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Note

# Importance of Scale in Nest-Site Selection by Arizona Gray Squirrels

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**ABSTRACT** Nests provide a place for individuals to rest, raise young, avoid predators, and escape inclement weather; consequently, knowledge of habitat characteristics important to nest placement is critical for managing species of conservation concern. Arizona gray squirrels (*Sciurus arizonensis*) are endemic to mountains of southwestern United States and northwestern Mexico. We investigated factors influencing nest-site selection at 4 spatial scales (forest-type, nest-site, nest-tree, and within-canopy placement) to provide ecological information and management recommendations for this sensitive species. Nest densities were 2.6 times higher in riparian than pine-oak woodlands. Nest sites had more large trees, snags, logs, and canopy cover and had lower slope. Arizona gray squirrels selected tall trees with more interlocking trees and tended to place nests adjacent to the main trunk. Regardless of scale, Arizona gray squirrels seemed to select nesting areas for their ability to provide protection from predators and the elements as well as access to food. Consequently, maintaining large trees with closed canopies and downed logs should be considered when determining land management plans. © 2011 The Wildlife Society.

**KEY WORDS** Arizona, drey, habitat, nest-site selection, *Sciurus arizonensis*, squirrel.

Nests are widely recognized for their importance to reproduction (e.g., Martin and Roper 1988, Wilson 1998, Madsen and Shine 1999, Rauter et al. 2002, Benson et al. 2008). However, for mammals, nests may provide year-round benefits to adults. Nests and burrows provide a place to rest, raise young, avoid predators, and escape inclement weather (Mahan and Yahner 1996, Steele and Koprowski 2001, Henner et al. 2004, Wolton 2009). Given the benefits of nests and because nest sites have been suggested to impose limitations on density and reproduction in a variety of mammals (Doncaster and Woodroffe 1993, Carey et al. 1997, Magoun and Copeland 1998, Smith et al. 2007, but see Carey 2002), knowledge of habitat characteristics important to nest placement is critical to conserve species of concern.

Tree squirrels are an excellent group for ecological study because they are common, highly detectable, and dependent upon mature forests for food and nest sites (Gurnell 1987, Steele and Koprowski 2001); consequently, squirrel abundance and behavior may serve as ecological indicators of environmental change (Carey 2000, Steele and Koprowski 2001, Koprowski 2005). Three types of nests are commonly used by squirrels: ground nests, cavity nests, and leaf nests lined with grass, moss, and fur, also known as dreys (Gurnell 1987). Dreys (hereafter nests) are constructed and maintained by individual squirrels (Gurnell 1987), thus individuals can be more selective in nest placement.

Arizona gray squirrels (*Sciurus arizonensis*) inhabit the Madrean Archipelago of southwestern United States and northwestern Mexico, an area recognized for high biodiversity and endemism for many taxa (Hoffmeister 1986, Felger and Wilson 1995, McCord 1995, McLaughlin 1995, Turner et al. 1995). Arizona gray squirrels are endemic to riparian areas of deciduous and mixed forest at elevations >1,120 m (Brown 1984, Best and Riedel 1995). Despite being federally listed as threatened in Mexico as a consequence of habitat loss (Alvarez-Castañeda and Patton 1999) and the subspecies in the Catalina Mountains in Arizona (*S. a. catalinae*) being listed as sensitive by the United States Forest Service (Best and Riedel 1995), data on the species are sparse. In fact, with only 2 publications in the primary ecological literature (Frey et al. 2008, Cudworth and Koprowski 2010), the International Union for the Conservation of Nature (IUCN) designated the species data deficient (IUCN 2009). A better understanding of the ecology of the Arizona gray squirrel may enhance understanding of environmental conditions necessary to promote forest health; however, no information exists on nest-site selection by Arizona gray squirrels.

Our objective was to investigate factors influencing nest-site selection and determine at what scale Arizona gray squirrels select nest areas. The scale at which nest-site selection is analyzed has not been consistent in other tree squirrel studies (Snyder and Linhart 1994, Taulman 1999, Menzel et al. 2004, Edelman and Koprowski 2005, Salsbury 2008). Therefore, we examined multiple scales: forest-type, nest-site, nest-tree, and within-canopy nest placement to determine selection criteria at each scale.

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## STUDY AREA

We investigated nest-site selection by Arizona gray squirrels in the Huachuca Mountains in southwestern Cochise County, Arizona, USA. The Huachuca Mountains are approximately 26,000 ha and vary from 1,500 m to 2,880 m in elevation; Arizona gray squirrels are the only tree squirrel in the mountain range (Cockrum 1960, Brown 1984, Hoffmeister 1986). We delineated 3 distinct forest types: Madrean pine-oak, mixed conifer, and riparian woodlands. Madrean pine-oak forest and woodlands were dominated by Chihuahuan pine (*Pinus leiophylla*), Apache pine (*P. engelmannii*), ponderosa pine (*P. ponderosa*), silverleaf oak (*Quercus hypoleucoides*), and Arizona white oak (*Q. arizonica*). Emory oak (*Q. emoryi*), Gambel oak (*Q. gambelii*), alligator juniper (*Juniperus deppeana*), Douglas-fir (*Pseudotsuga menziesii*), piñon pine (*Pinus edulis*), manzanita (*Arctostaphylos pungens*), and Arizona madrone (*Arbutus arizonica*) were also present at lower densities. Mixed conifer forests and woodlands were dominated by Douglas-fir, southwestern white pine (*Pinus strobiformis*), ponderosa pine, white fir (*Abies concolor*), and aspen (*Populus tremuloides*). Riparian woodland and shrublands were dominated by Arizona sycamore (*Platanus wrightii*), Fremont cottonwood (*Populus fremontii*), Arizona walnut (*Juglans major*), velvet ash (*Fraxinus velutina*), and bigtooth maple (*Acer grandidentatum*). New Mexican locust (*Robinia neomexicana*), box-elder (*Acer negundo*), and sandbar willow (*Salix exigua*) were also present (Wallmo 1955, Felger et al. 2001, United States Geological Survey [USGS] 2005).

## METHODS

Nests are highly visible and reliable indicators of squirrel presence (Bouffard 1982, Don 1985); therefore, we applied distance-sampling methods to data collected from line transects to assess density of nests within the study area and relative density among forest types (Anderson et al. 1979, Don 1985). The short trees ( $12.0 \pm 1.0$  m) and low density of large trees ( $\geq 40$  cm dbh;  $33.3 \pm 7.2$  trees/ha) in the study area provided an ideal environment in which to locate nests and assess density; consequently, we are confident we met distance-sampling assumptions of 100% detectability on the transect line (Buckland et al. 2001). We used Hawth's Analysis Tools for ArcGIS (Version 3.27, [www.spatialecology.com/htools](http://www.spatialecology.com/htools), accessed 9 Nov 2006) to generate 50 random points within each of the 3 dominant forest types throughout the Huachuca Mountains. We acquired land-cover data on forest type from Southwest Regional Gap Analysis Program (USGS 2004). Random points served as the beginning of line transects to determine density of nests within each forest type (Bouffard 1982). We walked randomly oriented transects for 500 m or until we exited the forest type under study. We surveyed all transects in winter and early spring to maximize detection of nests in leafless trees. We used binoculars to locate nests along transects and measured perpendicular distance, noted tree species, and recorded coordinates with a Global Positioning System unit (GPS; eTrex Vista GPS unit, Garmin International,

Inc., Olathe, KS). Although, we observed squirrels and squirrel sign (nests, feeding) on transects in the upper mixed conifer habitat, they were at very low densities that did not permit density estimation.

We randomly selected 41 nest locations (21 riparian and 20 pine-oak sites) from line transects and 24 random locations from the beginning of line transects (13 riparian and 11 pine-oak sites) to quantify tree and site characteristics. The number of transects completed and nest-locations measured depended upon access and the amount of these areas available in the study area. Nest measurements included height above ground, structural support (main trunk, side branches, witches broom [dense growth at branch tips]), and aspect. Nest-tree measurements included species, condition (live or dead), diameter at breast height, tree height, number of access routes (trees with branches  $\leq 0.5$  m from branches of nest tree), and live crown height, from which we also calculated proportion live crown. We used 10-m-radius circular vegetation plots centered on nest trees (Smith and Mannan 1994, Litvaitis et al. 1996, Edelman and Koprowski 2005) to record nest-site information, including slope, aspect (degree measurements converted to 1 of 8 directions), canopy cover (densitometer readings at 0 m, 5 m, and 10 m from the nest or random tree in 4 cardinal directions), and number of shrub stems and logs ( $\geq 20$  cm diameter and  $\geq 2$  m in length); we also calculated total canopy cover, total basal area, and log volume per hectare. We recorded species, condition, and diameter at breast height of each tree ( $\geq 3$  cm) in the plot and calculated Shannon-Wiener diversity index of tree species within the plot, as well as number of live trees and snags per hectare, number of large trees and snags per hectare ( $> 40$  cm dbh), and number of shrub stems and logs per hectare. We collected identical information at random plots centered on the nearest tree with diameter at breast height  $\geq 12.7$  cm to the randomly selected start point of each line transect. We classified trees as available if diameter at breast height was  $\geq 12.7$  cm, because that was the smallest tree with a nest. We tallied species of trees within random plots to calculate nest-tree species availability and compared those data to use of nest-tree species as determined by nests located along line transects.

Between April 2007 and December 2008, we trapped and uniquely marked 48 individuals, 37 of which received radio-collars (18 F, 19 M; Cudworth and Koprowski 2010). We used a Yagi antenna (Model F164-165-3FB, Wildlife Materials International, Inc., Carbondale, IL) and receiver (Model R-1000, Communications Specialists Inc., Orange, CA) to track squirrels to nocturnal nests once per month and a GPS unit to record night-nest locations. Dreys were the most commonly used nocturnal nest in our population and comprised 81% of our night-nest observations (82 of 101 nests). We recorded the same information collected for within-canopy placement and nest-tree selection at these nests. Because our trapping area encompassed both riparian and pine-oak forest types, we combined data collected from nests located along transects ( $n = 41$ ) with nests located during telemetry ( $n = 82$ ) to further describe nest placement. Trapping and handling procedures were approved by

Arizona Game and Fish Department and The University of Arizona Institutional Animal Care and Use Committee (IACUC protocol 08-025).

We used Program Distance (Version 5.0, Release 2, <http://www.ruwpa.st-and.ac.uk/distance/>, accessed 10 Mar 2009) to estimate density of nests from transect data. We developed 8 models, including 4 key functions (half-normal, hazard rate, negative exponential, and uniform) each for forest type combined and stratified. We used Akaike's information criterion (AIC) to select among competing models. We determined minimum number of unique nests used per squirrel from radio-telemetry data to calibrate density estimations and report nest and individual densities.

We conducted all habitat analyses in JMP 7 (SAS Institute, Inc., Cary, NC). To meet assumptions of normality, we used arcsine square root, cube root, and natural log transformations (Ramsey and Schafer 2002). We report transformed parameter estimates ( $\pm$ SE) but report mean ( $\pm$ SE) as untransformed values. We selected a hypothesis-testing approach because ours is the first study on nest-site selection in this species, and our objective was to describe the structural differences between nest and random sites (Steidl 2006). Therefore, we selected several variables known to be important in other tree squirrel species and used a Pearson's chi-squared goodness-of-fit test to analyze categorical data (nest-tree species, seasonal use, and nest and slope aspect) and logistic regression to determine factors important in nest-tree and nest-site selection for riparian and pine-oak forest types separately. We identified highly correlated variables ( $r > 0.7$ ) prior to analysis and only included the variable that best explained differences between nest and random areas (higher  $F$ -value in logistic regression). We used stepwise logistic regression with a liberal probability to enter ( $P = 0.250$ ) to narrow our data set and select variables for inclusion in nest-site and nest-tree models.

## RESULTS

We walked 25 line transects of 432 m ( $\pm 24$  m), totaling 10.8 km of forest traversed, and located 43 nests on 11 riparian transects and 39 nests on 14 pine-oak transects. All models had  $\Delta$ AIC  $< 4$ ; therefore, we selected the top model for nest density estimation (uniform key function with cosine adjustment, 5% truncation, stratified by forest type; AIC = 488.86; Kolmogorov-Smirnov goodness-of-fit: riparian = 0.08,  $P = 0.966$ ; pine-oak = 0.13,  $P = 0.625$ ). Density was 4.68 nests/ha (95% CI = 2.65–8.28) in riparian woodlands, 1.83 nests/ha (95% CI = 1.22–2.74) in pine-oak woodlands, and 3.26 nests/ha (95% CI = 2.14–4.95) when we combined vegetation types. We located 82 unique nests with telemetry for an average of 2.48 nests/individual throughout the study. Correcting for multiple nests, estimated overall density was 1.31 individuals/ha (95% CI = 0.86–2.00). Squirrel density estimates were 2.6 times higher in riparian woodlands (1.89 individuals/ha, 95% CI = 1.06–3.34) than pine-oak woodlands (0.74 individuals/ha, 95% CI = 0.49–1.10).

Slope aspect did not differ between nest and random sites for riparian ( $\chi^2_2 = 2.93$ ,  $n = 34$ ,  $P = 0.231$ ) or pine-oak woodlands ( $\chi^2_3 = 2.51$ ,  $n = 31$ ,  $P = 0.474$ ). Only number of dead trees and canopy cover at 5 m were selected by squirrels in riparian woodlands (whole model test:  $R^2 = 0.11$ ,  $\chi^2_2 = 4.78$ ,  $P = 0.092$ ), with nest sites tending to have more dead trees ( $\beta = 0.23 \pm 0.16$ ,  $\chi^2_1 = 2.12$ ,  $P = 0.145$ ) and higher canopy cover at 5 m ( $\beta = 3.60 \pm 2.98$ ,  $\chi^2_1 = 1.60$ ,  $P = 0.206$ ) than random sites in riparian woodlands, although these differences were not significant (Table 1). For pine-oak woodlands, large trees, slope, logs, and dead trees were selected by squirrels (whole model test:  $R^2 = 0.32$ ,  $\chi^2_4 = 12.89$ ,  $P = 0.012$ ; Table 1). Nest sites had lower slope ( $\beta = -6.84 \pm 3.13$ ,  $\chi^2_1 = 6.82$ ,  $P = 0.009$ ) and over twice as many large trees ( $\geq 40$  cm dbh;  $\beta = 0.70 \pm 0.34$ ,  $\chi^2_1 = 5.39$ ,  $P = 0.020$ ) and logs ( $\beta = 0.50 \pm 0.29$ ,  $\chi^2_1 = 3.45$ ,  $P = 0.063$ ) than random sites in pine-oak woodlands (Table 1). Although nest sites had fewer dead trees on average, when we held all other variables constant nest sites also had more dead trees than random sites, although this difference was not significant ( $\beta = 0.41 \pm 0.32$ ,  $\chi^2_1 = 1.79$ ,  $P = 0.181$ ).

Nests were located nonrandomly among tree species in riparian woodlands ( $\chi^2_{11} = 48.26$ ,  $P < 0.001$ ), with Arizona sycamore used nearly 3 times more than expected and white fir, Apache pine, and Fremont cottonwood each used 1.6 times more than expected (Table 2). Nests were also distributed nonrandomly among tree species in pine-oak woodlands ( $\chi^2_{12} = 42.73$ ,  $P < 0.001$ ), with Chihuahua pine used 5.6 times, Douglas-fir and white fir used 3.4 times, and southwestern white pine used 2.2 times more than expected (Table 2). All nests but one were located in live trees (99.2%,  $n = 122$ ). Tree height was highly correlated with diameter at breast height and live crown height; therefore, we used only tree height, proportion live crown, and number of access routes in nest-tree models. Only tree height was selected by squirrels in riparian woodlands (whole model test:  $R^2 = 0.23$ ,  $\chi^2_1 = 10.20$ ,  $P = 0.001$ ); nest trees were 1.4 times taller than random focal trees ( $\beta = 0.27 \pm 0.10$ ,  $\chi^2_1 = 10.20$ ,  $P = 0.001$ ; Table 3). Tree height and number access routes were selected by squirrels in pine-oak woodlands (whole model test:  $R^2 = 0.35$ ,  $\chi^2_2 = 14.00$ ,  $P = 0.001$ ); nest trees were 1.3 times taller ( $\beta = 0.37 \pm 0.18$ ,  $\chi^2_1 = 8.01$ ,  $P = 0.005$ ) and had 1.6 times more access routes ( $\beta = 5.28 \pm 2.13$ ,  $\chi^2_1 = 11.43$ ,  $P = 0.001$ ) than random focal trees (Table 3).

We located 123 nests during line transects and radio-telemetry. On average, nests were located in the upper 25% of trees (95% CI = 22–27%). Nests were most often placed on or directly adjacent to the main trunk (59.2%) and were rarely located in witches brooms (2.5%;  $\chi^2_2 = 59.15$ ,  $n = 120$ ,  $P < 0.001$ ); however, nests were randomly oriented ( $\chi^2_7 = 7.36$ ,  $n = 123$ ,  $P = 0.392$ ). The use of nest trees by radio-collared squirrels located with telemetry differed among seasons ( $\chi^2_1 = 13.10$ ,  $P = 0.003$ ,  $n = 138$ ). Nests placed in deciduous trees (Arizona sycamore and Fremont cottonwood) were 5.4 times more likely to be used in summer (Apr–Sep;  $n = 27$ ) than winter (Oct–Mar;  $n = 5$ ); nests in

**Table 1.** Physical and vegetation characteristics ( $\bar{x} \pm SE$ ) at nest (riparian:  $n = 21$ ; pine-oak:  $n = 20$ ) and random (riparian:  $n = 13$ ; pine-oak:  $n = 11$ ) sites for Arizona gray squirrels, Huachuca Mountains, Arizona, USA, 2007–2008.

Site characteristic	Nest		Random	
	$\bar{x}$	SE	$\bar{x}$	SE
<b>Riparian</b>				
Plot slope (%)	24.6	10.1	21.5	3.4
Canopy cover 0 m (%)	89.2	1.2	84.3	2.8
Canopy cover 5 m (%) <sup>a</sup>	87.2	1.4	80.4	4.4
Canopy cover 10 m (%)	83.8	2.2	81.2	3.8
Canopy cover average (%)	86.7	1.3	82.0	3.6
Live trees (no./ha)	987.3	113.2	810.3	135.7
Dead trees (no./ha) <sup>a</sup>	168.3	40.0	112.8	43.6
Large trees (no./ha) <sup>b</sup>	50.8	9.7	51.3	9.7
Large snags (no./ha) <sup>b</sup>	1.6	1.6	2.6	2.6
Shrub stems (no./ha)	1358.9	261.0	1401.4	324.0
Logs (no./ha)	34.9	10.2	33.3	10.7
Logs (vol./ha)	7.9	3.1	14.0	6.1
Basal area (m <sup>2</sup> /ha)	37.1	4.9	35.2	5.7
Shannon–Wiener diversity index	1.2	0.1	1.3	0.2
<b>Pine-Oak</b>				
Plot slope (%) <sup>a</sup>	43.5	4.7	54.7	5.8
Canopy cover 0 m (%)	84.5	3.0	81.9	5.0
Canopy cover 5 m (%)	81.5	3.3	78.9	4.1
Canopy cover 10 m (%)	83.9	2.4	81.8	4.3
Canopy cover average (%)	83.3	2.6	81.8	4.2
Live trees (no./ha)	1371.7	186.4	1439.4	754.8
Dead trees (no./ha) <sup>a</sup>	303.3	43.8	397.0	108.9
Large trees (no./ha) <sup>a,b</sup>	30.0	5.4	12.1	6.8
Large snags (no./ha) <sup>b</sup>	10.0	4.3	6.1	4.1
Shrub stems (no./ha)	2134.0	478.9	1679.4	330.3
Logs (no./ha) <sup>a</sup>	65.0	16.3	30.3	15.5
Logs (vol./ha)	15.9	4.4	8.7	4.8
Basal area (m <sup>2</sup> /ha)	26.8	1.9	26.0	2.5
Shannon–Wiener diversity index	1.0	0.1	1.1	0.4

<sup>a</sup> Indicates variable selected by stepwise logistic regression.

<sup>b</sup> >40 cm dbh.

evergreen trees (Arizona white oak, Emory oak, silverleaf oak, alligator juniper, Chihuahua pine, and piñon pine) were used equally between seasons ( $n = 53$ /season).

## DISCUSSION

Densities of Arizona gray squirrels in the Huachuca Mountains are similar to other *Sciurus* species (1.31 individ-

uals/ha; Nash and Seaman 1977, Carraway and Verts 1994, Koprowski 1944<sup>a,b</sup>, Pasch and Koprowski 2004). The Huachuca Mountains are in the center of the geographic range of Arizona gray squirrels and are believed to hold among the highest densities (Brown 1984, Hoffmeister 1986). However, our estimates of squirrel density are expected to be maximal as we likely missed nests during

**Table 2.** Percent use and availability of nest-tree species for Arizona gray squirrels, Huachuca Mountains, Arizona, USA, 2007–2008. Expected values based upon availability of tree species.

Tree species	Riparian		Pine-oak	
	% Observed	% Expected	% Observed	% Expected
Alligator juniper	2.5	16.1	0.0	4.6
Apache pine	2.5	1.3	7.7	6.9
Arizona madrone	0.0	1.9	0.0	0.6
Arizona sycamore	50.0	8.4	0.0	0.0
Arizona white oak	12.5	38.7	12.8	21.4
Bigtooth maple	10.0	13.6	0.0	3.5
Chihuahua pine	0.0	0.0	2.6	0.0
Douglas-fir	0.0	1.9	23.1	2.9
Fremont cottonwood	5.0	2.6	0.0	0.0
Gambel oak	0.0	0.0	0.0	0.6
Piñon pine	0.0	0.0	7.7	16.8
Silverleaf oak	12.5	8.4	28.2	38.7
Southwestern white pine	0.0	2.6	5.1	1.7
Velvet ash	2.5	3.2	0.0	0.6
White fir	2.5	1.3	12.8	1.7

**Table 3.** Focal tree comparisons at nest and random sites for Arizona gray squirrels, Huachuca Mountains, Arizona, USA, 2007–2008.

Habitat	n	Dbh (cm)		Height (m)		Live crown (m)		Proportion live crown		No. access routes <sup>a</sup>	
		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
Riparian											
Nest	21	60.7	7.2	19.3 <sup>b</sup>	1.2	11.4	1.0	0.580	0.028	6.0	0.7
Random	13	37.8	3.7	13.6	1.0	7.5	0.9	0.549	0.040	4.8	0.7
Pine-Oak											
Nest	20	29.7	2.4	13.2 <sup>b</sup>	1.1	6.7	0.7	0.501	0.033	4.9 <sup>b</sup>	0.5
Random	11 <sup>c</sup>	28.5	3.3	10.0	1.8	4.3	0.7	0.510	0.061	3.1	1.6

<sup>a</sup> No. of trees with branches  $\leq 0.5$  m from branches of nest tree.

<sup>b</sup> Indicates variable selected by stepwise logistic regression.

<sup>c</sup> One focal tree was dead and had no live crown.

radio-telemetry and consequently underestimated number of nests used per individual. Densities were higher in riparian than pine-oak woodlands, in agreement with scant existing information on the habitat of Arizona gray squirrels (Theobald 1983, Brown 1984, Hoffmeister 1986, Frey et al. 2008). Riparian areas may contain more tall trees suitable for nesting and provide an increased supply of drinking water and walnuts, suggested to be an important food item for Arizona gray squirrels (Theobald 1983; Brown 1984; Hoffmeister 1986; N. Cudworth and J. Koprowski, The University of Arizona, unpublished data).

Arizona gray squirrels select nest-site and nest-tree structures similar to other tree squirrel species, including canopy cover, live crown height, and number of access routes, logs, large trees, and snags (Halloran and Bekoff 1994, Edelman and Koprowski 2005, Merrick et al. 2007). Greater canopy cover and live-crown height of nest trees may provide more cover and protection from aerial predators, including goshawks (*Accipiter gentilis*), red-tailed hawks (*Buteo jamaicensis*), and an observed unsuccessful predation attempt by a Cooper's hawk (*Accipiter cooperii*; Brown 1984; Smith and Mannan 1994; Carey et al. 1997; N. Cudworth and J. Koprowski, unpublished data), and the greater number of trees with interlocking branches provide more access routes to and from nest trees (Rothwell 1979, Hall 1981, Halloran and Bekoff 1994, Edelman and Koprowski 2005). Logs also provide runways for travel (Douglass and Reinert 1982, Smith and Mannan 1994, Bakker 2006), and decaying logs and snags increase heterogeneity and complexity of the local environment, which may provide increased diversity of food resources, nest sites, and cover from predators (Smith and Mannan 1994, Carey and Harrington 2001, Carey and Wilson 2001). The lower slopes selected in pine-oak forests may provide higher soil moisture and more productive trees (Kantola and Humphrey 1990). Large trees with extensive crowns are indicative of mature trees and often associated with increased food crops (Goodrum et al. 1971, Burns and Honkala 1990); consequently, more large trees within a nest site may increase access to food and provide potential trees for nest construction (Edelman and Koprowski 2005).

Most selected nest-tree species also provide food resources, potentially minimizing travel distances (Theobald 1983; Brown 1984; Carey et al. 1997; N. Cudworth and J. Koprowski, unpublished data). Arizona sycamores seem es-

pecially important as nest trees in riparian areas and provide many characteristics selected by Arizona gray squirrels, including tall trees with dense canopy cover and branching to provide access routes. Placement of nests near the top of trees and adjacent to the trunk provides thick foliage cover, increased nest stability, and protection from wind and elements (Farentinos 1972, Halloran and Bekoff 1994, Edelman and Koprowski 2005); selected nest-tree species were among the tallest in the Huachuca Mountains. Deciduous trees were less likely to be used in winter, likely due to lack of protection during leaf-free months, and co-nesting did occur but predominantly in winter (N. Cudworth and J. Koprowski, unpublished data), probably as a mechanism to conserve heat during colder nights (Edelman and Koprowski 2007). However, nests were oriented randomly within trees, suggesting increased solar exposure may not be a strategy employed by Arizona gray squirrels to aid thermoregulation (Farentinos 1972, Edelman and Koprowski 2005).

Arizona gray squirrels demonstrated selection at all spatial scales. Riparian woodlands seem especially important, potentially providing a greater food supply. The nonsignificant variable selection and weak site-selection models at riparian nest sites may indicate decreased selectivity by squirrels or increased homogeneity at these sites, further suggesting that any site within a riparian system is a quality nest site, given availability of adequate nest trees. Habitat features selected by squirrels at nest-site and nest-tree scales also suggest benefits in terms of access to food, protection from predators, and buffers from elements. Nest placement and seasonal use of deciduous trees and co-nesting further emphasize the importance of nests for thermoregulation. Regardless of scale, Arizona gray squirrels select nesting areas based upon their ability to provide protection from predators and elements as well as access to food resources.

### Management Implications

Densities of Arizona gray squirrels were highest in riparian woodlands, suggesting these limited areas may be especially important. Within riparian woodlands, Arizona sycamores were used extensively as nest trees. Consequently, measures should be taken to promote reproduction and growth of sycamore populations. Locally, Arizona gray squirrels select forest structures maximizing local habitat heterogeneity and travel pathways both on the ground and through the canopy.

Measures to maintain large trees with closed canopies to supply access routes and downed logs to provide runways should be considered when developing land management plans, including prescribed burning and thinning. Throughout their range, Arizona gray squirrels are exposed to habitat loss due to logging, fire, agricultural clearing of forests, and introduced competitors (e.g., Abert's squirrel [*Sciurus aberti*]), which has led to decline (Best and Riedel 1995, Alvarez-Castañeda and Patton 1999). Consequently, minimizing anthropogenic, large-scale disturbances may also be necessary to maintain adequate numbers of Arizona gray squirrels.

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### LITERATURE CITED

Alvarez-Castañeda S. T., and J. L. Patton. 1999. Mamíferos del Noreste de México. La Paz, Baja California Sur, México.

Anderson, D. R., J. L. Laake, B. B. Crain, and K. P. Burnham. 1979. Guidelines for line transect sampling of biological populations. *The Journal of Wildlife Management* 43:70–78.

Bakker, V. J. 2006. Microhabitat features influence the movements of red squirrels (*Tamiasciurus hudsonicus*) on unfamiliar ground. *Journal of Mammalogy* 87:124–130.

Benson, J. F., M. A. Lotz, and D. Jansen. 2008. Natal den selection by Florida panthers. *The Journal of Wildlife Management* 72:405–410.

Best T. L., and S. Riedel. 1995. *Sciurus arizonensis*. *Mammalian Species* 496:1–5.

Bouffard, S. H. 1982. Tree squirrels. Pages 160–161 in D. E. Davis, editor. *CRC handbook of census methods for terrestrial vertebrates*. CRC Press, Inc., Boca Raton, Florida, USA.

Brown, D. E. 1984. Arizona's tree squirrels. Arizona Game and Fish Department, Phoenix, USA.

Buckland, S. T., D. R. Anderson, K. P. Burnham, L. L. Laake, D. L. Borchers, and L. Thomas. 2001. *Introduction to distance sampling*. Oxford University Press, London, United Kingdom.

Burns R. M., and B. H. Honkala. 1990. *Silvics of North America: 1. conifers; 2. hardwoods*. United States Forest Service, Washington, D.C., *Agriculture Handbook* 654:1–377.

Carey, A. B. 2000. Effects of new forest management strategies on squirrel populations. *Ecological Applications* 10:248–257.

Carey, A. B. 2002. Response of northern flying squirrels to supplementary dens. *Wildlife Society Bulletin* 30:547–556.

Carey A. B., and C. A. Harrington. 2001. Small mammals in young forests: implications for management for sustainability. *Forest Ecology and Management* 154:289–309.

Carey A. B., and S. M. Wilson. 2001. Induced spatial heterogeneity in forest canopies: responses of small mammals. *The Journal of Wildlife Management* 65:1014–1027.

Carey, A. B., T. M. Wilson, C. C. Maguire, and B. L. Biswell. 1997. Dens of northern flying squirrels in the Pacific Northwest. *The Journal of Wildlife Management* 61:684–699.

Carraway L. N., and B. J. Verts. 1994. *Sciurus griseus*. *Mammalian Species* 474:1–7.

Cockrum, E. L. 1960. *The recent mammals of Arizona*. The University of Arizona Press, Tucson, USA.

Cudworth N. L., and J. L. Koprowski. 2010. Influences of mating strategy on space use of Arizona gray squirrels. *Journal of Mammalogy* 91:1235–1241.

Don, B. A. C. 1985. The use of drey counts to estimate grey squirrel populations. *Journal of Zoology* 50:282–286.

Doncaster C. P., and R. Woodroffe. 1993. Den site can determine shape and size of badger territories: implications for group-living. *Oikos* 66:88–93.

Douglass N. J., and H. K. Reinert. 1982. The utilization of fallen logs as runways by small mammals. *Proceedings of the Pennsylvania Academy of Science* 56:162–164.

Edelman A. J., and J. L. Koprowski. 2005. Selection of drey sites by Abert's squirrels in an introduced population. *Journal of Mammalogy* 86:1220–1226.

Edelman A. J., and J. L. Koprowski. 2007. Communal nesting in asocial Abert's squirrels: the role of social thermoregulation and breeding strategy. *Ethology* 113:147–154.

Farentinos, R. C. 1972. Nests of the tassel-eared squirrel. *Journal of Mammalogy* 53:900–903.

Felger, R. S., M. B. Johnson, and M. F. Wilson. 2001. *The trees of Sonora, Mexico*. Oxford University Press, New York, New York, USA.

Felger R. S., and M. F. Wilson. 1995. Northern Sierra Madre Occidental and its Apachian outliers: a neglected center of biodiversity. Pages 36–51 in L. F. DeBano, G. J. Gottfried, R. H. Hamre, and C. B. Edminster, technical coordinators. *Biodiversity and management of the Madrean Archipelago: the sky islands of southwestern United States and northwestern Mexico*. U.S. Forest Service General Technical Report RM-GTR-264, Fort Collins, Colorado, USA.

Frey, J. K., M. T. Hill, B. L. Christman, J. C. Truett, and S. O. MacDonald. 2008. Distribution and habitat of the Arizona gray squirrel (*Sciurus arizonensis*) in New Mexico. *The Southwestern Naturalist* 53:248–255.

Goodrum, P. D., V. H. Reid, and C. E. Boyd. 1971. Acorn yields, characteristics, and management criteria of oaks for wildlife. *Journal of Wildlife Management* 35:520–532.

Gurnell, J. 1987. *The natural history of squirrels*. Facts On File Publications, New York, New York, USA.

Hall, J. G. 1981. A field study of the Kaibab squirrel in Grand Canyon National Park. *Wildlife Monographs* 75.

Halloran M. E., and M. Bekoff. 1994. Nesting-behavior of Abert squirrels (*Sciurus aberti*). *Ethology* 97:236–248.

Henner, C. M., M. J. Chamberlain, B. D. Leopold, and L. W. Burger, Jr., 2004. A multi-resolution assessment of raccoon den selection. *Journal of Wildlife Management* 68:179–187.

Hoffmeister, D. F. 1986. *Mammals of Arizona*. The University of Arizona Press, Tucson, USA.

International Union for Conservation of Nature and Natural Resources [IUCN]. 2009. *IUCN Red List of Threatened Species*. Version 2009. 1. <[www.iucnredlist.org](http://www.iucnredlist.org)>. Accessed 19 Oct 2009.

Kantola A. T., and S. R. Humphrey. 1990. Habitat use by Sherman's fox squirrel (*Sciurus niger shermani*) in Florida. *Journal of Mammalogy* 71:411–419.

Koprowski, J. L. 1994a. *Sciurus carolinensis*. *Mammalian Species* 480:1–9.

Koprowski, J. L. 1994b. *Sciurus niger*. *Mammalian Species* 479:1–9.

Koprowski, J. L. 2005. The response of tree squirrels to fragmentation: a review and synthesis. *Animal Conservation* 8:369–376.

Litvaitis, J. A., K. Titus, and E. M. Anderson. 1996. Measuring vertebrate use of terrestrial habitats and foods. Pages 254–274 in T. A. Bookhout, editor. *Research and management techniques for wildlife and habitats*. The Wildlife Society, Bethesda, Maryland, USA.

Madsen T., and R. Shine. 1999. Life history consequences of nest-site variation in tropical pythons (*Liasis fuscus*). *Ecology* 80:989–997.

Magoun A. J., and J. P. Copeland. 1998. Characteristics of wolverine reproductive den sites. *Journal of Wildlife Management* 62:1313–1320.

Mahan C. G., and R. H. Yahner. 1996. Effects of forest fragmentation on burrow-site selection by the eastern chipmunk (*Tamias striatus*). *American Midland Naturalist* 136:352–357.

- Martin T. E., and J. J. Roper. 1988. Nest predation and nest-site selection of a western population of the hermit thrush. *Condor* 90:51–57.
- McCord, R. D. 1995. Phylogeny and biogeography of the land snail, *Sonorella*, in the Madrean Archipelago. Pages 317–324 in L. F. DeBano, G. J. Gottfried, R. H. Hamre, and C. B. Edminster, technical coordinators. Biodiversity and management of the Madrean Archipelago: the sky islands of southwestern United States and northwestern Mexico. U.S. Forest Service General Technical Report RM-GTR-264, Fort Collins, Colorado, USA.
- McLaughlin, S. P. 1995. An overview of the flora of the sky islands, southeastern Arizona: diversity, affinities, and insularity. Pages 60–70 in L. F. DeBano, G. J. Gottfried, R. H. Hamre, and C. B. Edminster, technical coordinators. Biodiversity and management of the Madrean Archipelago: the sky islands of southwestern United States and northwestern Mexico. U.S. Forest Service General Technical Report RM-GTR-264, Fort Collins, Colorado, USA.
- Menzel, J. M., W. M. Ford, J. W. Edwards, and M. A. Menzel. 2004. Nest tree use by the endangered Virginia flying squirrel in the central Appalachian Mountains. *American Midland Naturalist* 151: 355–368.
- Merrick, M. J., S. R. Bertelsen, and J. L. Koprowski. 2007. Characteristics of Mount Graham red squirrel nest sites in a mixed conifer forest. *Journal of Wildlife Management* 71:1958–1963.
- Nash D. J., and R. N. Seaman. 1977. *Sciurus aberti*. *Mammalian Species* 80:1–5.
- Pasch B. S., and J. L. Koprowski. 2004. Correlates of vulnerability in Chiricahua fox squirrels. Pages 426–428 in G. J. Gottfried, B. S. Gebow, L. G. Eskew, and C. B. Edminster, compilers. Connecting mountain islands and desert seas: biodiversity and management of the Madrean Archipelago II. U.S. Forest Service General Technical Report RMRS-P-36, Fort Collins, Colorado, USA.
- Ramsey F. L., and D. W. Schafer. 2002. *The statistical sleuth: a course in methods of data analysis*. Second edition. Duxbury, Thompson Learning, Pacific Grove, California, USA.
- Rauter, C. M., H.-U. Reyer, and K. Bollmann. 2002. Selection through predation, snowfall and microclimate on nest-site preferences in the water pipit *Anthus spinoletta*. *Ibis* 144:433–444.
- Rothwell, R. 1979. Nest sites of red squirrels (*Tamiasciurus hudsonicus*) in the Laramie range of southeastern Wyoming. *Journal of Mammalogy* 60:404–405.
- Salsbury, C. M. 2008. Distribution patterns of *Sciurus niger* (eastern fox squirrel) leaf nests within woodlots across a suburban/urban landscape. *Northeastern Naturalist* 15:485–496.
- Smith A. A., and R. W. Mannan. 1994. Distinguishing characteristics of Mount Graham red squirrel midden sites. *Journal of Wildlife Management* 58:437–445.
- Smith, G. C., M. Mathieson, and L. Hogan. 2007. Home range and habitat use of a low-density population of greater gliders, *Petauroides volans* (Pseudocheiridae: Marsupialia), in a hollow-limiting environment. *Wildlife Research* 34:427–483.
- Snyder M. A., and Y. B. Linhart. 1994. Nest-site selection by Abert's squirrel: chemical characteristics of nest trees. *Journal of Mammalogy* 75:136–141.
- Steele M. A., and J. L. Koprowski. 2001. *North American tree squirrels*. Smithsonian Books, Washington, D.C., USA.
- Steidl, R. J. 2006. Model selection, hypothesis testing, and risks of condemning analytical tools. *Journal of Wildlife Management* 70:1497–1498.
- Taulman, J. F. 1999. Selection of nest trees by southern flying squirrels (*Sciuridae: Glaucomys volans*) in Arkansas. *Journal of Zoology* 248:369–377.
- Theobald, D. P. 1983. *Studies on the biology and habitat of the Arizona gray squirrel*. Thesis. Arizona State University, Tempe, USA.
- Turner, D. S., S. Brandes, M. Fishbein, and P. W. Hirt. 1995. Preserve design for maintaining biodiversity in the sky island region. Pages 524–530 in L. F. DeBano, G. J. Gottfried, R. H. Hamre, and C. B. Edminster, technical coordinators. Biodiversity and management of the Madrean Archipelago: the sky islands of southwestern United States and northwestern Mexico. U.S. Forest Service General Technical Report RM-GTR-264, Fort Collins, Colorado, USA.
- United States Geological Survey [USGS] National Gap Analysis Program. 2004. Provisional Digital Land Cover Map for the Southwestern United States. Version 1.0. RS/GIS Laboratory, College of Natural Resources, Utah State University, Logan, USA.
- United States Geological Survey [USGS] National Gap Analysis Program. 2005. Southwest Regional GAP Analysis Project—Land Cover Descriptions. RS/GIS Laboratory, College of Natural Resources, Utah State University, Logan, USA.
- Wallmo, O. C. 1955. Vegetation of the Huachuca Mountains, Arizona. *American Midland Naturalist* 54:466–480.
- Wilson, D. S. 1998. Nest-site selection: microhabitat variation and its effects on the survival of turtle embryos. *Ecology* 79:1884–1892.
- Wolton, R. 2009. Hazel dormouse *Muscardinus avellanarius* (L.) nest site selection in hedgerows. *Mammalia* 73:7–12.

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