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SELECTION OF DREY SITES BY ABERT'S SQUIRRELS IN AN INTRODUCED POPULATION

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Abert's squirrels (*Sciurus aberti*) are reported to depend on ponderosa pine (*Pinus ponderosa*) for food and nest sites. Introduced Abert's squirrels in the Pinaleño Mountains of Arizona, however, occupy mixed-conifer forests that contain almost no ponderosa pine (about 2%). We examined selection of drey sites in this introduced population. Dreys (i.e., spherical nests) were built adjacent to the trunk at 75% of the tree height. Dreys were found in 5 different conifer species and <2% were in ponderosa pine. Drey trees were larger and had more access routes than did random trees. Drey sites were steeper, had more large trees, Douglas-fir (*Pseudotsuga menziesii*), and southwestern white pine (*Pinus strobiformis*), and less corkbark fir (*Abies lasiocarpa* var. *arizonica*) than random sites. The structural characteristics of drey trees in the Pinaleños population also were very similar to drey trees used by natural populations of Abert's squirrels in ponderosa pine forests. Our results suggest that the dependence of Abert's squirrels on ponderosa pine is not as strong as previously reported. Structural features such as tree size and access routes appear to be more important to selection of drey sites than tree species.

Key words: Arizona, bolus nest, exotic species, Mt. Graham red squirrel, nest-site selection, Pinaleño Mountains, obligate, *Sciurus aberti*, *Tamiasciurus hudsonicus grahamensis*, tassel-eared squirrel

Colonizing populations are frequently exposed to novel conditions ranging from environmental changes in climate, vegetation, and food sources to variations in interspecific interactions with predators, competitors, and parasites (Lever 1994). As a result, differentiation from source populations in morphology or behavior can occur (Goheen et al. 2003; Johnston and Selander 1971; St. Louis and Barlow 1991). In herbivores with specialized plant associations, exposure to novel plant species can cause modifications in diet and habitat use (Carroll and Boyd 1992; Trowbridge 2004) among individuals in colonizing populations. Behavioral changes in response to novel plant species can be the result of intrinsic characteristics in the colonizing population such as founder effects, genetic drift, local adaptation, phenotypic plasticity, preadaptation that allows use of novel species, and modification of behavior through learning or can be extrinsic conditions including quality and abundance of plant species and interactions with interspecific competitors (Fox and Morrow 1981; Losos et al. 1997, 2001; Marohasy 1996; Thomas et al. 2001).

Abert's squirrel (*Sciurus aberti*) is reportedly a specialized herbivore that depends on ponderosa pine (*Pinus ponderosa*) for food and nest sites (Hall 1981; Halloran and Bekoff 1994; Keith 1965; Patton and Green 1970; Pederson et al. 1976; Snyder 1993; States and Wettstein 1998; Stephenson 1975). The extent of dependence of Abert's squirrels on ponderosa pine has been compared to highly specialized mammalian herbivores such as the koala (*Phascolarctos cinereus*) and giant panda (*Ailuropoda melanoleuca*—Murphy and Linhart 1999; Synder and Linhart 1994). However, a review of evidence from natural and introduced populations suggests that the dependence of Abert's squirrels on ponderosa pine is overstated (Edelman and Koprowski, in press a). One example of Abert's squirrels occupying vegetative communities other than ponderosa pine forests occurs in the Pinaleño 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. The introduced population of Abert's squirrels in the Pinaleño Mountains provides a natural experiment for examining the reported dependence of this species on ponderosa pine. Anecdotal observations in the Pinaleño Mountains indicate that Abert's squirrels use a variety of conifer species for food and nest sites (Edelman and Koprowski, in press a; Hutton et al. 2003).

Nests are important resources for tree squirrels that provide a location to raise young, rest, avoid predators, and escape inclement weather (Steele and Koprowski 2001). Tree squirrels use ground nests, cavity nests, and spherical nests constructed from leaves and twigs called dreys (Gurnell 1987). The most

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common nests used by Abert's squirrels are dreys; cavities are rarely used and burrows are never used (Halloran and Bekoff 1994). Abert's squirrel dreys are almost exclusively built in ponderosa pine trees that are larger and more connected with neighboring trees than are nondrey trees (Halloran and Bekoff 1994). Tree chemistry also is reported to differ between ponderosa pine drey and nondrey trees (Snyder and Linhart 1994), suggesting that species-specific chemical cues may aid in nest-site selection of Abert's squirrels.

The objective of our study was to examine selection of drey sites by an introduced population of Abert's squirrels occupying a mixed-conifer forest where ponderosa pine is extremely uncommon. Based on our previous observations of this population, we expected Abert's squirrels in the Pinaleño Mountains to construct dreys in a variety of conifer species other than ponderosa pine. We predicted that structural characteristics of drey sites would be similar to those described in previous studies on Abert's squirrels in ponderosa pine forests.

MATERIALS AND METHODS

Study area.—The study area was located in the Pinaleño Mountains, 25 km southwest of Safford, Arizona. Abert's squirrels were introduced to the Pinaleño Mountains in the 1940s (Davis and Brown 1988) and inhabit all forested environments from pine–oak forests through spruce–fir forests (Edelman and Koprowski, in press a). Our site encompassed 110 ha of mixed-conifer forest from about 2,850 to 3,170 m in elevation. Dominant tree species were corkbark fir (*Abies lasiocarpa* var. *arizonica*, 41%), Engelmann spruce (*Picea engelmannii*, 20%), aspen (*Populus tremuloides*, 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%). The 1st published record of a sighting of Abert's squirrels on our study site occurred in 1952 (Hoffmeister 1956).

Nest identification.—We used 48 × 15 × 15-cm box traps constructed of 1.3 × 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.) were attached to captured squirrels. Adults (>600 g) were fitted with radiocollars (model SOM 2380, Wildlife Materials, Inc., Carbondale, Illinois) that weighed <5% of body mass. Handling of animals was in accordance with the University of Arizona Institutional Animal Care and Use Committee and the guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998). Nest locations were obtained by homing (White and Garrott 1990) on radiocollared squirrels from September 2001 to September 2003. Average number (± *SE*) of nests found per squirrel ($n = 37$) was 5.7 ± 0.8. Dreys accounted for the majority of nests found (90.2%); cavity nests were excluded from analyses.

Tree and site measurements.—For each drey, we recorded height, support structure, distance from trunk, and compass direction from trunk. Drey support structure consisted of lateral branches or natural depressions created by branches at the apex of trees. For each tree with a drey, we recorded species, condition, diameter at breast height (DBH), height, live canopy length (i.e., the vertical length of tree that was covered in live branches), and number of trees (≥10 cm DBH) with branches within 0.5 m of any part of the drey tree (i.e., access routes). We used a clinometer to measure tree height, drey height, and live canopy length.

Within a 10-m-radius circular plot (0.03 ha) surrounding the drey tree, we recorded species, condition, and DBH of each tree ≥3 cm DBH and number of logs ≥20 cm diameter and ≥2 m length. Percent slope (% slope) and slope aspect were measured at each site. Canopy cover was measured by using a spherical densiometer (model C, Forest Densiometers, Bartlesville, Okalahoma) at 0, 5, and 10 m from the nest tree in the 4 cardinal directions (north, south, west, and east); measurements for each plot were averaged for each distance (% canopy cover at 0, 5, and 10 m) and for the plot (% canopy cover). Coefficient of variation of canopy cover (canopy cover *CV*) was calculated to measure the variability of canopy cover within the plot. Tree condition was classified by using the following 5 classes: (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 each site. Based on the measurements taken at sites, we calculated the following variables (number per ha): logs (logs/ha), trees (trees/ha), live trees (live trees/ha), dead trees (dead trees/ha), trees with <20 cm DBH (small trees/ha), trees with ≥20 cm DBH and ≤40 cm DBH (medium trees/ha), trees with >40 cm DBH (large trees/ha), Engelmann spruce (Engelmann spruce/ha), corkbark fir (corkbark fir/ha), Douglas-fir (Douglas-fir/ha), white fir (white fir/ha), aspen (aspen/ha), southwestern white pine (southwestern white pine/ha), ponderosa pine (ponderosa pine/ha), and deciduous trees excluding aspen (deciduous trees/ha).

For comparison with drey trees and sites, we selected a stratified sample ($n = 69$) of random trees (≥10 cm DBH) in the study area and measured the same variables as at the drey trees and sites. Random trees were selected in 5 categories based on tree types used by Abert's squirrels for dreys: live corkbark fir, live Engelmann spruce, live Douglas-fir, live southwestern white pine, and recently dead conifers (condition class 2). A subset of random trees ($n = 28$) along with associated sites was randomly selected from the 5 strata based on the proportional availability of each strata in the study area (Krebs 1998).

Data analysis.—We conducted all statistical analyses by using JMP-IN (SAS Institute Inc. 2003) and SAS (SAS Institute Inc. 2002). Count variables were cube root transformed, proportions were arcsine transformed, and DBH was log transformed to better meet the assumptions of parametric and multivariate tests (Zar 1984); however, means ± *SE* reported in results are calculated from untransformed values. We analyzed categorical data by using Pearson chi-square tests. We used 2-tailed *t*-tests to test for differences between characteristics of drey trees and random trees. One-way analysis of variance (ANOVA) followed by post hoc Tukey–Kramer tests were used to compare variation in characteristics of random trees between tree species. Differential use of tree species for dreys was compared to availability of tree species on the study site by using a chi-square goodness-of-fit test with Bonferroni-corrected confidence intervals (Manly et al. 2002).

Stepwise discriminant function analysis (DFA) was used to select variables that best discriminated between drey and random trees and sites. Selection criteria for entry and removal of variables in stepwise DFA was $F = 0.15$. Variables selected in stepwise DFA were then analyzed by using DFA. To prevent multicollinearity, high pairwise correlations ($r > 0.70$) between variables were identified before stepwise DFA. For each pair of highly correlated variables, only the variable that best discriminated between drey and random trees or sites

Table 1.—Abert's squirrel (*Sciurus aberti*) use of tree species for dreys compared to tree-species availability in a mixed-conifer forest of the Pinaleño Mountains, Arizona.

	Drey tree frequency		
Tree species	*n*	% ± 95% *CI*[a]	% availability
Corkbark fir	30	23.3 ± 9.6	57.0
Douglas-fir	61	47.3 ± 11.3	18.2
Engelmann spruce	22	17.1 ± 8.5	16.3
Southwestern white pine	14	10.9 ± 7.0	7.2
Ponderosa pine	2	1.6 ± 2.8	1.3

[a] *CI* = Bonferroni-corrected confidence interval.

(higher F value in 1-way ANOVA) was used in stepwise DFA (McGarigal et al. 2000).

Results

Dreys.—Almost all dreys were built against the main trunk of trees (distance to trunk = 0.1 ± 0.1 m, range = 0–8 m, n = 129). Most dreys were supported by a lateral branch (91%, n = 117), although a small number were placed in natural depressions at the apex of trees (9%, n = 12). Dreys were built at a height of 15.6 ± 0.3 m (n = 129) and at about 75% of the tree height (ratio of drey height to tree height = 0.733 ± 0.012, n = 129). Dreys were built most frequently on the south (32.8%) and east (29.3%) sides of trees and less frequently on north (22.4%) and west (15.5%) sides ($\chi^2 = 8.14$, $d.f. = 3$, $n = 116$, $P = 0.043$).

Drey trees.—Dreys were usually built in live trees (94.6%, n = 122), but a small number (5.4%, n = 7) also were found in recently dead trees (condition class 2). Abert's squirrels used 5 species of conifers for drey trees (Table 1), which differed from the availability of tree species ($\chi^2 = 76.93$, $d.f. = 4$, $n = 129$, $P < 0.001$). Use of Douglas-fir for dreys was more than twice the availability and almost one-half of dreys were found in this species. About 25% of dreys were found in corkbark fir, but use by Abert's squirrels was one-half of the availability. Smaller amounts of Engelmann spruce, southwestern white pine, and ponderosa pine were used for dreys in similar proportions to their availability.

Drey trees were larger and taller than random trees (Table 2). Live canopy length was larger in drey trees than random trees, and the live canopy length to tree height ratio (live canopy length/tree height) was smaller in drey trees than random trees (Table 2). Drey trees also had more access routes than did random trees (Table 2). Differences between drey and random trees varied between the 5 tree types used by Abert's squirrels (Table 2). For all tree types, drey trees were taller with greater girth than random trees. Live canopy length was larger in live corkbark fir, live Douglas-fir, and live southwestern white pine drey trees than random trees, but was not different between live Engelmann spruce drey trees and random trees. Live canopy length/tree height did not differ between drey trees and random trees of any tree types except live corkbark fir, where drey trees had smaller live canopy length/tree height than random trees. Number of access routes was greater for live corkbark fir and live Douglas-fir drey trees than for random trees, but did not

Table 2.—Characteristics of drey trees of Abert's squirrels (*Sciurus aberti*) compared to random trees in a mixed-conifer forest of the Pinaleño Mountains, Arizona. Asterisk (*) denotes difference between drey and random trees ($P < 0.05$, 2-sided t-test).

		Tree measurements				
		DBH (cm)	Height (m)	Live canopy length (m)	Live canopy length/tree height	Number of access routes[a]
Tree group	*n*	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$	$\bar{X} \pm SE$
All combined						
Drey	129	59.9 ± 2.4	21.7 ± 0.4	14.4 ± 0.5	0.668 ± 0.020	5.1 ± 0.2
Random	28	28.6 ± 5.2*	13.7 ± 0.9*	10.0 ± 1.0*	0.750 ± 0.044*	3.7 ± 0.4*
Live Engelmann spruce						
Drey	18	38.0 ± 2.4	18.9 ± 1.0	12.6 ± 1.0	0.667 ± 0.046	4.8 ± 0.7
Random	15	26.1 ± 2.6*	13.3 ± 1.0*	9.8 ± 1.1	0.753 ± 0.051	5.5 ± 0.7
Live corkbark fir						
Drey	27	39.3 ± 1.7	20.6 ± 0.7	16.4 ± 0.6	0.799 ± 0.021	5.7 ± 0.4
Random	15	24.0 ± 2.3*	13.4 ± 1.0*	11.7 ± 0.8*	0.895 ± 0.028*	4.1 ± 0.5*
Live Douglas-fir						
Drey	61	77.7 ± 3.8	23.0 ± 0.7	15.7 ± 0.6	0.684 ± 0.09	4.7 ± 0.3
Random	14	42.4 ± 8.0*	15.8 ± 1.5*	10.0 ± 1.3*	0.663 ± 0.040	3.1 ± 0.6*
Live southwestern white pine						
Drey	14	58.0 ± 4.6	21.6 ± 1.4	15.5 ± 1.0	0.721 ± 0.041	5.6 ± 0.6
Random	16	32.5 ± 4.2*	15.7 ± 1.3*	9.7 ± 1.0*	0.653 ± 0.043	4.5 ± 0.6
Recently dead trees						
Drey	7	44.5 ± 5.2	22.0 ± 1.7	—	—	4.9 ± 0.9
Random	9	29.1 ± 4.7*	14.1 ± 1.5*	—	—	4.2 ± 0.7

[a] Number of trees (≥10 cm diameter at breast height) that have branches within 0.5 m of any part of the focal tree.

Table 3.——Physical and vegetational characteristics of drey sites of Abert's squirrels (*Sciurus aberti*) compared to random sites in a mixed-conifer forest of the Pinaleño Mountains, Arizona.

	Drey ($n = 129$)	Random ($n = 28$)
Site characteristics	$\bar{X} \pm SE$	$\bar{X} \pm SE$
Basal area (m^2/ha)	69.1 ± 2.0	56.9 ± 4.2
% slope	22.8 ± 1.1	12.0 ± 2.4
% canopy cover[a]	80.3 ± 1.0	76.6 ± 2.1
% canopy cover at 0 m	87.9 ± 1.1	87.1 ± 2.3
% canopy cover at 5 m	77.7 ± 1.2	72.2 ± 2.6
% canopy cover at 10 m	75.3 ± 1.4	70.6 ± 2.9
Canopy cover *CV*[b]	23.3 ± 1.2	28.1 ± 2.6
Logs/ha	103.4 ± 9.0	143.2 ± 19.3
Trees/ha	1382.8 ± 53.8	1526.8 ± 115.5
Live trees/ha	935.2 ± 47.0	1131.1 ± 100.8
Dead trees/ha	447.6 ± 25.0	395.6 ± 53.6
Small trees/ha[c]	867.6 ± 49.8	1074.3 ± 106.8
Medium trees/ha[d]	369.6 ± 18.8	355.8 ± 40.3
Large trees/ha[e]	146.6 ± 6.2	96.6 ± 13.4
Engelmann spruce/ha	269.5 ± 26.7	279.7 ± 57.4
Corkbark fir/ha	489.1 ± 49.5	841.3 ± 106.2
Douglas-fir/ha	230.0 ± 24.5	110.3 ± 52.6
White fir/ha	29.1 ± 9.2	1.1 ± 19.7
Aspen/ha	178.4 ± 32.9	216.0 ± 70.6
Southwestern white pine/ha	143.6 ± 12.9	63.7 ± 27.7
Ponderosa pine/ha	22.7 ± 4.2	13.6 ± 8.9
Deciduous trees/ha[f]	14.1 ± 3.8	0.0 ± 8.2
Simpson's diversity index	2.68 ± 0.09	2.37 ± 0.18

[a] All distances combined.
[b] *CV* = Coefficient of variation.
[c] Trees < 20 cm diameter at breast height (DBH).
[d] Trees ≥ 20 cm DBH and ≤ 40 cm DBH.
[e] Trees > 40 cm DBH.
[f] Excluding aspen.

differ within any other tree types. The 4 species of random trees (Table 2) differed in DBH ($F = 3.6$, *d.f.* = 3, 64, $P = 0.019$), but not tree height, live canopy length, live canopy length/tree height, or number of access routes ($F < 2.2$, *d.f.* = 3, 64, $P > 0.10$). Douglas-fir random trees were similar in DBH to southwestern white pine random trees (Tukey–Kramer, $P > 0.05$), but Douglas-fir random trees were larger than Engelmann spruce and corkbark fir random trees (Tukey–Kramer, $P < 0.05$). Southwestern white pine, live Engelmann spruce, and live corkbark fir random trees did not differ in DBH (Tukey–Kramer, $P > 0.05$).

Tree size as indicated by DBH and number of access routes discriminated between drey and random trees (Wilks' $\lambda = 0.625$, $F = 46.23$, *d.f.* = 2, 154, $P < 0.0001$). The discriminant function (eigenvalue = 0.600, $F = 46.23$, *d.f.* = 2, 154, $P < 0.0001$) was correlated with tree size ($r = 0.886$, $P < 0.0001$) and number of access routes ($r = 0.381$, $P < 0.0001$). Drey trees were larger and had more access routes than did random trees (mean discriminant scores: drey trees = 0.369 ± 0.088, random trees = −1.653 ± 0.189).

Drey sites.—Aspect of slope did not differ between drey and random sites ($\chi^2 = 1.90$, *d.f.* = 3, $n = 157$, $P = 0.593$). Out of 23 site variables (Table 3), 6 discriminated between drey and random sites (Wilks' $\lambda = 0.768$, $F = 7.57$, *d.f.* = 6, 150, $P < 0.0001$). Drey and random sites differed among all characteristics except medium trees/ha, as indicated by the correlation between the discriminant function (eigenvalue = 0.303, $F = 7.57$, *d.f.* = 6, 150, $P < 0.0001$) and original variables (Table 4). Drey sites were steeper with more large trees, southwestern white pine, and Douglas-fir, but less corkbark fir than random sites (mean discriminant scores: drey sites = 0.255 ± 0.088, random sites = −1.174 ± 0.189).

Table 4.—Correlation between original variables selected in stepwise discriminant function analysis and discriminant function for drey sites of Abert's squirrels (*Sciurus aberti*) and random sites.

	Correlation with discriminant function	
Sites characteristics	*r*	*P*
% slope	0.669	< 0.001
Large trees/ha[a]	0.552	< 0.001
Corkbark fir/ha	−0.529	< 0.001
Southwestern white pine/ha	0.456	< 0.001
Douglas-fir/ha	0.293	< 0.001
Medium trees/ha[b]	0.065	0.420

[a] Trees > 40 cm diameter at breast height (DBH).
[b] Trees ≥ 20 cm DBH and ≤ 40 cm DBH.

Discussion

Dreys.—Similar to drey placement in ponderosa pine forests (Farentinos 1972; Halloran and Bekoff 1994; Snyder and Linhart 1994), Abert's squirrels in mixed-conifer forests of the Pinaleño Mountains also built dreys against the trunk and at approximately 75% of tree height. Placement of dreys in the upper part of conifers may increase structural stability and protect the drey from wind and rain as branches at this height are more dense than on the lower part of the tree, but larger than branches at the top of the tree (Farentinos 1972). Dreys were more frequently oriented toward the south and east, which may provide increased solar exposure during early morning (Farentinos 1972). In winter, we observed that Abert's squirrels often stayed in dreys well past sunrise, possibly gaining thermoregulatory benefits from the solar radiation at the drey.

Drey trees.—Abert's squirrels likely built dreys in larger trees because tall trees with thick trunks provide stability and protection from the effects of wind and rain. In addition, large trees have large branches that provide stable platforms for dreys (Halloran and Bekoff 1994). Drey trees may have had more access routes to allow squirrels to easily travel to and from the drey through the tree canopy, rather than on the ground where they are more exposed to aerial and terrestrial predators (Hall 1981; Rothwell 1979). In addition to structural features, tree chemistry may also influence selection of nest sites. Phloem of drey trees for Abert's squirrels in ponderosa pine forest contained more carbohydrates and sodium and less copper, iron, and silicon than did phloem of nondrey trees (Snyder and Linhart 1994).

Structural characteristics of drey trees for Abert's squirrels in mixed-conifer forests were similar to those found in ponderosa pine forests. Drey trees were larger, taller, and had more access routes than did nondrey trees in ponderosa pine forests

(Halloran and Bekoff 1994). Other arboreal sciurids including red squirrels (*Tamiasciurus hudsonicus*), fox squirrels (*Sciurus niger*), and northern flying squirrels (*Glaucomys sabrinus*) also build dreys in trees that are larger than nondrey trees (Fancy 1980; Hackett and Pagels 2003; Kantola and Humphrey 1990; Menzel et al. 2004; Salsbury et al. 2004; Young et al. 2002).

Abert's squirrels used 5 conifer species for dreys, but 2 species, Douglas-fir and corkbark fir, were used at proportions differing from availability, possibly because of the size characteristics of these tree species. Abert's squirrels likely used Douglas-fir at twice the availability because Douglas-fir trees are one of the largest conifer species on the study area and larger trees are selected for dreys. Corkbark fir is one of the smaller conifer species on the study area, likely making it less suitable for use as a drey tree. Abert's squirrels in natural populations almost exclusively use ponderosa pine trees for dreys (Brown 1984), although piñon pine (*Pinus edulis*) also is used (Hoffmeister 1971).

Drey sites.—The steeper slopes with larger trees and different abundances of certain tree species at drey sites likely not only reflect selection of drey sites, but also habitat selection. By having larger trees on drey sites, Abert's squirrels have access to more potential drey trees. Larger trees also produce more conifer seeds (Burns and Honkala 1990), resulting in more food resources. At drey sites, corkbark fir was found in lower numbers, whereas southwestern white pine and Douglas-fir were found at higher numbers, possibly reflecting their differential use as food resources. Douglas-fir and southwestern white pine seeds are commonly eaten by Abert's squirrels on our study area, whereas corkbark fir seeds are rarely eaten (Edelman and Koprowski 2005b; Hutton et al. 2003). Steeper slopes may be drier, sunnier, and have a shorter fire interval that would favor the growth of Douglas-fir and southwestern white pine over corkbark fir (Burns and Honkala 1990; Dieterich 1983; Jones 1974). In addition, steeper slopes may have more difficult access for timber harvesting, possibly resulting in larger trees in these areas.

Abert's squirrels and ponderosa pine.—The dogma that Abert's squirrels are dependent on ponderosa pine suggests that this relationship is an adaptation. However, use of other tree species and forest types, as seen in our studies on dreys and cavity nests (Edelman and Koprowski 2005b), indicates that Abert's squirrels are selective about structural components of forests instead of specific tree species. Furthermore, additional studies on Abert's squirrels in the Pinaleño Mountains indicate that this species relies mostly on non–ponderosa pine conifer species as food and cover resources (Edelman and Koprowski 2005b; Hutton et al. 2003). Natural populations of Abert's squirrels also occasionally build dreys in piñon pine (Hoffmeister 1971) and use nest boxes (Pederson et al. 1978), indicating that tree species is of lesser importance in the selection of nest sites. Structural characteristics of drey trees in the Pinaleño Mountains were similar to those in ponderosa pine forests (Farentinos 1972; Halloran and Bekoff 1994), further suggesting that structural cues may be most influential in selection of nest sites. Abert's squirrels in ponderosa pine occasionally feed on tree species other than ponderosa pine (reviewed in Edelman and Koprowski 2005a). Ponderosa pine may be the only tree species typically used for food, cover, and nest sites by Abert's squirrels in natural populations, simply because other conifer species are not available in monotypic ponderosa pine forests. However, association of Abert's squirrels with ponderosa pine does not indicate an obligate relationship. Structural components appear important in selection of nest sites in other arboreal sciurids including red squirrels, fox squirrels, and northern flying squirrels (Fancy 1980; Hackett and Pagels 2003; Kantola and Humphrey 1990; Menzel et al. 2004; Salsbury et al. 2004; Young et al. 2002).

Examination of our results suggests that the dependence of Abert's squirrels on ponderosa pine is not as strong as previously reported and is likely facultative. Other factors such as interspecific competition with sympatric tree squirrel species may prevent Abert's squirrels from extensively using non–ponderosa pine forests in their natural range (Edelman and Koprowski 2005a; Ferner 1974). Abert's squirrels are naturally sympatric with red squirrels over much of their range in the United States. In these areas, Abert's squirrels are found in lower-elevation ponderosa pine forests and red squirrels occur in higher-elevation mixed-conifer and spruce–fir forests (Brown 1984; Rasmussen 1941). Where Abert's squirrels are absent, red squirrels often occupy ponderosa pine forests as well (Ferner 1974). In the Pinaleño Mountains, however, the endemic Mt. Graham red squirrel (*T. h. grahamensis*) has been isolated for approximately 10,000 years from other tree squirrel species (Lomolino et al. 1989) until the recent introduction of Abert's squirrels. Because of a relaxation of competition, adaptations that could allow red squirrels to exclude Abert's squirrels from mixed-conifer and spruce–fir forests may be reduced in the Pinaleño Mountains population (Minckley 1968). Additionally, the low density of the endangered Mt. Graham red squirrels also may reduce interspecific levels of competition for Abert's squirrels (Edelman and Koprowski 2005a).

The introduction of Abert's squirrels into the Pinaleño Mountains and their spread and persistence for >60 years (Edelman and Koprowski 2005a) suggests that the reported dependence of this species on ponderosa pine forests is overstated. The successful introductions of Abert's squirrels into 10 sites within the southwestern United States (Davis and Brown 1988) indicate that future management and conservation efforts must consider this lack of dependence to be effective. In addition, the mechanisms for exclusion of Abert's squirrels from mixed-conifer forests in other locations warrant further study and may provide important insight into species distributions. The reported obligate relationship between Abert's squirrels and ponderosa pine cannot solely explain the inability of Abert's squirrels to persist in other conifer forest types because nest sites in this introduced population are selected based on structural components rather than tree species.

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