

DIET AND TREE USE OF ABERT'S SQUIRRELS (*SCIURUS ABERTI*) IN A MIXED-CONIFER FOREST

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ABSTRACT—Abert's squirrels (*Sciurus aberti*) are reported to be dependent on ponderosa pine (*Pinus ponderosa*) forests for food, cover, and nest sites. Introduced Abert's squirrels in the Pinaleno Mountains of Arizona, however, occupy forests that contain little to no ponderosa pine. We documented diet and tree use of Abert's squirrels in mixed-conifer forests of the Pinaleno Mountains using observations of marked animals. Individuals ate similar food items as Abert's squirrels in ponderosa pine forests, including seeds, inner bark, buds, and fungi, but 5 conifer species were used as food sources. Douglas-fir (*Pseudotsuga menziesii*) and southwestern white pine (*Pinus strobiformis*) were the most frequently eaten conifer species. Abert's squirrels also were observed in all tree species. Our results suggest that the dependence of Abert's squirrels on ponderosa pine is not as strong as previously reported.

RESUMEN—Se registra que las ardillas arbóreas de Abert (*Sciurus aberti*) son dependientes de los bosques del pino ponderosa (*Pinus ponderosa*) para comida, cobijo, y sitios para anidar. Las ardillas arbóreas de Abert que fueron introducidas en las Montañas Pinalenos de Arizona, sin embargo, ocupan bosques que contienen poco a ningún pino ponderosa. Documentamos la dieta y el uso de los árboles de las ardillas arbóreas Abert en bosques de coníferas mixtas de las Montañas Pinalenos observando animales marcados. Los individuos ingirieron comida similar que las ardillas de Abert viviendo en los bosques de pino ponderosa, incluyendo semillas, corteza interior, retoños, y hongos, pero cinco especies de coníferas fueron usadas como fuentes de alimento. Abeto de Douglas (*Pseudotsuga menziesii*) y pino blanco (*Pinus strobiformis*) fueron las especies de coníferas más ingeridas. También se observaron las ardillas arbóreas de Abert en todas las especies de árboles. Nuestros resultados sugieren que la dependencia de las ardillas arbóreas de Abert al pino ponderosa no es tan fuerte como se registró antes.

The Abert's squirrel (*Sciurus aberti*) typically occurs in ponderosa pine (*Pinus ponderosa*) forests in Arizona, Colorado, New Mexico, Utah, and Wyoming in the United States and in Chihuahua and Durango in Mexico (Nash and Seaman, 1977). The Abert's squirrel is reportedly 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). Ponderosa pine seeds, apical buds, staminate cones, inner bark, and associated hypogeous fungi are the primary food sources of Abert's squirrels in ponderosa pine forests (Keith, 1965; Stephenson, 1975; Farentinos et al., 1981; Kotter and Farentinos, 1984; States et al., 1988). A review of evidence from natural and

introduced populations, however, suggests that the dependence of Abert's squirrels on ponderosa pine might be overstated (Edelman and Koprowski, in press). Individuals have been observed in oak-dominated woodland (Baker and Greer, 1962), piñon pine (*Pinus edulis*) woodland (Reynolds, 1966), mixed-conifer forests (Findley et al., 1975; Hall, 1981), spruce-fir forests (Allen, 1895; Pedersen et al., 1976), and alpine tundra (Cooper, 1987).

One example of Abert's squirrels occupying vegetative communities other than ponderosa pine forests occurs in the Pinaleno Mountains of Arizona. In this isolated mountain range, introduced Abert's squirrels occupy mixed-conifer and spruce-fir forests that contain little to no ponderosa pine. Observations in the Pinaleno Mountains have recorded Abert's squir-

rels using a variety of conifer species for food and nest sites (Hutton et al., 2003; Edelman, 2004). Herein, we document diet and tree use of Abert's squirrels in a mixed-conifer forest of the Pinaleno Mountains.

METHODS—Study Area—Abert's squirrels were introduced into the Pinaleno Mountains, 25 km southwest of Safford, Arizona in the 1940s (Davis and Brown, 1988) and inhabit all forested environments from pine-oak forests (elevation 1,830 m) through spruce-fir forests (elevation 3,270 m) (Edelman and Koprowski, in press). Our study site encompassed 110 ha of mixed-conifer forest from ca. 2,850 to 3,170 m elevation. Dominant tree species were corkbark fir (*Abies lasiocarpa* var. *arizonica*, 52.2%), Engelmann spruce (*Picea engelmannii*, 17.6%), Douglas-fir (*Pseudotsuga menziesii*, 12.2%), and aspen (*Populus tremuloides*, 10.5%), with smaller amounts of southwestern white pine (*Pinus strobiformis*, 6.0%), ponderosa pine (1.1%), and white fir (*Abies concolor*, 0.4%). The first published sighting of Abert's squirrels on the study site occurred in 1952 (Hoffmeister, 1956).

Live-trapping—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 peanut butter to trap squirrels. 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 ($n = 47$ individuals). Adults (>600 g) were fitted with radio collars (Model SOM 2380, Wildlife Materials, Inc., Carbondale, Illinois) that weighed $<5\%$ of body mass ($n = 35$ individuals).

Observations—We observed diet ($n = 85$) and tree use ($n = 216$) of Abert's squirrels opportunistically during the course of a radio-telemetry study from September 2001 to September 2003 (Edelman, 2004). We identified food items and recorded tree species used by individuals. Observations in nest trees were excluded from tree-use data. Most observations of diet (81.2%, $n = 15$ individuals) and tree use (93.5%, $n = 19$ individuals) were taken from marked individuals.

Data Analysis—We conducted statistical analyses using JMP-IN (SAS Institute, Inc., 2003). Observations of diet were tested using Pearson's χ^2 goodness-of-fit test. Observations of Abert's squirrels in different tree species and feeding on conifer species were compared to availability of tree species on the study

site using a χ^2 goodness-of-fit test with Bonferroni-corrected confidence intervals (Manly et al., 2002).

RESULTS—Diet—Abert's squirrels were observed foraging on 11 food items, including conifer seeds ($n = 42$), conifer apical buds ($n = 15$), conifer inner bark ($n = 10$), conifer staminate flowers ($n = 8$), hypogeous fungi ($n = 3$), pecans left by humans ($n = 3$), epigeous fungi ($n = 1$), dwarf mistletoe (*Arceuthobium microcarpum*) in Engelmann spruce ($n = 1$), road dirt ($n = 1$), and water ($n = 1$).

Frequency of foraging on the 4 conifer food items differed (Table 1; $\chi^2 = 39.83$, $df = 3$, $P < 0.0001$). Seeds were the most frequent conifer food item (56.0%), whereas apical buds (20.0%), inner bark (13.3%), and staminate flowers (10.7%) were less frequently ingested. Abert's squirrel use of conifer species for food differed from availability on the study area ($\chi^2 = 1534.15$, $df = 4$, $P < 0.0001$). Douglas-fir ($44.0 \pm 14.7\%$ observed vs. 13.7% expected) and southwestern white pine ($34.7 \pm 14.1\%$ observed vs. 6.7% expected) were used more than expected by availability. Engelmann spruce ($13.3 \pm 10.1\%$ observed vs. 19.8% expected) and ponderosa pine ($5.3 \pm 6.7\%$ observed vs. 1.2% expected) were used as frequently as expected by availability. Corkbark fir ($2.7 \pm 4.8\%$ observed vs. 58.6% expected) was used less than expected by availability. Use of conifer seeds (Table 1; $\chi^2 = 15.86$, $df = 2$, $P = 0.0004$) and apical buds (Table 1; $\chi^2 = 14.80$, $df = 2$, $P = 0.0006$) differed between conifer species. Southwestern white pine (59.5%) and Douglas-fir (31.0%) were the most common species of seeds eaten, whereas use of ponderosa pine seeds (9.5%) occurred at lower amounts and corkbark fir and Engelmann spruce seeds were never eaten. Most foraging on apical buds occurred in Douglas-fir (80.0%) with lesser amounts in corkbark fir (13.3%) and southwestern white pine (6.7%) and none in Engelmann spruce or ponderosa pine. Foraging on inner bark and staminate flowers only occurred in Engelmann spruce and Douglas-fir, respectively (Table 1). Signs of inner bark feeding (i.e., peeled twigs and cut terminal branches beneath trees) on southwestern white pine, ponderosa pine, and corkbark fir also were observed on the study area, but not during observations of squirrels.

Tree Use—Abert's squirrel use of tree species

TABLE 1—Observations of food items of different conifer species eaten by Abert's squirrels (*Sciurus aberti*) in a mixed-conifer forest of the Pinaleno Mountains, Arizona.

Conifer species	n	Food item frequency			
		Seeds	Apical buds	Inner bark	Staminate flowers
Douglas-fir	33	13	12	0	8
Southwestern white pine	26	25	1	0	0
Engelmann spruce	10	0	0	10	0
Ponderosa pine	4	4	0	0	0
Corkbark fir	2	0	2	0	0
Total	75	42	15	10	8

differed from availability on the study area (Table 2; $\chi^2 = 250.33$, $df = 6$, $P < 0.0001$). Douglas-fir was the most commonly used tree species by Abert's squirrels, with use 3 times more frequent than expected by availability. Southwestern white pine and ponderosa pine also were used more frequently than expected by availability. Engelmann spruce and white fir were used as frequently by Abert's squirrels as expected by availability. Corkbark fir and aspen were both used less than expected by availability.

DISCUSSION—Abert's squirrels introduced into the Pinaleno Mountains ate conifer food items, such as apical buds, staminate flowers, seeds, and inner bark and associated mistletoe and fungi, as in natural populations; however, ponderosa pine represented only a small percentage of conifer food, and all conifer species except the rare white fir (0.4%) were eaten. We observed a wider range in diet than previously recorded for Abert's squirrels in the Pin-

aleño Mountains, probably due to the large number of observations (Hutton et al., 2003). Previous observations only recorded Abert's squirrels feeding on fungi and seeds from Douglas-fir, southwestern white pine, and corkbark fir (Hutton et al., 2003). Abert's squirrels in mixed-conifer forests used all tree species as cover. In natural populations, Abert's squirrels typically only use ponderosa pine trees for cover (Patton, 1975; Lema, 2001).

The use of multiple conifer species for food and cover by Abert's squirrels in mixed-conifer forests suggests that this species is not strictly dependent on ponderosa pine as previously reported. Abert's squirrels in natural populations also have been observed eating non-ponderosa pine food items, including seeds and inner bark of piñon pine (Reynolds, 1966; Ratcliff et al., 1975; Soderquist, 1987) and Douglas-fir (Ratcliff et al., 1975; Stephenson, 1975), Gambel oak (*Quercus gambeli*) acorns (Stephenson, 1975; Soderquist, 1987; Forbes, 1997), juniper (*Juniperus osteosperma*) seeds (Soderquist,

TABLE 2—Abert's squirrel (*Sciurus aberti*) observed use of trees species compared to availability in a mixed-conifer forest of the Pinaleno Mountains, Arizona.

Tree species	Tree frequency		% availability
	n	% \pm 95% C.I. ^a	
Douglas-fir	83	38.4 \pm 8.9	12.2
Engelmann spruce	52	24.1 \pm 7.8	17.6
Southwestern white pine	36	16.7 \pm 6.8	6.0
Corkbark fir	31	14.3 \pm 6.4	52.2
Ponderosa pine	12	5.6 \pm 4.2	1.1
White fir	1	0.5 \pm 1.2	0.4
Aspen	1	0.5 \pm 1.2	10.5

^a C.I. = Bonferroni-corrected half width.

1987), and dwarf mistletoe (*Arceuthobium vaginatum*) berries and tissue (Stephenson, 1975; Pederson et al., 1987). Ponderosa pine might be the main food and cover source for Abert's squirrels in natural populations simply because other conifer species are not common in monotypic ponderosa pine forests (Brown, 1982). Other factors, such as interspecific competition with sympatric tree squirrel species, might prevent Abert's squirrels from extensively using non-ponderosa pine forests in their natural range (Ferner, 1974; Edelman, 2004).

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). Mount Graham red squirrels feed on many of the same food items as Abert's squirrels, including epigeous and hypogeous fungi and seeds of all conifer species (Froehlich, 1990). Abert's squirrel use of these food and cover resources could limit their availability for the Mount Graham red squirrel. The ecological impacts of the other 9 introduced populations of Abert's squirrels in Arizona and New Mexico (Davis and Brown, 1988) are still unknown.

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