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Nest-site characteristics of the montane endemic Mearns's squirrel (*Tamiasciurus mearnsi*): an obligate cavity-nester?

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Many animals depend on nests for their survival and reproduction, with some species considered obligate tree cavity-nesters. Mearns's squirrel (*Tamiasciurus mearnsi*) is a species endemic to the Sierra de San Pedro Mártir, Baja California, Mexico, that relies on tree cavities for nesting. Federally listed as threatened in Mexico, and as endangered by the International Union for Conservation of Nature, the ecology of this southernmost *Tamiasciurus* is poorly known. The aim of this study was to examine the nesting requirements of Mearns's squirrels. We used telemetry to locate the nests and 10-m-radius circular plots to compare habitat characteristics between nest sites and random sites, nest sites of males and females, and nest sites of breeding and nonbreeding females. Nest tree species, nest tree condition, nest tree size (diameter at breast height), canopy cover, and occurrence of white firs (*Abies concolor*) are important characteristics for nesting. Nest sites of males did not differ from those of females except for nest tree condition. Females apparently do not have specific nesting requirements for rearing young. Unlike other congeners that also build leaf nests and underground burrows for nesting, large trees and snags that facilitate cavity formation are critical for the conservation of this species.

Key words: Baja California, cavity nests, endemic species, Mexico, nest sites, *Sciurus*, secondary cavity-nester, Sierra de San Pedro Mártir, tree cavities

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Cavity-nesting species in forest ecosystems comprise a structured community that interacts through the creation and competition for nest sites (Martin et al. 2004). Cavity-nesters are commonly grouped as weak excavators, strong excavators, and secondary cavity-nesters (Steger and Dulisse 2002). Weak and strong excavators build their own cavities, whereas secondary cavity-nesters always use old, existing cavities (Wiebe et al. 2007). Secondary cavity-nesters include a variety of passerines, ducks, birds of prey, and small mammals that require but cannot excavate cavities. Thus, they rely on nests created by excavators or a limited number of naturally occurring holes (Martin et al. 2004). In particular, densities of secondary cavity-nesters are often assumed to be primarily limited by nest sites (Miller 2010). Nests are critical for raising young, rest, predator avoidance, and shelter from adverse weather (Steele and Koprowski 2001). Because males and females have specific but often divergent biological needs, especially in mammals where pair-bonding is rare (Curley and Keverne 2005), nesting requirements are expected to differ between sexes (i.e., Edwards and Guynn 1995); however, this seldom has been examined by researchers. Quality of nest sites

also has been associated with fitness correlates such as probability of predation and nesting success (Li and Martin 1991). As a result, information on nest-site characteristics may allow researchers to assess habitat suitability and management (Ramos-Lara and Cervantes 2007).

In mammals, few cavity-using animals are obligates (Carey 2002). Tree squirrels in particular use 3 types of nests for resting and rearing young: spherical nests constructed from leaves and twigs (known as dreys), cavities within live trees and snags, and occasionally holes in the ground (Gurnell 1987). However, in some tree and flying squirrels females commonly rear their young in tree cavities rather than dreys (Carey et al. 1997; Edwards and Guynn 1995), suggesting that female squirrels may have specific nesting requirements compared to males. This also seems to be the case of the tree squirrels in the genus *Tamiasciurus*. The genus contains 3 species (Thorington and Hoffmann 2005): Douglas's squirrels



(*T. douglasii*), red squirrels (*T. hudsonicus*), and Mearns's squirrels (*T. mearnsi*). Douglas's and red squirrels frequently use natural tree cavities for nesting, but where suitable cavities are lacking, squirrels construct dreys and occasionally underground burrows (Gurnell 1987; Steele 1998, 1999). In contrast, Mearns's squirrels are known to use only tree cavities for nesting (Koprowski et al. 2006; Ramos-Lara and Koprowski 2012), suggesting that unlike the other 2 species, Mearns's squirrels may be obligate secondary cavity-nesters. As a result, Mearns's squirrels may have specific nesting requirements compared to Douglas's and red squirrels, which also use dreys and underground nests (Arsenault 2004). However, little information on the nesting requirements of Mearns's squirrels exists to date (i.e., Koprowski et al. 2006; Ramos-Lara and Koprowski 2012), despite the 100 years since the species was described (Allen 1893; Townsend 1897). Other than food, few other resources are more important to tree squirrels than nests (Steele and Koprowski 2001), with tree cavities considered an important and potentially limiting resource. However, the importance of nests in different forest types and tree species is unknown (Edelman and Koprowski 2006).

Tamiasciurus mearnsi is an endemic species that occurs only in the coniferous forests of the Sierra de San Pedro Mártir (SSPM), Baja California, Mexico (Lindsay 1981). Mearns's squirrels are separated from the nearest populations of Douglas's and red squirrels by approximately 600 km of mostly nonforested lowlands (Yensen and Valdés-Alarcón 1999). However, the exact distribution of Mearns's squirrels in SSPM is unknown, except for 3 locations < 10 km apart reported in the literature (Lindsay 1981; Yensen and Valdés-Alarcón 1999). The species is known from approximately 2,100 m to 2,750 m elevation in the coniferous forests of SSPM (Yensen and Valdés-Alarcón 1999). Considered a rare species (Huey 1964), Mearns's squirrels are federally listed as threatened in Mexico (Secretaría de Medio Ambiente y Recursos Naturales 2010) due to their restricted distribution, low population density, and isolation, and as endangered by the International Union for Conservation of Nature (de Grammont and Cuarón 2008). Herein, the aim of our study was to examine the nesting requirements of Mearns's squirrels. Because males and females have divergent biological needs, we expected differences in nesting requirements between sexes and between breeding and nonbreeding females.

MATERIALS AND METHODS

Study area.—The Sierra de San Pedro Mártir is located approximately 100 km southeast of Ensenada, Baja California, Mexico (Stephens et al. 2003). SSPM was established as a Forest Reserve in 1932, as a National Park in 1947, and has been proposed as a Biosphere Reserve (Bojórquez-Tapia et al. 2004). SSPM National Park comprises 65,000 ha, of which coniferous forests cover about 40,655 ha (Minnich et al. 2000). Forests are composed of Jeffrey pine (*Pinus jeffreyi*), sugar

pine (*P. lambertiana*), lodgepole pine (*P. contorta*), white fir (*Abies concolor*), and limited amounts of quaking aspen (*Populus tremuloides*) and incense cedar (*Calocedrus decurrens*). The most common forest types are Jeffrey pine, Jeffrey pine–mixed conifer, and mixed white fir forests (Stephens et al. 2003). Mixed-conifer forest on the summit plateau is replaced by chaparral and Sonoran Desert scrub at lower elevations. The most striking feature of the mixed-conifer forests is an open, parklike aspect that consists of mature trees reaching 30–45 m, with few pole-sized trees and saplings, and an open shrub cover (Bojórquez-Tapia et al. 2004). Elevation averages 2,600 m in the north and decreases to 1,800 m in the southern portion of the range with the highest peaks over 3,000 m (Stephens et al. 2003). Compared to other forests in North America, forests in SSPM have not experienced disturbance from logging and fires always have spread without human interference (Minnich et al. 2000). Summers are dry except for afternoon thunderstorms of the North American monsoon (Minnich et al. 2000). According to data recorded by Servicio Meteorológico Nacional at Ejido San Matías, located about 25 km north of SSPM, mean ($\pm SD$) monthly temperature in the region remained similar throughout the study ($19.2^{\circ}\text{C} \pm 6.59^{\circ}\text{C}$, $n = 36$). In contrast, mean ($\pm SD$) monthly precipitation in 2005 (22.8 ± 25.7 mm, $n = 12$) was greater than in 2006 (9.0 ± 16.5 mm, $n = 12$) and 2007 (10.7 ± 13.5 mm, $n = 12$). Hairy woodpeckers (*Picoides villosus*) and northern flickers (*Colaptes auratus*) are the most common species of tree-cavity excavators recorded above 2,600 m in SSPM (Gómez de Silva 2002).

Large-scale surveys.—During 2005, we surveyed approximately 2,500 ha of forest in the margins of the Vallecitos Meadow, where the species was collected previously for museum specimens (Lindsay 1981; Yensen and Valdés-Alarcón 1999), to detect direct (animal sighting) and indirect (remnants of food with characteristic gnawing) occurrence of Mearns's squirrels and to establish potential capture sites. The area was explored systematically using a topographic map (Schad 1988).

Trapping and telemetry.—We captured animals during May–August of 2006 and 2007. Live traps (model 201; Tomahawk Live Trap Co., Hazelhurst, Wisconsin) were placed at the base of large-diameter trees, baited with peanuts and peanut butter, covered with tree bark, and checked at 1-h intervals. Captured squirrels were transferred to a cloth handling cone (Koprowski 2002), where we collected data on sex, age class, reproductive condition, and body mass. Adult animals (≥ 240 g) were fitted with radiocollars (model SOM-2190; Wildlife Materials International, Inc., Carbondale, Illinois) and uniquely numbered Monel ear tags (style 1005-1; National Band and Tag Co., Newport, Kentucky) with colored plastic washers (style 1842; National Band and Tag Co.) on both ears. We distinguished adults and juveniles based on reproductive condition and body mass of captured animals. All squirrels were released at the capture site after ≤ 8 min of handling time; no animals were injured during the study. Trapping and handling procedures were conducted

with approval from the University of Arizona Institutional Animal Care and Use Committee (protocol 05-038), in accordance with guidelines of the American Society of Mammalogists (Sikes et al. 2011), and with permits from the following Mexican authorities: Dirección Forestal y de la Fauna Parque Nacional Sierra de San Pedro Mártir and Dirección General de Vida Silvestre.

Nest identification.—We tracked squirrels to their nests using a 3-element yagi directional antenna (Wildlife Materials International, Inc.) and receiver (model R-1000; Communications Specialists, Inc., Orange, California) in spring (April) and fall (September–November) and weekly during summer (May–August); we did not monitor animals during winter (December–March) because of snow and limited access. Based on the presence of litters and the reproductive condition of radiocollared females observed entering and leaving their nests, we recorded which tree cavities were used by breeding females (known as maternity nests) and nonbreeding females (hereafter referred to as nonmaternity nests).

Habitat characteristics.—For each cavity nest, we recorded height and aspect (degrees) of the entrance. For each nest tree, we recorded species, height, diameter at breast height (DBH), condition (live or dead), crown size of live trees (radius of 4 cardinal directions averaged), and number of trees (≥ 5 -cm DBH) with interlocked crowns to the nest tree. For each nest site, we recorded distance to nearest tree (≥ 5 -cm DBH), total number of trees (≥ 5 -cm DBH), total number of logs (≥ 15 -cm diameter and ≥ 1.5 -m length), slope (degrees), slope aspect (degrees), and percentage canopy cover at 0 m, 5 m, and 10 m from the nest tree in the 4 cardinal directions (north, south, west, and east); measurements were averaged for each distance (percentage canopy cover at 0 m, 5 m, and 10 m) and for the entire nest site (percentage canopy cover). In addition, we recorded species, condition, and DBH of all trees (≥ 5 -cm DBH) at each nest site. Tree condition was classified using the following classes: live (class 1), dead with intact branches (class 2), and snag with trunk broken (class 3). Based on the habitat characteristics recorded at nest sites, we calculated the following variables (number per hectare): small trees/ha (trees with ≥ 5 -cm DBH and < 40 -cm DBH), medium trees/ha (trees with ≥ 40 -cm DBH and < 85 -cm DBH), large trees/ha (trees with ≥ 85 -cm DBH), Jeffrey pines/ha, lodgepole pines/ha, white firs/ha, trees/ha, live trees/ha, dead trees/ha, snags/ha, logs/ha, basal area of all trees (m^2/ha), and species richness. Relative dominance, relative density, and relative frequency of each species of tree were determined for all nest sites (Muller-Dombois and Ellenberg 1974). The Shannon diversity index (H') and evenness (E) also were calculated for all nest sites (Magurran 1988).

We measured nest-site characteristics using 10-m-radius circular plots (0.03 ha) with the nest tree at the center (Muller-Dombois and Ellenberg 1974). Nest height, nest tree height, and slope were measured using a Hagl f electronic clinometer (Hagl f Sweden; Forestry Suppliers, Inc., Jackson, Mississippi). Crown size, DBH, and distances were measured using

a metric fabric diameter tape (model 283D; Forestry Suppliers, Inc.). Distances were marked using plain, vinyl, stake wire flags (Forestry Suppliers, Inc.). Percentage canopy cover was measured using a GRS Densitometer (Forestry Suppliers, Inc.). For comparison with nest sites, we used random trees to measure habitat availability by walking randomly within the study area using randomly generated numbers to denote distance and direction. The nearest tree with ≥ 40 -cm DBH was used as the center of a 10-m-radius circular plot from which the same data were collected; focal random trees with ≥ 40 -cm DBH are large enough to contain cavities that may be used by Mearns's squirrels for nesting (Gurnell 1987).

Data analysis.—We used unpaired t -tests, Mann–Whitney (U) tests, and the Mardia–Watson–Wheeler (W) test for circular analysis (Magurran 1988; Zar 1996) to examine differences between nest sites and random sites, nest sites of males and females, and nest sites of females with maternity and nonmaternity nests. Rayleigh's (Z) test was used to analyze random distributions around 360° for both nest aspect and slope aspect (Zar 1996). We used chi-square (χ^2) to compare categorical variables between sites, with subsequent Bonferroni simultaneous confidence intervals to establish selection (Neu et al. 1974). Pearson correlation (r) was used to explore relationship between nest tree height and cavity nest height. We used stepwise discriminant function analyses to determine the habitat characteristics that best discriminated between nest sites and random sites, nest sites of males and females, and nest sites of females with maternity and nonmaternity nests (McGarigal et al. 2000). Selection criteria for entry and removal of variables for nest sites and random sites were: F , entry = 3.0 and removal = 2.5, and for both nest sites of males and females and nest sites of females with maternity and nonmaternity nests: F , entry = 2.0 and removal = 1.5. Prior to stepwise discriminant function analysis, we removed highly correlated variables ($r > 0.70$) to prevent multicollinearity. For each pair of highly correlated variables, only the variable that best discriminated (higher F -value in 1-way analysis of variance) was used in stepwise discriminant function analysis (McGarigal et al. 2000). For the interpretation of the discriminant functions, we examined the correlations between each habitat characteristic and the discriminant function. The relative contribution of each habitat characteristic was assessed based on the structure coefficients. Habitat characteristics with higher correlations contributed more to the discriminant function than those with lower correlations (McGarigal et al. 2000).

We conducted all statistical analyses with SPSS 17.0 (SPSS Inc., Chicago, Illinois) and Oriana 3.0 (Kovach 2009). When necessary, variables were log-transformed to better meet the assumptions of univariate and multivariate tests (McGarigal et al. 2000; Zar 1996); however, means \pm SD shown in the results are from untransformed values. Because the same data were used for multiple comparisons, we adjusted our alpha level to 0.017 with a Bonferroni correction for all our analyses (Pallant 2007).

TABLE 1.—Habitat characteristics used in univariate analysis (†) and stepwise discriminant function analysis (‡) to compare nest sites of Mearns's squirrels (*Tamiasciurus mearnsi*) with random sites, nest sites of males and females, and nest sites of females with maternity and nonmaternity nests, in a coniferous forest of the Sierra de San Pedro Mártir, Baja California, Mexico. Sample size for each habitat characteristic corresponds to the number of sites except: cavity height (nests, $n = 79$; random, $n = 2$; males, $n = 26$; females, $n = 35$; maternity, $n = 20$; nonmaternity, $n = 22$), cavity aspect (nests, $n = 76$; random, $n = 2$; males, $n = 26$; females, $n = 32$; maternity, $n = 18$; nonmaternity, $n = 19$), focal tree crown size (nests, $n = 63$; random, $n = 109$; males, $n = 20$; females, $n = 35$; maternity, $n = 15$; nonmaternity, $n = 22$), and slope aspect (random, $n = 114$). DBH = diameter at breast height.

Habitat characteristics	Use		Sex		Reproduction	
	Nests ($n = 115$)	Random ($n = 115$)	Males ($n = 47$)	Females ($n = 48$)	Maternity ($n = 21$)	Nonmaternity ($n = 32$)
Cavity						
† Height (m)	14.8 ± 6.1	10.0 ± 10.2	12.8 ± 5.0	15.6 ± 6.5	16.7 ± 6.1	16.5 ± 5.9
† Aspect (degrees)	286.8 ± 128.9	305.0 ± 94.2	285.1 ± 95.3	153.0 ± 128.9	323.4 ± 114.6	194.0 ± 88.3
Focal tree						
‡ Height (m)	24.6 ± 9.0	25.0 ± 6.4	22.6 ± 9.2	26.0 ± 8.7	28.1 ± 10.4	25.4 ± 7.5
‡ DBH	95.6 ± 26.9	65.3 ± 17.5	92.7 ± 26.9	94.6 ± 28.2	103.5 ± 34.1	92.0 ± 22.0
† Crown size (m)	4.5 ± 1.3	2.7 ± 1.0	4.8 ± 1.4	4.2 ± 1.3	4.3 ± 1.4	4.3 ± 1.2
‡ Interlocked trees	1.3 ± 2.5	2.4 ± 3.6	1.3 ± 2.3	1.5 ± 2.8	1.1 ± 1.6	1.7 ± 3.2
Site						
‡ Nearest tree (m)	5.1 ± 3.3	4.15 ± 2.6	5.2 ± 3.2	4.8 ± 3.4	5.3 ± 3.3	4.6 ± 3.3
‡ % canopy cover 0 m	75.1 ± 26.4	86.4 ± 16.7	70.1 ± 26.7	80.7 ± 23.8	78.1 ± 25.6	83.3 ± 21.9
‡ % canopy cover 5 m	30.9 ± 23.3	24.9 ± 17.8	28.3 ± 22.2	35.5 ± 25.2	36.5 ± 24.4	36.7 ± 25.3
‡ % canopy cover 10 m	18.8 ± 17.18	20.0 ± 14.5	20.4 ± 18.6	18.7 ± 17.7	21.2 ± 13.6	17.9 ± 19.4
† % canopy cover ^a	41.6 ± 15.9	43.8 ± 9.8	39.6 ± 14.8	45.0 ± 16.4	45.3 ± 16.2	46.0 ± 16.2
† Small trees/ha ^b	130.1 ± 161.5	166.1 ± 271.1	128.4 ± 164.5	161.1 ± 174.3	152.4 ± 177.5	153.1 ± 169.1
‡ Medium trees/ha ^c	37.1 ± 46.3	44.1 ± 43.6	45.4 ± 54.0	33.3 ± 42.4	22.2 ± 35.5	38.5 ± 44.1
‡ Large trees/ha ^d	9.3 ± 17.4	4.9 ± 12.7	6.4 ± 15.0	8.3 ± 16.1	15.9 ± 20.1	7.3 ± 16.4
‡ Jeffrey pines/ha	134.8 ± 128.4	198.6 ± 271.2	131.9 ± 114.8	156.3 ± 150.5	155.6 ± 151.4	147.9 ± 144.7
‡ Lodgepole pines/ha	18.3 ± 51.5	11.6 ± 33.1	23.4 ± 70.5	16.7 ± 36.4	11.1 ± 26.5	20.8 ± 40.4
‡ White firs/ha	23.2 ± 53.2	4.6 ± 18.7	24.8 ± 66.1	29.9 ± 48.3	23.8 ± 38.2	30.2 ± 51.8
† Trees/ha	176.5 ± 167.1	215.1 ± 268.3	180.1 ± 171.5	202.8 ± 180.0	190.5 ± 175.2	199.0 ± 177.5
† Live trees/ha	167.0 ± 163.1	210.4 ± 268.4	169.5 ± 166.8	193.1 ± 176.7	182.5 ± 172.4	189.6 ± 173.6
‡ Dead trees/ha	9.6 ± 20.1	4.6 ± 12.4	10.6 ± 22.1	9.7 ± 19.4	7.9 ± 14.6	9.4 ± 21.1
‡ Logs/ha ^e	62.3 ± 58.8	47.8 ± 40.3	70.2 ± 63.4	63.2 ± 58.9	46.0 ± 46.5	67.7 ± 63.6
‡ Basal area (m ² /ha)	21.8 ± 20.7	20.7 ± 16.5	21.9 ± 21.9	21.3 ± 19.5	24.3 ± 19.2	21.5 ± 21.1
‡ Slope (degrees)	22.2 ± 13.0	19.9 ± 10.9	23.0 ± 14.0	23.8 ± 13.1	22.5 ± 11.6	23.2 ± 14.0
† Slope aspect (degrees)	246.8 ± 119.5	261.5 ± 101.7	209.1 ± 101.9	310.8 ± 105.0	324.3 ± 124.0	295.8 ± 114.5
‡ Species richness (trees)	1.4 ± 0.8	1.2 ± 0.6	1.3 ± 0.8	1.6 ± 0.8	1.5 ± 0.7	1.6 ± 0.9

^a All distances combined (0 m, 5 m, and 10 m).

^b ≥5-cm DBH and <40-cm DBH.

^c ≥40-cm DBH and <85-cm DBH.

^d ≥85-cm DBH.

^e ≥15-cm diameter and ≥1.5-m length.

RESULTS

We captured 38 adult Mearns's squirrels (20 males and 18 females). Squirrels used tree cavities in 424 (99.5%) of 426 nesting events, with only 1 adult male nesting underground on 2 (0.5%) consecutive nights during August 2007. In total, we located 115 cavity nests, of which 21 were used as maternity nests. As a result, we used 115 random trees to measure habitat availability for nesting to maintain equal sample sizes.

We detected only 3 (2.6%) cavities in the 115 random trees. On average, cavity nests were located higher than tree cavities found in random trees (Table 1). However, cavity height was not correlated with nest tree height ($r = 0.12$, $n = 79$, $P = 0.29$). Entrances to cavities in nest trees ($Z = 0.48$, $n = 76$, $P = 0.62$) were not oriented in any particular direction (Table 1). Tree species were not used relative to their availability ($\chi^2_2 = 13.019$, $P = 0.0015$); Jeffrey pines were used similarly to their

availability (98% confidence interval [98% CI] = 0.70–0.90), whereas lodgepole pines were used 7.5 times less (98% CI = 0.00–0.11) and white firs 14.0 times more (98% CI = 0.06–0.23; Fig. 1). Because dead trees (class 2) and snags (class 3) did not differ within nest trees ($U = 6,098.5$, $n_1 = 115$, $n_2 = 115$, $P = 0.07$) and focal random trees ($U = 6,437.0$, $n_1 = 115$, $n_2 = 115$, $P = 0.42$), we pooled both classes into a single variable, hereafter referred to as dead trees. Live and dead trees were not used relative to their availability ($\chi^2_1 = 48.79$, $P < 0.0001$); live trees were used 1.7 times less than their availability, whereas dead trees were used 8.7 times more (Fig. 2). Nest trees had crowns 1.7 times greater than focal trees at random sites ($t_{170} = 9.67$, $P < 0.0001$; Table 1). Four of the 17 characteristics used in stepwise discriminant function analysis (Table 1) differed between nest sites and random sites (Wilks' $\lambda = 0.48$, $\chi^2_7 = 164.24$, $P < 0.001$; Table 2). Nest sites had nest trees 1.5 times larger (DBH), with 1.8 times fewer

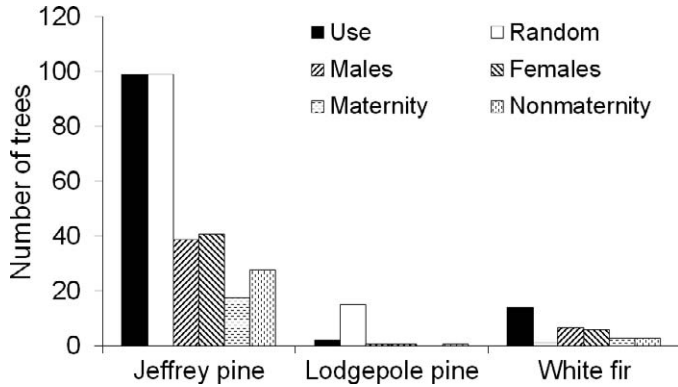


FIG. 1.—Number of Jeffrey pines (*Pinus jeffreyi*), lodgepole pines (*P. contorta*), and white firs (*Abies concolor*) used by Mearns's squirrels (*Tamiasciurus mearnsi*) at nest sites ($n = 115$), compared to random sites ($n = 115$), nest sites of males ($n = 47$) and females ($n = 48$), and nest sites of females with maternity ($n = 21$) and nonmaternity nests ($n = 32$) in the Sierra de San Pedro Mártir, Baja California, Mexico.

interlocked trees, 1.2 times less canopy cover at 0 m, and 5.0 times more occurrence of white firs/ha than those at random sites (eigenvalue = 1.08, $\chi^2_7 = 164.24$, $P < 0.001$; Table 1). Slope aspect at nest sites was not oriented in any particular direction ($Z = 1.48$, $n = 115$, $P = 0.23$) and did not differ from random sites ($W = 2.58$, $P = 0.28$; Table 1). Similarly, percentage canopy cover, trees/ha, live trees/ha, and small trees/ha did not differ between nest sites and random sites (all $P > 0.05$; Table 1). Tree diversity (H') at nest sites ($H' = 0.72$, $S = 5$, $E = 0.45$, $n = 609$) was 2.3 times higher than that at random sites ($H' = 0.32$, $S = 5$, $E = 0.20$, $n = 742$; $H'_{\max} = 1.61$; $t_{1,318} = 8.60$, $P < 0.0001$). This difference was due to the absence of sugar pines and quaking aspens at nest sites and random sites, respectively, and to the difference in abundance among tree species (Table 3). Jeffrey pines had the greatest relative dominance, relative density, and relative frequency at

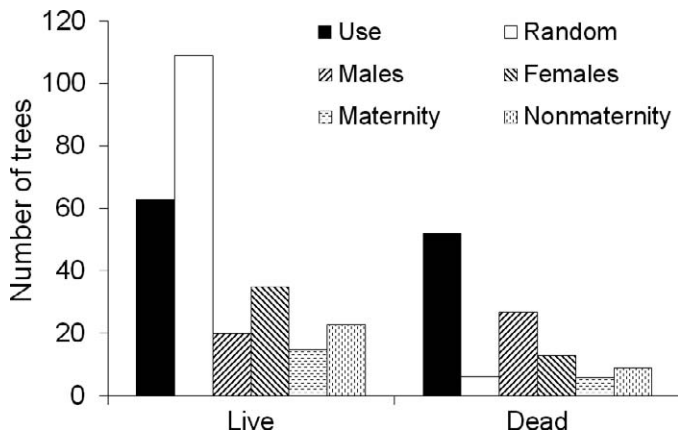


FIG. 2.—Number of live and dead trees used by Mearns's squirrels (*Tamiasciurus mearnsi*) at nest sites ($n = 115$) compared to random sites ($n = 115$), nest sites of males ($n = 47$) and females ($n = 48$), and nest sites of females with maternity ($n = 21$) and nonmaternity nests ($n = 32$) in the Sierra de San Pedro Mártir, Baja California, Mexico.

TABLE 2.—Correlations between original characteristics selected in stepwise discriminant function analysis to compare nest sites of Mearns's squirrels (*Tamiasciurus mearnsi*) with random sites, and nest sites of males and females, in the Sierra de San Pedro Mártir, Baja California, Mexico. Significance ($P < 0.017$) is marked with an asterisk (*). DBH = diameter at breast height.

Habitat characteristics	Correlation with discriminant function	
	<i>r</i>	<i>P</i>
Use versus random		
Focal tree DBH	0.659	<0.0001*
% canopy cover 0 m	-0.247	<0.0001*
White firs/ha	0.241	<0.0001*
Interlocked trees	-0.185	0.004*
% canopy cover 5 m	0.141	0.028
Large trees/ha ^a	0.138	0.031
Focal tree height	-0.022	0.734
Males versus females		
% canopy cover 0 m	0.510	0.043
Species richness (trees)	0.478	0.058
Focal tree height (m)	0.456	0.070
Lodgepole pines/ha	-0.146	0.559

^a ≥ 85 -cm DBH.

nest sites and random sites. However, unlike Jeffrey pines, white firs at nest sites had higher relative dominance, relative density, and relative frequency than those at random sites (Table 3).

Nest sites of males and females only differed in nest tree condition ($\chi^2_1 = 8.98$, $P = 0.003$), with no differences in any other of the characteristics analyzed using univariate tests (all $P > 0.06$; Table 1). Females used 1.8 times more live trees for nesting, whereas males used 2.1 times more dead trees (Fig. 2). In contrast, tree species used for nesting did not differ between males and females ($\chi^2_2 = 0.08$, $P = 0.96$; Fig. 1). Stepwise discriminant function analysis indicated a difference between sexes (Wilks' $\lambda = 0.85$, $\chi^2_4 = 14.53$, $P = 0.006$), but none of the variables included in the model were significant after the Bonferroni correction (Table 2). Similarly, tree diversity did not differ between nest sites of males ($H' = 0.77$, $E = 0.48$) and females ($H' = 0.69$, $E = 0.43$; $t_{542} = 1.62$, $P = 0.24$; Table 3).

Nest sites of females with maternity and nonmaternity nests did not differ in any of the habitat characteristics analyzed using univariate tests (all $P > 0.18$; Table 1) and stepwise discriminant function analysis (Wilks' $\lambda = 0.91$, $\chi^2_2 = 4.80$, $P = 0.09$; Table 1). Tree species ($\chi^2_2 = 0.43$, $P = 0.81$; Fig. 1) and tree condition ($\chi^2_1 = 0.001$, $P = 0.97$; Fig. 2) did not differ between sites. Similarly, tree diversity did not differ between sites with maternity nests ($H' = 0.59$, $E = 0.37$) and nonmaternity nests ($H' = 0.74$, $E = 0.46$; $t_{239} = 1.62$, $P = 0.11$; Table 3).

DISCUSSION

Mearns's squirrels used primarily tree cavities for nesting (Koprowski et al. 2006; Ramos-Lara and Koprowski 2012); although 1 adult nested underground, this behavior was rare. As potentially obligate secondary cavity-nesters, access to tree

TABLE 3.—Relative dominance (Rdo), relative density (Rde), and relative frequency (Rfr) for each species of tree found at nest sites of Mearns's squirrels (*Tamiasciurus mearnsi*), random sites (availability), nest sites of males and females, and nest sites of females with maternity and nonmaternity nests in a coniferous forest of the Sierra de San Pedro Mártir, Baja California, Mexico. Sp = species of trees, J = Jeffrey pine (*Pinus jeffreyi*), L = lodgepole pine (*P. contorta*), S = sugar pine (*P. lambertiana*), F = white fir (*Abies concolor*), A = quaking aspen (*Populus tremuloides*).

Sp	Use						Sex						Reproduction					
	Nests (n = 115)			Random (n = 115)			Males (n = 47)			Females (n = 48)			Maternity (n = 21)			Nonmaternity (n = 32)		
	Rdo	Rde	Rfr	Rdo	Rde	Rfr	Rdo	Rde	Rfr	Rdo	Rde	Rfr	Rdo	Rde	Rfr	Rdo	Rde	Rfr
J	84.8	76.4	64.0	89.5	92.3	77.3	87.3	73.2	66.2	76.8	77.1	60.6	73.3	81.7	61.3	84.8	74.3	60.4
L	2.9	10.3	16.3	7.2	5.4	15.6	2.4	13.0	16.9	4.0	8.2	15.5	0.8	5.8	12.9	5.4	10.5	18.8
S	0	0	0	0.6	0.1	0.7	0	0	0	0	0	0	0	0	0	0	0	0
F	12.3	13.1	19.0	2.7	2.2	6.4	10.3	13.8	16.9	19.2	14.7	23.9	25.9	12.5	25.8	9.8	15.2	20.8
A	0	0.2	0.7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
%	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100

cavities in SSPM is critical for the survival and reproduction of Mearns's squirrels. To compensate for lack of suitable tree cavities, other species of arboreal squirrels construct dreys and underground burrows (Edwards and Guynn 1995; Gurnell 1987). However, the reason for the lack of dreys in Mearns's squirrels compared to other arboreal squirrels remains unknown. Inadequate nesting material or high predation by raptors may be responsible for Mearns's squirrels nesting only in tree cavities; however, more research is needed. Reported as rare and occurring in limited numbers (Huey 1964; Yensen and Valdés-Alarcón 1999), the Mearns's squirrel population may be influenced by access to suitable nest sites, as suggested for other secondary cavity-nesters (Boyle et al. 2008; Miller 2010).

Mearns's squirrels have specific nesting requirements, with white firs, large trees, and snags being important resources for nesting, similar to other species of arboreal squirrels (e.g., Merrick et al. 2007; Meyer et al. 2005). As secondary cavity-nesters, large snags are expected to be important resources for Mearns's squirrels because cavity nests are typically found in large diseased or damaged trees, but particularly in large snags (Holloway and Malcolm 2007). However, large snags are not common resources in the study area, which may account for the high use of cavities in live trees. Because woodpeckers use mostly live trees and hard snags for nesting (Steeger and Dulisse 2002), Mearns's squirrels may depend strongly on these primary cavity-nesters for suitable nest sites. Higher frequency of cavity nests in live trees also has been reported in other species of tree and flying squirrels (Bendel and Gates 1987; Edelman and Koprowski 2006). Contrary to dead trees, live trees may be more suitable as nest sites for cavity-nesters because overhead branches provide protection from weather, increased cover, and structural complexity for predator avoidance (Cotton and Parker 2000).

Cavities in larger trees may provide more stability and protection from the effects of wind and cold temperatures (Halloran and Bekoff 1994). Larger trees also have more time to develop suitable cavities and thick trunks facilitate formation of natural cavities (Edelman and Koprowski 2006) and by other primary cavity-nesters. However, because density of

large trees is lower than that of small and medium-sized trees, this also possibly limits excavation of cavities by birds such as woodpeckers. Largest trees within younger stands are known to limit northern flying squirrel (*Glaucomys sabrinus*) populations in British Columbia, Canada (Cotton and Parker 2000). Nest trees with larger crowns also may provide more routes to escape from predators (Ramos-Lara and Cervantes 2007) and more access to food sources. Larger trees with larger crowns produce more cones than do younger conifers (Holimon et al. 1998). Although nest trees with larger crowns may be selected initially by primary cavity-nesters such as northern flickers, which tend to excavate their cavities in sites surrounded by denser forest (Arsenault 2004), Mearns's squirrels also may benefit from nesting in these trees.

Fewer interlocked trees at nest sites possibly was due to the open forests in SSPM (Bojórquez-Tapia et al. 2004). Similarly, the higher proportion of dead trees used by Mearns's squirrels for nesting also may account for less canopy cover at 0 m. Interlocked trees and more canopy cover in other forests commonly provide routes to escape from predators, easy access to food sources, and allow squirrels to travel through the trees rather than on the ground where they are more exposed to aerial and terrestrial predators (Edelman and Koprowski 2005; Ramos-Lara and Cervantes 2007). However, because of the open forests in SSPM, Mearns's squirrels commonly travel on the ground from tree to tree in search of food and potential tree cavities, increasing the time exposed to terrestrial and aerial predators. Nest sites with higher density of white firs may provide Mearns's squirrels with more cavity nests, safer sites for resting and hiding from aerial predators, and easy access to more sources of food. Basidiomycete fungi, such as veiled polypores (*Cryptoporus volvatus*), commonly grow on the trunks of white firs and are an important source of food for Mearns's squirrels (Koprowski et al. 2006). Similarly, cavity nests located at sites with greater diversity of trees may increase the variety of foods nearby. For instance, lodgepole pines were rarely used for nesting but their cones were heavily consumed by Mearns's squirrels throughout the study. Nesting near favored food trees during the summer also has been

reported in other species of tree squirrels (Edwards and Guynn 1995).

Distribution of animals is influenced by factors such as the abundance of and competition for resources, predation pressure, tactics of mate acquisition, and breeding systems (Clutton-Brock and Harvey 1978). Differential reproductive investment is more pronounced in polygynous mammals that lack male parental care (Curley and Keverne 2005). As a result, differences in nesting requirements may be expected between sexes (e.g., Edwards and Guynn 1995). Nonetheless, nests sites of male and female Mearns's squirrels only differed in nest tree condition, suggesting that both sexes may have similar nesting requirements. Using more live trees for nesting may provide female Mearns's squirrels with more protection against predators (Wiebe et al. 2006) and easier access to cavities and food sources (Holimon et al. 1998), especially during the breeding season. In other species, such as eastern fox squirrels (*Sciurus niger*), use of dreys and cavities by males and females is proportional within seasons, whereas in eastern gray squirrels (*S. carolinensis*) it differs between sexes (Edwards and Guynn 1995). More studies are needed to learn more about the sources of variation in nesting behavior between sexes in arboreal squirrels.

Nest sites of females did not differ between maternity and nonmaternity nests, suggesting that female Mearns's squirrels do not have specific nesting requirements for raising litters. Suitable cavities in live and dead trees may be the primary nesting requirement for females during both breeding and nonbreeding seasons. Female eastern fox squirrels and eastern gray squirrels use tree cavities more often during the winter reproductive period, than at other times of the year, to increase the survival of their nestlings (Edwards and Guynn 1995). Other characteristics such as cavity size also are known to influence use by secondary cavity-nesters (Boyle et al. 2008; Martin et al. 2004); however, the importance for Mearns's squirrels is still unknown.

Evidence indicates that Mearns's squirrels may be obligate secondary cavity-nesters (Koprowski et al. 2006; Ramos-Lara and Koprowski 2012) with specific nesting requirements. As a result, conservation of Mearns's squirrels requires both suitable nest sites and healthy populations of primary cavity-nesters such as woodpeckers and flickers. Large trees and snags that facilitate cavity formation are primarily important for the conservation of this endemic species. Dominance of large snags in forests of SSPM is presumed to be due to the lack of fire suppression (Stephens 2004). In other parts of North America, fire suppression has altered wildfire patterns, increasing the frequency of stand-replacing crown fires and greatly reducing standing snags (Dwyer and Block 2000). Because Mearns's squirrels rely strongly on dead trees for nesting, fire suppression in SSPM may impact the occurrence of these structures and consequently of tree cavities. However, the reason for the lack of dreys in Mearns's squirrels compared to other squirrels and the implications of this behavior in their ecology and conservation remains unknown.

RESUMEN

Muchos animales dependen de nidos para su sobrevivencia y reproducción con algunas especies consideradas anidadoras de cavidad obligadas. La ardilla de Mearns (*Tamiasciurus mearnsi*) es una especie endémica de la Sierra de San Pedro Mártir, Baja California, México, la cual depende de cavidades de árboles para anidar. Listada federalmente como amenazada en México, y como en peligro por la Unión Internacional para la Conservación de la Naturaleza, la ecología de esta *Tamiasciurus* sureña es pobremente conocida. El objetivo de este estudio fue examinar los requerimientos de anidación de las ardillas de Mearns. Utilizamos telemetría para localizar los nidos y cuadrantes circulares de 10 m de radio para comparar características del hábitat entre los sitios de anidación y sitios al azar, sitios de anidación de machos y hembras, y sitios de anidación de hembras reproductivas y no reproductivas. La especie del árbol de anidación, la condición del árbol de anidación, el tamaño (diámetro a la altura del pecho) del árbol de anidación, la cobertura del dosel y la abundancia de abetos blancos (*Abies concolor*) son características importantes para anidar. Los sitios de anidación de los machos no difirieron de las hembras excepto por la condición del árbol de anidación. Las hembras aparentemente no tienen requerimientos específicos de anidación al tener crías. A diferencia de otros congéneres que también construyen nidos de hoja y madrigueras subterráneas para anidar, los árboles grandes y tocones que facilitan la formación de cavidades son críticos para la conservación de esta especie.

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