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Feeding behavior and activity patterns of Amazon red squirrels

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 where feeding sign was located, site characteristics of the forest immediately surrounding the feeding sign, and the tree exhibiting feeding sign. We measured the site characteristics inside a 10-m radius circular plot, the physical characteristics of the tree exhibiting feeding sign, and 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 with 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.

Keywords: foraging behavior; habitat use; palm trees; *Sciurus igniventris*; *Sciurus spadiceus*.

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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 the 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, Doerr 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, Guldmond 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. 2005, Zong et al. 2010). 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 are indistinguishable in the field (Emmons and Feer 1997, Eisenberg and Redford 1999, Gwinn et al. 2012). Both are considered solitary (Emmons and Feer 1997, Youlatos 1999, Thorington et al. 2012), but forage in groups of four or fewer individuals (Eason 2010). Individuals feed on large palm nuts with thick and hard endocarps (Emmons 1984, Silvius 2002, Thorington et al. 2012); however, little is known about their feeding behavior and the characteristics of their 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. As 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 Yavari 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 because of 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, $n=365$). The total rainfall was 21% greater (3914 mm) in the wet year of 2009 than 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. 2013). Owing 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 \times 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 two transects that were parallel to each other. Each year, we surveyed a total of 85 km, walking two entire transect lines in a single day from 600 until 16:00 h. Sunrise during our study was between 05:00 and 06:00 h, and sunset was between 17:50 and 17:57 h. Day length did not vary greatly owing to the similar schedule between years. Our low frequency of sightings precluded a distance-sampling-based analysis but suggests that

density is quite low (approximately 1.0 individual/km²). We searched for squirrels and squirrel feeding sign, and recorded coordinates (GPS; eTrex Vista GPS unit; Garmin International Inc., Olathe, KS, USA). For each squirrel encountered, we recorded the 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 affected the behaviors of individuals, we ceased our observations. We worked in Amazon red squirrel habitat daily from 06:00 to 16:00 h; therefore, we believe that our observations capture an adequate sample of behaviors across all periods.

We used χ^2 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, CA, 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 χ^2 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 et al. 1996) to evaluate the 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 the total number, species, condition (live, dead), and diameter at breast height (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 2005b). We calculated the Shannon-Wiener diversity index; total basal area (m²/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 χ^2 goodness-of-fit test to examine availability versus use. We used the 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), 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 two-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, Prather et al. 2006, Merrick et al. 2007, Cudworth and Koprowski 2011, Jessen 2013, Palmer et al. in press). We built a set of eight 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 ($r = 0.75$, $n = 18$) with the size of the live crown and the height of the tree was also highly correlated ($r = 0.88$, $n = 18$) with the DBH of the tree, and these 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, USA) 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 min (range, 2–120 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 s (range=10–20 s). Amazon red squirrels were observed alone 50 times and twice two individuals were <10 m from each other. Seven of 54 individuals were melanistic. Males and females including two lactating females on June 7, 2009, and July 17, 2010, were observed; however, we were unable to calculate an accurate sex ratio because of their wary behavior (one male, three females, 50 sex unknown). The frequency of sightings differed by hour of the day ($\chi^2 = 20.8$, $df = 8$, $p = 0.014$), with more squirrels sighted during the morning and a peak in activity between 10:00 and 11:00 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 ($\chi^2 = 1.9$, $df = 3$, $p = 0.60$). Squirrels traveled 57%, foraged 33%, vocalized 4%, had agonistic interactions 4%, and groomed 2% of the time ($\chi^2 = 65.8$, $df = 4$, $p < 0.001$).

The frequency of behaviors of Amazon red squirrels was similar among time periods ($\chi^2 = 40.8$, $df = 32$, $p = 0.14$; Figure 1); however, behaviors differed among story levels ($\chi^2 = 27.6$, $df = 12$, $p = 0.006$; 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

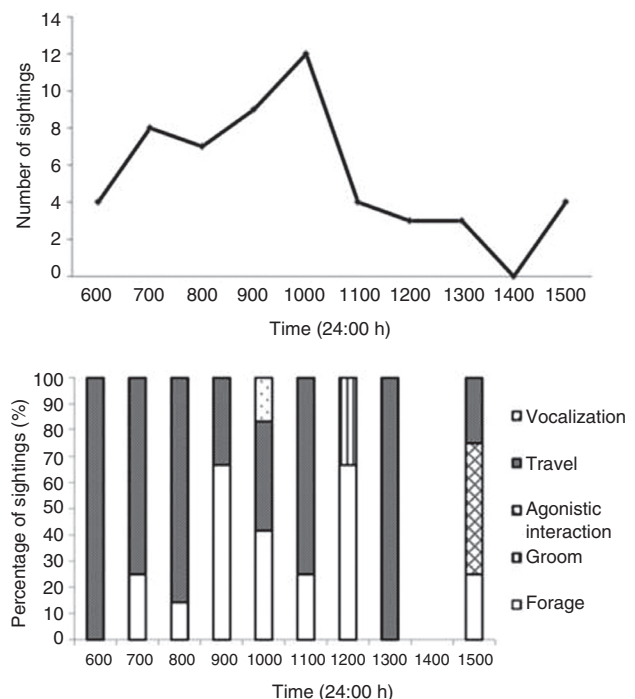


Figure 1 Distribution of sightings of Amazon red squirrels (*Sciurus igniventris*, *S. spadiceus*) by time (top) and percentage of behavior by time from 600 to 1600 (bottom) at the Amazon Research Center in Tamshiyacu-Tahuayo Reserve, Loreto, Peru, from June to July 2009 and 2010.

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 s (range, 25–35 s) to first remove the exocarp, and approximately 3 min to consume a nut and drop the

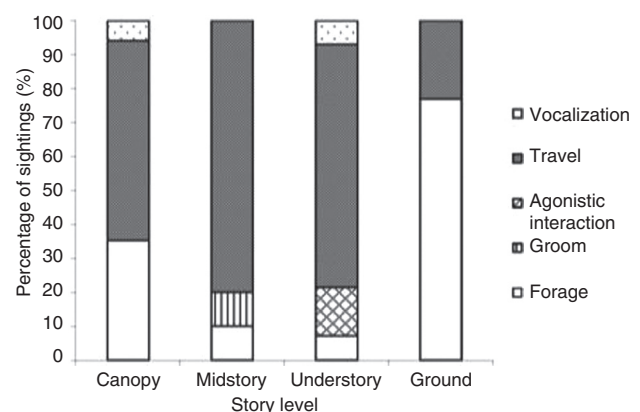


Figure 2 Percentage of Amazon red squirrel (*Sciurus igniventris*, *S. spadiceus*) behaviors by story level (canopy, ground, midstory, and understory) at the Amazon Research Center in Tamshiyacu-Tahuayo Reserve, Loreto, Peru, from June to July 2009 and 2010.

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, 34–90 s), stopped for 10–20 s, and then resumed gnawing. Up to two individuals were observed foraging within 10–15 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 one 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 owing to the unique incisor 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 ($\chi^2=33.8$, $df=3$, $p<0.001$), foraging in *bajiales* 0.5 and palm swamps 0.8 times less than available, in high restinga 5.3 times more than available,

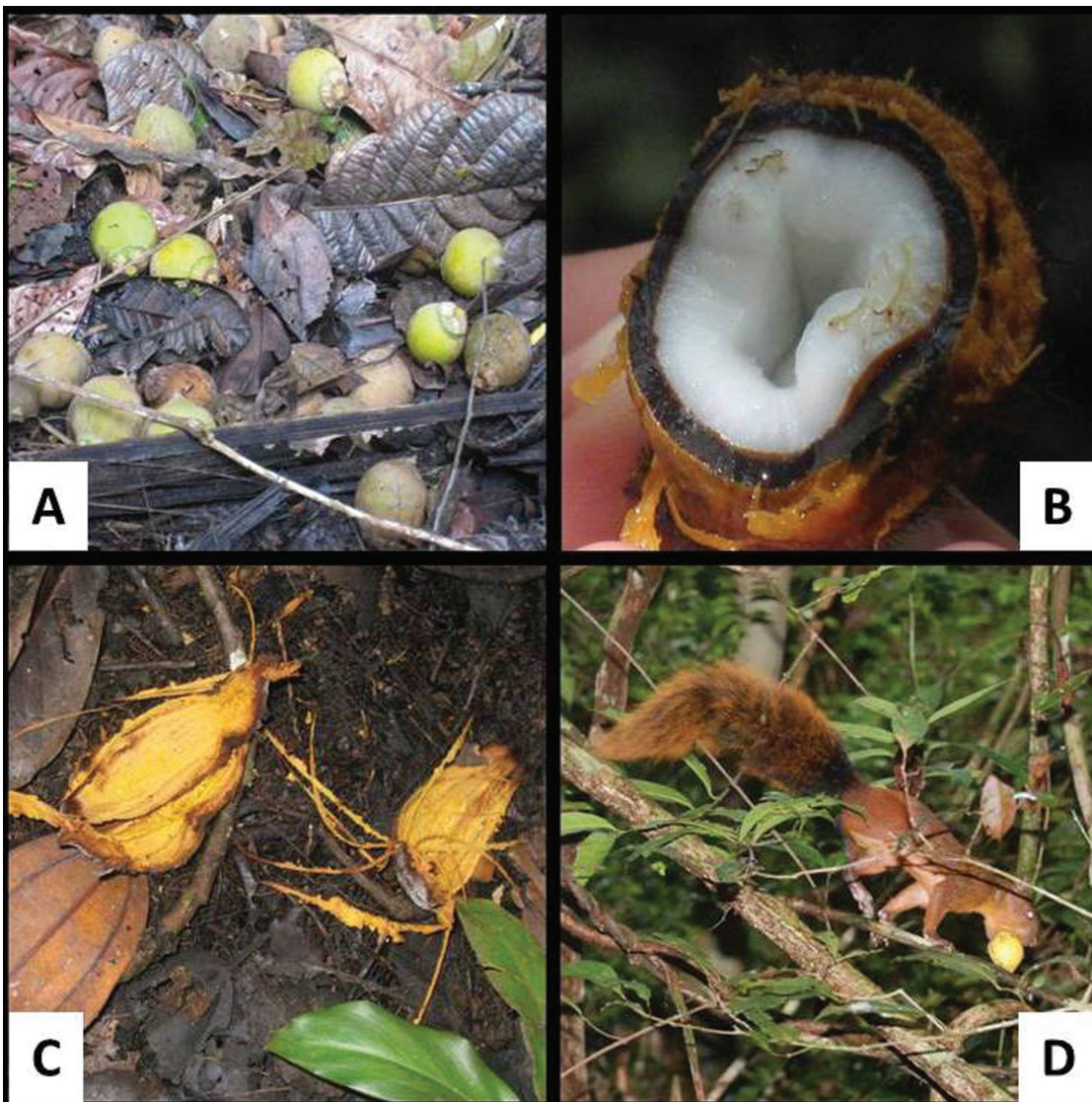


Figure 3 *Astrocaryum chambira* fruit on ground (A); inside of *Astrocaryum murumuru* (B); Amazon red squirrel feeding sign on ground, exocarp of *Astrocaryum chambira* (C); and adult northern Amazon red squirrel (*Sciurus igniventris*) carrying *Astrocaryum chambira* (D); photo: Geoffrey H. Palmer) at the Amazon Research Center in Tamshiyacu-Tahuayo Reserve, Loreto, Peru, from June to July 2009 and 2010.

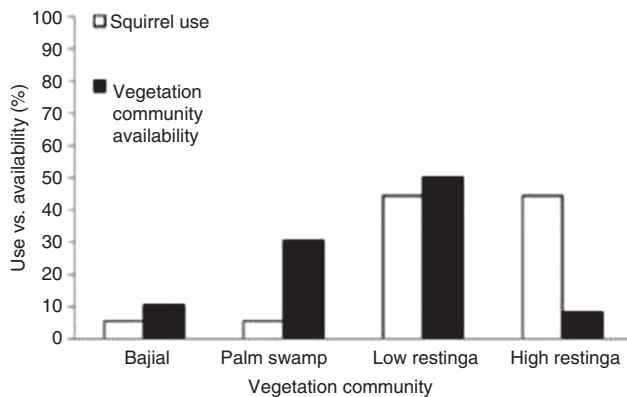


Figure 4 Habitat use vs. availability by Amazon red squirrels (*Sciurus igniventris*, *S. spadiceus*) at the Amazon Research Center in Tamshiyacu-Tahuayo Reserve, Loreto, Peru, from June to July 2009 and 2010.

and foraged in low restinga almost equal to availability (Figure 4).

Trees at which Amazon red squirrel sign was found were five 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 two 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 ($\beta=7.19\pm 3.61$, $\chi^2=3.97$, $p=0.046$) compared with 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 ($\chi^2=2193.7$, $df=76$, $p<0.001$). 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 with random locations (Table 1). As Amazon red squirrels did not appear to be selecting for

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 to July 2009 and 2010.

	Feeding site	Random location
Characteristics of trees		
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		
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

^aIndicates variables are different at $\alpha\leq 0.008$ (Bonferroni-adjusted value for focal tree characteristic analysis) in two-tailed t-test.

^bNo feeding site characteristics differed from random sites at ≤ 0.004 (Bonferroni-adjusted value for site characteristic analysis) in two-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 to July 2009 and 2010.

Tree characteristics models					
Model ^a	K ^b	AIC ^c	Δ AIC ^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

^aDBH, 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).

^bK, number of parameters.

^cAIC, Akaike's information criterion values.

^d Δ AIC, AIC relative to the most parsimonious model.

^ew_i, AIC model weight.

forest characteristics when foraging, we did not build logistic regression models.

Discussion

Behavioral observations

Amazon red squirrels at ARC were active for a 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 (*Sciurus vulgaris*; Linnaeus 1758) during the winter season (Thompson 1977, Tonkin 1983, Wauters 2000).

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. Although squirrels had to travel considerable distances owing 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 (*Sciurus 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, Gurnell 1987, Wauters et al. 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 as these story levels can be very dense, squirrels might be more protected from predators while vocalizing.

Foraging sites

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 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 2005b, Cudworth and Koprowski 2011, Jessen 2013, Palmer et al. in press). Characteristics of focal trees were similar to characteristics important to other tree squirrels (Edelman and Koprowski 2005b, Cudworth and Koprowski 2011, Jessen 2013, Palmer et al. in press). Feeding sign was located at the base of tall trees with large girth. These trees are able to provide more food, as 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 et al. 1992, Edelman and Koprowski 2005a), 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).

Conservation implications

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 et al. 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: Observations were made during field research authorized by Peruvian permit no. 0246-2010-AG-DGFFS-DGEFFS from The Dirección General de Fauna y Flora Silvestre and by The University of Arizona Institutional Care and Use Committee (AICUC protocol 09-035). Thanks to Dr. Paul Beaver and the staff at the Amazonia Expeditions, especially Jeisen Shahuano, Alfredo Do Santos, and Rafael Flores Pinedo for their enthusiasm and assistance in the field. We also wish to thank Stephanie Beaver, Tim Jessen, Zachary Koprowski, and Geoffrey Palmer for help in the field. Thanks also to Melissa Merrick for help in the field 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, Tinker Summer Field Grant Program from The University of Arizona, the Latin American Student Field Research Award from the American Society of Mammalogists, and The University of Arizona.

Received May 12, 2013; accepted October 8, 2013; previously published online November 9, 2013

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