

## CHARACTERISTICS OF ABERT'S SQUIRREL (*SCIURUS ABERTI*) CAVITY NESTS

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**ABSTRACT**—Cavity nests are rarely used by Abert's squirrels (*Sciurus aberti*) in ponderosa pine (*Pinus ponderosa*) forests. Introduced Abert's squirrels in the Pinaleno Mountains of Arizona, however, exhibit occasional use of cavity nests (ca. 10%). We examined characteristics of cavity nest sites in this introduced population. Cavity nests were located at two-thirds of the tree height and were found mainly in both dead and live aspen (*Populus tremuloides*). Aspen cavity trees were larger than aspen random trees. Aspen cavity sites had more large snags and less ponderosa pine and were less steep than aspen random sites. Abert's squirrels possibly use cavities in large aspen trees because thick trunks and older trees might allow larger cavities to form, might provide greater thermal and wind protection, or both. The greater use of cavity nests by the Abert's squirrels in our study could be due to the higher frequency of cavity-forming aspens or harsher winter conditions in mixed-conifer forests of the Pinaleno Mountains than in ponderosa pine forests where Abert's squirrels typically occur or both.

**RESUMEN**—Nidos en cavidades raramente son usados por las ardillas de Abert (*Sciurus aberti*) en bosques de pino ponderosa (*Pinus ponderosa*). Las ardillas de Abert introducidas en las Pinaleno Mountains de Arizona, sin embargo, exhiben uso moderado de nidos en cavidades (cerca de 10%). Examinamos las características de los sitios de nidos en cavidades en esta población introducida. Los nidos en cavidades se localizaron a  $\frac{2}{3}$  de la altura del árbol y fueron encontradas principalmente en el álamo temblón (*Populus tremuloides*) vivo o muerto. Los álamos temblones con cavidades fueron más grandes que los álamos al azar. Sitios con cavidades en álamos tuvieron más árboles muertos grandes y menos pinos ponderosa y fueron menos empinados que sitios con álamos al azar. Las ardillas de Abert posiblemente usan cavidades en álamos grandes porque los troncos gruesos y árboles más viejos pueden permitir que se formen cavidades, pueden proveer más protección termal y contra el viento, o ambos. El mayor uso de nidos en cavidades por las ardillas de Abert en nuestra investigación puede ser debido a la más alta frecuencia de álamos con cavidades, o a los inviernos más duros en los bosques mixtos de coníferas en las Pinaleno Mountains que en los bosques de pino ponderosa donde las ardillas de Abert son encontradas típicamente, o ambos.

Nests are important resources for many species of mammals (von Frisch, 1974). Tree squirrels (*Sciurus* and *Tamiasciurus*) use nests for raising young, rest, predator avoidance, and cover during inclement weather (Steele and Koprowski, 2001). Tree squirrels use a variety of nest types: spherical nests constructed from leaves and twigs (dreys), cavities within live trees and snags, and occasionally ground nests (Gurnell, 1987). In some species of tree squirrels and flying squirrels, females prefer to rear young in cavities rather than dreys (Edwards and Gynn, 1995; Carey et al., 1997). Ar-

tificial cavities (i.e., nest boxes) provide protection from adverse weather by maintaining mean temperatures of 25.9°C greater than ambient temperature when occupied (Havera, 1979). Cavities also can facilitate communal nesting (Koprowski, 1996; Steele and Koprowski, 2001). Provisioning of artificial cavities increases densities and survivorship among some age and sex classes of tree squirrels (Barkalow and Soots, 1965; Burger, 1969; Nixon and Donohoe, 1979; Nixon et al., 1984), suggesting that cavities can be an important and limiting resource; however, the effect of cavities in different forest types and species is not known.

Abert's squirrel (*Sciurus aberti*) is native primarily to ponderosa pine (*Pinus ponderosa*) forests of the southwestern United States and northern Mexico (Brown, 1984). Abert's squirrel reportedly is dependent on ponderosa pine for food, cover, and nest sites (Keith, 1965; Patton and Green, 1970; Stephenson, 1975; Pederson et al., 1976; Hall, 1981; Snyder, 1993; Halloran and Bekoff, 1994; States and Wettstein, 1998). Nests are typically dreys built in large conifer trees that have inter-connected branches with neighboring trees (Halloran and Bekoff, 1994; Edelman and Koprowski, 2005). Burrows are never used, and cavity nests (2% of nests found) are rarely used (Halloran and Bekoff, 1994). The few cavity nests noted were in ponderosa pine (Halloran and Bekoff, 1994), Gambel oak (*Quercus gambeli*; Patton and Green, 1970; Patton, 1975), aspen (*Populus tremuloides*; Brown, 1984), and cottonwood (*Populus fremontii*; Keith, 1965). Abert's squirrels also nest in nest boxes when available (Pederson et al., 1978). Due to infrequent use of cavity nests by Abert's squirrels, characteristics of cavity nests have never been reported.

The objective of our study was to observe use of cavity nests by Abert's squirrels. We examined cavity nest sites of an introduced population of Abert's squirrels in a mixed-conifer forest in the Pinaleno Mountains of Arizona. Abert's squirrels were introduced to the Pinaleno Mountains in the 1940s to provide hunting opportunities (Davis and Brown, 1988). Unlike most natural populations, Abert's squirrels in the Pinaleno Mountains inhabit mixed-conifer and spruce-fir (*Picea-Abies*) forests that contain little to no ponderosa pine (Hutton et al., 2003; Edelman, 2004).

**METHODS—Study Area**—Our study area was in the Pinaleno Mountains, 25 km southwest of Safford, Arizona, and encompassed 110 ha of mixed-conifer forest at elevations from ca. 2,850 to 3,170 m. Dominant tree species were corkbark fir (*Abies lasiocarpa* var. *arizonica*, 41%), Engelmann spruce (*Picea engelmannii*, 20%), aspen (17%), and Douglas-fir (*Pseudotsuga menziesii*, 10%), with smaller amounts of southwestern white pine (*Pinus strobiformis*, 8%), ponderosa pine (2%), and white fir (*Abies concolor*, 1%).

**Nest Identification**—We used 48-cm × 15-cm × 15-cm box traps constructed of 1.3-cm × 2.5-cm wire mesh (Custom Model 202, Tomahawk Live Trap Co., Tomahawk, Wisconsin) baited with peanuts and pea-

nut butter to trap squirrels (Edelman, 2004). Captured squirrels were transferred to a cloth handling-cone (Koprowski, 2002) to assess sex, reproductive condition, age class, and body mass. Numbered metal ear tags (Model 1005-1, National Band and Tag Co., Newport, Kentucky) with plastic colored washers (1-cm Model 1842, National Band and Tag Co., Newport, Kentucky) were attached to captured squirrels. Adults (>600 g) were fitted with radio-collars (Model SOM 2380, Wildlife Materials, Inc., Carbondale, Illinois) that weighed <5% of body mass. Nest locations were obtained by homing (White and Garrott, 1990) on radio-collared squirrels ( $n = 37$  individuals) from September 2001 to September 2003.

**Tree and Site Measurements**—For each cavity nest, we assessed number of entrances and their height and aspect. For each cavity tree, we recorded tree species, tree condition, diameter at breast height (DBH), tree height, and number of trees ( $\geq 10$  cm DBH) with branches within 0.5 m of any part of nest tree (i.e., access routes). We measured tree height and entrance height with a clinometer.

Within a 10-m-radius circular plot (0.03 ha) surrounding the cavity tree, we recorded species, condition, and DBH of each tree  $\geq 3$  cm DBH, as well as the number of logs  $\geq 20$  cm diameter and  $\geq 2$  m long (Smith and Mannan, 1994). Percent slope and slope aspect were measured at each site. Canopy cover was measured using a spherical densiometer (Model C, Forest Densiometers, Bartlesville, Oklahoma) at 0, 5, and 10 m from nest trees in the 4 cardinal directions (north, south, west, and east); measurements were averaged for each distance (% canopy cover at 0, 5, and 10 m) and for plots (% canopy cover; Young et al., 2002). Coefficient of variation of canopy cover (canopy cover CV) was calculated to measure variability of canopy cover in the plot. Tree condition was classified as: 1) live; 2) dead with intact branches and twigs, trunk pointed, and almost all bark remaining; 3) dead with branches present but broken, tree trunk broken near top, and most bark remaining; 4) dead with branches broken near trunk, tree trunk broken, and little bark remaining; and 5) dead with branches gone, tree trunk broken near breast height, and bark gone. Simpson's diversity index was calculated for trees at each site (Magurran, 1988). Based on the measurements taken at sites, we calculated the following variables (number per ha): logs/ha, trees/ha, live trees/ha, dead trees/ha, trees with <20 cm DBH (small trees/ha), trees with  $\geq 20$  cm DBH and  $\leq 40$  cm DBH (medium trees/ha), trees with >40 cm DBH (large trees/ha), dead trees with DBH >40 cm (large snags/ha), Engelmann spruce/ha, corkbark fir/ha, Douglas-fir/ha, white fir/ha, aspen/ha, southwestern white pine/ha, ponderosa pine/ha, and deciduous trees (excluding aspen)/ha. For

comparison with aspen cavity trees and sites, we randomly selected aspen trees ( $\geq 10$  cm DBH) in the study area ( $n = 17$ ) and measured the same variables as at aspen cavity trees and sites.

**Data Analysis**—We conducted all statistical analyses using JMP-IN (SAS Institute, 2003) and SAS (SAS Institute, 2002). When necessary, variables were transformed for data analyses to better meet assumptions of parametric and multivariate tests (Zar, 1984); however, means  $\pm$  SE presented in results are from untransformed values. We analyzed categorical data using Pearson chi-square tests. Characteristics of aspen cavity nest trees and random trees were analyzed using 2-tailed *t*-tests.

We used stepwise discriminant function analysis (DFA) to select variables that best discriminated aspen cavity and random sites. Selection criterion for entry and removal of variables in stepwise DFA was  $F = 0.15$ . Variables selected in stepwise DFA were analyzed using DFA. To prevent multicollinearity, high pairwise correlations ( $r > 0.70$ ) between variables were identified prior to stepwise DFA. For each pair of highly correlated variables, only the variable that best discriminated between aspen cavity and random sites (higher *F* value in one-way ANOVA) was used in stepwise DFA (McGarigal et al., 2000).

**RESULTS**—Average number of nests found per squirrel was  $5.7 \pm 0.8$ . Cavity nests ( $n = 14$ ) accounted for 9.8% of nests found, whereas the majority of nests were dreys. All cavity nests had one entrance except one cavity that had 2 entrances. Cavity entrances were located at a mean height of  $14.6 \pm 1.6$  m and at two-thirds of tree height (ratio of cavity entrance to tree height =  $0.646 \pm 0.049$ ). Cavity entrances were distributed equally with respect to orientation ( $\chi^2 = 2.57$ ,  $df = 3$ ,  $n = 14$ ,  $P = 0.463$ ).

The most common tree species ( $\chi^2 = 17.29$ ,  $df = 2$ ,  $P = 0.0002$ ) used for cavity nests was aspen ( $n = 12$ ), but cavity nests also were found in corkbark fir ( $n = 1$ ) and ponderosa pine ( $n = 1$ ). Live trees ( $n = 9$ ) were not used for cavity nests more frequently ( $\chi^2 = 1.14$ ,  $df = 1$ ,  $P = 0.285$ ) than dead trees ( $n = 5$ ). Cavity nests occurred equally in dead trees of condition classes 2 to 4 ( $\chi^2 = 0.40$ ,  $df = 2$ ,  $n = 5$ ,  $P = 0.819$ ), but none occurred in the most heavily decayed trees of condition class 5. Aspen trees with cavities were almost 2 times larger in DBH than random aspen trees (cavity trees =  $52.6 \pm 4.1$  cm; random trees =  $28.3 \pm 3.4$  cm;  $t = 4.59$ ,  $df = 27$ ,  $P < 0.0001$ ), but did not differ in tree height (cavity trees =  $18.1 \pm 1.6$

m; random trees =  $15.5 \pm 1.3$  m;  $t = 1.27$ ,  $df = 27$ ,  $P = 0.216$ ) or number of access routes (cavity trees =  $3.1 \pm 0.5$  trees; random trees =  $3.9 \pm 0.4$  trees;  $t = 1.38$ ,  $df = 27$ ,  $P = 0.180$ ).

Slope aspect did not differ between aspen cavity and random sites ( $\chi^2 = 0.63$ ,  $df = 3$ ,  $n = 29$ ,  $P = 0.889$ ). Out of 24 site variables (Table 1), 5 discriminated between aspen cavity and random sites (Table 2: Wilks'  $\lambda = 0.324$ ,  $F = 9.59$ ,  $df = 5$ , 23,  $P < 0.0001$ ). Aspen cavity and random sites differed among all selected characteristics except dead trees/ha and medium trees/ha, as indicated by the correlation between the discriminant function (eigenvalue = 2.084,  $F = 9.59$ ,  $df = 5$ , 23,  $P < 0.0001$ ) and original variables (Table 2). Aspen cavity sites had more large snags and less ponderosa pine and were less steep than aspen random sites (mean discriminant scores: aspen cavity sites =  $-1.658 \pm 0.203$ ; aspen random sites =  $1.170 \pm 0.282$ ).

**DISCUSSION**—Abert's squirrels possibly used cavities in larger aspen trees because trees with thick trunks provide stability and protection from the effects of wind and cold (Halloran and Bekoff, 1994), older trees have more time to develop suitable cavities, or thick trunks facilitate formation of cavities large enough to be used by Abert's squirrels. Eastern gray squirrels (*S. carolinensis*), fox squirrels (*S. niger*), and northern flying squirrels (*Glaucomys sabrinus*) also select cavity nest trees that are larger than random trees (Sanderson et al., 1975; Kantola and Humphrey, 1990; Hackett and Pagels, 2003; Menzel et al., 2004).

The higher number of large snags on aspen cavity sites compared to random sites could allow Abert's squirrels access to more potential cavity nest trees. The steeper slopes found on aspen random sites compared to cavity sites might be drier, sunnier, and have a shorter fire interval that would favor growth of ponderosa pine over large aspen (Burns and Honkala, 1990) and decrease persistence of snags.

The rare use (2% of nests found) of cavities by Abert's squirrels in monotypic ponderosa pine forests (Halloran and Bekoff, 1994) might be due to the paucity of large cavity-forming tree species. Ponderosa pine is resistant to rot and rarely forms cavities (Brown, 1984). Aspens are susceptible to rot, which allows birds to excavate cavities easily (Aitken et al., 2002).

TABLE 1—Physical and vegetational characteristics (mean  $\pm$  SE) of aspen (*Populus tremuloides*) random sites and cavity nest sites used by Abert's squirrel (*Sciurus aberti*) in mixed-conifer forests of the Pinaleno Mountains, Arizona.

Site characteristics	Cavity ( $n = 12$ )	Random ( $n = 17$ )
Basal area (m <sup>2</sup> /ha)	72.9 $\pm$ 7.8	57.7 $\pm$ 6.5
% slope	10.9 $\pm$ 2.3	21.8 $\pm$ 2.0
% canopy cover <sup>a</sup>	78.2 $\pm$ 3.5	78.5 $\pm$ 3.0
% canopy cover at 0 m	84.5 $\pm$ 3.1	88.8 $\pm$ 2.6
% canopy cover at 5 m	79.6 $\pm$ 4.4	74.7 $\pm$ 3.7
% canopy cover at 10 m	70.4 $\pm$ 5.6	71.8 $\pm$ 4.7
Canopy cover CV <sup>b</sup>	25.6 $\pm$ 4.9	28.3 $\pm$ 4.1
Logs/ha	186.1 $\pm$ 35.9	118.0 $\pm$ 30.2
Trees/ha	1,500.0 $\pm$ 182.9	1,769.4 $\pm$ 153.6
Live trees/ha	1,044.4 $\pm$ 142.3	1,144.0 $\pm$ 119.6
Dead trees/ha	455.6 $\pm$ 111.5	625.4 $\pm$ 93.7
Small trees/ha <sup>c</sup>	975.0 $\pm$ 200.2	1,284.5 $\pm$ 168.2
Medium trees/ha <sup>d</sup>	350.0 $\pm$ 58.5	387.6 $\pm$ 49.2
Large trees/ha <sup>e</sup>	175.5 $\pm$ 25.4	97.4 $\pm$ 21.3
Large snags/ha <sup>f</sup>	41.7 $\pm$ 10.5	19.6 $\pm$ 8.9
Engelmann spruce/ha	547.2 $\pm$ 90.5	271.5 $\pm$ 76.0
Corkbark fir/ha	586.1 $\pm$ 146.7	458.7 $\pm$ 123.3
Douglas-fir/ha	102.8 $\pm$ 44.9	134.8 $\pm$ 37.7
White fir/ha	2.8 $\pm$ 2.5	1.9 $\pm$ 2.1
Aspen/ha	197.2 $\pm$ 204.5	711.5 $\pm$ 171.8
Southwestern white pine/ha	63.9 $\pm$ 71.1	166.6 $\pm$ 59.7
Ponderosa pine/ha	0.0 $\pm$ 4.4	13.1 $\pm$ 3.7
Deciduous trees/ha <sup>g</sup>	0.0 $\pm$ 5.2	5.6 $\pm$ 4.3
Simpson's diversity index	2.49 $\pm$ 0.28	2.44 $\pm$ 0.23

<sup>a</sup> All distances combined.

<sup>b</sup> CV = Coefficient of variation.

<sup>c</sup> Trees <20 cm diameter at breast height (DBH).

<sup>d</sup> Trees  $\geq$ 20 cm DBH and  $\leq$ 40 cm DBH.

<sup>e</sup> Trees >40 cm DBH.

<sup>f</sup> Dead trees >40 cm DBH.

<sup>g</sup> Excluding aspen.

Thus, secondary cavity nesters, such as the Abert's squirrels, likely had greater access to cavities at our study site because aspens are common in mixed-conifer forests of the Pinaleno Mountains. Abert's squirrels in ponderosa pine forests will use nest boxes (Pederson et al., 1978), suggesting that the lack of suitable cavity nests in this forest type rather than nesting behavior explains the rare use of cavity nests.

Harsher winter conditions might also contribute to the higher use of cavity nests seen in our study. Mixed-conifer forests are located higher in elevation than ponderosa pine forests and, as a result, have more extreme winters (i.e., cold and snow) (Brown, 1982). The higher frequency of communal nesting by Abert's

squirrels in mixed-conifer forests than ponderosa pine forests also suggests that thermal conditions are harsher in the former (Lema et al., 1999; Edelman and Koprowski, unpublished data). Furthermore, Abert's squirrels use cavity nests for communal nesting at a higher frequency than expected by availability in mixed-conifer forests (Edelman and Koprowski, unpublished data). Thus, the additional insulation that cavity nests provide compared to dreys possibly contributes to the increased use of cavity nests in our population.

Use of cavity nests in mixed-conifer forests by Abert's squirrels, suggests that this species is not strictly dependent on ponderosa pine for nest sites as previously reported. Other factors, such as interspecific competition with sympat-

TABLE 2—Correlation between original variables selected in stepwise discriminant function analysis and discriminant function for aspen (*Populus tremuloides*) random sites and cavity nest sites used by Abert's squirrel (*Sciurus aberti*) in mixed-conifer forests of the Pinaleno Mountains, Arizona.

Site characteristics	Correlation with discriminant function	
	<i>r</i>	<i>P</i>
% slope	0.702	<0.001
Ponderosa pine/ha	0.519	0.004
Large snags/ha <sup>a</sup>	-0.467	0.011
Dead trees/ha	0.298	0.116
Medium trees/ha <sup>b</sup>	-0.035	0.857

<sup>a</sup> Dead trees >40 cm diameter at breast height (DBH).

<sup>b</sup> Trees  $\geq$ 20 cm DBH and  $\leq$ 40 cm DBH.

ric tree squirrel species, might prevent Abert's squirrels from extensively using non-ponderosa pine forests in their natural range (Ferner, 1974; Edelman, 2004). Future research should focus on examining the specific mechanisms that restrict natural populations of Abert's squirrels to ponderosa pine forests. Forest management prescriptions also must incorporate the potential value of cavities to Abert's squirrels because the availability of cavities might provide a tool to increase or decrease abundance of this species.

The endangered Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) also inhabits mixed-conifer and spruce-fir forests of the Pinaleno Mountains (Froehlich, 1990). Introduced Abert's squirrels have been suggested to compete for resources with the Mount Graham red squirrel, possibly contributing to their decline (Spicer, 1985). Almost 50% of Mount Graham red squirrel nests are found in cavities (Young et al., 2002). Competition for limited nest sites with Abert's squirrels could negatively impact the Mount Graham red squirrel. The potential negative consequences further emphasize the need for management plans to address the response of introduced Abert's squirrels relative to that of the endangered native red squirrel. Currently, we are comparing nest use between these 2 species to determine the amount of overlap in nest characteristics and the potential for nest site competition.

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