



## How do Neotropical pygmy squirrels (*Sciurillus pusillus*) use seasonally flooded forests in the Peruvian Amazon?

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Tree squirrels are important components of ecosystems but to understand their role, we must learn how squirrels select and use habitat. Tree squirrel species richness is highest in the tropics and, according to the International Union for Conservation of Nature, is also where the greatest number of data deficient species occurs. The Neotropical pygmy squirrel (*Sciurillus pusillus*) is one of these species. In 2009 and 2010, we conducted distance sampling to estimate population density, we measured vegetation variables to investigate forest characteristics that influence habitat selection at 3 different scales, and conducted observations to obtain knowledge about activity patterns and behavior of Neotropical pygmy squirrels in igapó forest in the Peruvian Amazon. Density of squirrels was 0.10 and 0.14 individuals/ha, respectively, for each year. Squirrel activity peaked at 0800h, individuals were found mainly in the canopy and never on the ground, and frequency of squirrel behaviors differed by time and story level. Squirrels mainly used high and low restinga and areas that had more trees that were  $\geq 30$  cm diameter at breast height (DBH)/ha compared to random areas in our site in igapó forest. Squirrels used trees that were larger in DBH, taller, and had a larger live crown compared to random trees. Neotropical pygmy squirrels are associated with features related to mature forests.

Las ardillas arborícolas son un componente importante de los ecosistemas, pero para entender su rol debemos aprender cómo estas ardillas seleccionan y usan su hábitat. La riqueza de especies de ardillas arborícolas es mayor en los trópicos y de acuerdo a la Unión Internacional para la Conservación de la Naturaleza, es también ahí donde se encuentra el mayor número de especies en la categoría de datos deficientes. La ardilla neotropical de Buffon (*Sciurillus pusillus*) es una de estas especies. Durante el 2009 y 2010, realizamos muestreos a distancia para estimar la densidad poblacional de esta especie al tiempo que medimos variables de la vegetación para investigar las características del bosque que influyen en la selección de hábitat a 3 escalas diferentes y realizamos observaciones para obtener información sobre los patrones de actividad y el comportamiento de la ardilla neotropical de Buffon en el bosque igapó de la Amazonía peruana. La densidad de ardillas fue 0.10 y 0.14 individuos/ha respectivamente para cada año. La actividad en esta especie de ardilla alcanzó su punto máximo a las 0800 hr, la mayoría de individuos se encontraron principalmente en el dosel y nunca en el suelo, y la frecuencia de comportamientos fue diferente de acuerdo al horario y nivel vertical en el bosque. Las ardillas utilizaron principalmente las restingas altas y bajas y las áreas con más árboles que tenían  $\geq 30$  cm DAP/ha comparado con otras áreas escogidas al azar en el bosque de igapó. Las ardillas usaron árboles con un DAP mayor, más altos y con una corona viva más grande, comparado con árboles al azar. La ardilla neotropical de Buffon está asociada con características relacionadas con los bosques maduros.

Key words: activity pattern, *Caryocar*, mature forest, population density, rainforest, *Tachigali*, tree squirrel, tropical forest

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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 such as seed dispersal and pollination (Gessman and MacMahon 1984; Terborgh 1988; Stoner et al. 2007). Mammals also drive the dynamics and complexity of biological communities by serving

as predators and providing a prey base for a range of rainforest species (Gessman and MacMahon 1984; 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 percentage of mammal species worldwide 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 understand and evaluate the importance and role these species play in rainforest ecosystems. Arboreal-dwelling species are likely to be particularly sensitive to changes in forest condition.

Tree squirrels are a group of mammals found on 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 little-known obligate species is critical to assess how loss of tropical habitats will affect global biodiversity and ecosystem function.

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). Several studies in temperate forests of the United States and Europe support use of tree squirrels as indicator species of forest condition (Munch 1996; Bayne and Hobson 2000; Carey 2000; Kremsater et al. 2003; Koprowski 2005; Smith et al. 2005), but a similar value as indicator species in rainforests is still unknown (Koprowski and Nandini 2008). Squirrels also provide ecosystem services and in some cultures squirrels have an important economic value (Adeola 1992; Steele and Koprowski 2001; Durojaye 2008).

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 (38–48 g—Jessen et al. 2013a). Not surprisingly, this secretive squirrel is listed as data deficient (Eisenberg and Redford 1999; Amori et al. 2008; Thorington et al. 2012). *S. pusillus* has a fragmented distribution (Emmons and Feer 1997), is diurnal, is believed to be solitary but has been seen foraging in groups, and several individuals were recently documented to share a nest (Heymann

and Knogge 1997; Eason 2010; Jessen et al. 2013b). However, important details about their life history and ecology are still lacking. In addition, *S. pusillus* forms part of the Sciurillinae, which together with Ratufinae are believed to be the most ancient lineages within the Sciuridae (Thorington et al. 2012). Learning more about *S. pusillus* could shed light on the ancestral behavior and ecology of the Sciuridae family.

In 2009 and 2010, we conducted a study on *S. pusillus* in the Amazon forest of Peru, with the objective to investigate characteristics of the forest that influence habitat selection at 3 different scales (landscape, forest, and focal tree), 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 the area 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—Prance 1979; Kvist and Nebel 2001; Myster 2009).

In 2009, the study site experienced above average total rainfall (3,914 mm) and in 2010, a severe drought affected the area (21% less than 2009: 3,100 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,  $n = 365$ ).

*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 and to estimate density in the 400-ha ARC research grid. The 2- × 2-km research grid was initially created to study primates and was completed at the beginning of 2009. The grid has 21 two-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 1700h. We measured perpendicular distance from transect to *S. pusillus* locations with a range finder and recorded each location with a handheld global positioning system (Garmin eTrex Legend Cx, Olathe, Kansas—estimated accuracy 2–5 m). 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 squirrels 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 6.0 release 1 (Thomas et al. 2010). 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, for each squirrel encountered, we used time of day (hour), initial 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 individual was sighted from data collected through distance sampling as well as opportunistic observations. We worked in *S. pusillus* habitat each day from approximately 0600h (time of sunrise) to approximately 1700h (time of sunset), 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 3 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 (ESRI

2011). 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 et al. 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  $\geq 3$  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 (Strickler 1959; Smith and Mannan 1994; Edelman and Koprowski 2005). 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 ( $\text{m}^2/\text{ha}$ ), total number of trees/ha, number of live trees/ha, number of dead trees/ha, number of logs/ha, and number of trees  $\geq 20$  cm DBH/ha,  $\geq 30$  cm DBH/ha, and  $\geq 40$  cm DBH/ha within each circular plot. Although we attempted to identify all trees to species, we could only classify 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  $\geq 20$  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  $\geq 30$  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  $\alpha$  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 (Pereira and Itami 1991; Halloran and Bekoff 1994; Prather et al. 2006; Merrick et al. 2007; Cudworth

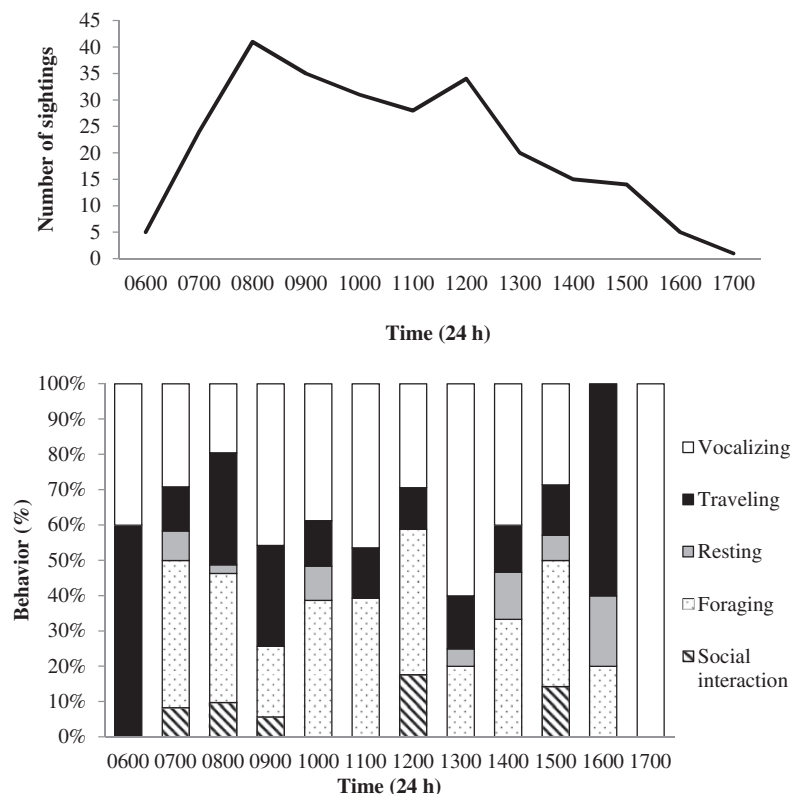
and Koprowski 2011). We built a set of 13 candidate logistic regression models to determine characteristics of focal trees most important to *S. pusillus* presence and another set of 19 candidate logistic regression models to determine characteristics of forest most important in predicting *S. pusillus* presence (Table 2). We used 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 2012) 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  $\Delta\text{AIC} < 4$ , 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 2 years. The frequency of sightings differed by hour of the day ( $\chi^2 = 91.11$ ,  $n = 253$ ,  $P < 0.001$ ). More squirrels were sighted during the morning mainly between 0800 and 1200h with a peak activity at 0800h (Fig. 1). Squirrels used story levels differently ( $\chi^2 = 391.81$ ,  $n = 253$ ,  $P < 0.001$ ). *S. pusillus* were sighted in the canopy 77.5%, midstory 15%, and understory 7.5% of the time but were never sighted on the ground. The frequency of each behavior differed ( $\chi^2 = 108.96$ ,  $n = 253$ ,  $P < 0.001$ ) 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,



**Fig. 1.**—Distribution of sightings of Neotropical pygmy squirrels (*Sciurillus pusillus*) by time (top) and percentage of behaviors by time, from 0600 to 1700h (bottom). Amazon Research Center in Tamshiyacu–Tahuayo Reserve, Loreto, Peru, from June to July 2009 and 2010.

and interacting with other squirrels, and if we reclassify those observations to vocalization, squirrels were vocalizing 95.7% of the time.

The frequency of *S. pusillus* behaviors differed among time periods ( $\chi^2 = 71.32, n = 253, P = 0.006$ ) as well as among story levels ( $\chi^2 = 61.36, n = 253, P < 0.001$ ). *S. pusillus* vocalized and traveled frequently right after sunrise and before sunset (Fig. 1). Squirrels foraged, traveled, and interacted in all story levels except for the ground, and vocalized and rested only in the midstory and canopy (Fig. 2).

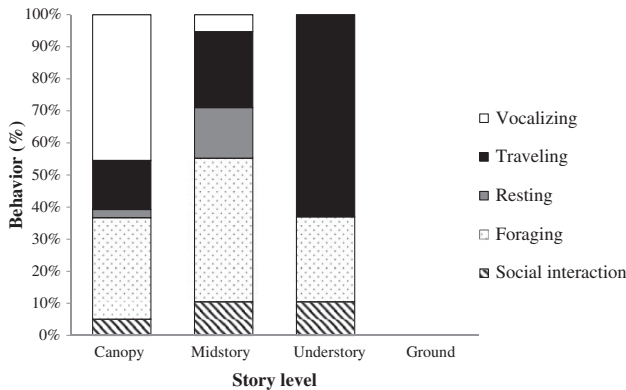
**Habitat use.**—We successfully detected *S. pusillus* at 159 locations distributed unequally across vegetation communities ( $\chi^2 = 17.01, n = 159, P < 0.001$ ). *S. pusillus* used bajiales 0.4 and palm swamps 0.35 times less than their availability, but used high restinga 1.6 and low restinga 1.3 times more than their availability (Fig. 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  $\geq 30$  cm DBH ( $t_{101} = -3.37, P = 0.001$ ) and 80% more trees that were  $\geq 40$  cm DBH/ha compared to random sites in the forest ( $t_{101} = -3.52, P < 0.001$ ; Table 1). Total canopy cover, number of trees  $\geq 30$  cm DBH/ha, and number of trees  $\geq 40$  cm DBH/

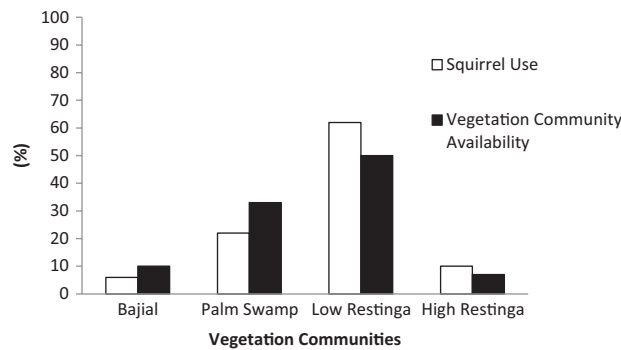
ha were forest characteristics included in the top 4 performing logistic regression candidate models (Table 2). When we consider the simplest top model: *S. pusillus* locations had 80% more trees that were  $\geq 40$  cm DBH/ha on average ( $\beta = 0.02 \pm 0.01, \chi^2 = 8.44, P = 0.004$ ) and 1% more 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 ( $\chi^2 = 283.92, n = 54, df = 17, P < 0.001$ ; 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 ( $t_{101} = -13.29, P < 0.001$ ), 2.3 times taller ( $t_{101} = -11.25, P < 0.001$ ), and had 2.3 times larger live crown ( $t_{101} = -8.45, P < 0.001$ ) 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



**Fig. 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 to July 2009 and 2010.



**Fig. 3.**—Vegetation type availability versus use by Neotropical pygmy squirrels (*Sciurillus pusillus*). Amazon Research Center in Tamshiyacu–Tahuayo Reserve, Loreto, Peru from June to July 2009 and 2010.

**Table 1.**—Forest and tree characteristics comparison ( $\bar{X} \pm SE$ ) at squirrel detection sites ( $n = 54$ ) and random sites ( $n = 49$ ) for Neotropical pygmy squirrels (*Sciurillus pusillus*), Amazon Research Center in Tamshiyacu–Tahuayo Reserve, Loreto, Peru from June to July 2009 and 2010. DBH = diameter at breast height.

C	Squirrel location	Random location
Characteristics of forest		
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 $\geq 20$ cm DBH (no./ha)	247.5 ± 10.8	213.6 ± 11.2
Trees $\geq 30$ cm DBH (no./ha) <sup>a</sup>	121.0 ± 7.7	85.0 ± 7.2
Trees $\geq 40$ cm DBH (no./ha) <sup>a</sup>	57.4 ± 5.3	32.7 ± 4.5
Basal area (m <sup>2</sup> /ha)	1363.4 ± 74.4	1220.7 ± 62.7
Shannon–Wiener diversity index	1.68 ± 0.08	1.46 ± 0.07
Characteristics of trees		
DBH (cm) <sup>b</sup>	46.3 ± 2.8	12.4 ± 1.3
Height (m) <sup>b</sup>	29.1 ± 0.8	12.9 ± 1.1
Live crown size (m) <sup>b</sup>	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

<sup>a</sup> Variables are different at  $\alpha \leq 0.004$  (Bonferroni-adjusted value for forest characteristic analysis) in 2-tailed *t*-test.

<sup>b</sup> Variables are different at  $\alpha \leq 0.008$  (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 to July 2009 and 2010. 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<sup>2</sup>/ha); # logs = logs (no./ha); # dead trees = dead trees (no./ha); D.I. = Shannon/Wiener diversity;  $K$  = number of parameters; AIC = Akaike's Information Criterion values;  $\Delta$ AIC = AIC relative to the most parsimonious model;  $w_i$  = AIC model weight; 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).

Forest characteristics models					
Model	$K$	AIC	$\Delta$ AIC	$w_i$	$R^2$
Trees $\geq 40$ , C.C., Trees $\geq 40 \times$ C.C.	3	129.78	0.00	0.256	0.15
C.C., Trees $\geq 30$ , Trees $\geq 30 \times$ C.C.	3	130.69	0.92	0.162	0.14
Trees $\geq 40$ , C.C.	2	131.26	1.48	0.122	0.12
C.C., Trees $\geq 30$ , Trees $\geq 40$	3	131.69	1.91	0.098	0.14
C.C., Trees $\geq 30$ , Trees $\geq 40$ , Trees $\geq 30 \times$ C.C., Trees $\geq 40 \times$ C.C.	5	131.80	2.03	0.093	0.17
C.C., Trees $\geq 30$	2	132.09	2.31	0.080	0.12
Trees $\geq 40$ , B.A., C.C.	3	133.42	3.64	0.041	0.12
Trees $\geq 40$ , D.I., # dead trees	3	134.54	4.76	0.024	0.12
Trees $\geq 40$	1	134.58	4.80	0.023	0.08
Trees $\geq 30$ , Trees $\geq 40$ cm	2	134.65	4.88	0.022	0.10
Trees $\geq 40$ , D.I., # dead trees, # logs	4	135.76	5.99	0.013	0.12
Trees $\geq 30$	1	135.76	5.99	0.013	0.08
Trees $\geq 40$ , B.A., D.I.	3	135.78	6.00	0.013	0.11
Trees $\geq 30$ , Trees $\geq 40$ cm, B.A., D.I., C.C., # log, # dead trees	7	135.99	6.21	0.011	0.17
Trees $\geq 30$ , Trees $\geq 40$ , B.A., D.I.	4	136.11	6.33	0.011	0.12
Trees $\geq 40$ , B.A.	2	136.58	6.81	0.008	0.09
Trees $\geq 30$ , Trees $\geq 40$ , 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	$K$	AIC	$\Delta$ AIC	$w_i$	$R^2$
DBH, Height, P.C.	3	44.84	0.00	0.481	0.74
DBH, Height, P.C., DBH $\times$ 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 $\times$ 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 $\times$ 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

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. 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 are no other population density studies on *S. pusillus*, when we compared densities of Neotropical pygmy squirrels with densities of other members of the 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 (Nash and Seaman 1977; Gurnell 1983; Carraway and Verts 1994; Koprowski 1994a, 1994b; Pasch and Koprowski 2005; Jathanna et al. 2008; Cudworth and Koprowski 2011).

Although there was a large difference in total rainfall between these 2 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; Heymann 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

**Table 3.**—Tree use (observed) by Neotropical pygmy squirrels (*Sciurillus pusillus*) and availability (expected) in random sites on the Amazon Research Center in Tamshiyacu–Tahuayo Reserve, Loreto, Peru from June to July 2009 and 2010. UNK tree = unknown tree species.

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

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 although occasionally more than 2 individuals nest together (Wells and Giacalone 1985; Koprowski 1996).

*Sciurillus pusillus* at ARC are diurnal and have an active period of 11 h per day. Individuals were observed exiting and entering their nest at sunrise and sunset (Jessen et al. 2013b), 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 1200h. This activity pattern is similar to observations of other tree squirrel species during the spring, summer, and fall seasons in the northern hemisphere (Thompson 1977; Tonkin 1983; Wauters et al. 1992; Koprowski and Corse 2005).

*Sciurillus 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* is more social than other species of tree squirrels (Jessen et al. 2013b) since communal nesting only rarely occurs in some species of tree squirrels in temperate forests, most often between 2 individuals during cold weather (Wells and Giacalone 1985; Halloran and Bekoff 1994; Koprowski

1996; Edelman and Koprowski 2007). 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 squirrels (*Sciurus vulgaris*) and eastern gray squirrels (*Sciurus carolinensis*) spend more time foraging and similar time resting (Erossy 1973; Tonkin 1983; Hampshire 1985; Gurnell 1987; Wauters et al. 1992) compared to *S. pusillus*. Although individuals 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 vocalized mainly from the canopy.

*Sciurillus pusillus* selected biotic and physical forest characteristics both at the plot and focal tree level, which is similar to other tree squirrel species (Pereira and Itami 1991; Lurz et al. 2000; 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 Lecythydaceae (Myster 2009). *S. pusillus* selected larger trees and trees from the genera *Tachigali* (Fabaceae family) and *Eschweilera* (Lecythydaceae 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. 2013b). *Eschweilera* and *Caryocar* trees are also used by native human populations for timber, rope making, and artisan crafts (Vásquez Martínez 1997).

*Sciurillus 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 (Gurnell 1987; Edelman and Koprowski 2005; Cudworth and Koprowski 2011; Thorington et al. 2012; Palmer et al. 2013). Larger trees with larger live crown may provide protection for tree squirrels against predators (Edelman and Koprowski 2005; Cudworth and Koprowski 2011), and this may be even more important for a small squirrel such as *S. pusillus*. Small tree squirrel species have 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).

*Sciurillus pusillus* at ARC is associated with 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). Old growth forests are associated with a great diversity of species, and *S. pusillus* may serve as an indicator species because they are easy to survey; however, more studies are needed. 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 known Neotropical mammal and shows the potential of the species as a conservation tool for mature forests and the great biodiversity found in these areas.

### ACKNOWLEDGMENTS

Thanks to P. Beaver and the staff at Amazonia Expeditions, especially J. Shahuano, A. Do Santos, and R. Flores Pinedo for their enthusiasm and assistance in the field. We also thank S. Beaver, T. Jessen, Z. Koprowski, and G. Palmer for help in the field. Thanks also to M. Merrick for field efforts and for sharing her expertise with GIS and digital maps. Financial support was provided by the Scott Neotropical Fund from the Cleveland Metroparks Zoo and the Cleveland Zoological Society, The Exploration Fund from The Explorers Club, the Tinker Summer Field Grant Program from University of Arizona, the Latin American Student Field Research Award from the American Society of Mammalogists, and the University of Arizona.

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Submitted 9 February 2015. Accepted 17 August 2015.

Associate Editor was Ricardo A. Ojeda.