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# Nest Site Selection by Western Gray Squirrels at Their Northern Range Terminus

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**ABSTRACT** The western gray squirrel (*Sciurus griseus*) in Washington, USA, is limited to 3 disjunct areas and is a state threatened species. Information is lacking for the North Cascades population, which is the northernmost population for the species. Squirrels in this population exist without oaks (*Quercus* spp.) that provide forage and cavities for maternal nests elsewhere in their range. During May 2003 to August 2005, we studied selection of nest sites and nest trees by 18 radiocollared squirrels in Okanogan County, Washington. Without oak cavities, females reared their young in dreys. General nest-tree characteristics were similar to characteristics of western gray squirrel nest trees in Southeastern Cascades: relatively tall ponderosa pines (*Pinus ponderosa*)  $\geq 40$  cm diameter at breast height. Results from conditional logistic models determined that the odds of a squirrel selecting a tree for nesting increased with greater diameter at breast height and with infection by dwarf mistletoe (*Arceuthobium* spp.). Nest sites with high selection probability by squirrels had greater basal area and number of tree species than available unselected sites. Retention of forest patches that include a mix of conifer species or conifer and deciduous trees and moderate to high basal area could promote nesting opportunities, connectivity for arboreal travel, as well as abundance and diversity of hypogeous fungi. Experiments to test the efficacy of retaining untreated patches of varying size (including trees infected with mistletoe) on nesting by western gray squirrels within stands managed for fire suppression and forest health would provide important information about the effects of forest fuel management on arboreal wildlife.

**KEY WORDS** mistletoe, nest selection, *Sciurus griseus*, threatened species, Washington, western gray squirrel.

Fire suppression over the past 100 years in the interior dry forests of western North America has resulted in dense stands of young, suppressed trees, and increased coarse woody debris and vulnerability to disease and catastrophic fire (Agee 1993, 2003). As a result, managers are in need of strategies for restoring forest health and adequate habitat for a suite of wildlife species, many of which are threatened or endangered. The western gray squirrel (*Sciurus griseus*) is one such species. This arboreal rodent is the largest tree squirrel native to Washington, Oregon, and California, USA. In Washington, it inhabits forest habitats in 3 disjunct areas: the Southeastern Cascades adjacent to the Columbia Gorge, the southern Puget Trough, and the North Cascades (Linders and Stinson 2007). Citing concerns over increasing population fragmentation and habitat loss, the Washington Department of Fish and Wildlife (WDFW) listed the western gray squirrel as threatened in 1993.

Tree squirrels serve various ecological functions in forest communities. They forage for and consequently spread the spores of hypogeous fungi; these fungi serve to facilitate nutrient and water uptake in pine (*Pinus ponderosa*), oak (*Quercus* spp.), and Douglas-fir (*Pseudotsuga menziesii*) roots (Maser et al. 1981). Squirrels also disperse seeds and acorns by burying them throughout their home range. They recover some, but not all, buried seeds, leaving many to germinate (Smith 1970). Along with providing ecological functions, squirrels have specific basic requirements for forest structure: connectivity between branches for travel, trees of suitable size for nesting, and mast-producing species for forage. As a

result, tree squirrels are useful indicators of the efficacy of forest management strategies (Patton et al. 1985, Pederson et al. 1987, Carey 2000, Koprowski 2005).

Suitable nest trees and nest sites are an essential habitat component for tree squirrels (Steele and Koprowski 2001). Without appropriate nesting opportunities, tree squirrels are vulnerable to predators and weather extremes and cannot reproduce successfully. Tree squirrels typically construct 3 types of nests: 1) the den is a nest that occurs inside tree cavities; 2) the drey, a spherical mass of intertwined branches, needles, and other vegetation, also provides squirrels complete enclosure; and 3) the platform nest resembles a flattened drey and may include more leafy vegetation. Studies of various tree squirrel species have highlighted the importance of canopy connectivity, tree size, and a variety of tree species to nest site selection (Sanderson et al. 1975, Halloran and Bekoff 1994, Edelman and Koprowski 2005). Tree squirrels also frequently use deformations (i.e., witches' brooms) caused by infection of trees with dwarf mistletoe (*Arceuthobium* spp.) for nesting (Garnett et al. 2004, 2006; Hedwall et al. 2006).

Throughout most of its range, the western gray squirrel inhabits conifer-hardwood forests (Ingles 1947, Carraway and Verts 1994). In the southern Puget Trough and Southeastern Cascades of Washington, the western gray squirrel is described as an oak-obligate species that depends on a diverse mixture of oak and conifer trees (Dalquest 1948, Rodrick 1986, Foster 1992, Linders 2000, Bayrakçi et al. 2001). When oak is present, western gray squirrels harvest acorns for food and use oak cavities almost exclusively for natal dens (Cross 1969, Linders 2000). As

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observed in other sciurid species, large trees that form a well-connected canopy are an important habitat component for western gray squirrels, providing arboreal escape routes (Ingles 1947, Rice 1977, Gilman 1986, Foster 1992, Ryan and Carey 1995).

The North Cascades of Washington represent not only the northern extent of the western gray squirrel's range, but one of the only areas where it survives without oak. Because oak woodlands are in decline in Washington, it is important to understand the conditions where western gray squirrel populations persist without oak (Larsen and Morgan 1998). Moreover, this species inhabits primarily dry forests in this region and such forests are undergoing increasing management for disease prevention and restoration of more natural fire regimes; managers need information on wildlife habitat requirements to accommodate species that depend on these dry forests.

Our objectives were to 1) describe the characteristics of western gray squirrel nests in an area lacking oak; 2) quantify western gray squirrel nest selection relative to availability at 2 spatial scales, the nest tree and nest site; and 3) develop management recommendations for maintaining appropriate nesting opportunities in a dry forest habitat.

## STUDY AREA

The study area was located in the Black Canyon Creek Watershed, Okanogan National Forest, 11 km west of Pateros, Washington. Mean temperatures varied from  $-9^{\circ}\text{C}$  in January to  $31^{\circ}\text{C}$  in August, with cold, wet winters and hot, dry summers. Average annual precipitation was 32 cm and total annual snowfall averaged 103 cm (35-yr means; Western Regional Climate Center 2005). Elevation ranged from 437 m to 1,196 m. Ponderosa pine dominated south-facing slopes. Douglas-fir was the dominant conifer species on east and north aspects, or where vegetation had a riparian component. Vegetation in riparian zones included the following deciduous tree species: cottonwood (*Populus balsamifera*), aspen (*Populus tremuloides*), and alder (*Alnus rubra*).

## METHODS

Between June 2003 and September 2004, we trapped squirrels with  $15 \times 15 \times 48$ -cm (model 202) and  $23 \times 23 \times 66$ -cm (model 205) wire mesh Tomahawk live traps (Tomahawk Live Trap Co., Tomahawk, WI) baited with whole English walnuts. We weighed, sexed, and assessed the reproductive condition of captured squirrels in a cloth handling cone (Koprowski 2002) modified with a ventral flap. We attached eartags (model 1005-3; National Band and Tag Co., Newport, KY) to all captured squirrels and fitted those weighing  $>650$  g with a 16-g radiotransmitter (model SI-2C; Holohil Systems Ltd., Carp, ON, Canada). We used a braided stainless steel cable fastened with a brass crimp to help reinforce the zip-tie collar against removal by chewing. We located nests year-round by homing on inactive collared squirrels and inspecting trees from the ground with binoculars (White and Garrott 1990). Our study was approved by the University of Washington

Institutional Animal Care and Use Committee (protocol no. 2479-24).

## Nest, Tree, and Site Characteristics

We delineated the 1,300-ha study area using a minimum convex polygon (MCP; The Home Range Extension for ArcView) around all locations ( $n = 1,014$ ) of 18 (9 F, 9 M) radiocollared squirrels surrounded by a 500-m buffer, the average interfix movement of male squirrels (Gregory 2005). We examined selection of nests at 2 scales: the nest tree and the site (i.e., the area within a 25-m radius of the nest tree) containing the nest tree. For every nest, we recorded its type (den, drey, or platform) and species of nest tree. Natal nests were nests where a female gave birth, as confirmed by direct observation of young in or around the nest.

Due to time limitations, we randomly selected a sample of 50 nest trees from the 64 nest trees that we identified by radiotelemetry. To increase representation of nests that multiple squirrels used repetitively, we replaced 2 of the randomly selected trees that a squirrel had used once with 2 nest trees that  $>1$  squirrel had used multiple times. Because individual squirrels often used multiple nests, not all nests were statistically independent. The 50 nest trees represented 15 individual squirrels (6 M, 9 F). For each nest, we noted nest aspect in relation to the tree's trunk, measured the nest height above ground, and calculated the ratio of nest height to nest tree height. We also recorded whether the nest occurred in a mistletoe broom as visible from the ground.

Within a 0.2-ha plot centered on each nest tree, we randomly sampled 8 unused available trees  $>20$  cm diameter at breast height (i.e., minimum dbh of nest trees) for comparison with the nest tree (Skalski 1987). Eight random trees per nest tree provided a measure of variability and, on some sites, was the maximum number present in our sample plot. For each of these available trees and the nest tree, we recorded species, total height, height to lowest live crown (i.e., crown base height), and diameter at breast height. We made categorical observations of percent live canopy (i.e., tree condition; 0–50% live, 50–75% live, or  $>75\%$  live), presence or absence of mistletoe brooms visible from the ground, and height relative to other trees in the stand (taller than, equal ht as, or shorter than surrounding trees). We also measured connectivity by counting surrounding trees with branches  $\leq 1$  m away (i.e., the estimated max. distance that a western gray squirrel will jump between trees; Linders 2000, Gregory 2005). We measured height with an Impulse IP200 laser (Laser Technology Inc., Englewood, CO).

To compare nest sites to available unused sites we used a Geographic Information System (GIS) to plot the 50 nest tree locations together with each squirrel's 95% MCP home range. We generated a number of random locations corresponding to the number of nest trees within each home range using the ArcView Animal Movements extension. If a nest tree occurred within the overlap of 2 home ranges, we confined the corresponding random location to the home range of the squirrel that had used the nest most frequently. Our largest sampling area for vegetation measurements was a circular plot with a radius of 25 m (see below); therefore, if a

random location fell within 50 m of a nest tree, we reselected the point. Each home range served as a separate stratum for selection of random locations, with individual squirrels contributing a variable number of nests to the study. One female used a nest and died after only 2 relocations; lacking a home range, we selected the corresponding random location for this nest tree within an area equal to the average female 95% MCP home range (35 ha) centered on the nest tree. We used Global Positioning System receivers to position each random location; the tree nearest to the coordinates served as the focal tree for the available site.

To characterize nest and available sites we used nested 0.2-ha, 0.04-ha, and 0.01-ha circular plots centered on the nest and focal tree. We measured connectivity on nest sites by averaging the connectivity of the nest tree and the 8 available trees used for tree selection analysis (see above) and on available sites by averaging the connectivity of the focal tree and 8 randomly selected trees within a circular 0.2-ha plot centered on the focal tree. Within the 0.04-ha plot, we estimated percent overstory canopy cover by taking the average of 28 readings from a moosehorn cover scope (Moosehorn Cover Scopes, Medford, OR) at 4 evenly spaced points along the plot radius in the 4 cardinal directions and at 3 points to the northwest, northeast, southwest, and southeast. We recorded species of all trees (>5 cm dbh) and created a binary variable, Tree Species (i.e.,  $\geq 90\%$  ponderosa pine vs. any other mixture of species), to summarize this information. We also measured diameter at breast height of all live trees  $\geq 5$  cm diameter at breast height (summarized as quadratic mean dbh) and used these stem data to calculate basal area ( $m^2/ha$ ). Within the 0.01-ha plot, we visually estimated the percent cover of shrubs and saplings ( $\leq 5$  cm dbh) and tallied them by species. We categorized ground cover as primarily litter, primarily vegetation, or equal litter and vegetation. For each site, we utilized GIS to obtain aspect and elevation and calculate the distance from the nest and focal tree to the nearest perennial water source and to the nearest maintained road. We conducted all vegetation sampling May–August 2005.

### Statistical Analysis

To identify factors that could be contributing to squirrels' selection of nest trees and nest sites, we used conditional logistic models to estimate the logit of selection probability (Hosmer and Lemeshow 2000). We then evaluated the relative importance of predictors using the information-theoretic approach (Anderson et al. 2000, Burnham and Anderson 2002).

We collected tree and site data under matched case-control designs. We matched or stratified nest and available trees by nest site, whereas we matched nest and available sites by squirrel home range. Sample size, including the cases for each matched set (stratum), varied from 2 to 16. Most matched sets for the tree data had 9 observations (nest tree plus 8 available trees), whereas most matched sets for the site data had  $\leq 6$  observations (nest site plus 5 available sites). Under this study design, we fit conditional logistic models instead of the usual logistic models. We eliminated

**Table 1.** Means and percentages for characteristics of selected ( $n = 49$ ) and available unused trees ( $n = 387$ ) within the nest sites ( $n = 49$ , 0.2 ha) of 15 western gray squirrels, Okanogan County, Washington, USA (May–Aug 2005).

Variable	Nest trees	SE	Available trees	SE
Connectivity (count)	2.7	0.3	2.3	0.1
Crown base ht (m)	6.0	0.5	4.7	0.2
Dbh (cm)	45.4	1.8	37.5	1.0
Mistletoe (%)				
Present	46.9		6.7	
Absent	53.1		93.3	
Relative ht (%)				
Taller	24.5		9.0	
Equal	67.3		63.8	
Shorter	8.2		27.1	
Condition—% live canopy (%)				
0–50%	18.4		17.8	
50–75%	32.6		30.5	
>75%	49.0		51.7	
Tree ht (m)	23.0	1.0	20.0	0.5
Tree species (%)				
Ponderosa pine	83.7		76.7	
Douglas-fir or cottonwood	16.3		23.2	

the stratum-specific parameters by conditioning on the observed predictor values, the stratum total, and the number of cases in each stratum; this method allowed estimation of parameters associated with uncontrolled predictors with reduced bias and increased efficiency (Pike et al. 1980).

Predictors of squirrels' nest tree selection fell into 4 categories:

1. Species: tree species.
2. tree size: tree height, diameter at breast height, and crown base height.
3. Tree condition: percent live canopy and mistletoe.
4. Tree relative to stand: connectivity and relative height.

Similarly, predictors of squirrels' nest site selection formed 3 categories:

1. Stand characteristics: basal area, connectivity, mean diameter at breast height, and count of tree species.
2. Ground characteristics: ground cover, shrub cover, and count of understory species.
3. Site placement: aspect, elevation, distance to water, and distance to road (Tables 1, 2).

Lists of a priori candidate models included those suggested by Foster (1992), WDFW (E. A. Rodrick, WDFW, unpublished report), and Linders (2000), as well as models utilizing a combination of predictors from the categories of tree and site characteristics mentioned above (Tables 3, 4).

We evaluated the level of association between each pair of predictors. For continuous predictor pairs we used correlation coefficients, for categorical predictor pairs we used contingency tables with chi-square tests, and for continuous-categorical predictor pairs we used one-way analysis of variance (ANOVA) with  $F$ -tests. Collinearity problems are likely to occur between predictors in the same category. When we found a strong correlation ( $r \geq 0.5$ ) in any pair or

**Table 2.** Means and percentages for characteristics of selected ( $n = 50$ ) and available unused ( $n = 50$ ) nest sites (0.2 ha, 0.04 ha, or 0.01 ha) within the home ranges of 15 western gray squirrels, Okanogan County, Washington, USA (May–Aug 2005).

Variable	Nest sites	SE	Available sites	SE
Aspect (%)				
South	42.0		62.0	
Other	58.0		38.0	
Basal area <sup>a</sup> (m <sup>2</sup> /ha)	27.2	1.7	14.7	1.1
Canopy cover <sup>a</sup> (%)	45.4	2.6	30.3	2.3
Connectivity <sup>b</sup> (count)	2.4	0.2	1.9	0.1
Distance to road (m)	430	40	430	40
Distance to water (m)	540	50	530	50
Elevation (m)	760	20	760	20
Ground cover <sup>c</sup> (%)				
>50% litter	68.0		60.0	
>50% vegetation	16.0		22.0	
Litter = vegetation	16.0		18.0	
Quadratic mean dbh <sup>a</sup> (cm)	31.7	1.1	27.6	1.1
Shrub cover <sup>c</sup> (%)	10.9	2.1	11.9	2.0
Tree species <sup>a</sup> (%)				
≥90% ponderosa pine	56.0		88.0	
Other mixture	44.0		12.0	
Understory species <sup>c</sup> (count)	3.0	0.2	2.3	0.2

<sup>a</sup> Plot area = 0.04 ha.

<sup>b</sup> Plot area = 0.2 ha.

<sup>c</sup> Plot area = 0.01 ha.

group of continuous predictors in a proposed model, we considered multiple versions of that model, each containing only one predictor from the pair or a subset from the group that were not highly correlated. Thus, we retained every predictor in the analysis.

We used SAS procedure PHREG (SAS Institute, Cary, NC) for the calculation of parameter estimates and the Akaike's Information Criterion (AIC). We note that the AIC reported by PHREG is derived from the conditional likelihood and should differ from the AIC derived from the full likelihood by a constant. Simulation studies indicated that the performance of AIC in selecting the correct model with small sample sizes was similar to other proposed extensions of AIC (Pan 1999). Therefore, we proceeded with model selection and model averaging using the SAS-reported AIC. After calculating the difference in AIC values ( $\Delta\text{AIC}$ ), we ranked the models in ascending order and used their Akaike weights ( $w_i$ ) to obtain the likelihood that each was the best model in the set. We included models that were within 4 AIC units of the top model to form an approximate 95% confidence set for the best model (Burnham and Anderson 2002). We used model averaging over models in the confidence set to identify the most influential predictors (Burnham and Anderson 2002). In addition, we assessed the relative importance of predictors by adding the weights of each model in which they were included to obtain a cumulative weight (Burnham and Anderson 2002). We used odds ratios with 95% confidence intervals that did not include 1 to identify significant predictors of nest trees and sites in conditional logistic regression models (Agresti 1990).

After reviewing the model averaging results, we found the presence of mistletoe to be the most prominent predictor for

**Table 3.** A priori models used to compare nest trees ( $n = 49$ ) used by western gray squirrels to available unused trees ( $n = 387$ ) within nest sites ( $n = 49$ ) in Okanogan County, Washington, USA (May–Aug 2005). The difference in Akaike's Information Criterion values ( $\Delta\text{AIC}$ ) and Akaike weights ( $w_i$ ) are listed.

Model <sup>a</sup>	$\Delta\text{AIC}$	$w_i$
Tree structure		
Cond, Dbh, Mist, Spp	0.00	0.355
CBH, Cond, Dbh, Mist, Spp	1.01	0.214
Cond, Ht, Mist, Spp	2.74	0.090
CBH, Cond, Mist, Spp	14.77	0.000
Global		
CBH, Con, Cond, Dbh, Mist, RHt, Spp	0.46	0.282
Con, Cond, Ht, Mist, RHt, Spp	3.61	0.058
Predator escape		
Con, Cond, Mist	13.64	0.000
Foster (1992)		
Dbh, Spp	47.65	0.000
Linders (2000)		
Con, Dbh, RHt	48.04	0.000
Con, Ht, RHt	52.99	0.000

<sup>a</sup> Variables: CBH = crown base height; Con = connectivity; Cond = tree condition; Dbh = diameter at breast ht; Ht = tree ht; Mist = mistletoe; RHt = relative tree ht; Spp = tree species.

nest tree selection, and it was included in all candidate models in the 95% confidence set. Because one-way ANOVA  $F$ -tests indicated significant associations between mistletoe and the continuous variables diameter at breast height, connectivity, and tree height, we further evaluated the contribution of the three continuous predictors by controlling for the presence of mistletoe in a post hoc analysis. Using all nest and available trees, we identified the subset of matched sets in which mistletoe was not present. We then fit this subset with 2 additional conditional logistic models containing only connectivity, diameter at breast height, and tree height. We used odds ratios with 95% confidence intervals to illustrate the significance of each continuous predictor.

## RESULTS

### Nest Characteristics

We radiotracked 18 squirrels (9 M, 9 F) and found them associated with 64 nests. Twenty-five percent of all squirrel relocations were at nests ( $n = 252$  nest locations out of 1,014 total telemetry relocations). We located squirrels in 39% of the nests only once and in 61% of the nests  $\geq 2$  times. Ninety-eight percent of nests were either drey (78%) or platform (20%). Ninety-seven percent of nests occurred in either ponderosa pine (81%) or Douglas-fir (16%) trees. One platform nest was in a cottonwood, and a den was in an alder cavity. Natal nests comprised 9% of the nests. Of the 6 natal nests, 1 was the den and the other 5 were dreys. Four of 5 natal dreys occurred in ponderosa pine.

Of the 50 nests we sampled for selection analyses, 40% occurred on the south side of the nest tree, 21% were on the west side, 15% were on the north side, and 15% were on the east side. We categorized 5 nests (10%) built in the crotch of the nest tree as having no aspect. Mean nest height was 11.8

**Table 4.** A priori models used to compare western gray squirrel nest sites ( $n = 50$ ) and available unused sites ( $n = 50$ ) within home ranges ( $n = 15$ ) in Okanogan County, Washington, USA (May–Aug 2005). The difference in Akaike’s Information Criterion values ( $\Delta AIC$ ) and Akaike weights ( $w_i$ ) are listed.

Model <sup>a</sup>	$\Delta AIC$	$w_i$
Stand characteristics		
BA, Qdbh, TSpp	0.00	0.582
Global		
Asp, BA, DW, GCov, Qdbh, SCov, TSpp, USpp	1.37	0.293
Asp, BA, DR, Elev, GCov, Qdbh, SCov, TSpp, USpp	3.07	0.125
Asp, CON, DW, GCov, Qdbh, SCov, TSpp, USpp	21.19	0.000
Asp, CON, DR, Elev, GCov, Qdbh, SCov, TSpp, USpp	23.60	0.000
Linders (2000)		
CON, Qdbh, TSpp	22.14	0.000
Washington Department of Fish and Wildlife (E. A. Rodrick, Washington Department of Fish and Wildlife, unpublished report)		
DW, TSpp	30.87	0.000
Predator escape		
CON, SCov	38.53	0.000
Ground characteristics		
GCov, SCov, USpp	38.56	0.000
Site placement		
Asp, DW	40.31	0.000
Asp, DR, Elev	42.32	0.000

<sup>a</sup> Variables: Asp = aspect; BA = basal area; CON = connectivity; DR = distance to road; DW = distance to water; Elev = elevation; GCov = ground cover; Qdbh = quadratic mean diameter at breast ht; SCov = shrub cover; TSpp = tree species; USpp = understory species.

m (SE = 0.5,  $n = 48$ ). Most nests were halfway up the tree, as indicated by a mean ratio of nest height to tree height of 0.53 (SE = 0.03, range: 0.20–0.92,  $n = 48$ ). These values exclude the den nest and one drey obscured by mistletoe. Forty-six percent of the nests occurred in a mistletoe broom.

### Nest Tree Selection

We compared 10 models using data from 49 nest trees and 387 available trees within 49 nest sites. There were 3 nest tree plots that contained <8 available trees. In addition, we omitted the den nest tree from this analysis because there were no suitable trees within 0.2 ha for comparison. The model with the greatest support from the data indicated that nest trees, when compared with available trees, had greater diameter at breast height, presence of mistletoe, and percent live canopy, and were more likely to be ponderosa pine (Table 3). This model’s weight was 1.3 times greater than the second best model. Three of the 4 variables in the best model (mistletoe, tree condition, and tree species) were included throughout the top model set and each had a cumulative weight of 0.999, providing additional evidence of their importance. Odds ratios indicated that increasing diameter at breast height and presence of mistletoe had the strongest effect on squirrels’ nest tree selection (Table 5).

Mistletoe was the dominant predictor whenever present in a model. Almost half of nest trees (23/49) contained

**Table 5.** Odds ratios and 95% confidence intervals for explanatory variables of western gray squirrel nest tree selection in Okanogan County, Washington, USA (May–Aug 2005), based on model-averaged coefficients from 10 models.

Variable	Coeff.	SE	Odds ratio	CI
Connectivity	0.130	0.101	1.139	0.935, 1.387
Crown base ht	0.021	0.046	1.021	0.933, 1.118
Dbh*	0.065	0.020	1.067	1.026, 1.111
Mistletoe*	3.618	0.631	37.27	10.82, 128.3
Relative ht1	0.078	0.384	1.082	0.510, 2.295
Relative ht2	0.072	0.262	1.075	0.643, 1.797
Tree condition2	−0.259	0.617	0.772	0.230, 2.587
Tree condition3	−0.578	0.695	0.561	0.144, 2.189
Tree ht	0.028	0.026	1.029	0.978, 1.083
Tree species	0.268	0.649	1.307	0.367, 4.661

\* Significant result (i.e., CI does not include 1).

mistletoe brooms compared with 7% (26/387) of available trees. There were 27 out of 49 matched sets containing  $\geq 1$  tree with mistletoe, and 23 of those 27 sets had mistletoe in the nest tree. Twelve of those nest trees were the only trees with mistletoe in their respective matched sets. The post hoc analysis using only the 22 matched sets with no mistletoe presence identified connectivity and tree height as significant predictors in addition to diameter at breast height (Table 6).

### Nest Site Selection

We compared 11 models using data from 50 nest sites and 50 available sites within 15 western gray squirrel home ranges. The model with the most support from the data included mean tree diameter at breast height, stand basal area, and number of tree species; all were greater at nest sites than at available sites (Tables 2, 4). This model’s weight was 1.9 times greater than the second best model. The 3 variables in the best model also were included in the top model set, each with a cumulative weight of 1, providing additional evidence of their importance. Of these variables, stand basal area had the strongest support (Table 7), indicating that western gray squirrels were more likely to choose nest sites with higher stand basal area.

## DISCUSSION

Lacking oak trees that provide cavities used as natal dens in more southerly populations, most western gray squirrels in our North Cascades study area reared young in dreys. Squirrels in Washington’s Southeastern Cascades and

**Table 6.** Odds ratios and 95% confidence intervals for explanatory variables of western gray squirrel nest tree selection in Okanogan County, Washington, USA (May–Aug 2005), based on post hoc analysis using 22 matched sets of trees without mistletoe ( $n = 196$  trees).

Model <sup>a</sup>	Variable	Coeff.	SE	Odds ratio	CI
1	Connectivity*	0.527	0.221	1.694	1.099, 2.611
	Dbh*	0.160	0.040	1.173	1.085, 1.269
2	Connectivity	0.336	0.199	1.399	0.947, 2.067
	Tree ht*	0.283	0.083	1.327	1.128, 1.562

<sup>a</sup> Two models were considered because of the high correlation ( $r = 0.69$ ) between Dbh and Tree ht.

\* Significant result (i.e., CI does not include 1).

**Table 7.** Odds ratios and 95% confidence intervals for explanatory variables of western gray squirrel nest site selection in Okanogan County, Washington, USA (May–Aug 2005), based on model-averaged coefficients from 11 models.

Variable	Coeff.	SE	Odds ratio	CI
Aspect	−0.344	0.382	0.709	0.335, 1.499
Basal area*	0.168	0.047	1.183	1.079, 1.298
Distance to road	0.000	0.000	1.000	1.000, 1.001
Distance to water	0.001	0.001	1.001	0.999, 1.002
Elevation	0.000	0.001	1.000	0.998, 1.002
Ground cover1	0.249	0.435	1.283	0.547, 3.009
Ground cover2	−0.078	0.475	0.925	0.365, 2.347
Quadratic mean dbh	0.152	0.123	1.164	0.916, 1.481
Shrub cover	0.023	0.019	1.024	0.986, 1.062
Tree species	−0.522	0.706	0.593	0.149, 2.366
Understory species	0.207	0.166	1.210	0.889, 1.702

\* Significant result (i.e., CI does not include 1).

southern Puget Trough primarily used cavities in oaks but also Douglas-fir and big leaf maple (*Acer macrophyllum*) as natal dens (Linders 2000; Vander Haegen et al. 2005; W. M. Vander Haegen, WDFW, unpublished data). Female squirrels in the North Cascades may rear young in dreys because of a low density of suitable tree cavities. The widespread use of cavities by other western gray squirrel populations as well as studies suggesting that enclosures such as nest boxes facilitate tree squirrel population growth suggest a benefit not realized by this population (Burger 1969, Nixon and Donohoe 1979, Nixon et al. 1984).

Presence of mistletoe had a strong positive effect on squirrels' selection of a nest tree on our study area. All nests built in trees with mistletoe used the broom as part of the nest structure; in many cases, the broom supporting the nest was the only visible broom in the tree. In northern Arizona, USA, Abert's squirrels (*S. aberti*) were more likely to use ponderosa pine with brooms than without brooms (Garnett et al. 2004). Mistletoe brooms also were found to be important denning or cover microhabitat for northern flying squirrels (*Glaucomys sabrinus*; Lehmkuhl et al. 2006b) and bushy-tailed woodrats (*Neotoma cinerea*; Lehmkuhl et al. 2006a) in similar dry forests of the eastern Washington Cascades. The structure created by mistletoe deformations seems to be enhancing nesting opportunities for western gray squirrels, perhaps filling a gap created by the lack of oak cavities for dens.

Western gray squirrel nest trees we identified share several characteristics with nest trees in the Southeastern Cascades (i.e., ponderosa pines  $\geq 40$  cm dbh and taller than or equal ht to the tallest surrounding trees; Linders 2000). The tendency for squirrels to choose trees with a larger stem diameter than the mean diameter of the surrounding stand is similar to that reported for other squirrel populations (Byrne 1979, Halloran and Bekoff 1994, Linders 2000). Squirrels most likely select larger trees for nesting because larger trees typically have branches substantial enough to support a nest and withstand adverse weather conditions, especially wind (Halloran and Bekoff 1994).

Nesting in clumps of trees rather than isolated trees provides squirrels with avenues of escape, among other benefits; however, the proximity of trees surrounding a nest tree varies among populations. Squirrels in our study built nests in trees with an average of 2.7 interlocking crowns versus 4.1 observed for the Southeastern Cascades population (Linders 2000). The mean connectivity of Abert's squirrel nest trees ( $2.8 \pm 1.2$ ; Halloran and Bekoff 1994) in Colorado was similar to our observations, perhaps a result of a greater similarity in overall forest type between the North Cascades and the predominantly ponderosa pine stands of Colorado where trees can be more dispersed throughout a stand.

Sites selected for nesting by western gray squirrels in the North Cascades had greater basal area but similar mean diameter at breast height to available sites. Within these nest sites, squirrels selected nest trees with greater diameter at breast height; combined, these findings suggest that sites with more and larger trees have greater value than sites with fewer, smaller trees. The average basal area of selected nest sites (27 m<sup>2</sup>/ha) is similar to the basal area measured at western gray squirrel nest and core-use areas in the Southeastern Cascades (25.4 m<sup>2</sup>/ha; Linders 2000) and stands where squirrels frequently were observed in western Washington's Puget Trough (27 m<sup>2</sup>/ha; Ryan and Carey 1995). Thus, squirrels in the 3 Washington populations seem to select stands with similar basal area. Experimental studies of Kaibab squirrels (*S. aberti kaibabensis*) in Arizona found higher densities on control sites relative to treatment sites where timber harvest had reduced basal area and average stem diameter (Patton et al. 1985). Larger, more established ponderosa pines tend to have higher mast production and provide increased structure for nesting, perhaps explaining this pattern (Patton et al. 1985, Krannitz and Duralia 2004).

In general, larger trees and reduced probability of stand-replacing wildfire that result from forest thinning and prescribed burning should benefit western gray squirrel populations. However, if applied uniformly on the landscape, these treatments would likely reduce the number of tree species, tree connectivity, and the number of mistletoe brooms available for nesting, as well as reducing stand basal area to levels associated with sites not used for nesting by squirrels in this study. Moreover, thinning could reduce availability of hypogeous fungi, an important food for western gray squirrels and other small mammals (Dodd et al. 2003, Lehmkuhl et al. 2006b).

## MANAGEMENT IMPLICATIONS

Silvicultural prescriptions at the scale of the forest stand may be able to balance squirrel conservation and the various goals of dry forest management (Lehmkuhl et al. 2007). Retention of patches that include a mix of conifer species or conifer and deciduous trees and moderate to high basal area could promote nesting opportunities, connectivity for arboreal travel, as well as abundance and diversity of hypogeous fungi (Dodd et al. 2003; Lehmkuhl et al. 2004, 2006b). We recommend experimental studies to explore the

effect of patch retention on western gray squirrels, including assessment of optimal patch size and efficacy of the treatment for retaining mistletoe structure for wildlife use while protecting the surrounding stand from mistletoe spread and wildfire (Bull et al. 2004). To enhance nesting opportunities for western gray squirrels, we recommend retaining trees >20 cm diameter at breast height (min. size used for nesting) with mistletoe brooms in the upper one-half of the crown. Because mistletoe is not common on all sites used by western gray squirrels and is not a prerequisite for nesting, we recommend 3 additional characteristics of nest trees (dbh, connectivity, and ht) associated with use by squirrels that should be considered in future modeling efforts. With careful management, the North Cascades can continue to support this threatened species and serve as an important region for investigating the effects of forest fuel management on arboreal wildlife.

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