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POTENTIAL FOR NEST SITE COMPETITION BETWEEN NATIVE AND EXOTIC TREE SQUIRRELS

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In communities where strong interspecific competition between native species is lacking, exotic and native species often exhibit intense resource competition resulting in decline of native populations. We examined the potential for interspecific competition for nest sites between co-occurring native Mt. Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) and exotic Abert's squirrels (*Sciurus aberti*) in the Pinaleño Mountains of Arizona. Comparison of nest use between red and Abert's squirrels at different scales (nest, nest tree, and nest site) revealed contrasting results. Competition for nests and nest trees appears unlikely given the dissimilarity in use of nest types and tree characteristics. Abert's squirrels predominately used dreys, whereas red squirrels mostly used cavity nests. Neither squirrel species occupied a nest used by the other species. Nest trees differed in size and species between squirrels for dreys, but not for cavities. Abert's squirrel nest sites were found in a wider range of microhabitats including almost all microhabitats in which red squirrel nest sites were located. Although there was significant overlap, each species showed distinct trends in microhabitat. In general, red squirrel nest sites were characterized as more densely forested areas dominated by corkbark fir (*Abies lasiocarpa* var. *arizonica*), whereas Abert's squirrel nest sites were more open and contained greater tree species diversity. Overlap in microhabitat characteristics increases the likelihood of interspecific competition and could increase the vulnerability of red squirrels to extinction.

Key words: coexistence, introduced species, niche overlap, pine squirrel, *Sciurus aberti*, *Tamiasciurus hudsonicus*, tassel-eared squirrel

The introduction and establishment of exotic species is a major anthropogenic influence on global biodiversity (Sax et al. 2005; Williamson 1996). In communities where strong interspecific competition between native species is lacking, exotic and native species often exhibit intense resource competition resulting in decline of native populations (Williamson 1996). Interspecific competition for limited resources occurs in invaded communities when exotic and native species occupy similar niches. Long-term interspecific competition between exotic and native species can result in competitive exclusion of the less-competitive species or competitive coexistence (Bruno et al. 2005; Williamson 1996). However, competitive coexistence between ecologically similar species requires an axis of environmental heterogeneity along which species can partition niches through species-specific trade-offs. These trade-offs allow each species to outcompete others within a portion of the axis of environmental heterogeneity and maintain a nondecreasing population (Brown et al. 1994).

Exotic Abert's squirrels (*Sciurus aberti*), which were introduced to many isolated mountain ranges in the southwestern United States (Davis and Brown 1988), are implicated in the decline of several native species of tree squirrels (Lange 1960; Minckley 1968). Although Abert's squirrels are native to the southwestern United States and northern Mexico, before translocations, they were not present in introduced areas (Brown 1984; Davis and Brown 1989). In the Pinaleño Mountains of Arizona, exotic Abert's squirrels may have negatively affected the native Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*), an isolated subspecies of the North America red squirrel (Spicer 1985). In other areas of the southwestern United States, Abert's squirrels and red squirrels naturally have extensive range overlap in montane, forested environments (Brown 1984). Within areas of sympatry, Abert's squirrels and red squirrels are spatially segregated by macrohabitat; the former occupy ponderosa pine (*Pinus ponderosa*) forests and the latter inhabit higher-elevation mixed-conifer and spruce–fir forests (Ferner 1974). However, in the Pinaleño Mountains, Abert's squirrels and Mt. Graham red squirrels do not exhibit macrohabitat segregation

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and both species occupy mixed-conifer and spruce–fir forests containing little ponderosa pine (Hutton et al. 2003).

Since introduction in the 1940s, Abert's squirrels have quickly spread throughout conifer forests of the Pinaleño Mountains, coinciding with an apparent decrease in abundance of Mt. Graham red squirrels (Minckley 1968). The population of Mt. Graham red squirrels (hereafter referred to as red squirrel) is estimated at only 214 individuals (Rushton et al. 2006) and is listed as federally endangered (United States Fish and Wildlife Service 1993). Spatially explicit models of population dynamics have shown that competition from Abert's squirrels could significantly decrease the long-term viability of red squirrels (Rushton et al. 2006). Competition between Abert's squirrels and red squirrels is probable because both species are diurnal, arboreal squirrels that feed on similar conifer seeds and fungi and nest in tree cavities and dreys (Edelman and Koprowski 2005a, 2005b, 2006; Young et al. 2002). However, the extent to which Abert's squirrels and red squirrels compete for resources such as nest sites, space, and food is unknown, yet has important implications for the long-term persistence of the critically endangered native.

Our objective was to examine the potential for competition between native red squirrels and exotic Abert's squirrels in the Pinaleño Mountains for one aspect of resource use, nests. Nest sites are an important resource for tree squirrels and reflect habitat use (Gurnell et al. 2002). Nests provide a location for raising young, rest, predator avoidance, and cover during inclement weather (Steele and Koprowski 2001). We examined nest use at the scale of the nest, nest tree, and nest site. Specifically, we sought to address the following questions: Do native and exotic squirrels use similar types of nests? Are nest trees similar between native and exotic squirrels? Is microhabitat at nest sites similar between native and exotic squirrels? We hypothesized that nest use would differ between these species because of differences in body size and known nesting preferences in other populations (Halloran and Bekoff 1994; Koprowski 2005; Nash and Seaman 1977; Young et al. 2002). However, the amount of overlap in nest-use characteristics between squirrel species is difficult to predict because mixed-conifer forest is a novel habitat for Abert's squirrel and these species typically do not co-occur in the same habitat. Similarity in nest use would indicate potential for interspecific competition, whereas differences in nest use could contribute to coexistence between squirrel species and the persistence of the endangered red squirrel.

Materials and Methods

Study area.—The study area was 110 ha of mixed-conifer forest from approximately 2,850 to 3,170 m in elevation in the Pinaleño Mountains (32°42′N, 109°53′W), 25 km southwest of Safford, Arizona. Mixed-conifer forest on the study area was dominated by corkbark fir (*Abies lasiocarpa* var. *arizonica*), but included a variety of other conifer and deciduous species (Edelman and Koprowski 2005b, 2007).

Nest identification.—Two sizes of live traps were used to capture squirrels: 48 × 15 × 15-cm box traps constructed of 1.3 × 2.5-cm wire mesh (custom model 202; Tomahawk Live Trap Co., Tomahawk, Wisconsin) and 40.6 × 12.7 × 12.7-cm box traps (model 201; Tomahawk Live Trap Co.). Baited traps were placed on the ground at middens, nests, feeding sign, or squirrel sightings. Trapping was conducted periodically (every 1–3 months) from September 2001 to August 2003 as part of a larger study on nest and space use of Abert's squirrels and red squirrels (Edelman and Koprowski 2005a, 2005b, 2006). Traps were open during the day and checked every 2 h. Sex, reproductive condition, age, and body mass of livetrapped squirrels were recorded. 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. All adults were fitted with radiocollars (Abert's squirrels: model SOM 2380; red squirrels: model SOM 2190; Wildlife Materials International, Inc., Murphysboro, Illinois) that weighed <5% of body mass. Handling of animals was in accordance with the guidelines of the American Society of Mammalogists (Gannon et al. 2007) and the University of Arizona Institutional Animal Care and Use Committee with permits from the Arizona Game and Fish Department and the United States Fish and Wildlife Service, Endangered Species Office.

Nest use was observed by tracking radiocollared animals to nest sites with a TRX-1000S or TRX-2000S receiver and a 3-element yagi directional antenna (Wildlife Materials International, Inc.). Twenty-six radiocollared Abert's squirrels (15 males and 11 females) and 41 red squirrels (16 males and 25 females) were monitored. Squirrels were tracked either before emergence from the nest at sunrise or after individuals entered nests near sunset. The nest of each radiocollared individual was typically located more than 1 time each month with 2–3 weeks between locations from September 2002 to September 2003 (Abert's squirrels, $\bar{X} = 1.5$ locations/month ± 0.1 *SE* and $\bar{X} = 19.0$ days between locations ± 1.2 *SE*; red squirrels, $\bar{X} = 2.2 \pm 0.1$ locations/month and $\bar{X} = 14.2 \pm 1.2$ days between locations). Squirrels used multiple nests during the study (Abert's squirrels, $\bar{X} = 6.2$ nests/individual ± 0.7 *SE*; red squirrels, $\bar{X} = 2.7 \pm 0.3$ nests/individual). Location and nest type (cavity, ground, or drey) were recorded and the nest tree was marked with a uniquely numbered tag.

Nest-tree measurements.—For each nest tree, we measured species, condition, diameter at breast height (DBH), height, nest 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). A clinometer (model PC5 360PC; Suunto, Ogden, Utah) was used to measure tree height and nest height. Dead tree condition was classified into 4 decay classes: 1) dead with intact branches and twigs, trunk pointed, and almost all bark remaining; 2) dead with branches present, but broken, tree trunk broken near top, and most bark remaining; 3) dead with branches broken near trunk, tree trunk broken, and little bark remaining; and 4) dead with branches gone, tree trunk broken near breast height, and bark shed.

Microhabitat measurements.—Within a 10-m-radius circular plot (0.03 ha) surrounding nest tree, we measured species, condition, and DBH of each tree $\geq$3 cm DBH and number of logs ≥20 cm diameter at one end and ≥2 m length. Percent slope (% 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 tree in each cardinal direction (north, east, south, and west); 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. Simpson's diversity index was calculated for trees at each site (Magurran 2004). Based on the measurements of trees taken at sites, we calculated 15 variables (Table 1).

TABLE 1.—Vegetation and physical characteristics (mean ± *SE*) of Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*; $n = 79$) and Abert's squirrel (*Sciurus aberti*; $n = 104$) microhabitat at nest sites (see "Materials and Methods" for full descriptions of each habitat characteristic).

Microhabitat characteristics	Red squirrel	Abert's squirrel
% slope	15.5 ± 0.8	24.2 ± 1.4
% canopy cover[a]	85.5 ± 0.7	80.1 ± 0.9
% canopy cover at 0 m	89.9 ± 0.8	87.6 ± 1.0
% canopy cover at 5 m	83.9 ± 0.9	77.6 ± 1.2
% canopy cover at 10 m	82.6 ± 1.0	75.2 ± 1.5
Canopy cover *CV*[b]	16.4 ± 0.8	23.4 ± 1.3
Logs/ha	243.5 ± 15.0	109.2 ± 9.0
Basal area (m^2/ha)	75.9 ± 2.7	70.2 ± 2.2
Trees/ha	1,918.6 ± 71.7	1,387.2 ± 58.4
Live trees/ha	1,387.8 ± 60.9	915.3 ± 50.6
Dead trees/ha	530.0 ± 30.7	471.0 ± 28.9
Large snags/ha[c]	38.4 ± 4.0	32.1 ± 3.5
Small trees/ha[d]	1,317.3 ± 74.3	871.6 ± 53.6
Medium trees/ha[e]	449.8 ± 19.6	366.3 ± 20.5
Large trees/ha[f]	151.5 ± 10.2	149.4 ± 7.3
Simpson's diversity index	1.80 ± 0.06	2.69 ± 0.10
Engelmann spruce/ha	248.9 ± 21.5	283.0 ± 31.0
Corkbark fir/ha	1,396.2 ± 71.5	467.5 ± 52.1
Douglas-fir/ha	78.9 ± 12.2	238.1 ± 29.1
White fir/ha	3.4 ± 1.9	34.6 ± 12.5
Quaking aspen/ha	138.0 ± 28.1	168.9 ± 37.2
Southwestern white pine/ha	34.6 ± 7.8	149.8 ± 16.1
Ponderosa pine/ha	4.2 ± 2.6	24.5 ± 5.3
Deciduous trees/ha[g]	8.0 ± 6.5	15.9 ± 5.1

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

Data analysis.—We conducted statistical analyses using JMP version 7.0.1 (SAS Institute Inc., Cary, North Carolina) and SAS version 9.00 (SAS Institute Inc.). Each nest and associated tree and site were treated as independent from other nests because squirrels frequently switched nests (Abert's squirrels, median = 23 days between nest switching; red squirrels, median = 31.4 days between nest switching) and nests were often used by more than 1 individual (Abert's squirrels, $\bar{X} = 1.5$ individuals/nest ± 0.1 *SE*; red squirrels, $\bar{X} = 1.3 \pm 0.3$ individuals/nest) and across several generations (J. L. Koprowski, pers. obs.). Count variables were cube-root transformed, proportions were arcsine transformed, and DBH was log transformed before statistical analyses. However, means (±*SE*) reported are from untransformed values. We analyzed categorical data using Pearson chi-square tests. We used 2-tailed *t*-tests to examine differences in nest height. For each squirrel species, Levin's niche breadth for nest-tree species was calculated separately for drey and cavity nests as:

$$B = 1/\left(n \sum p_i^2\right), \tag{1}$$

where n is the number of tree species and p_i is proportion of nest trees found in the ith category of tree species (Hurlbert 1978). B ranges from $a_{\min}/A$ (when only 1 nest-tree species is used) to 1 (when each tree species is used in proportion to natural abundance), where $a_{\min}$ is the abundance of the least-abundant tree species and A is the total abundance of all tree species. Niche overlap between squirrel species for nest-tree species was calculated separately for drey and cavity nests as:

$$L = (A/XY) \sum (x_i y_i / a_i), \tag{2}$$

where X is the sum of all tree species used by red squirrels, Y is the sum of all tree species used by Abert's squirrels, x_i is the sum of the ith category of tree species used by red squirrels, y_i is the sum of the ith category of tree species used by Abert's squirrels, and a_i is the abundance of a tree species in the ith category. L is 0 when no tree species are shared between species, a value of 1 when both species utilize each tree species in proportion to natural abundance, and a value >1 when each species uses some tree species more than others and this use is similar between species (Hurlbert 1978). Abundance of each tree species was estimated from measurements taken at random sites throughout the study area (Hutton et al. 2003). Tree species availability for dreys included only live trees, whereas for cavity nests dead and live trees were included in calculations. Quaking aspen (*Populus tremuloides*) was excluded from calculation of tree species availability for drey trees because this species was never used for dreys.

Multivariate analyses of variance were used to determine if nest trees and microhabitat differed between squirrel species. Bonferroni-corrected *t*-tests were used to examine differences between species for specific nest-tree characteristics. Stepwise discriminant function analysis (DFA) was used to select variables that best discriminated between Abert's squirrel and red squirrel microhabitat. Stepwise DFA described the maximum difference between nest sites of Abert's and red squirrels based on a linear combination of selected microhabitat variables. Selection criteria for entry and removal of variables in stepwise DFA was $P = 0.15$. 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 species (higher F-value in 1-way analysis of variance) was used in stepwise DFA (McGarigal et al. 2000). To determine the relative contribution of each selected microhabitat variable to the discriminant function, we examined the

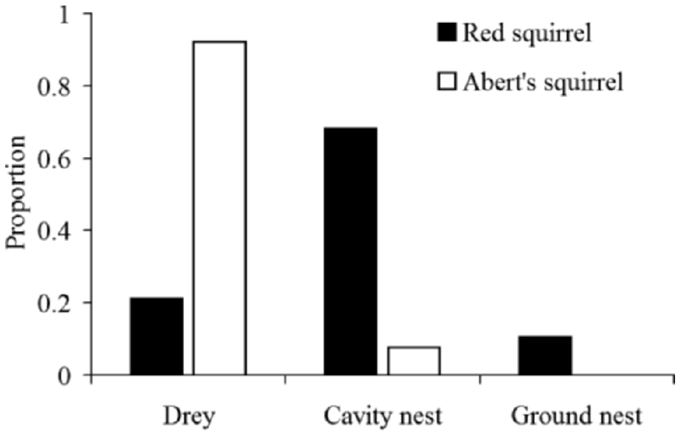

Fig. 1.—Proportion of nest types (drey, cavity, and ground) found for red squirrels (*Tamiasciurus hudsonicus grahamensis*; $n = 85$) and Abert's squirrels (*Sciurus aberti*; $n = 104$).

Table 2.—Number of dreys and cavity nests of red squirrels (*Tamiasciurus hudsonicus grahamensis*) and Abert's squirrels (*Sciurus aberti*) found in different tree condition classes. Increasing decay class number (1–4) correlates with increasing decay of tree (see "Materials and Methods" for full descriptions of each decay class).

	Red squirrel		Abert's squirrel	
Nest-tree condition	Drey ($n = 18$)	Cavity nest ($n = 57$)	Drey ($n = 96$)	Cavity nest ($n = 8$)
Live	14	23	91	5
Total dead	4	34	5	3
Decay class 1	3	2	5	1
Decay class 2	1	11		
Decay class 3		17		2
Decay class 4		4		

correlations (also called structure coefficients or canonical loadings) between each variable and the discriminant function. Higher correlations indicated that the microhabitat variable contributed more to the discriminant function than lower correlated variables (McGarigal et al. 2000). When compared to the discriminant scores for each species, the correlations can be used to interpret the biological meaning of the discriminant function. Positively correlated microhabitat variables are greater in magnitude on nest sites with positive discriminant scores and lesser in magnitude on nest sites with negative scores. Conversely, negatively correlated variables are greater in magnitude on sites with negative scores and lower on sites with positive scores. Standard deviation of discriminant scores is considered a measure of habitat breadth with larger *SD* signifying greater habitat breadth (Carnes and Slade 1982). We compared *SD* of discriminant scores between squirrel species using a 2-tailed *F*-test.

Results

Nests.—Nests were species specific; no squirrels were observed using a nest that had been previously occupied by the other species. Abert's squirrels used a higher proportion of drey to cavity nests than red squirrels ($\chi^2 = 89.05$, *d.f.* = 1, $P < 0.0001$; Fig. 1). Most Abert's squirrel nests were dreys (92.3% of 104 nests), whereas more red squirrel nests were in cavities (76.3% of 76 nests). Red squirrels also used a small number of ground nests (Fig. 1). Abert's squirrel dreys were built higher than red squirrel dreys (Abert's squirrel, $\bar{X} = 15.7 \pm 0.4$ m; red squirrel, $\bar{X} = 8.6 \pm 0.8$ m; $t = 7.72$, *d.f.* = 112, $P < 0.0001$). Cavity nests of Abert's squirrels were located higher than those used by red squirrels (Abert's squirrel, $\bar{X} = 14.7 \pm 2.1$ m; red squirrel, $\bar{X} = 7.5 \pm 0.6$ m; $t = 4.42$, *d.f.* = 53, $P < 0.0001$).

Nest trees.—Red squirrels more frequently built dreys in dead trees than Abert's squirrels ($\chi^2 = 6.03$, *d.f.* = 1, $P = 0.014$), although the majority of dreys for both species were built in live trees (Table 2). The few dreys built by red squirrels and Abert's squirrels in dead trees were located in the least decayed trees (decay class 1 and 2). Niche breadth (*B*) was <1 for both species, signifying that neither squirrel used tree species for dreys in proportion to natural abundance (Abert's squirrel, $B = 0.61$; red squirrel, $B = 0.44$; Table 3). A lower niche breadth value for red squirrels compared to Abert's squirrels indicated that the former used fewer tree species for dreys. Most red squirrel dreys were built in corkbark fir or Engelmann spruce (*Picea engelmannii*), whereas Abert's squirrel dreys were mostly built in Douglas-fir (*Pseudotsuga menziesii*) with lesser numbers in corkbark fir, Engelmann spruce, and southwestern white pine (*Pinus strobiformis*; Table 3). Niche overlap (*L*) was <1, indicating that tree species used for dreys were not heavily shared between squirrel species ($L = 0.74$; Table 3). Red squirrel drey trees differed from Abert's squirrel drey trees ($F = 14.32$, *d.f.* = 3, 110, $P < 0.0001$; Fig. 2) by being half the DBH and more than 1.5 times shorter in height ($t < 2.4$, *d.f.* = 112, $P < 0.016$), but similar in number of access routes ($t > 2.4$, *d.f.* = 112, $P > 0.016$).

Squirrel species used cavity nests in live and dead trees at similar proportions ($\chi^2 = 1.40$, *d.f.* = 1, $P = 0.24$), but almost all types of dead trees (decay class 1–4) were used for cavity nests by both species (Table 2). Niche breadth was low for both species, indicating that neither squirrel used tree species for cavity nests in proportion to natural abundance (Abert's squirrel, $B = 0.21$; red squirrel, $B = 0.35$; Table 3). Niche breadth was higher for red squirrels, signifying that they used more tree species for cavity nests than Abert's squirrels. Most cavity nests of both species were found in quaking aspen, the primary deciduous softwood. Red squirrels also frequently used corkbark fir for cavity nests (Table 3). Niche overlap was >1, indicating that squirrel species used some tree species more intensively than others and that use was similar between squirrel species ($L = 5.12$; Table 3). Cavity nest trees were similar between species in all structural characteristics ($F = 0.36$, *d.f.* = 3, 61, $P = 0.78$; Fig. 2).

Nest microhabitat.—Slope aspect of red squirrel microhabitat at nest sites differed from that of Abert's squirrels ($\chi^2 = 13.65$, *d.f.* = 3, $P = 0.0034$). Red squirrel microhabitat was more frequently found on east-facing (46.8% of 79) and

Table 3.—Percentage use of tree species for nests by red squirrels (*Tamiasciurus hudsonicus grahamensis*) and Abert's squirrels (*Sciurus aberti*) compared to tree species availability in a mixed-conifer forest of the Pinaleño Mountains, Arizona.

	Dreys			Cavity nests		
		% use			% use	
Nest-tree species	% available	Red squirrel ($n = 18$)	Abert's squirrel ($n = 96$)	% available	Red squirrel ($n = 57$)	Abert's squirrel ($n = 8$)
Corkbark fir	57.0	61.1	22.9	51.4	28.0	0
Douglas-fir	18.2	5.6	49.0	14.0	1.8	0
Engelmann spruce	16.3	27.7	15.6	16.4	3.5	0
Southwestern white pine	7.2	5.6	10.4	5.5	1.8	0
Ponderosa pine	1.3	0	2.1	1.6	1.8	12.5
Quaking aspen[a]	—	—	—	11.1	63.1	87.5

[a] Quaking aspen was not included in calculations of tree species availability for dreys because dreys were never found in this species.

north-facing (30.4%) slopes than west-facing (13.9%) and south-facing (8.9%) slopes. Abert's squirrel microhabitat was most commonly found on east-facing slopes (38.5% of 104) and to a lesser extent on south-facing (25.0%), west-facing (22.1%), and north-facing (14.4%) slopes.

Red squirrel and Abert's squirrel nest sites differed in microhabitat characteristics ($F = 0.85$, *d.f.* = 24, 158, $P < 0.0001$; Table 1). Five of 17 microhabitat characteristics (Table 1) were selected by stepwise DFA to maximally describe the difference between Abert's and red squirrel nest sites (Wilks' $\lambda = 0.642$, $F = 100.77$, *d.f.* = 1, 181, $P < 0.0001$; Table 4). Based on the strength of their correlations with the discriminant function (eigenvalue = 0.973, $F = 28.53$, *d.f.* = 6, 176, $P < 0.0001$), abundance of corkbark fir and logs and tree species diversity at nest sites were characteristics that contributed most to the microhabitat difference between squirrel species (Table 4). Slope and canopy cover and to a lesser extent abundance of dead trees also contributed to microhabitat differences between species. A histogram of discriminant scores for nest sites (Fig. 3) revealed overlap in microhabitat at nest sites between species. Abert's squirrel nest sites were found in a wider range of microhabitats including almost all microhabitats in which red squirrel nest sites were located. Standard deviation of discriminant scores was greater for Abert's squirrels (mean discriminant score ± *SD*: Abert's squirrel = -0.855 ± 1.118; red squirrel = 1.125 ± 0.818; $F = 18.54$, *d.f.* = 1, 181, $P < 0.0001$), indicating a broader microhabitat breadth than red squirrels. Based on the mean discriminant scores and their correlation with microhabitat characteristics (Fig. 3; Table 4), red squirrel microhabitat (positive mean discriminant score) typically had more corkbark fir, dead trees, logs, and canopy cover and less tree species diversity and was less steep than typical Abert's squirrel microhabitat (negative mean discriminant score). The discriminant function correctly classified 80.8% of microhabitat sites according to species (88.6% of *T. h. grahamensis* and 73.1% of *S. aberti*).

Discussion

Success in the establishment of a species often depends on the level of competition between native and introduced species (Lockwood et al. 2007; Williamson 1996). Biological invasions consist of 4 stages: transport, establishment, spread, and impact (Lockwood et al. 2007). Biological resistance created by populations of native species is often considered to greatly reduce the risk of establishment and spread (Simberloff 1986). Because of the rarity of threatened and endangered species, biological resistance experienced by introduced species is frequently reduced and such populations may be particularly vulnerable to invasion. Perhaps not surprisingly, introduced species threaten 49% of federally protected species in the United States (Wilcove et al. 1998) potentially because of resource competition (Lockwood et al. 2007).

The potential for resource competition between endangered native red squirrels and exotic Abert's squirrels is greatest at the scale of the nest site. Many Abert's squirrel nest sites were similar in microhabitat characteristics to red squirrel nest sites with a broader range of conditions. Despite significant overlap, red squirrel nest sites were typically more densely forested and dominated by corkbark firs with dead and downed trees, whereas Abert's squirrel nest sites were usually more open with greater tree species diversity. Whether differences in microhabitat use can maintain stable, long-term coexistence between Abert's and red squirrels is unknown. A similar conservation dilemma exists in Europe, where native Eurasian red squirrels (*Sciurus vulgaris*) and exotic eastern gray squirrels (*S. carolinensis*) co-occur (Williamson 1996). The outcome of interspecific competition appears to vary in different forest types. In deciduous forests, Eurasian red squirrels and eastern gray squirrels exhibit considerable habitat overlap likely resulting in competitive exclusion of natives (Wauters et al. 2002). In coniferous forests, low habitat overlap occurs, possibly contributing to coexistence of Eurasian red squirrels and eastern gray squirrels (Bryce et al. 2002).

General microhabitat differences between species could represent competitive exclusion, with native red squirrels forced into reduced range of microhabitats directly or indirectly by exotic Abert's squirrels. Although it is possible that Abert's squirrels have reduced the available habitat for red squirrels, particularly in areas of microhabitat overlap, general differences in microhabitat more likely represent the disparity in diet and caching behavior of these species. Red squirrels may select microhabitat that is typically dominated by corkbark fir and Engelmann spruce because these species are frequently used

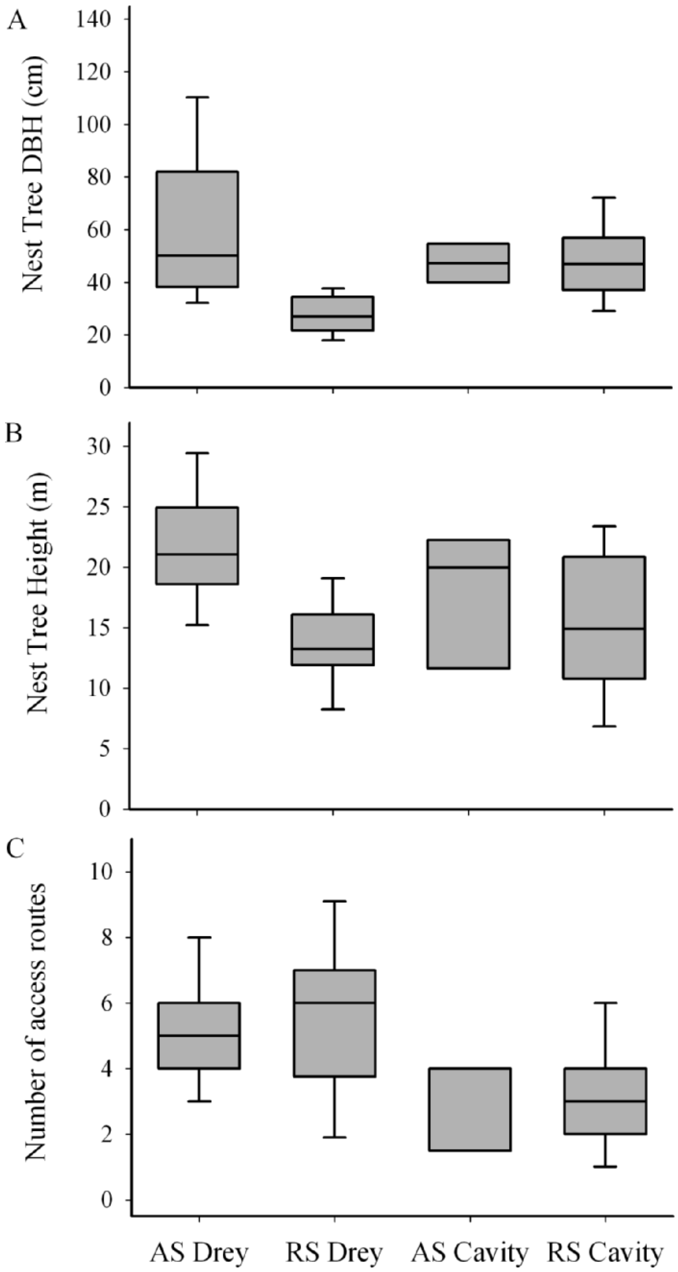

FIG. 2.—A) Tree diameter at breast height, B) tree height, and C) number of access routes for drey and cavity nest trees of red squirrels (*Tamiasciurus hudsonicus grahamensis*; RS) and Abert's squirrels (*Sciurus aberti*; AS). Boxes represent median and quartiles and bars show 10th and 90th percentiles.

TABLE 4.—Correlation of selected microhabitat characteristics from nest sites of red squirrels (*Tamiasciurus hudsonicus grahamensis*) and Abert's squirrels (*Sciurus aberti*) with discriminant function (see "Materials and Methods" for full descriptions of each microhabitat characteristic).

	Correlation with discriminant function	
Microhabitat characteristics	*r*	*P*
Corkbark fir/ha	0.852	<0.001
Simpson diversity index	−0.712	<0.001
Logs/ha	0.676	<0.001
% slope	−0.494	<0.001
% canopy cover	0.429	<0.001
Dead trees/ha	0.194	<0.01

for food (United States Fish and Wildlife Service 1993) and nest trees. In the Pinaleño Mountains, Abert's squirrels in mixed-conifer forests used corkbark fir for feeding, cover, and nest trees less frequently than expected by availability (Edelman and Koprowski 2005a, 2005b). Thus, Abert's squirrels likely select more species-rich microhabitat containing Douglas-fir and southwestern white pine that are primarily used for food, cover, and nest trees (Edelman and Koprowski 2005a, 2005b). Red squirrels are larder hoarders that cache large quantities of conifer seeds in cone scale piles called middens (Steele 1998), whereas Abert's squirrels rarely cache food (Nash and Seaman 1977). The greater canopy cover, tree density, number of downed logs, and number of dead trees found in red squirrel microhabitat may create the necessary microclimate conditions for seed storage in middens by decreasing desiccation from wind and solar radiation (Steele 1998). The more open microhabitats where only Abert's squirrels were found likely have fewer suitable areas for cone storage. Whether these suboptimal microhabitats could be occupied by red squirrels if Abert's squirrels were removed is unknown.

Competition for nests and nest trees appears unlikely given dissimilarity in use of nest types and tree characteristics. Abert's squirrels predominately used dreys, whereas red squirrels mostly used cavity nests, similar to populations where only a single species occurs (Halloran and Bekoff 1994; Young et al. 2002). In addition, neither squirrel species occupied a nest used by the other species. Lack of nest sharing and differential use of nest trees between red squirrels and Abert's squirrels also may reflect the divergent biology of these species. Abert's squirrels are large tree squirrels (600 g),

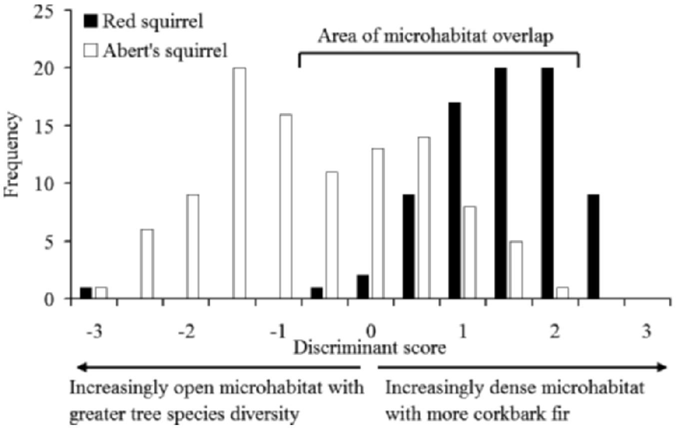

FIG. 3.—Histogram of discriminant scores of red squirrel (*Tamiasciurus hudsonicus grahamensis*) and Abert's squirrel (*Sciurus aberti*) microhabitat at nest sites. Interpretation of discriminant scores in relation to microhabitat characteristics is shown below histogram.

whereas red squirrels are small (225 g—Koprowski 2005; Nash and Seaman 1977). The body size and communal nesting of Abert's squirrels may necessitate use of large nests and nest trees (Edelman and Koprowski 2007). Differential use of tree species for dreys may reflect species-specific differences in tree size. Corkbark fir is a small conifer species and likely less suitable for use as a drey tree by Abert's squirrels but not red squirrels. Large-bodied Abert's squirrels may construct dreys in Douglas-fir because of its large size (Edelman and Koprowski 2005b). Thus, body size differences likely decrease overlap and reduce interspecific competition between these native and exotic squirrels for nests and nest trees.

Management of the Mt. Graham red squirrel.—Wildfire also is a serious threat to persistence of red squirrels (Koprowski et al. 2006). Forest thinning to reduce risk of catastrophic fire must avoid changes in forest composition and structure that favor exotic Abert's squirrels. Mixed-conifer and spruce–fir forests are novel for Abert's squirrels (Hutton et al. 2003) and response to silvicultural treatments is unknown. However, in other forest types, management to increase Abert's squirrels involves open areas interspersed with clumps of trees to promote open forests of shade-intolerant species (Dodd 2003). Nest sites of Abert's squirrels in the Pinaleños are more open than those of red squirrels, suggesting that structural preferences are similar to those of other populations of *S. aberti*. Management should focus on retention of red squirrel microhabitat and promotion of dense stands of corkbark fir, downed logs, closed canopy, and suitable cavity trees in mixed-conifer forests currently unoccupied by native red squirrels. Biological needs must be reconciled with fire management (Koprowski et al. 2006). Such a balance may prove difficult and requires small-scale experiments to assess species-specific squirrel responses (Pederson et al. 1987), while also developing large-scale, landscape-level approaches that incorporate distribution of habitat (Dodd 2003). Spatially explicit models successfully predict impact of forest management on Eurasian red squirrels (Gurnell et al. 2002; Lurz et al. 2003) and could be used to develop an appropriate conservation strategy for the red squirrel. Abert's squirrels have not excluded red squirrels over 65 years, yet any level of competition could decrease populations and increase vulnerability to extinction (Rushton et al. 2006). Other resources such as space, microclimate, and food are also important for tree squirrels (Steele and Koprowski 2001). Overlap between red squirrels and Abert's squirrels exists for these resources, but the extent and implications are unknown.

Conclusions.—As a group, tree squirrels are successful colonizers (Palmer et al. 2008), having been introduced to every continent except Antarctica, with introduction attempts numbering in the hundreds (Long 2004). Their abundance and ease of study make tree squirrels a model organism for examining the relationship between exotic and native species (Palmer et al. 2008). Our results indicate that overlap in resources between exotic and native species depends on the scale of analysis. Interspecific competition for nests and nest trees appears minimal between Abert's and red squirrels, likely because of differences in morphology and behavior. Overlap in microhabitat characteristics increases likelihood of interspecific competition and decreases probability of stable, long-term coexistence. When evaluating potential for competition between exotic and native species, researchers should consider the scale at which overlap in resource use would be greatest. Identifying the mechanisms that result in competition and promote coexistence between native and exotic species is a major scientific challenge, but essential to developing efficacious conservation strategies (Lockwood et al. 2007; Williamson 1996).

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