Characteristics of Mount Graham Red Squirrel Nest Sites in a Mixed Conifer Forest

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ABSTRACT The Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) is constrained to the Pinaleño Mountains in southeastern Arizona, USA. The population's endangered status and extensive forest damage from insects and fire warrants a better understanding of habitat variables important for nest site selection. We examined characteristics of cavity (n = 91) and drey (n = 38) nests and compared these to random sites (n = 113). Dreys were found primarily in Engelmann spruce (*Picea engelmannii*) and corkbark fir (*Abies lasiocarpa* var. *arizonica*). Cavity nests occurred primarily in aspen (*Populus tremuloides*) and corkbark fir. Squirrels selected nest sites with higher canopy cover and more corkbark fir, decayed logs, and living trees. Forest management plans emphasizing thinning must consider how altering these habitat characteristics could affect availability and suitability of tree stands for nesting squirrels. (JOURNAL OF WILDLIFE MANAGEMENT 71(6):1958–1963; 2007)

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Availability of nest sites is an important consideration in evaluating suitable tree squirrel habitat (Gurnell et al. 2002). Nest sites and the nest itself are critical in providing refuge from predators, a place to rear young, a source of thermal stability in harsh conditions, and serve a key role in food storage for many squirrels (Fancy 1980, Pauls 1981, Vahle and Patton 1983, Carey 1995, Steele and Koprowski 2001). Because of the dependence of tree squirrels on forests (Carey 2000, Steele and Koprowski 2001), a better understanding of what constitutes quality nest sites will aid in managing both critical forest habitat and the resident species. This is especially true in the case of endangered species, where limited availability or alteration of existing habitat could constrain population size or exacerbate population decline.

The Mount Graham red squirrel (Tamiasciurus hudsonicus grahamensis) is an endangered subspecies endemic to the Pinaleño Mountains of southeastern Arizona, USA. This locale represents the southernmost extent of the species in western North America (Hoffmeister 1986). Potential Mount Graham red squirrel habitat is estimated at 6,753-12,216 ha based on satellite imagery (Hatten 2000), and 9,083 ha based on forested area above 2,425 m as no middens have been found below 2,362 m (Smith and Mannan 1994, Hatten 2000). Red squirrel habitat was further compromised by the 2,718-ha Clark Peak fire in 1996 (Froehlich 1996), 11,898-ha Nuttall Complex fire in 2004 (Koprowski et al. 2006), and sustained outbreaks of bark beetles (Dryocoetes confusus, Dendroctonus rufipennis) and spruce aphids (Elatobium abietinum; United States Department of Agriculture Forest Service 2004, Koprowski et al. 2005). Decreasing habitat quality, plans for fuel load reduction, and a small population size (approx. 276 \pm 12 individuals in 2005; T. Snow, Arizona Game and Fish Department, personal communication) accentuate the need to understand habitat requirements. Currently, small-scale thinning has been initiated in an attempt to restore forested habitat to a more fire-tolerant, historic species composition with less densely spaced, large diameter trees and fewer snags (United States Department of Agriculture Forest Service 2005). More widespread thinning projects and prescribed burns to further reduce fuel loads are presently under consideration.

Previous studies on Mount Graham have examined characteristics of red squirrel habitat associated with middens and nest tree characteristics (Spicer et al. 1985, Froehlich and Smith 1990, Mannan and Smith 1991, Smith and Mannan 1994, Young et al. 2002) but none have focused specifically on nest site habitat characteristics associated with both the nest tree and surrounding forest structure. We focus on nest tree and nest site characteristics of Mount Graham red squirrels in a mixed-conifer to spruce-fir transition zone to identify key attributes and gain insight into how proposed thinning may affect this at-risk population. Squirrels in our study area use 3 types of nests for resting and rearing young: cavity nests, dreys (constructed of grass, leaves, lichen; Young et al. 2002), and occasionally log or ground nests. Our aim was to confirm nest use (visually and with radiotelemetry) and compare habitat parameters of cavity nests, dreys, and randomly located sites to determine whether habitat features important in nest site selection could be identified and if features differed between nest types.

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STUDY AREA

Our study area was located in the Pinaleño Mountains of southeastern Arizona, Graham County, USA. This mountain range is part of the Madrean Archipelago, a collection of high elevation mountain islands rising from the desert, known for their diversity and high degree of endemism of mammals (Koprowski 2005a, b). We used an established study site (Edelman and Koprowski 2005, Koprowski 2005a) that contained a 107-ha area of mixed-conifer habitat dominated by corkbark fir (Abies lasiocarpa var. arizonica, 45.6%), Engelmann spruce (Picea engelmannii, 19.1%), and aspen (Populus tremuloides, 18.4%) with interspersed Douglas fir (Pseudostuga menziesii, 8.5%), ponderosa pine (Pinus ponderosa, 9.3%), and southwestern white pine (P. strobiformis, 6.3%). Elevation at our site ranged between 2,870 m and 3,050 m with precipitation coming primarily from winter snowfalls (max. depth 1992-2003: 156.7 \pm 22.7 cm, range = 57–285 cm) and summer monsoons (total annual rainfall 1996–2003: 241.2 \pm 23.9 mm, range = 77.8–438.1 mm; Koprowski 2005*a*).

METHODS

Habitat Measurements

Nest identification.—We located nests by tracking radiocollared adult male and female squirrels (Koprowski et al. 2006) to nightly nests throughout the year from June 2002 to August 2005. This included nests used for raising litters and for resting. We identified a location as a nest site if we detected a squirrel in a nest (via radiotelemetry) or sighted it entering or exiting a nest. For each nest site (n =129), we established a 10-m (0.3-ha) radius circular plot with the nest tree as the plot center. We collected measurements for both the focal nest tree and nest stand (Smith and Mannan 1994). We handled animals for radiocollaring in accordance with the University of Arizona Institutional Animal Care and Use Committee and American Society of Mammalogists Animal Care and Use Committee (1998).

Focal tree and habitat measurements.-For each nest tree, we recorded tree species, tree condition (living or dead), tree height, living crown (vertical extent of tree with living branches), diameter at breast height, nest height or height of nest entrance, and the number of access routes (no. of trees ≥ 10 cm dbh with branches within 0.5 m of any part of the nest tree; Edelman and Koprowski 2005). We calculated 17 variables used to describe each site. We measured all trees ≥ 3 cm diameter at breast height within the 10-m circular plot and recorded species, condition, and diameter at breast height of each. We calculated average canopy cover using a spherical densiometer in each cardinal direction at 0 m, 5 m, and 10 m from the focal tree. We averaged canopy cover estimates for each distance and then for the entire plot. Within the plot, we counted number of decayed logs (logs slightly to completely friable) and intact logs ≥ 20 cm diameter and ≥ 2 m in length. We then recorded plot aspect and percent slope, and we calculated Simpson's diversity index (Magurran 2004).

The smallest nest tree we measured during this study contained a drey and had a diameter at breast height of 12 cm. Given that Mount Graham red squirrels occasionally use small trees for nest sites, we evaluated nest tree selection by comparing nests to randomly located focal trees (n = 113) ≥ 10 cm diameter at breast height within the study area (94% of random focal trees [n = 106] were ≥ 12 cm dbh). We used a random coordinate generator in ArcView 3.3 to produce random locations in red squirrel habitat. We also compared habitat characteristics within nest tree circular plots to 10-m radius circular plots centered on the random focal trees. We collected the same focal tree and stand data at random plots as collected at nest plots with the exception of nest height.

Statistical Analysis

We carried out all statistical analyses in SPSS (SPSS Inc., Chicago, IL), and MINITAB (MINITAB Inc., State College, PA). We assessed normality of each variable using Kolmogorov–Smirnov normality tests. We used log, arcsine, or square root transforms to better meet assumptions of normality of the data for univariate and multivariate tests. We present means and standard errors from untransformed data in the text.

We used a chi-square goodness-of-fit test and calculated 85% Bonferroni simultaneous confidence intervals for all species and 97.5% confidence for individual species to assess nest tree use compared to species availability in our study area (Marcum and Loftsgaarden 1980). We calculated species availability as a tally of the number of each species occurring at each random plot, summed across all random plots in the study area.

We explored habitat variables important in nest site selection and discrimination among cavity, drey, and random sites with discriminant function analysis (DFA). To identify distinguishing variables among sites and narrow our data set, we first performed stepwise DFA with probability of F = 0.05 to enter and probability of F =0.10 to remove. We followed with DFA on the resulting selected variables. We used a one-way analysis of variance with a Tukey's post hoc multiple comparison test to determine if significant differences exist among discriminant scores associated with each site type. We calculated Pearson's correlation coefficients between standardized canonical discriminant scores and the variables selected from stepwise discriminant analysis. For all analyses we chose an alpha level of 0.05 to indicate significance.

RESULTS

Focal Tree Comparisons

Cavity trees were on average 1.6 times larger, had less living crown, and fewer access routes than drey trees and random focal trees (Table 1). Cavity nests were more likely to be found in dead trees (57%, n = 91). Squirrels used aspen trees for cavity nests more than 3 times the availability of this species ($\chi^2 = 149.63$, df = 5, P < 0.001, n = 90, individual 97.5% CI around the difference: proportion

 Table 1. Focal tree comparisons ($\hat{x} \pm SE$) among cavity nest sites, drey nest sites, and random sites for Mount Graham red squirrels inhabiting mixed conifer

 forest, Pinaleño Mountains, Arizona, USA, 2002–2005.

Focal tree type	n	dbh (cm)		Ht (m)		Living crown (m)		No. access routes ^a	
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Cavity	91	49.5A ^b	2.0	15.7A	0.6	3.4A	0.5	3.7A	0.2
Drey	38	29.0B	1.5	14.0	0.7	6.7B	0.9	5.1B	0.3
Random	113	29.6B	1.4	13.5B	0.5	6.2B	0.5	3.8A	0.2

^a No. of trees (\geq 10 cm dbh) that have branches within 0.5 m of any part of the focal tree.

 $^{\rm b}$ Means followed by different letters differ significantly at $\alpha \leq 0.05$ (Tukey's method).

availability – proportion used for cavity nests in aspen = -0.460 ± 0.141 ; Table 2).

Drey nest trees had nearly twice the living crown area compared to cavity nest trees and more access routes than cavity nest trees or random trees (Table 1). Dreys were likely to be in living trees (73.7%, n = 38), and occurred most commonly in Engelmann spruce and corkbark fir (overall $\chi^2 = 48.66$, df = 5, P < 0.001, n = 37), although simultaneous confidence intervals do not detect differences in individual species selection for dreys (Table 2).

Nest Site Comparisons

Compared to random sites, cavity and drey nest sites had 10% more canopy cover, 20% more live trees per hectare, and twice the number of decayed logs per hectare and corkbark fir per hectare. Cavity nest sites also had 40% more large trees per hectare, >40% more large snags per hectare, and 23% higher basal area per hectare than drey and random sites. Cavity nest sites also had 71% more aspen per hectare than drey sites but 1.5 times fewer aspens per hectare than random sites. In contrast, random sites had 73% more ponderosa pine per hectare and 18% more Douglas fir per hectare than cavity and drey sites and 50% more southwestern white pine per hectare than cavity nest sites (Table 3).

Of the 17 variables used to characterize forest structure, 6 were selected via stepwise DFA as best discriminating among cavity, drey, and random sites (corkbark fir/ha, decayed logs/ha, large trees/ha, ponderosa pine/ha, Douglas-fir/ha, and aspen/ha). The overall Wilks' λ values were decreased from 0.783 in step 1 to 0.525 in step 6. Among the

6 selected variables, all correlation coefficients were ≤ 0.5 . Since multicollinearity was low among variables, we used all of them in subsequent DFA. Nest sites (both cavity and drey) were distinguished from random sites by discriminant function (DF) 1, which had scores positively correlated with corkbark fir, decayed logs, and large tree densities and negatively correlated with ponderosa pine, aspen, and Douglas fir densities (DF 1: eigenvalue = 0.506, Wilks' λ = 0.581, χ^2 = 128.479, P < 0.001). The separation of cavity sites from drey sites is evident in DF 2, which was positively correlated with, and heavily weighted by aspen and large tree density (DF 2: eigenvalue = 0.143, Wilks' λ = 0.875, χ^2 = 31.56, P < 0.001; Table 4). Classification accuracy based on the resulting discriminant functions was 61.2%.

Distinctions between site types (cavity, drey, and random) were further indicated by differences in DF scores (DF 1, $F_{2,239} = 60.527$, P < 0.001; DF 2, $F_{2,239} = 17.062$, P < 0.001). Discriminant function 1 scores were higher for nest sites compared to random sites (Tukey's Honestly Significant Differences [HSD], $\alpha = 0.05$) and discriminant function 2 scores were higher for cavity and random sites compared to drey sites (Tukey's HSD, $\alpha = 0.05$).

Because substantial similarity existed in forest structure between cavity nest and drey sites, we repeated the above analyses with cavity and drey sites combined. Of the original 17 variables, the same 6 variables were selected as best distinguishing red squirrel nest sites from random sites. Correlation among selected variables was low (≤ 0.5) and we conducted DFA on the 6 variables. Again, abundance of corkbark fir, decayed logs, large trees, and less ponderosa pine, aspen, and Douglas fir distinguished nest sites from

Table 2. Species availability (calculated from random plots) and species used for Mount Graham red squirrel cavity nests (n = 90) and dreys (n = 37) found in mixed conifer forest, Pinaleño Mountains, Arizona, USA, 2002–2005.^a

Tree species	n available	P _a	<i>n</i> used (cavity)	P _u (cavity)	P _a –P _u (cavity)	97.5% CI P _a –P _u (cavity)	n used (drey)	P _u (drey)	P _a -P _u (drey)	97.5% CI P _a –P _u (cavity)
Engelman spruce	984	0.19	3	0.03	0.16	-0.07 to 0.39	14	0.38	-0.19	-0.48 to 0.10
Corkbark fir	2,352	0.46	23	0.26	0.20	0.00 to 0.40	20	0.54	-0.08	-0.33 to 0.17
Douglas fir	439	0.09	2	0.02	0.06	-0.17 to 0.29	1	0.03	0.06	-0.30 to 0.42
Aspen	949	0.18	58	0.64	-0.46	-0.60 to -0.32 A ^b	1	0.03	0.16	-0.20 to 0.52
Southwestern white pine	326	0.06	2	0.02	0.04	-0.19 to 0.24	1	0.03	0.04	-0.32 to 0.40
Ponderosa pine	48	0.09	2	0.02	0.07	-0.18 to 0.32	0	0	0.09	

^a We recorded one cavity nest in an unknown tree species and one drey nest in a white fir. We did not include these in species use analyses. We present CIs (85% overall, 97.5% individual) for the difference in proportion available (P_a) and proportion used (P_u) for each tree species. Intervals containing zero indicate that species use is in proportion to its availability in the study area. CIs excluding zero with positive endpoints indicate that a species is used significantly less than its availability in the study area, and intervals excluding zero with negative endpoints indicate that a species is used significantly more than its availability in the study area.

^b CIs followed by different letters indicate use significantly differs from availability ($\alpha \leq 0.025$).

Table 3. Stand characteristics ($\tilde{x} \pm SE$) among cavity nest sites, drey nest sites, and random sites for Mount Graham red squirrels inhabiting mixed conifer
forest, Pinaleño Mountains, Arizona, USA, 2002–2005.

	Cavity (n	= 91)	Drey (n	= 38)	Random (<i>n</i> = 113)		
Stand characteristics	x	SE	x	SE	\bar{x}	SE	
Slope (%)	25.2	5.60	15.7	2.20	16.6	0.90	
\bar{x} canopy cover (%)	84.6A ^b	0.60	84.7A	1.40	75.3B	1.70	
Live trees/ha	1,326.4A	52.40	1,362.3A	88.50	1,068.4B	54.80	
Snags/ha	519.8	26.70	571.9	53.00	454.0	31.30	
Large trees/haª	167.4A	8.90	94.7B	9.40	105.9B	6.50	
Large snags/ha ^a	44.3A	4.00	21.9B	4.00	28.0B	3.20	
Logs/ha	82.2	8.80	71.1	10.60	54.9	6.60	
Log vol/ha (m ³)	44.4	5.50	43.7	8.70	32.9	5.90	
Decayed logs/ha	167.0A	12.00	164.0A	15.90	77.9B	8.30	
Basal area (m²/ha)	78.5A	2.50	63.6B	2.50	57.4B	2.40	
Simpson's D	0.5A	0.02	0.4B	0.02	0.6C	0.02	
Engelmann spruce/ha	274.7	21.40	262.3	35.60	290.3	25.10	
Corkbark fir/ha	1,237.0A	63.60	1,488.6A	109.10	693.8B	60.40	
Douglas-fir/ha	76.6A	10.80	58.8A	8.70	129.5B	15.60	
Aspen/ha	189.0	28.90	53.5A	11.20	279.9B	43.70	
Southwestern white pine/ha	46.9A	11.90	49.1	19.70	96.2B	14.70	
Ponderosa pine/ha	4.0A	2.30	1.8A	1.20	14.2B	2.50	

^a Trees >40 cm dbh.

 $^{\rm b}$ Means followed by different letters differ significantly at $\alpha \leq 0.05$ (Tukey's method).

random sites (DF eigenvalue 0.506, Wilks' $\lambda = 0.664$, $\chi^2 = 97.048$, P < 0.001; Table 4). By combining nest types, classification accuracy increased to 79.3%.

DISCUSSION

Nest site selection by Mount Graham red squirrels is strongly influenced by stand composition, particularly density of corkbark fir, mature (large) trees, and decaying logs. These indicators of old growth were consistently higher at nest sites, regardless of nest type. Availability of larger snags and cavity-containing trees, especially aspen, is also of particular importance for this population as they provide preferred nesting locations. Cavity nests may offer benefits such as increased insulation (Menzel et al. 2004), space for caching food (Vahle and Patton 1983) when food resources are scarce, and more protection from ever-present avian predators (Froehlich and Smith 1990, Carey 1995). Because cavities are more likely in dead trees, they also have fewer access routes and living canopy, which might offer further protection from some predators but make the nest cavity potentially more conspicuous. Red squirrels on Mount Graham used cavity nests at a much higher rate than do neighboring populations in the White Mountains of east-central Arizona (Young et al. 2002), and during our study Mount Graham red squirrels used cavities over dreys by more than 2:1. The difference between sites is likely due to differences in habitat structure as fewer aspen and resulting cavities and snags are available in the White

Table 4. Tests of equality among group means for variables entered into discriminant analysis and resulting standardized canonical discriminant function coefficients (DFC) for each variable and bivariate Pearson's correlation coefficients between discriminant function (DF) scores and the selected variables for A) cavity nests and dreys separate and B) cavity nests and dreys combined for Mount Graham red squirrels, Pinaleño Mountains, Arizona, USA, 2002–2005. Associated P values at 0.05 α level are given for F-tests (P_F) and Pearson's correlation coefficients (P_r).

А.									
Variable	Wilks' λ	F 2,239	P_F	DF 1 correlations	P_{r1}	DFC 1	DF 2 correlations	DFC 2	P_{r2}
Corkbark fir/ha	0.776	34.552	< 0.0001	0.799	< 0.01	0.454	-0.275	-0.223	< 0.01
Decayed logs/ha	0.809	28.268	< 0.0001	0.753	< 0.01	0.422	-0.079	-0.034	0.22
Large trees/ha	0.855	20.197	< 0.0001	0.466	< 0.01	0.412	0.756	0.808	< 0.01
Ponderosa pine/ha	0.919	10.540	< 0.0001	-0.488	< 0.01	-0.263	0.084	0.081	0.19
Aspen/ha	0.927	9.400	< 0.0001	-0.302	< 0.01	-0.186	0.582	0.571	< 0.01
Douglas fir/ha	0.950	6.305	< 0.0020	-0.377	< 0.01	-0.162	0.137	-0.115	0.03
В.									
Variable	Wilks' λ	F 1,239	P_F	DF correlations	P_{r1}	DFC			
Corkbark fir/ha	0.783	66.630	< 0.0001	0.804	< 0.01	0.460			
Decayed logs/ha	0.809	56.695	< 0.0001	0.754	< 0.01	0.422			
Ponderosa pine/ha	0.919	21.042	< 0.0001	-0.490	< 0.01	-0.264			
Large trees/ha	0.931	17.701	< 0.0001	0.452	< 0.01	0.412			
Douglas fir/ha	0.952	12.201	0.001	-0.379	< 0.01	-0.160			
Aspen/ha	0.967	8.154	0.005	-0.313	< 0.01	-0.202			

Mountains compared to Mount Graham (Young et al. 2002). For dreys, squirrels likely have more choice in nest tree species and associated stand characteristics; however, we found more similarities than differences between cavity nest and drey sites.

Corkbark fir is an important component of red squirrel nesting habitat in the mixed conifer transition zone on Mount Graham and is the dominant tree species (45.6%), constituting a large proportion of mature, cone-bearing trees. Spicer et al. (1985) note that red squirrels in mixed conifer habitat associated primarily with stands containing corkbark fir or Engelmann spruce, and cones of corkbark fir, Engelmann spruce, and Douglas fir were most common in red squirrel middens. In addition to providing important nesting habitat, these dense, corkbark fir dominated stands provide increased canopy closure and dead woody debris. Such stands are associated with cooler microclimates, facilitating cone storage within middens, and offer greater protection from predators (Vahle and Patton 1983, Spicer et al. 1985, Smith and Mannan 1994, Carey 1995, Goheen and Swihart 2005). In contrast, randomly located sites in the mixed conifer transition zone are characterized by less structural complexity, canopy closure, and more tree species associated with drier, open sites (Brown 1986, Smith and Mannan 1994).

Decadence in the form of fallen and decaying logs and snags is an important habitat component for many small mammals (Douglass and Reinert 1982, Tallmon and Mills 1994, Carey and Harrington 2001, Carey and Wilson 2001, Bull 2002) including red squirrels (Vahle and Patton 1983, Froehlich and Smith 1990, Smith and Mannan 1994, Bakker 2006). These features provide additional vertical and horizontal structural complexity to forest habitats and promote ecosystem function and biocomplexity (Carey and Harrington 2001). Decaying wood is correlated with species richness in boreal forests (Juutinen et al. 2006) and is increasingly recognized as an important component of forest ecosystem function (Carey 2000, Carey and Harrington 2001, Thomas 2002). Decaying logs and snags serve many purposes for squirrels and other small mammals. They provide cache locations both alongside and within the log (Gurnell 1984, Patton and Vahle 1986), nesting locations (Bull 2002, Menzel et al. 2004), and runways (Douglass and Reinert 1982, Bakker 2006), and they promote the growth of epigeous fungi (Tallmon and Mills 1994, Thomas 2002, Juutinen et al. 2006)-an important component of red squirrel diets (Koprowski et al. 2005).

Currently, plans to restore the mixed conifer region of the Pinaleños call for thinning of dense stands, which are dominated by corkbark fir and Engelmann spruce, and removal of many snags and downed wood to reduce risk of future catastrophic fires and insect outbreaks. Red squirrel nest sites were associated with many of these features thought to be detrimental to forest health, including a high density of corkbark fir, snags, and decaying logs. Although fuel reduction may be necessary for forest health, it is important to bear in mind how removing these potential fuels might affect not only red squirrel nesting habitat but also assemblages of plants, fungi, and other birds and mammals. Alteration and fragmentation of stand structure may also influence squirrel movements and perceived predation risk (Gurnell et al. 2002, Bakker and Van Vuren 2004, Bakker 2006) thereby limiting usable habitat. Intense thinning (>50% stem reduction) has been associated with population decline in many squirrel species (see Koprowski 2005b for review) and microhabitat changes that are detrimental to fungal growth and mycorrhizal associations (Dodd et al. 2003). Such changes may also increase habitat suitability for other species such as Abert's squirrel (Sciurus aberti) or northern goshawks (Accipiter gentilis) that could potentially out-compete or increase predation upon red squirrels (Dodd et al. 2003, Drennan and Beier 2003, Edelman and Koprowski 2005).

MANAGEMENT IMPLICATIONS

To promote both forest health and conservation of Mount Graham red squirrel nesting habitat, we recommend a dynamic management plan such as those proposed by Vahle and Patton (1983), Smith and Mannan (1994), and Carey (2000, 2001). Such plans propose active management of dead and decaying trees in addition to variable density thinning to provide dense, mixed-age stands of suitable squirrel habitat while also reducing fuel load potential. Such practices may mimic natural thinning and gap formation processes while maintaining stands of adequate density, species composition, and decadence that we have shown to be important for squirrels nesting in mixed-conifer habitat. We caution that further studies need to be conducted in small areas of localized thinning of variable intensities in order to determine the impact on red squirrel habitat use before widespread thinning operations are undertaken.

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