amazon red squirrels. For the landscape level analysis, we used ArcGIS 10.0 (Environmental Systems Research Institute, Inc., Redlands California, USA) to calculate the availability of each vegetation community based on the area of each vegetation community (palm swamps, bajial, high restinga, and low restinga) shown in the digital map of the research grid and plotted the feeding sign locations that we obtained after survey efforts. We used a chi-square goodness-of-fit test to compare vegetation community availability to frequency of feeding sign in each vegetation community to determine if squirrels used vegetation communities disproportionately.

We used a standard center-point vegetation-sampling plot (Litvaitis el at. 1996) to evaluate characteristics of individual trees and sites with feeding sign. We measured an equal number of random trees and plots for comparison. Random sites were located in a

random direction and distance (10 – 50 m) from the squirrel feeding sign location. For

foraging site characteristics, we used a 10-m radius plot (area = 0.03 ha) centered on the

feeding site tree. We determined total number, species, condition (live, dead) and DBH

for all woody stems ≥ 3 cm, and used a spherical densitometer to estimate canopy cover

(Strickler 1959, Smith and Mannan 1994, Edelman and Koprowski 2005*b*). We

calculated Shannon-Wiener diversity index, total basal area (m^2/ha), number of live and

dead trees/ha, number of logs/ha, and number of trees > 20 cm, >30 cm, and 40 cm of

DBH/ha within each circular plot. Although we attempted to identify all trees to species,

we were only able to identify many trees to genus (Gentry 1996, Vásquez Martínez

1997). We used a chi-square goodness-of-fit test to examine availability versus use. We

used total number of trees of each genus documented in all of the random plots to

calculate tree species availability and compared this to the number of trees with feeding

sign of each genus to determine if squirrels selected tree species disproportionately to

availability.

For feeding tree characteristics, we recorded species, total height (m), live crown

height (m), diameter at breast height (DBH), and condition (live or dead) of the tree. We

also recorded distance (m), species, and DBH of the closest tree to the foraging tree.

To meet assumptions of normality, we used log transformations for size of live

crown of focal tree, total number of trees, number of live trees, and basal area, and used

arcsine transformations for total canopy cover, canopy cover at center, canopy cover at 5

m from center, and canopy cover at 10 m from center (Ramsey and Schafer 2002). We

used 2-tailed *t*-tests (with a Bonferroni corrected α-value) to compare individual

characteristics of squirrel feeding sign trees and feeding sites with random trees and random sites.

We chose a model selection approach based on information-theoretic methods (Burnham and Anderson 2002) to assess tree and site characteristics that are most important to Amazon red squirrels. Because little is known about the ecology of these squirrels (Koprowski and Nandini 2008), we measured characteristics that are known to be important to other species of tree squirrels (Pereira and Itami 1991, Halloran and Bekoff 1994, Merrick et al. 2007, Prather et al. 2006, Cudworth and Koprowski 2011, Palmer et al. In press, Jessen 2013). We built a set of 8 logistic regression models as candidate models to determine characteristics of feeding sign trees most important to squirrels (Table 2). We used Akaike's Information Criterion (AIC) to rank and evaluate competing models. To reduce multicollinearity, we only included variables in the models if correlation was low ($r < 0.70$) and retained variables that accounted for the most variation (higher F-value). For focal tree analyses, the proportion of the live crown was highly correlated ($r = 0.748$) with the size of the live crown, and the height of the tree was also highly correlated ($r = 0.881$) with DBH of the tree and were not included in any model. We report transformed parameter estimates, but report means as untransformed values. We used JMP 10 (SAS Institute INC., Cary, NC) to conduct all statistical analyses.

Results

Behavioral observations

     We observed adult Amazon red squirrels 54 times. Twelve squirrels were observed for an average duration of 29 minutes (range = 2 to 120 min), although for the majority of the monitoring time, squirrels were only heard gnawing on food items in the canopy and were not seen, and 42 squirrels were observed for an average of 15 sec (range = 10 to 20 sec). Amazon red squirrels were observed alone 50 times and twice 2 individuals were < 10 m from each other. Seven of 54 individuals were melanistic. Males and females including two lactating females on 7 June 2009 and 17 July 2010 were observed, but we were unable to calculate an accurate sex ratio due to their wary behavior (1 male, 3 females, 50 sex unknown). The frequency of sightings differed by hour of the day ($X^2 = 20.81$, $n = 54$, $P = 0.014$), with more squirrels sighted during the morning and a peak in activity between 1000 and 1100 h (Figure 1). Squirrels used all vertical strata of the forest equally and were sighted in the canopy 31%, midstory 24%, understory 19%, and ground 26% of the time ($X^2 = 1.85$, $n = 54$, $P = 0.604$). Squirrels traveled 57%, foraged 33%, vocalized 4%, had agonistic interactions 4%, and groomed 2% of the time ($X^2 = 65.81$, $n = 54$, $P = < 0.001$).

     The frequency of behaviors of Amazon red squirrels was similar among time periods ($X^2 = 40.796$, $n = 54$, $P = 0.137$; Figure 1) but behaviors differed among story levels ($X^2 = 27.633$, $n = 54$, $P = 0.006$; Figure 2). Amazon red squirrels only vocalized in the canopy and understory, traveled through all story levels, and foraged mainly in the canopy and ground (Figure 2). We observed social tolerance at feeding sites; squirrels

were otherwise solitary except two individuals that aggressively chased each other in the understory.

Amazon red squirrels were located most often by sound while they chewed through the hard endocarp of palm nuts. Amazon red squirrels took approximately 30 sec (range = 25 to 35 sec) to first remove the exocarp, and approximately 3 min to consume a nut and drop the empty endocarp to the ground (Figure 3). Squirrels held the blossom and stem ends of the fruit while pulling the exocarp off with their incisors, and rotating the fruit away from their mouth. Amazon red squirrels chewed nuts for an average of 1 min (range = 34 to 90 sec), stopped for 10 to 20 sec, and then resumed gnawing. Up to 2 individuals were observed foraging within 10 to 15 m from each other. Both fresh and old remains of nuts consumed by squirrels littered the forest ground below mature palm trees, and older nuts were found often with small invertebrates (spiders and beetles) and fungi living on and within the remains. We also observed 1 individual eating a honeycomb fungus (*Favolus* sp.) from a tree trunk.

Foraging sites

We found 18 different sites with Amazon red squirrel feeding sign, which we compared with 18 random sites. Feeding sign was found on the forest floor or on logs at the base of a tree. Feeding sign was easy to detect due to the unique incisors marks that Amazon red squirrels left on the empty endocarp (Figure 3; Silvius 2002).

We plotted the 18 feeding sign locations on the digital map of the research grid. Squirrels used the vegetation communities differentially ($X^2 = 33.84$, $n = 18$, $P = <$

0.001), foraging in bajiales 0.5 and palm swamps 0.8 less than available, in high restinga

5.3 times more than available, and foraged in low restinga almost equal to availability

(Figure 4).

Trees at which Amazon red squirrel sign was found were 5 times larger in DBH

($t_{34} = 12.557$, $P = < 0.001$), 2.3 times taller ($t_{34} = 6.090$, $P = < 0.001$), and had 2.3 times

larger live crown ($t_{34} = 4.397$, $P = < 0.001$) than random trees in the forest (Table 1).

DBH and size of live crown were characteristics of trees included in the top 2 logistic

regression models (Table 2). When we consider the parsimonious model, Amazon red

squirrel feeding sign was located at the base of trees with larger DBH ($\beta = 7.19 \pm 3.61$, χ^2

$= 3.97$, $P = 0.046$) compared to random trees in the forest. Amazon red squirrel feeding

sign was only located at the base of live trees (100%, $n = 18$) and squirrels used certain

species of palm trees to forage more than their availability in the forest ($X^2 = 2193.67$, $n =$

77, $P < 0.001$). Feeding sign was located at the base of *Astrocaryum* 123 times more than

expected, *Attalea* 147 times more than expected, and *Licania* 74 times more than

expected. Eighty three percent of the feeding sign was located at the base of palm trees

from the genus *Astrocaryum* spp., 11% at the base of *Attalea* spp., and 6% at the base of

Licania spp., which corresponded to the feeding sign tree. In the case of *Astrocaryum* and

Attalea we were able to identify trees to species. From the genus *Astrocaryum*, 80% of

the feeding sign was from *A. chambira*, 13% from *A. murumuru*, and 7% from *A. jauari*.

From the genus *Attalea* 100% of feeding sign corresponded to *A. maripa*.

Characteristics of the forest at the site level were not different compared to random locations (Table 1). Since Amazon red squirrels did not appear to be selecting for forest characteristics when foraging, we did not build logistic regression models.

Discussion

Foraging sites at ARC were easy to locate because Amazon red squirrels leave noticeable feeding sign composed of seed hulls and husks (Silvius 2002). Foraging sites give us presence/absence knowledge but do not provide information for estimating density. Amazon red squirrels appear to be non-territorial as more than one individual can be found foraging in the same site and squirrels use the same feeding site repeatedly (Emmons and Feer 1997, Youlatos 1999, Silvius 2002, Eason 2010). Although distance sampling is useful to survey mammals (Buckland et al. 2001), including Indian giant squirrels (*Ratufa indica*; Erxleben 1777; Jathanna et al. 2008) and southern Amazon red squirrels (Gómez et al. 2003), the dense forest conditions of our study area precluded use of the technique due to low apparent detectability. Foraging sites are conspicuous and reliable places to sight and observe squirrels under these conditions of visual obstruction.

Amazon red squirrels at ARC were active for period of about 10 h each day, with the start and end of activity corresponding to sunrise and sunset. Squirrels were more frequently sighted in the morning, and had a single peak of activity in the late morning. This activity pattern is similar to that observed for eastern gray (*Sciurus carolinensis*; Gmelin 1788) and Eurasian red squirrels (*S. vulgaris*; Linnaeus 1758) during the winter season (Thompson 1977, Tonkin 1983).

Contrary to what we expected, Amazon red squirrels at ARC used all layers of the canopy, as reported for *Sciurus igniventris* in Ecuador (Youlatos 1999); however, Neotropical pygmy squirrels (*Sciurillus pusillus*; Geoffroy 1803) mainly use the canopy (Jessen 2013), and Amazon dwarf squirrels (*Microsciurus flaviventer*; Gray 1867) use mainly the understory (Youlatos 1999). Amazon red squirrels foraged in the canopy, taking fruit directly from trees, or on the ground, collecting fallen ripe fruit like congeners in Central America (Glanz 1984). Squirrels used the understory and midstory to travel and move between the canopy and the ground, similar to other tree squirrels in rainforests (Glanz 1984, Estrada and Coates-Estrada 1985, Jessen 2013). Although Amazon red squirrels have not previously been observed traveling in the canopy (Emmons and Feer 1997), 60% of our squirrel observations in the canopy were of individuals walking or running along limbs in the canopy. Even though squirrels had to travel considerable distances due to the patchy distribution of palm trees, we believe the frequency of sightings of Amazon red squirrels traveling could also be related to increased wariness and human disturbance. In Central America, red-tailed squirrels (*Sciurus granatensis*; Humboldt 1811) and variegated squirrels (*S. variegatoides*; Ogilby 1839) also flee from observers (Glanz 1984). However, the high and constant frequency of sightings of squirrels acquiring food was similar to the amount of time allocated to foraging by Eurasian red squirrels (Tonkin 1983, Hampshire 1985, Gurnell 1987, Wauters 1992).

Amazon red squirrels at ARC appear to be relatively asocial and vocalized infrequently. In southeast Peru, southern Amazon red squirrels that were alone almost

never vocalized, and vocalizations were frequent and loud when these squirrels were found in groups (Eason 2010). In our study, squirrels were either in the canopy or understory when vocalizing, and since these story levels can be very dense, squirrels might be more protected from predators while vocalizing.

Amazon red squirrels used mainly high and low restinga, but foraged in high restinga more than expected. Neotropical pygmy squirrels found in the same area also use high and low restinga more than their availability (Jessen 2013). Bajiales and palm swamps stayed flooded for longer periods when compared with high and low restinga (Prance 1979, Kvist and Nebel 2001, Myster 2009), and perhaps squirrels prefer drier areas of the forest to access the ground to forage and cache ripe fruit that has fallen from palm trees (Silvius 2002, Thorington et al. 2012). Interestingly, Amazon red squirrels did not select for characteristics of the forest at the site level. Lack of site selectivity at ARC differs from other tree squirrels that are usually associated with specific characteristics such as canopy cover, tree density, number of logs, number of large trees, number of live and dead trees/ha, and basal area (Pereira and Itami 1991, Edelman and Koprowski 2005*b*, Cudworth and Koprowski 2011, Palmer et al. In press, Jessen 2013). Characteristics of focal trees were similar to characteristics important to other tree squirrels (Edelman and Koprowski 2005*b*, Cudworth and Koprowski 2011, Palmer et al. In press, Jessen 2013). Feeding sign was located at the base of tall trees with large girth. These trees are able to provide more food, since large mature trees are associated with greater food crops (Goodrum et al. 1971, Burns and Honkala 1990).

Palm trees from the genus *Astrocaryum* and *Attalea* were selected as the main source of food for squirrels in 2009 when we found most of the feeding sign. In 2010, no *Astrocaryum* and *Attalea* on our study area produced fruit and squirrels may have been feeding on fruit of other species that does not leave noticeable feeding sign, or other sources of food such as insects or fungi. Although red-tailed and variegated squirrels consume *Astrocaryum* and other palm fruit, they also feed on soft fruit and flowers (Glanz 1984). Other species of tree squirrels are known to switch food sources according to season and dependent on availability (Setoguchi 1990, Wauters 1992, Edelman and Koprowski 2005*a*) and the northern Amazon red squirrel is known to feed on larvae of palm bruchid beetles (Bruchidae: Pachymerini) found in endocarp of rotten palm fruit (Silvius 2002). Because of the hard endocarp of palm fruit, squirrels must benefit from the high protein and fats that palm fruit provides and that may compensate for the high handling time (MacArthur and Pianka 1966, Sih and Christensen 2001).

Amazon red squirrels at ARC appear to select certain tree species for food resources, and chose large trees that produce more food (Goodrum et al. 1971, Burns and Honkala 1990). These small mammals may play an important role in the rainforest, providing ecological services by dispersing these seeds and driving the dynamics and complexity of biological communities in rainforests (Estrada and Coates-Estrada 1985, Jansen 2012). At the same time, conservation of palm forests would likely mean conservation of Amazon red squirrels. Understanding foraging behavior of key seed dispersers provides us with important knowledge for conservation and management of forests, and important associates.

Acknowledgments

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TABLES AND FIGURES
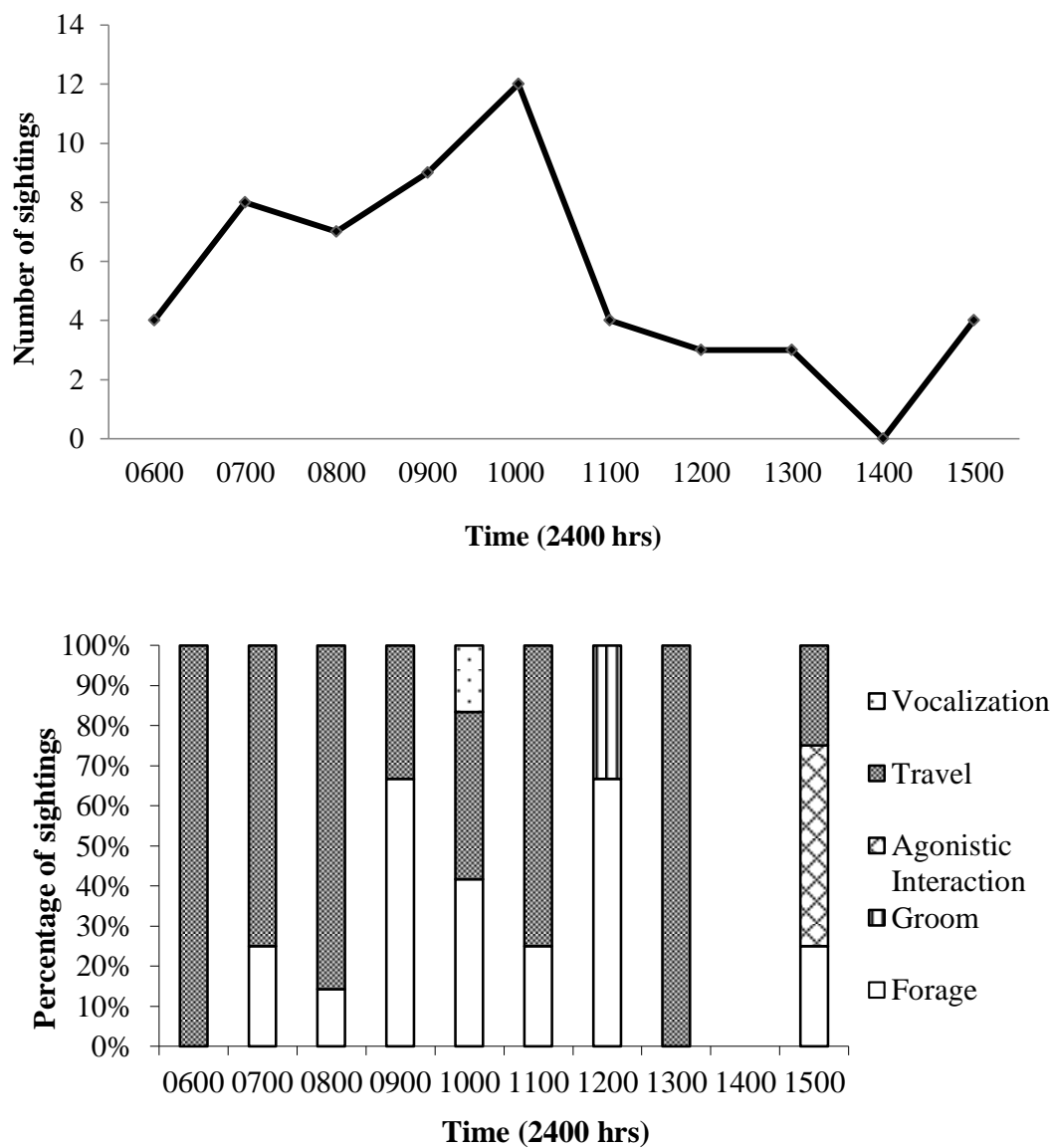
Figure 1: Distribution of sightings of Amazon red squirrels (*Sciurus igniventris*, *S. spadiceus*) by time (top) and percentage of behavior by time from 0600 to 1600 (bottom) at the Amazon Research Center in Tamshiyacu-Tahuayo Reserve, Loreto, Peru from June - July 2009 and 2010.
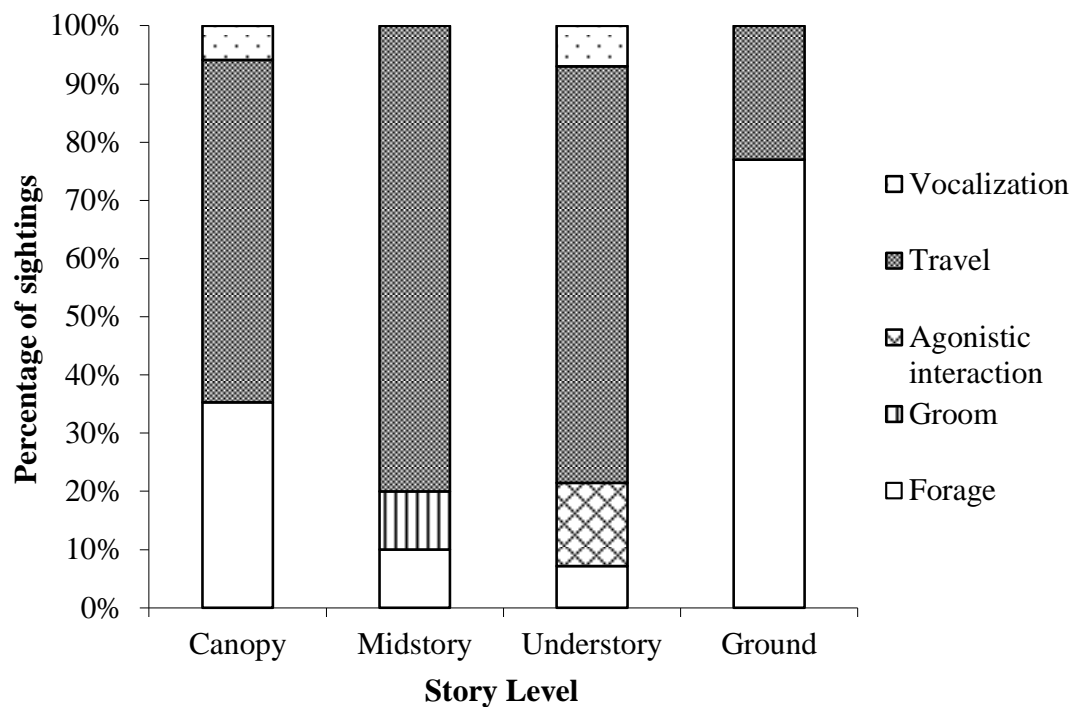
Figure 2: Percentage of Amazon red squirrel (*Sciurus igniventris*, *S. spadiceus*) behaviors by story level (canopy, ground, midstory, and understory) at the Amazon Research Center in Tamshiyacu-Tahuayo Reserve, Loreto, Peru from June - July 2009 and 2010.

Figure 3: *Astrocaryum chambira* fruit on ground (top left); inside of *Astrocarium murumuru* (top right); Amazon red squirrel feeding sign on ground, exocarp of *Astrocaryum chambira* (bottom left); and adult northern Amazon red squirrel (*Sciurus igniventris*) carrying *Astrocaryum chambira* (bottom right; photo: Geoffrey H. Palmer) at the Amazon Research Center in Tamshiyacu-Tahuayo Reserve, Loreto, Peru from June - July 2009 and 2010.
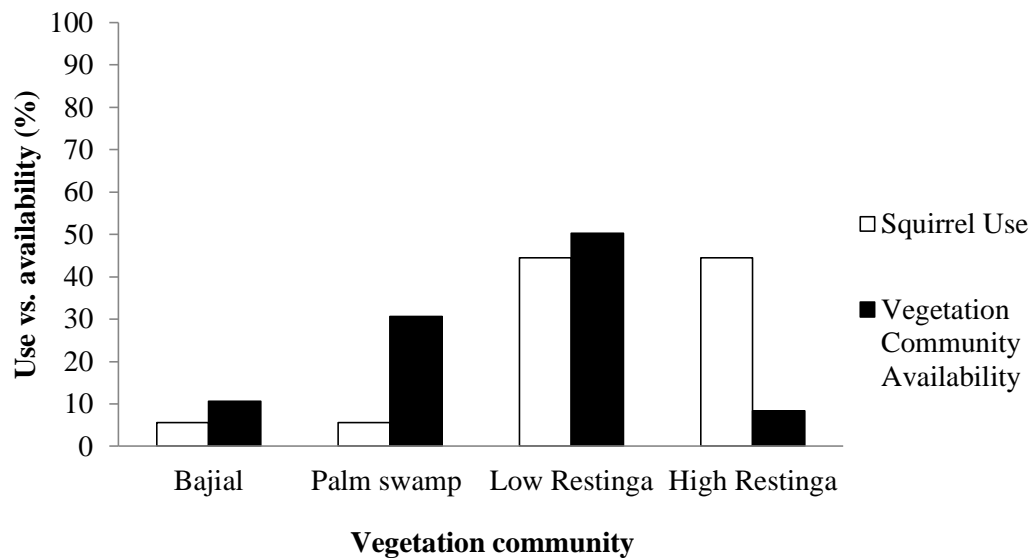
Figure 4: Habitat use vs. availability by Amazon red squirrels (*Sciurus igniventris*, *S. spadiceus*) at the Amazon Research Center in Tamshiyacu – Tahuayo Reserve, Loreto, Peru from June - July 2009 and 2010.

Table 1: Feeding sign tree and site characteristics comparison ($\bar{x} \pm$ SE) at squirrel (n = 18) and random sites (n = 18) for Amazon red squirrels (*Sciurus igniventris*, *S. spadiceus*) at the Amazon Research Center in Tamshiyacu-Tahuayo Reserve, Loreto, Peru from June - July 2009 and 2010.

| Characteristics of trees	Feeding site	Random location
DBH (cm)[a]	33.7 ± 2.4	6.5 ± 0.8
Height (m)[a]	20.4 ± 1.3	9.0 ± 1.3
Live crown size (m)[a]	7.0 ± 0.9	3.1 ± 0.5
Proportion of live crown	0.35 ± 0.04	0.37 ± 0.04
DBH of nearest tree (cm)	8.5 ± 1.1	9.6 ± 1.5
Distance to nearest tree (m)	1.33 ± 0.14	1.10 ± 0.16
Characteristics of sites[b]	**Feeding site**	**Random location**
Total canopy cover (%)	97.1 ± 0.6	97.2 ± 0.5
Canopy cover at center (%)	96.2 ± 0.7	97.8 ± 0.5
Canopy cover at 5 m from center (%)	97.6 ± 0.5	97.9 ± 0.4
Canopy cover at 10 m from center (%)	96.8 ± 0.7	96.5 ± 0.7
Total trees (no./ha)	2627.8 ± 180.2	2457.4 ± 114.2
Live trees (no./ha)	2561.1 ± 180.2	2407.4 ± 112.7
Dead trees (no./ha)	66.7 ± 14.5	51.9 ± 7.2
Logs (no./ha)	31.5 ± 11.9	22.2 ± 8.9
Trees > 20 cm DBH (no./ha)	203.7 ± 17.9	190.7 ± 21.4
Trees > 30 cm DBH (no./ha)	83.3 ± 11.2	85.2 ± 17.3
Trees > 40 cm DBH (no./ha)	31.5 ± 7.4	24.1 ± 5.3
Basal area (m^2/ha)	1318.3 ± 133.0	1129.7 ± 84.1
Shannon-Wiener diversity Index	1.53 ± 0.12	1.46 ± 0.07

[a] Indicates variables are different at $\alpha \leq 0.008$ (Bonferroni adjusted value for focal tree characteristic analysis) in 2-tailed *t*-test.
[b] No feeding site characteristics differed from random sites at ≤ 0.004 (Bonferroni adjusted value for site characteristic analysis) in 2-tailed *t*-test.

Table 2: Model selection statistics and performance measures for models using logistic regression to explain differences between feeding sign tree characteristics and random trees for Amazon red squirrels (*Sciurus igniventris*, *S. spadiceus*) at the Amazon Research Center in Tamshiyacu-Tahuayo Reserve, Loreto, Peru from June - July 2009 and 2010.

Tree Characteristics Models					
Model[a]	K[b]	AIC[c]	ΔAIC[d]	w_i[e]	R^2
DBH	1	10.52	0.00	0.468	0.88
DBH, Size of crown	2	10.93	0.40	0.383	0.92
DBH, DBH N.T.	2	12.81	2.29	0.149	0.88
Size of crown	1	38.26	27.73	4.45E-07	0.32
Size of crown, Distance	2	39.98	29.46	1.88E-07	0.35
Size of crown, DBH N.T.	2	40.00	29.48	1.86E-07	0.33
Size of crown, DBH N.T., Distance	3	41.29	30.76	9.78E-08	0.36
Null	0	52.02	41.50	5.00E-10	0.00

[a] DBH = Diameter at Breast Height of focal tree (cm), Size of crown = size of live crown of focal tree (m), Distance = distance of focal tree to nearest tree (m), DBH N.T. = Diameter at Breast Height of nearest tree (cm).
[b] K = number of parameters.
[c] AIC = Akaike's Information Criterion values.
[d] ΔAIC = AIC relative to the most parsimonious model.
[e] w_i = AIC model weight.

APPENDIX C: INFLUENCE OF TIME AND FLOOD ON DIURNAL MAMMAL DIVERSITY AND STORY LEVEL USE IN IGAPÓ FOREST OF THE PERUVIAN AMAZON

Paper was prepared to submit to a journal.

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ABSTRACT

Rainforests support the highest biodiversity in the world but are one of the most threatened ecosystems due forest destruction and predicted effects of climate change. Mammals are a very important component of rainforest ecosystems, and mammal diversity cannot be explained by forest type alone, but also by considering vertical stratification of the forest. We conducted surveys during a wet year and a dry year to estimate diversity indices of diurnal mammals that inhabit seasonally flooded igapó forest in the Peruvian Amazon. We considered the vertical stratification of the forest to assess whether diversity index varied by story level, and estimated alpha, beta, and gamma diversity. Mammal diversity did not differ between wet and dry years, although species richness was higher in the wet year and evenness was low for both years. Mammal diversity differed by story level between years, but was the highest in the canopy in both years. Alpha diversity was higher in the dry year compared to the wet year, and beta and gamma diversity were higher in the wet year compared to the dry year. During wet and dry year, frequency of sightings of species was influenced by time of day and varied by story level. Protection of continuous, mature forests with large canopies has important

conservation implications as these areas most likely protect the greatest diversity of mammals, while also providing shelter and food for other taxa.

INTRODUCTION

Rainforests support the highest biodiversity in the world (Wilson & Peter 1988) but are also among the most severely threatened ecosystems (Myers 1988, Phillips 1997, Laurance 2004) due to forest destruction, causing changes in species composition, species interactions, ecosystem processes, and microclimate modifications (Terborgh 1992, Bierregaard *et al*. 1992, Benitez-Malvido 1998, Laurance 1998). Rainforest deforestation is also predicted to affect local and global climate due to an increase in temperature, reduction of evapotranspiration and precipitation, and increase in runoff (Nobre *et al*. 1991, Laurence & Williamson 2002). Climate change is expected to have a great impact on rainforest ecosystems due to the narrow range of daily and yearly temperature that species are adapted to, as well as their dependence on rainfall (Malhi *et al*. 2009). Even subtle temperature changes, and most important, changes in precipitation such as extreme drought events, will affect species distribution, presence, and abundance, and are predicted to drive a great percentage of species to extinction (Thomas *et al*. 2004, Parry *et al*. 2007, Malhi *et al*. 2009). Techniques such as rapid inventories, systematic surveys, and monitoring programs are important to measure and document changes in species diversity and species distribution over time, and even some behavioral patterns (Wilson 1985, Haila & Margules 1996).

Rainforests, particularly the Peruvian Amazonian, have a more heterogeneous landscape than previously reported (Tuomisto *et al.* 1995). This has important implications since heterogeneity is positively correlated with species diversity (Pianka 1966). Species diversity is also related to forest structure and differs between canopy and story levels when forests are stratified vertically (Basset *et al*. 2001, Bernard 2001, Schulze *et al*. 2001, Viveiros Grelle 2003, Fermon *et al*. 2005). Each story has unique physical characteristics, microclimate, and resource availability, and harbors a unique flora and fauna (Frith 1984, Basset *et al*. 2001, Bernard 2001, Basset *et al*. 2003). Consideration of all vertical strata is necessary for accurate estimates of forest biodiversity and abundance since some species use multiple story levels (Bernard 2001, Viveiros Grelle 2003, Stork & Grimbacher 2006).

Rainforests are home to the greatest mammalian species richness, and mammals occupy all vertical strata (Estrada & Coates-Estrada 1985, Bernard 2001, Monteiro Vieira & Monteiro-Filho 2003, Viveiros Grelle 2003), however little is known about most rainforest species. In the Neotropics, mammalian diversity is being discovered at an average of one new genus and eight new species annually (Patterson 2000) but rate of extinction is unknown. Mammals play important roles in rainforests and can provide ecological services such as seed dispersal and pollination (Gessman & MacMahon 1984, Terborgh 1988, Jansen *et al*. 2012). Mammals also drive the dynamics and complexity of biological communities by serving as predators and providing a prey base (Gessman & MacMahon 1984, Terborgh 1988). Therefore, changes in mammal communities may

have implications for the dynamics and function of rainforest ecosystems with unknown consequences.

We conducted surveys in the Peruvian rainforest to determine what the diurnal mammalian diversity was and if this diversity was influenced by flood and varied by story level. To answer these questions, we considered the vertical stratification of the forest and predicted that the upper canopy would have the highest diversity index compared to the midstory, understory, and ground due to the advantages that a dense canopy offers for protection from predators and high food production. Use of lower levels would decrease in a year of flooding and deposition of silt at the ground level. We also predicted that diversity would be higher during a wet year compared to a dry year because of the positive influence that rainfall has on resource availability (Coe et al. 1976).

METHODS

STUDY SITE.- Our study site was a 400 ha research grid located in the Peruvian Amazon at the Amazon Research Center (ARC). The 2-km by 2-km research grid was initially created to study primates, and was completed at the beginning of 2009. The grid has 21 2-km line transects separated by 100-m intervals that run parallel northeast to southwest, with another set of 21 transects offset by 90° that run northwest to southeast. The ARC is located in Tamshiyacu - Tahuayo Reserve in the northeastern Peruvian Amazon between the Tamshiyacu - Tahuayo and Yavarí Miri rivers in the state of Loreto, near the

Brazilian border (4°39'S, 73°26'W). This 322,500 ha conservation area is a lowland,

evergreen, and seasonally flooded forest created by local communities due to

overexploitation of natural resources such as poaching, large scale commercial fishing,

fishing with chemicals, and large scale logging (Newing & Bodmer 2003). The plant

communities found within the study area include palm swamps (low-lying areas of poor

drainage, low tree diversity, most common species is moriche palm *Mauritia flexuosa*),

bajial (floods with a water level of 5-7 m, low tree diversity, small trees, none to sparse

vegetation in understory), high restinga (unflooded forest, clay soils, high tree diversity,

large trees are common), and low restinga (floods with a water level of 2.5-5 m, low tree

diversity; Prance 1979, Kvist & Nebel 2001, Myster 2009).

In 2009, the study site experienced above average total rainfall (3914 mm) and in

2010 a severe drought affected the area (21 % less than 2009: 3100 mm). In 2009, the

mean low was 23.3°C ($\pm$ 0.05 *SE*, n = 346) and the mean high was 28.2°C ($\pm$ 0.11 *SE*, n =

346). In 2010 the mean low was 23.2°C ($\pm$ 0.07 *SE*, n = 365) and the mean high was

29.4°C ($\pm$ 0.13 *SE*, n = 365). In 2009 most of the study site stayed under water until mid-

June, preventing ground dwelling mammals to occupy the area. In 2010, due to the

extreme drought, the study site stayed almost completely dry.

MAMMALIAN SURVEY.- In June and July of 2009 and 2010, we conducted mammal

surveys in forested habitat to compare species diversity of a wet versus a dry year. Each

year, we surveyed the entire 84-km grid system. We walked 2 entire transect lines in a

single day from 0600 until 1700 h. During surveys, we recorded species of mammals,

number of individuals, time of day, and story level where individuals were found, categorized as ground, understory (< 5 m, some cover and vegetation), midstory ($5 - 15$ m, little vegetation, mainly bare trunks from large trees), and canopy (> 15 m, usually very dense foliage). We stratified the forest vertically into these story levels to determine whether mammalian diversity varied by level. In the rainforest, these four story levels are distinct and easily recognizable.

ANALYSIS.- We used the Shannon - Wiener Diversity Index to estimate diurnal mammal diversity for wet (2009) and dry (2010) years as well as by story level. We analyzed differences between wet (2009) and dry (2010) years using the Shannon diversity t test in program PAST (Hammer *et al*. 2001). We estimated mammalian alpha, beta, and gamma diversity for the four different story levels as different types of habitat for wet, dry, and both years combined (Whittaker 1972). We created a contingency table in program JMP 10 (SAS Institute, INC., Cary, NC) and used a log-likelihood ratio to determine if the frequency of sightings by species varied by time of day or story level.

RESULTS

The diurnal mammalian diversity index did not differ between wet (2.01) and dry years (2.80; $t_{807.04} = -1.623$, $P = 0.105$). Species richness was marginally higher in the wet year, at 19 species, compared to 17 species sighted in the dry year, and evenness was low for both years (Figure 1). We sighted a total of 22 different species over two years and 14

species were detected in both years (Table 1). In the wet year we sighted a total of 438

individuals and 829 in the dry year.

The diversity index by story level differed between years, but diversity index was

the highest in the canopy for both years (2009: 1.88, 2010: 2.02). In the wet year, the

diversity index was second highest in the understory (1.34), followed by midstory (0.95)

and ground (0.69). Species richness was highest in the canopy, whereas evenness was

highest on the ground and canopy (Figure 2). In the dry year, the diversity index was

second highest in the midstory (1.64), followed by ground (1.48) and understory (0.80).

Species richness was highest in the canopy, whereas evenness was high for canopy and

understory (Figure 2). Alpha, beta, and gamma diversity were similar between wet and

dry years (α wet = 7, α dry = 8; β wet = 2.7, β dry = 2.1; γ wet = 19, γ dry = 17).

Species richness for the wet year and dry year combined was 22, representing six

orders of mammals (Table 1). Primates was most diverse and most abundant with eight

different species and 967 individuals sighted followed by Rodentia as represented by six

species with 171 individuals. During the wet and dry year, the frequency of sightings of

species was influenced by time of day (X^2 = 511.06, n = 438, P = < 0.001; X^2 = 473.40, n

= 829, P = < 0.001; Figure 3) and varied by story level (X^2 = 430.81, n = 438, P = <

0.001; X^2 = 403.85, n = 829, P = < 0.001; Table 1; Figure 4). We sighted more mammal

species during the late morning and early afternoon compared to the early morning and

late afternoon, an although there was a difference in the amount of flooding between

years, our frequency of sightings of species was similar across time periods for both

years (Table 1).

DISCUSSION

We observed 48 mammal species, including diurnal, nocturnal, terrestrial, arboreal, and aquatic mammals in the igapó forest. Diversity index did not differ between wet and dry year, and this is similar to patterns observed in other areas of Amazonia (Emmons 1984). Although Primates is not usually the most common taxon in Peru (Pacheco *et al*. 2009), sightings have become more frequent at the Tamshiyacu - Tahuayo Reserve since the decrease in hunting after creation of the reserve (Pitman *et al*. 2003). Most primates forage in groups, making them more visible compared to solitary species (Chapman 1990, Klein & Klein 2005). We sighted two more species of primates and had 463 more primate sightings during the dry year than the wet year, which could be explained by the low food availability observed in the dry year, forcing primates to move more while searching for food (Dawson 1979, Vedder 1984, Boinski 1987, Garber 2005, Di Bitetti 2006).

Although most of the mammal species sighted during our surveys were diurnal (Emmons & Feer 1997, Eisenberg & Redford 1999), species sightings varied by time of day and by story level, which is similar to other areas in the tropics, where species were associated with certain forest strata (Basset *et al*. 2001, Bernard 2001, Schulze *et al*. 2001, Viveiros Grelle 2003, Fermon *et al*. 2005). Each story level offers unique resources and includes different physical and environmental characteristics, which allows for a complex community with a great diversity of species (Frith 1984, Basset *et al*. 2001, Bernard 2001, Schulze *et al*. 2001, Viveiros Grelle 2003, Fermon *et al*. 2005).

As we predicted, the upper forest canopy at ARC had the highest diversity, which suggests the importance of protection and management of forests with large trees and closed canopy due to their contribution to biological diversity (Estrada & Coates-Estrada 1985, Dean *et al*. 1999, Andersson & Östlund 2004, Ishii *et al*. 2004, Sorensen 2004). Large, mature trees with large and continuous canopies provide travel routes (Emmons 1995, Laurance & Laurance 1999), protection, offer greater seed and fruit production to species using different story levels, and create different microclimates that support a high biodiversity (Goodrum *et al*. 1971, Estrada & Coates-Estrada 1985, Burns & Honkala 1990, Bierregaard *et al*. 1992). Mammal movements are restricted with reduced canopy connectivity; mammals and bird species will emigrate from areas where canopy is destroyed due to fire and where food sources are depleted (Kinnaird & O'Brien 1998, Wilson *et al*. 2007). Gaps in the canopy or lack of canopy connectivity can bring important ecological changes such as alteration of the plant community in the understory and subsequently the animal community (Frumhoff 1995, Kinnaird & O'Brien 1998). Observed and predicted impacts of rainforest alteration on mammal communities are more alarming when considering effects of climate change in rainforests (Laurance 1998).

Mammal diversity on the ground was approximately twice as high in the dry year than in the wet year. This could be explained by two factors that are influenced by the above average rainfall observed in 2009. First, water inundated the area during the wet year but not during the dry year. With increases in water level such as experienced in wet years, most of the ground-dwelling species move to higher ground, or terra firma, seeking

larger areas of dry land (Bodmer 1990*b*, Alho 2008). Only a few individuals stay in high restinga, the small patches of forest surrounded by water and high enough in elevation to avoid inundation in most years (Bodmer 1990*b*, Alho 2008). When the water recedes, terrestrial wildlife move through the forest to areas of lower elevation (Bodmer 1990*b*, Alho 2008). Alternatively, moriche palm is one of the main sources of food for many terrestrial mammals (Bodmer 1990*a*, Bodmer 1991, Tobler 2008, Bowler & Bodmer 2011). Ripe fruit drops to the ground and many mammal species forage around these palm trees. In the wet year, we observed fruit production, but, because of the above average rainfall, the fruit fell in the water and rotted. In the dry year, however, fruit production was very low and perhaps individuals were actively looking for food, making our ground sightings more common (Vedder 1984, Bonaventura *et al*. 1992, Dussault *et al*. 2005).

Mammals play a crucial role in ecosystem function (Gessman & MacMahon 1984, Terborgh 1988, Jansen *et al*. 2012). Conservation of mammals as well as their diversity is important for maintaining the complexity of biological communities (Gessman & MacMahon 1984, Terborgh 1988), and this is especially true in the tropics, host to some of the most complex biotic communities (Covich 1988, Tuomisto *et al*. 1995, Giller 1996, Scarano 2002). Protection of continuous, mature forests with large canopies has important conservation implications as these areas most likely protect the greatest diversity of mammals while also providing shelter and food for other taxa (Bierregaard *et al*. 1992, Dean *et al*. 1999, Andersson & Östlund 2004, Ishii *et al*. 2004, Sorensen 2004). These continuous forests also facilitate movements of ground and

canopy dwellers between lowland and higher elevation areas during wet and dry season as well as years with above average rainfall (Frumhoff 1995, Kinnaird & O'Brien 1998, Wilson *et al*. 2007). Forest characteristics such as large trees with large canopies and flood regimes need to be taken into consideration when designing management and conservation plans that aim to conserve and protect rainforest biodiversity.

ACKNOWLEDGMENTS

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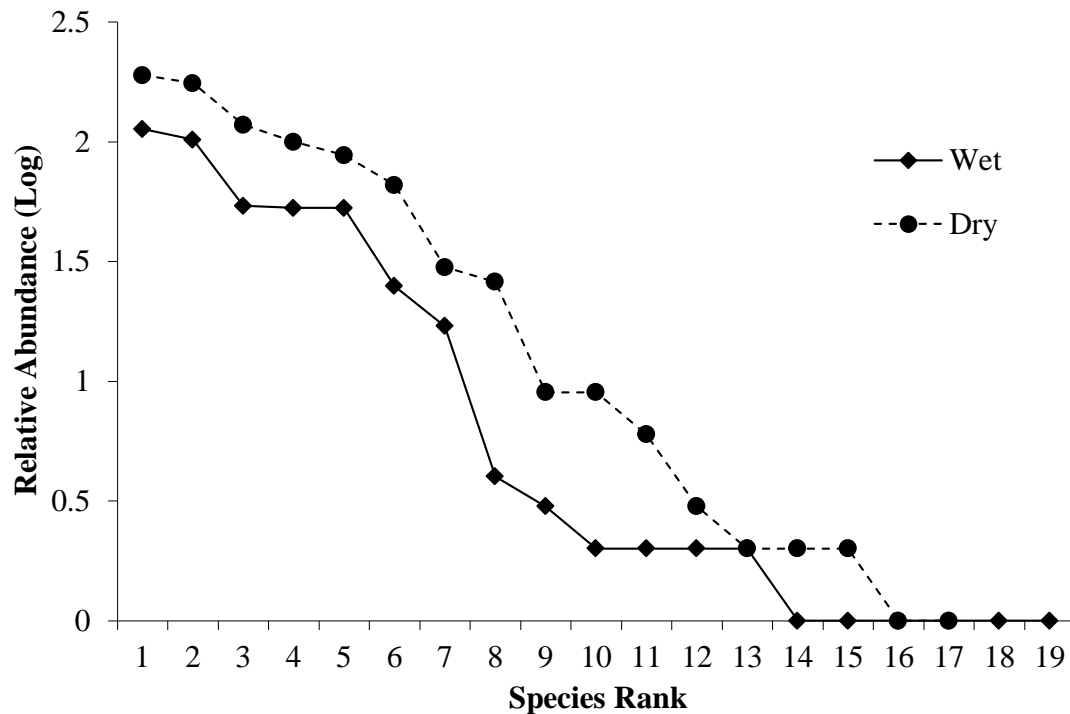
TABLES AND FIGURES

Figure 1: Rank abundance curve that compares species richness between wet and dry years, relative species abundance, as well as evenness for both years. On the x-axis, each number represents a species and is ranked by the relative abundance. A steep slope indicates low evenness and a shallow slope indicates high evenness since relative abundance among species is similar. Amazon Research Center in Tamshiyacu – Tahuayo Reserve, Loreto, Peru from June - July 2009 and 2010.

Table 1: Mammal abundance and story level where sighted (percentage of sightings from both years combined) in 2009 and 2010. Amazon Research Center in Tamshiyacu – Tahuayo Reserve, Loreto, Peru from June - July 2009 and 2010.

Order	Common Name	Scientific Name	Abundance		Story Level			
			Wet (2009)	Dry (2010)	Ground	Understory	Midstory	Canopy
Didelphimorphia	Common opossum	Didelphidae marsupialis	1	0	100	-	-	-
Pilosa	Two-toed sloth	Choloepus sp	1	0	-	-	-	100
	Southern tamandua	Tamandua tetradactyla	1	2	-	-	-	100
Primates	Pygmy marmoset	Cebuella pygmaea	0	9	-	-	78	22
	Saddleback tamarin	Saguinus fuscicollis	53	190	-	14	51	35
	Black-chested mustached tamarin	Saguinus mystax	54	176	-	1	50	49
	White-fronted capuchin	Cebus albifrons	0	30	-	-	-	100
	Tufted capuchin	Cebus apella	1	66	-	-	30	70
	Common squirrel monkey	Saimiri sciureus	102	100	-	15	12	73
	Dusky titi monkey	Callicebus moloch	17	26	2	7	47	44
	Monk saki	Pithecia monachus	25	118	-	-	12	88
Rodentia	Neotropical pygmy squirrel	Sciurillus pusillus	53	88	-	6	15	79
	Northern and Southern Amazon red squirrel*	Sciurus igniventris, S. spadiceus	2	6	50	13	-	38
	Black agouti	Dasyprocta fuliginosa	4	9	100	-	-	-
	Green acouchy	Myoprocta pratti	0	2	100	-	-	-
	Paca	Cuniculus paca	2	0	100	-	-	-
	Yellow-crowned brush-tailed rat	Isothrix bistriata	3	2	-	80	20	-
Carnivora	Tayra	Eira barbara	2	1	67	-	-	33
	South American coati	Nasua nasua	113	0	73	-	-	27
Artiodactyla	Collared peccary	Tayassu tajacu	2	0	100	-	-	-
	Red brocket deer	Mazama americana	1	3	100	-	-	-
	Gray brocket deer	Mazama gouazoubira	1	1	100	-	-	-

*Northern and Southern Amazon red squirrel are too similar to identify in the field due to similar size and color.
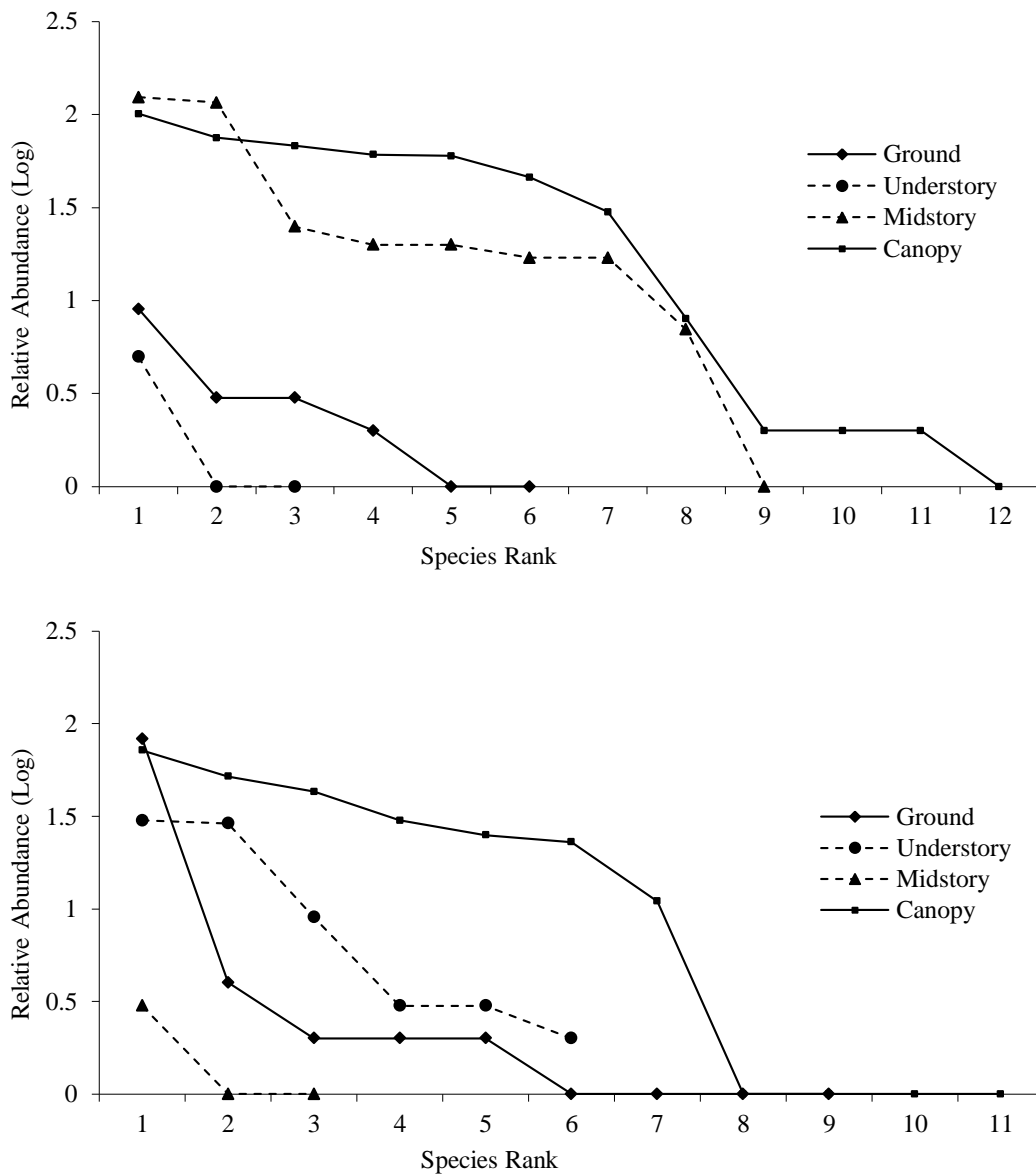
Figure 2: Rank abundance curve that compares species richness between the four different story levels in the forest, relative species abundance, and evenness in wet (2009; top) and dry (2010; bottom) year. On the x-axis, each number represents a species and is ranked by the relative abundance. A steep slope indicates low evenness and a shallow slope indicates high evenness since relative abundance among species is similar. Amazon Research Center in Tamshiyacu – Tahuayo Reserve, Loreto, Peru from June - July 2009 and 2010.
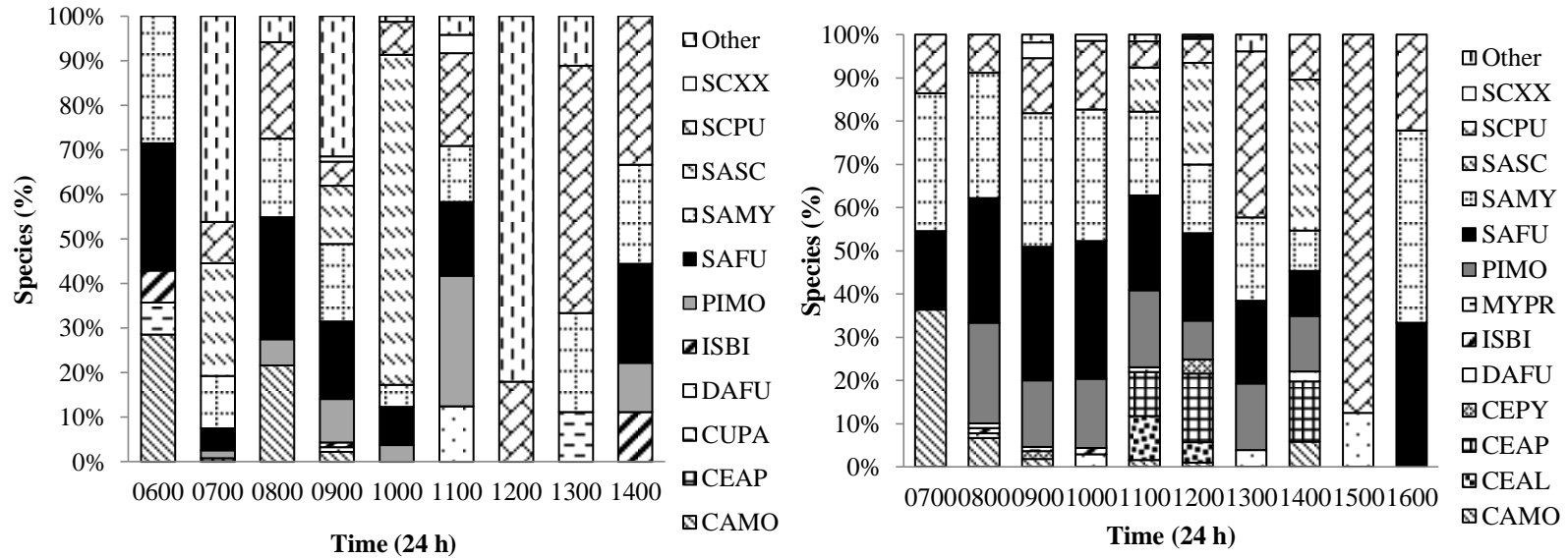
Figure 3: Percentage of Rodent and Primate species sighted by time in wet (2009; left) and dry years (2010; right) at the Amazon Research Center in Tamshiyacu − Tahuayo Reserve, Loreto, Peru from June - July 2009 and 2010. CAMO = *Callicebus moloch*, CEAL = *Cebus albifrons*, CEAP = *Cebus paella*, CEPY = *Cebuella pygmaea*, CUPA = *Cuniculus paca*, DAFU = *Dasyprocta fuliginosa*, ISBI = *Isothrix bistriata*, MYPR = *Myoprocta pratti*, PIMO = *Pithecia monachus*, SAFU = *Saguinus fuscicollis*, SAMY = *Saguinus mystax*, SASC = *Saimiri sciureus*, SCPU = *Sciurillus pusillus*, SCXX = *Sciurus igniventris*, *S. spadiceus*, Other = other mammal species.
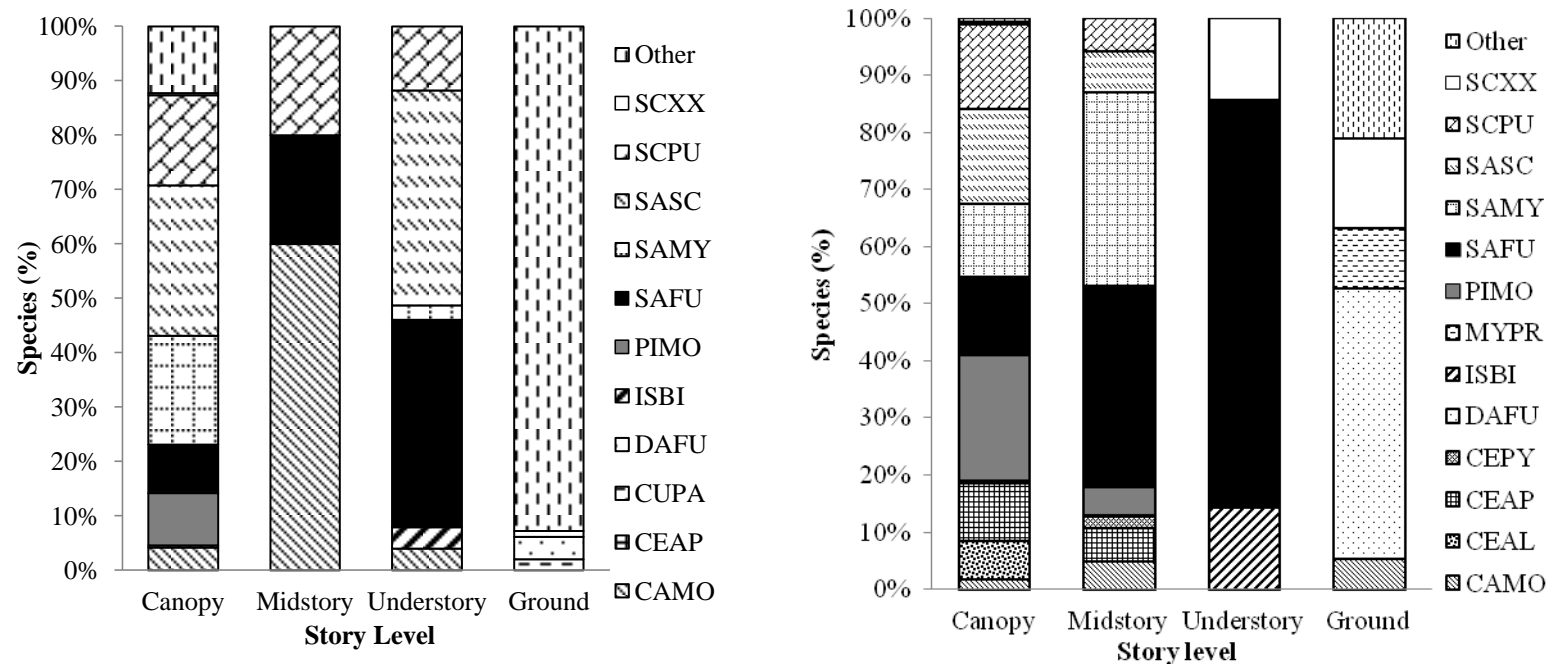
Figure 4: Percentage of Rodent and Primate species sighted by story level in wet (2009; left) and dry years (2010; right) at the Amazon Research Center in Tamshiyacu – Tahuayo Reserve, Loreto, Peru from June - July 2009 and 2010. CAMO = *Callicebus moloch*, CEAL = *Cebus albifrons*, CEAP = *Cebus paella*, CEPY = *Cebuella pygmaea*, CUPA = *Cuniculus paca*, DAFU = *Dasyprocta fuliginosa*, ISBI = *Isothrix bistriata*, MYPR = *Myoprocta pratti*, PIMO = *Pithecia monachus*, SAFU = *Saguinus fuscicollis*, SAMY = *Saguinus mystax*, SASC = *Saimiri sciureus*, SCPU = *Sciurillus pusillus*, SCXX = *Sciurus igniventris*, *S. spadiceus*, Other = other mammal species.