Seasonal Movements and Nest Site Selection of the Western Gray Squirrel (*Sciurus griseus*) in the Methow River Watershed

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Master of Science
College of Forest Resources
University of Washington
December 2005


Sue Misao/Methow Valley news 2004

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A thesis submitted in partial fulfillment of the
requirements for the degree of

Master of Science

University of Washington

2005

Program Authorized to Offer Degree:
College of Forest Resources

University of Washington

Abstract

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Chair of the Supervisory Committee:
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Listed as a state threatened species, the distribution of the western gray squirrel (*Sciurus griseus*) in Washington is limited to three disjunct areas. Little is known about the North Cascades population, which is the northernmost population for the species. Here, squirrels exist without oaks that provide winter forage and cavities for maternal nests elsewhere in its range. During May 2003 to August 2005, we studied movements and nesting habits, for eight female and four male radio-collared squirrels in Okanogan County, Washington. All movements and total home-range estimates were significantly larger than estimates reported for populations in California, Oregon, and south-central Washington. Average 95% fixed kernel home ranges were 142 ha for males and 49 ha for females, a significant difference. Fifty percent core home-range estimates for females averaged 6 ha and were not significantly different from those in south-central Washington. These results indicate that squirrels in this region are traveling increased distances to obtain necessary resources. In the absence of oak cavities, females reared their young in stick nests. General nest-tree characteristics were similar to characteristics of nest trees in Klickitat County: dominant or co-dominant ponderosa pines equal or greater than 40 cm diameter at breast height (dbh) with an interior or marginal stand position. The odds of a squirrel selecting a tree for nesting increased with mistletoe infection, dbh, and connectivity of the tree canopy. Nest sites with high selection probability by squirrels had greater basal area, larger mean dbh, and higher richness of tree species than control sites. To enhance squirrel habitat in this region, we recommend retaining trees larger than 22 cm dbh with mistletoe deformations in the upper portion of their crown that are large enough to accommodate a nesting squirrel (at least 20 cm diameter). Potential nest sites in these predominantly ponderosa pine forests should be managed for high basal area (>15 m^2/ha), large mean dbh (>25 cm), and a mix of conifer and deciduous tree species.

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ACKNOWLEDGEMENTS

This project would not have been possible without the contributions and commitment of many individuals. Success is, beyond doubt, a combination of dedication, timing, and teamwork.

I would first like to thank my advisory committee, Steve West, Matt Vander Haegen, and G. James Kenagy. Their perspectives on wildlife ecology have contributed substantially to my growth as a scientist.

The Washington Department of Fish and Wildlife (WDFW) provided funding for this research including a grant from the Aquatic Lands Enhancement Account (ALEA) fund. The U.S. Forest Service provided dependable logistical support including vehicles and housing, with special thanks to John Rohrer. Todd Thompson of the Bureau of Land Management generously procured a trailer for additional field housing.

Gene Orth, Liana Aker, and Sue Van Leuven of the WDFW provided invaluable volunteer field training. I am further indebted to Gene Orth for his consistent devotion to this project from start to finish. His 20+ years of wildlife field experience made this project more of a success than I ever expected.

I was also very fortunate to have exceptional assistance in the field from my volunteers. In addition to hard work, each of the following people provided unwavering enthusiasm and appreciation for this project: Janeen Hetzler, Claire Eldridge, Jesse Tigner, Kiersten Lippmann, Justina Harris, Scott Fields, Laura Hughes, Lindsay Malone, Jennifer Leach, Katie Rodd, and Josh Young.

Gary J. Reed of the U.S. Forest Service was very responsive to my requests for GIS data. Mary Linders of the WDFW was always ready and willing to share data and valuable advice founded on her knowledge and dedication to the western gray squirrel. I am especially grateful to Bob Gitzen of the Wildlife Science Group for his unlimited statistical advice and support.

My parents, Norm Gregory and Camille Seligman, my brother, Arthur Gregory, and sister-in-law, Bridget Gregory stood by me throughout this significant portion of my life with unconditional love and encouragement. Finally, I am grateful for Jeffree T. Ensing who has taught me that love truly is patient and kind.

DEDICATION

To Dr. Norman Wayne Gregory, Sr.

Introduction

The characteristics of an animal's seasonal movements and home-range size (Burt 1943) are thought to be indicative of many aspects of its ecology including habitat quality. A low quality habitat may include high numbers of predators or competitors and sparse opportunities for forage or mate selection (Gurnell 1983). For tree squirrels, opportunities for nesting are an additional, essential component of a suitable habitat (Steele and Koprowski 2001). Without appropriate nest sites and trees, tree squirrels are more vulnerable to predators and weather extremes and cannot reproduce successfully. Thus, an examination of space use in addition to variables contributing to a squirrel's selection of nest sites could contribute substantially to our understanding of its overall ecology.

The western gray squirrel (*Sciurus griseus*) is the largest tree squirrel native to the western states of Washington, Oregon, and California. Range of body mass is 520-942 g and total length 500-615 mm with adults showing no sexual dimorphism (Carraway and Verts 1994). This squirrel's pelage is silver-gray dorsally with a creamy white underside and a very bushy white-tipped tail (Dalquest 1948, Ingles 1965, Maser et al. 1981, Carraway and Verts 1994). Western gray squirrels can be distinguished from the nonnative congeners, the eastern gray squirrel (*Sciurus carolinensis*) and fox squirrel (*Sciurus niger*), by its longer ears and lack of brown coloration.

The western gray squirrel's distribution (Figure 1) follows the Upper Sonoran and Transition life zones including the eastern slopes of the Californian Cascade, Sierra

Figure 1. Distribution of the western gray squirrel.

Nevada, Tehachapi, Little San Bernardino, Santa Rosa, and Laguna mountains. Occasionally it inhabits the Lower Sonoran and Canadian Life Zones (Ingles 1947). In western California, it occurs throughout the Coast Ranges and to the east reaching into Nevada (Carraway and Verts 1994). The Cascade Range of Oregon is home to the western gray squirrel along the east side and west to Coos County (Maser et al 1981). In Washington State, the western gray squirrel once had a continuous distribution from the south central portion of the state, north to Okanogan county, and northwest to the Southern Puget trough (Dalquest 1948, Ingles 1965, Hall 1981). Currently, however, the western gray squirrel is confined to three disjunct areas in Washington: the Southeastern Cascades adjacent to the Columbia Gorge, the southern Puget Trough, and along the border between Okanogan and Chelan counties (WDFW 1993; Figure 2).

Historically abundant, western gray squirrels were harvested throughout the species' range. It was also labeled a pest that damaged pine and fir trees by removing their bark (Bowles 1921, Scheffer 1923). Today, western gray squirrel hunting is illegal in southern California but continues in northern counties. In Oregon, the western gray squirrel is on the state's Sensitive Species List and has an "Undetermined" status meaning there is limited knowledge about its population's persistence (ONHIC 2004). Despite the listing, and an estimate by Verts and Carraway (1998) of a greater than 28% reduction in areas inhabited by western gray squirrels, the Oregon Department of Fish and Wildlife still allows western gray squirrel hunting. Protection of western gray squirrels in Washington State began in 1954 with the removal of the species from hunting pamphlets. This did little to stop the decline of the population, which the

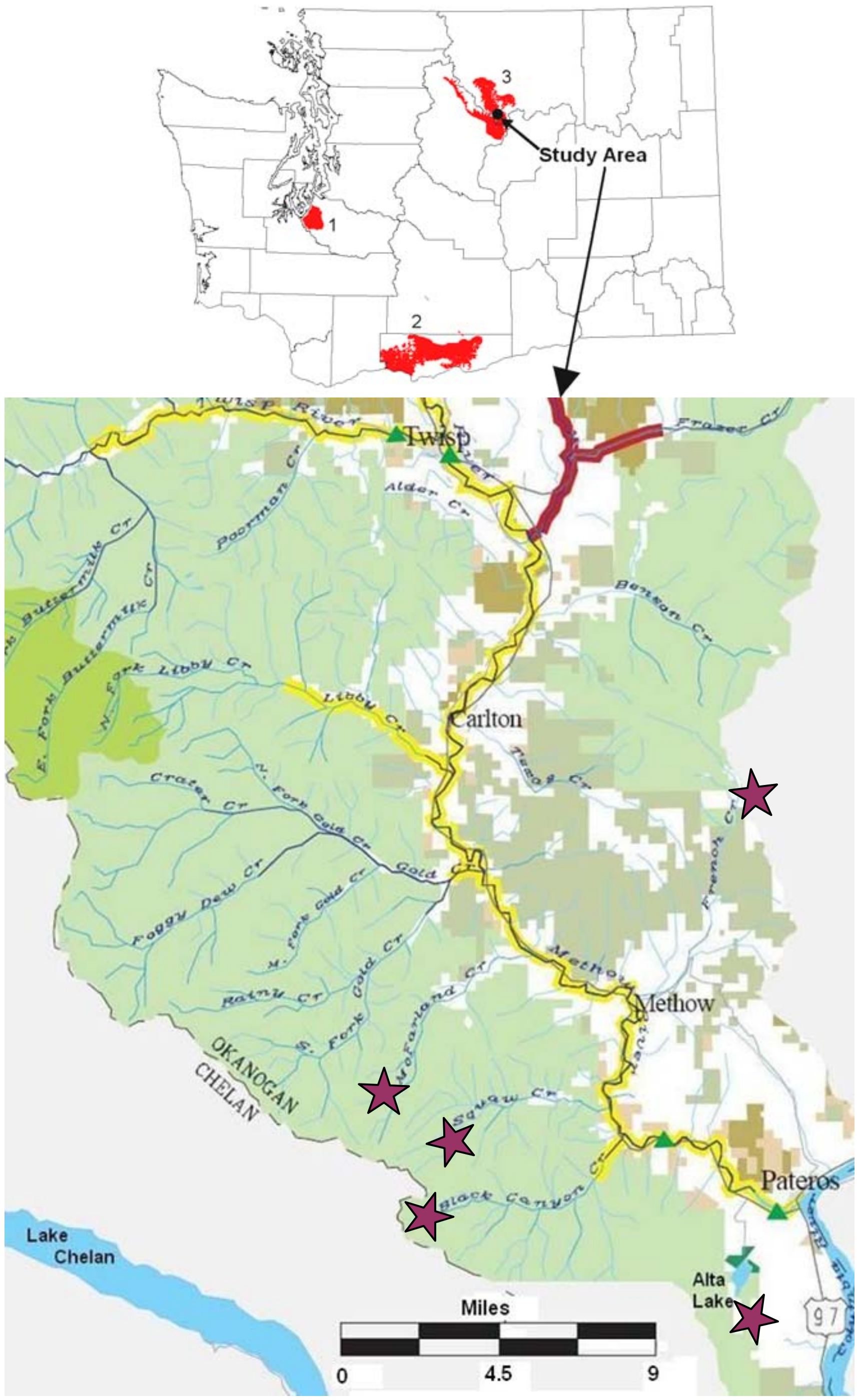


Figure 2. Washington range of the western gray squirrel in 1) Pierce, 2) Klickitat, and 3) Chelan and Okanogan counties with focus Methow River Watershed. Stars indicate areas visited during site selection process: French, McFarland, Squaw, and Black Canyon Creeks, as well as Alta Lake. Maps from WDFW and Washington State Department of Ecology.

Washington Department of Fish and Wildlife (WDFW) listed as threatened in 1993. A state threatened species is "any wildlife species native to the state of Washington that is likely to become an endangered species within the foreseeable future throughout a significant portion of its range within the state without cooperative management or removal of threats" (WAC 232-12-297, Section 2.5). At the federal level, the western gray squirrel is a species of concern. The Washington population was recently rejected for listing as a federal endangered species as it is not considered a "significant population segment to the taxon to which it belongs" (Federal Register, Vol. 69, No. 188). Clear reasons for the declining numbers of western gray squirrels in Washington have yet to be determined. However, some factors that many authors have noted as detrimental to western gray squirrel populations are habitat destruction, mange, and automobiles (Ingles 1947, Asserson 1974, Byrne 1979, Ryan and Carey 1995, Bayrakçi 1999, Linders 2000).

While recovery of the western gray squirrel in Washington is becoming a priority, distributional and life history information for the species is incomplete. According to Burt (1943), home range is a variable influenced by an animal's biology as well as ecological factors. Linder's (2000) study of western gray squirrels in Klickitat County revealed home ranges many times larger than studies done in Oregon and California (Ingles 1947, Cross 1969, Gilman 1986, Foster 1992). This result may be attributable to food scarcity and low population density (Don 1983).

All of the above studies occurred in the oak-conifer habitat that supports most western gray squirrel populations. This study took place in Okanogan County, Washington, an area at the northern extent of the western gray squirrel's range that lacks oaks as a food source and could therefore be classified as low quality (Gurnell 1983). Given little attention until recently, squirrels inhabiting this area were suspected of a dependence on walnut orchards for winter survival. The results of a survey by Barnum (1975) state that squirrels made a yearly, winter-long visit to walnut groves and then dispersed during the summer. Thus, one of this study's primary objectives was to track squirrels' movements using radio-telemetry techniques and compare them to those of other populations. This will begin to shed light on geographic variations in this species' use of space.

The second primary objective of this study was to characterize the nesting habitat of squirrels and identify some of the variables important to nest-site and nest-tree selection in a primarily coniferous habitat. Tree squirrels typically use three types of nests. Cavity nests or dens are nests that occur inside tree cavities. The shelter nest, a spherical mass of intertwined branches, needles and other vegetation, also offers squirrels complete enclosure. The platform nest resembles a flattened shelter nest and may include more leafy vegetation.

Throughout most of its range, the western gray squirrel inhabits conifer-hardwood forests. Results of studies in the southern Puget Trough and Columbia Gorge in Washington State describe the western gray squirrel as an oak-obligate species that depends on a diverse mixture of oak and conifer trees often near water (Dalquest 1948, Barnum 1975, Rodrick 1986, Foster 1992, Ryan and Carey 1995, Bayrakçi et al. 2001). In Klickitat County near the Columbia River Gorge, western gray squirrels frequent areas that are 58% ponderosa pine (*Pinus ponderosa*), 30% Oregon white oak (*Quercus garryana*), and 12% Douglas-fir (*Pseudotsuga menziesii*) (Linders 2000). On the west side of the state, in the southern Puget Trough, high use stands for western gray squirrels consist of 53% Douglas-fir, 34% Oregon white oak, higher basal area, and a greater overall diversity of tree species than low use stands (Ryan and Carey, 1995). Large trees that form a well-connected canopy are also considered an important habitat component as they provide arboreal routes of escape for this wary, secretive species (Ingles 1947, Rice 1977, Gilman 1986, Foster 1992, Ryan and Carey 1995). Oaks are regarded as critical to western gray squirrels as well because they provide cavities for maternal dens (Cross 1969, Linders 2000). However, during her study of western gray squirrel nesting habits, Foster (1992) observed maternal nests to be twig and leaf nests built in pines with no selection of oak cavities by pregnant females. While Ingles (1947) determined that western gray squirrels in California place maternal nests in tree cavities, he found that they used other tree species (e.g. cottonwood) in addition to oak. Among other tree squirrel species, eastern gray squirrels use cavities in chestnut and maple trees as well as oak (Sanderson et al. 1975). Abert squirrels (*Sciurus aberti*), the western gray squirrel's closest relative, have never been observed nesting in a cavity as their preferred nest-tree species, the rot resistant ponderosa pine, rarely provides them (Halloran and Bekoff 1994). Thus, western gray squirrels are able to persist in habitats without oak, selecting cavities in other tree species or stick nests for rearing young. Reports from WDFW nest surveys in the North Cascades described nesting areas as riparian areas with a diverse mixture of mature tree species (Bartels 2000).

This study sought to begin describing the specific characteristics of nest sites and nest trees that are important to western gray squirrels in areas that lack an oak component. We explored squirrels' nesting behavior at two scales; selection of a nest site within their home range and on a smaller scale, selection of a nest tree within the nest site.

Objectives as Hypotheses

Objective 1: To explore the western gray squirrel's use of space in the Black Canyon Creek watershed.

$H1_0$: Male and female squirrels do not differ in their year-round (total), breeding, or non-breeding movements.

$H2_0$: Male and female squirrels do not differ in their total home-range size.

$H3_0$: Male and female squirrels do not differ in their total, breeding, or non-breeding home-range overlap with other squirrels.

$H4_0$: There is no difference between total home-range estimates or their overlap for squirrels at Black Canyon Creek and those of other western gray squirrel populations.

$H5_0$: Squirrels do not shift the general location of their home range throughout the year.

Objective 2: To explore the nesting habits of the western gray squirrel in the Black Canyon Creek watershed.

$H1_0$: Squirrels use pine and fir trees for nesting in equal proportions.

$H2_0$: Nest use (quantity of nests and amount of use) does not differ between males and females.

$H3_0$: Characteristics of nest trees in Black Canyon Creek are not different from trees that squirrels in Klickitat County used for nesting.

$H4_0$: There is no difference between the importance of the following candidate models for explaining the variation in western gray squirrel nest-tree selection at Black Canyon Creek (Variables are defined in Table 1, p 26):

- Klickitat County comparison: *Dom* + *DBH* + *Stand_pos* + *Con*
- Predator escape: *Stand_pos* + *Con* + *TBV* + *Tree_cond*
- Oregon (Foster 1992): *DBH* + *Spp*
- Tree structure: *TBV* + *CBH* + *Tree_cond* + *Tree_ht* + *Spp*

$H5_0$: There is no difference between the importance of the following candidate models for explaining the variation in western gray squirrel nest-site selection at Black Canyon Creek (Variables are defined in Table 2, p 27):

- Ground cover characteristics: *Shrubcov* + *Underspp* + *Grndcov*
- Klickitat County comparison: *Con* + *QDBH* + *Trees*
- Predator escape: *Con* + *Shrubcov*
- Stand level characteristics: *QDBH* + *Trees* + *StandBA*
- Site placement characteristics: *Elev* + *Asp* + *DW* + *DR*
- WDFW comparison: *Trees* + *DW*

$H6_0$: There is no difference between selected characteristics of natal and non-natal nest sites and nest trees.

Methods

Study site selection and description

Site selection for trapping occurred during spring 2003 in the Methow Valley on the east side of the Cascade Mountains in north central Washington State, USA (Figure 2). Using the current WDFW western gray squirrel database, surveyors visited areas with a history of squirrel sightings and attempted to relocate previously documented nest sites and make opportunistic squirrel observations. According to the database, the southern end of the Methow Valley had the most sightings of squirrels and their nests. Additionally, the report produced by Bartels (2000) included specific coordinates of nest sites and squirrel observations. We attempted to follow up on these locations and assess their suitability for more focused study. We made trips to French Creek, McFarland Creek, Squaw Creek, Black Canyon Creek, and Alta Lake (Figure 2). In several instances, we had difficulty accessing pockets of public land surrounded by private residences. In addition, many of the nests that Bartels (2000) observed 3-4 years earlier were in disrepair or missing. After these initial, informal surveys, we determined Black Canyon Creek to be the most appropriate area for further study. This drainage had the most squirrel activity (i.e. nests and sightings of individuals) on a continuous piece of public land. Private land only occurs along the last mile of the creek near the Methow River.

The Black Canyon Creek Watershed is part of the Okanogan National Forest managed by the United States Forest Service (USFS). The creek is a class III, perennial stream at the southern end of the Methow River Watershed fed by several smaller streams before it flows into the Methow River. This area experiences cold, wet winters and hot, dry summers. Temperatures vary from a mean minimum of -9°C in January to a mean maximum of 31°C in August. Average annual precipitation is approximately 32 cm and total annual snowfall averages approximately 103 cm (Western Regional Climate Center 2005).

At the completion of radio telemetry, we established the boundaries of the study site using all locations of radio-collared squirrels surrounded by a 500 m buffer (Figure 3). The 500 m buffer is the average movement of male squirrels at Black Canyon Creek as determined during this study. This process delineated an area of ~1,300 hectares located on a primarily south-facing slope at the lower reach of Black Canyon Creek. The creek flows west-east through the southern portion of the site and is paralleled by Black Canyon Creek Road, a single lane gravel track. With elevations of 437-1196 m, this area consists of a series of dry drainages, most running north-south toward the creek. In addition to Black Canyon Creek, one corollary stream of ~700 m length serves as a perennial water source (Figure 3). The study area falls in the ponderosa pine (*Pinus ponderosa*) zone with vegetation associations of ponderosa pine/antelope-bush (*Purshia tridentata*) or ponderosa pine/antelope bush-snowbrush (*Ceanothus velutinus*) (Franklin and Dyrness 1973). Variations in vegetation occur with aspect and proximity to water. Douglas-fir (*Pseudotsuga menziesii*) often becomes the climax tree species where aspect shifts east or north and where vegetation has a riparian component. Deciduous species found in riparian zones include cottonwood (*Populus balsamifera),*

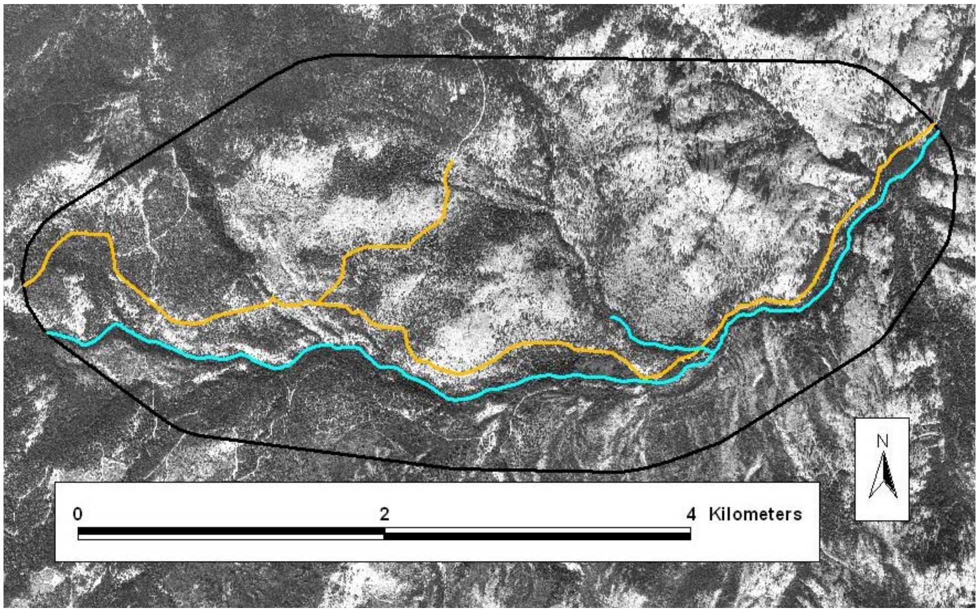


Figure 3. Aerial and ground photos of the Black Canyon Creek study area, Okanogan County, Washington. Orange lines and blue lines on aerial photo are maintained roads and creeks, respectively. Ground photo is of the eastern side of the study area.

alder (*Alnus rubra)*, and aspen (*Populus tremuloides*) (Franklin and Dyrness 1973). Four fires have burned this area in the last 90 years but only one, the Camas Creek fire in 1929, affected a large percentage of the study site (91%). Mammal species most commonly observed in this area are the red squirrel (*Tamiasciurus hudsonicus*), yellow pine chipmunk (*Tamias amoenus*), mule deer (*Odocoileus hemionus*), coyote *(Canis latrans)*, and black bear (*Ursus americanus*). Though this area is open to the public and receives visitors year round who camp, hunt, snowmobile, and gather firewood, people do not seem to venture far from maintained roads.

Trapping

We trapped squirrels to attach radio collars periodically from May 2003 to April 2004. Trapping began in places where we had made opportunistic observations of squirrels or their nests during the initial survey period and where the habitat seemed to resemble squirrel habitat in other portions of its range. As the study progressed, we adjusted trapping sites and effort when telemetry revealed additional sites frequented by squirrels. The need for trapping also increased as squirrels tended to have their collars chewed off. A final trapping effort in October 2004 served to remove collars. At the peak of trapping, we used approximately 100 traps across the study area. We arranged traps in lines or grid patterns separating them by an average distance of 50 meters. We used wire mesh Tomahawk live traps (Tomahawk Live Trap Co. Tomahawk WI, USA) ranging in size from 15 x 15 x 48 cm (model 202) to 23 x 23 x 66 cm (model 205) with no perceived change in trapping success. We preferred the smaller traps as they were easier to transport and with less space inside, a trapped animal was not as likely to incur injuries from impact with the trap walls. Each trapping session began with a prebaiting period where we wired traps open and baited them with whole English walnuts to “train” animals to enter the traps. Trapping began when squirrels removed bait from approximately half of the prebaited traps. Initially, this required about two weeks but later in the study, after squirrels became accustom to entering traps, prebating only lasted 2-3 days. Duration of trapping sessions was variable, also lasting 2-3 days. Heavy rain postponed trapping sessions. To minimize squirrels’ trapping stress, we placed traps against trees on the shady, northern side and checked them about every 2 hr.

Handling

We processed captured squirrels at the trapping site with a handling bag designed by Koprowski (2002) modified with an additional ventral flap. This method eliminated the mortality that can result from chemical restraint and allowed for efficient handling. Eartags (model 1005-3, National Band and Tag Co., Newport, KY, USA) attached to each ear provided animals with a unique number. We weighed squirrels in the handling bag to the nearest 10 g with a 2500-g Pesola spring scale. Female squirrels weighing over 650 g were favored for collaring. Collars consisted of a plastic zip tie supporting a 16 g radio transmitter (model SI-2C, Holohil Systems Ltd., Carp, Ontario Canada) with a wire whip antenna. Braided, stainless steel cable fastened with a brass crimp helped to reinforce the zip tie after squirrels started chewing off collars. A clip of a hind foot toenail provided a blood sample for future genetic analysis.

Radio telemetry

From June 2003 to September 2004 we relocated collared squirrels a maximum of three times per week; once in each of three time blocks (dawn-1000, 1001-1400, 1401-dusk) to assure independence between fixes (Otis and White 1999; Swihart and Slade 1997; White and Garrott 1990). Thirty-eight percent (10/26) of the deployed collars were chewed off, hampering our efforts to track squirrels throughout the year. Telemetry equipment included two-element, hand-held directional antennas (model RA-2A, Telonics, Mesa Arizona, USA) and portable TR-4 receivers (Telonics, Mesa, Arizona, USA) which allowed homing on collared animals and resulting behavioral and specific habitat observations. Garmin Etrex Venture Geographical Positioning System receivers (GPS; Garmin International, Inc. Olathe, Kansas, USA) provided location data in Universal Transverse Mercator (UTM) coordinates. We improved the accuracy of locations by determining if an animal was active before pursuing its signal and abandoned tracking if the sharp signal fluctuations, indicative of a fleeing animal, occurred.

We defined active nests as nests that we found in association with a radio-collared squirrel. If we found a squirrel inside a nest or in a tree supporting a nest, we labeled that nest as active. Upon location of an active nest, we made note of its type (den, platform, or shelter), aspect in relation to the trunk of the tree, height, color, and condition (good, fair, poor). We also recorded the species of the nest tree and its diameter at breast height (dbh). Natal nests were nests where we found a female repetitively for at least two weeks during the breeding season (~Feb.-June).

Nest-tree and nest-site sampling

To examine differences between the trees and sites that squirrels selected for nesting and those they did not, we collected data at 100 plots during May-August 2005. We generated a random sample of 50 nest trees from the 64 active nests identified with radio telemetry. On two occasions, nests representing multiple relocations replaced those used only once. Next, using ArcView GIS 3.2 (Environmental Systems Research Institute 1999) we plotted the 50 nest trees with each squirrel's 95% MCP total home-range estimate. We obtained 95% MCP estimates for each squirrel using the home range extension for ArcView (Rodgers and Carr 2002) by connecting outermost locations after we had removed the 5% that were furthest from the arithmetic mean of all points. Within each home range, we tallied the number of active nest trees and with the Animal Movements extension to ArcView (Hooge et al. 1999), randomly identified a corresponding number of unused sites for a total of 50 available sites to serve as controls (Figure 4). If an active nest tree fell within the overlap of two home ranges, we placed the corresponding control site within the home range for the squirrel that used the nest the most. Therefore, each home range served as a separate stratum when selecting unused sites, with squirrels contributing a variable number of nests to the study. One female used a nest and was depredated after only two relocations. Because

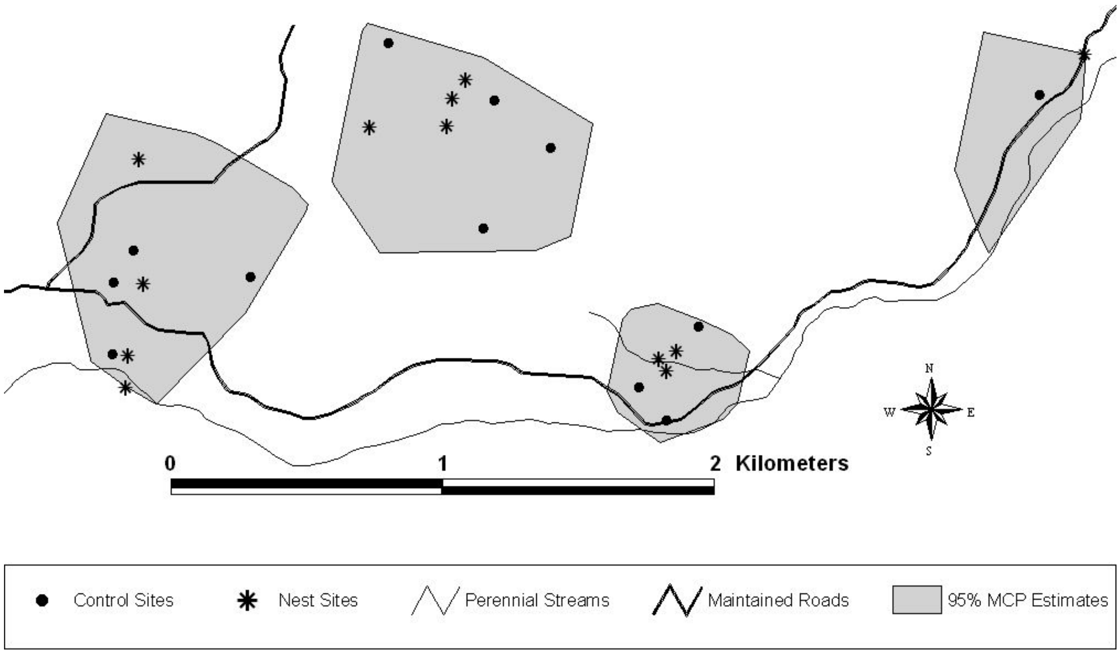


Figure 4. A selection of 95% minimum convex polygon western gray squirrel total home-range estimates with plots of nest sites and random available sites sampled for analysis.

we could not calculate a home range, we selected a control site for this squirrel within an area that corresponded to the average female 95% MCP total home-range size (35 ha) centered on the nest tree. On the ground, we used a GPS to locate each control site and labeled the tree nearest to the coordinates generated in ArcView as the focal tree. On one occasion, we reselected one control site because there were no trees within 10.6 m of the random location.

Sampling at all sites occurred within nested circular plots (25.25 m, 10.6 m radius and 5.6 m radius) using the nest tree or focal tree as the center point. Within the 25.25 m radius plot (0.2 ha), we sampled eight trees as unused, control nest trees (Figure 5). We randomly selected trees using the procedure of Skalski (1987). A basic random sampling scheme that uses only random bearings and distances from plot center results in a bias toward the center of the plot. For a uniform sample of points in a circular area, Skalski (1987) suggests using pairs of random numbers between zero and one, multiplying one of each pair by 360˚ to obtain a bearing and the square root of the other by the radius of the plot to obtain a distance. For each of these eight trees and the tree at plot center, we recorded total height and height to lowest live crown (CBH) using an Impulse IP200 laser (Laser Technology Inc., Englewood, CO) and measured dbh. We made categorical observations of percent live canopy, deformations from mistletoe infection (TBV; Parker and Mathiasen 2004) and stand dominance and position. We also recorded tree species and measured connectivity by counting the number of surrounding trees with branches ≤1 m away. One meter is the estimated

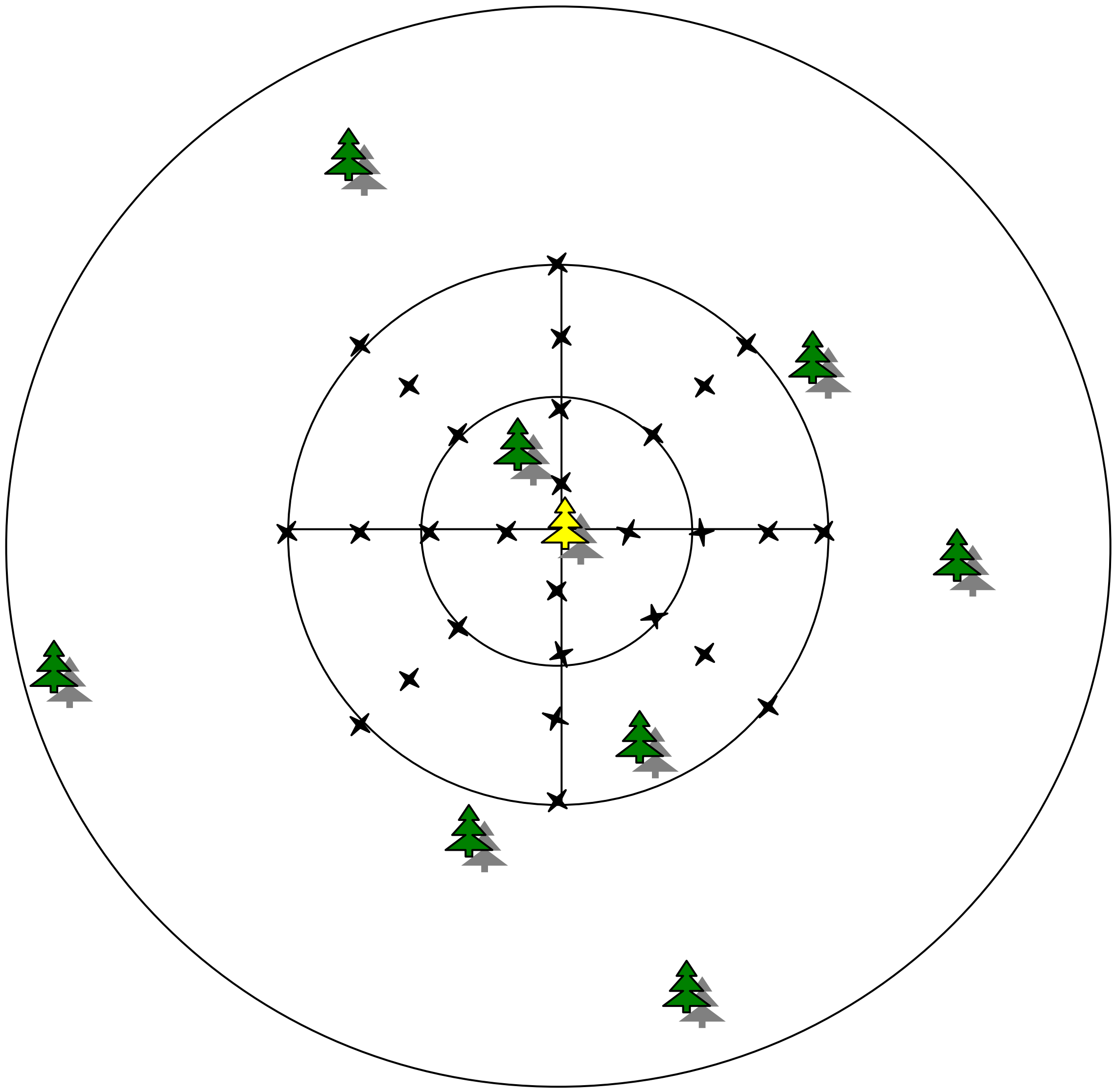


Figure 5. Diagram of vegetation sampling scheme centered on nest (selected site) or focal (control site) tree (in yellow). Largest circle represents the area (0.2 ha) for sampling of 8 control trees. The middle circle represents the area (0.035 ha) for stem measurements of all trees ≥5 cm dbh and canopy cover (at each✦). Smallest circle represents the area (0.01 ha) for understory and ground cover measurements.

maximum distance that a squirrel will jump between trees (Linders 2000, pers. obs.). Within each 10.6 m radius plot (0.035 ha), we recorded the species, condition (live or dead) and dbh of all trees ≥5 cm dbh. We summarized dbh in terms of quadratic mean dbh (QDBH), which corresponds to the dbh of a tree of average basal area for the stand. We also used the stem data to calculate stand basal area (m^2/ha). To estimate percent overstory cover of trees larger than 12 cm dbh, we took 28 readings with a moosehorn cover scope (Moosehorn Cover Scopes, Medford, OR) at four evenly spaced points along the 10.6 m radius in the four cardinal directions and three points to the NW, NE, SW, and SE. We also made a tally of coarse woody debris (CWD) measuring ≥10 cm diameter at the large end and indexed it according to three decay classes. Within each 5.6 m radius plot (0.01 ha), we tallied shrubs and saplings ≤5 cm dbh by species within two height classes, 0.5-2 m and 2.8 m. In addition, we visually estimated percent cover of deciduous and evergreen trees and shrubs within each height class using categories (0-1%, 2-5%, 6-25%, 26-50%, 51-75%, >75%). If total cover within either height class was over 6%, we estimated modal height also. We recorded the percent ground cover of vegetation ≤5 cm tall in the following categories: total vegetation, grasses/forbs, conifer seedlings, deciduous tree seedlings, moss, litter, CWD, rock, and bare soil. For each site, we utilized ArcView and GIS shapefiles from the USFS to obtain its aspect and elevation and calculate its distance from the nearest perennial water source and maintained road. We also photographed all sites including trees at plot center with a digital camera for additional reference.

Data Analysis

Movements

Using the Animal Movements extension, we calculated distances between fixes for all squirrels. We compared movements for animals with ≥30 relocations (8 females and 5 males). We also averaged monthly movements and plotted them by sex (6 breeding females and 5 males) to observe fluctuations indicating the onset of the breeding and non-breeding seasons. We categorized breeding females as those that exhibited reduced movement and close association with a nest site typical of this species during reproduction. We restricted this plot of interfix movements to this group rather than all females because they would have the highest probability of displaying the behavior that we were trying to measure.

We also used the Animal Movements extension to produce 100% minimum convex polygon (MCP; Mohr 1947) and 95% fixed kernel (FK; Worton 1989) home-range estimates with least-squares cross-validation (LSCV). Determining a smoothing parameter with LSCV does not require that the data conform to a bivariate normal distribution. However, to calculate the minimal smoothing parameter accurately using LSCV it was necessary to remove replicate locations (e.g. repetitive fixes at a nest) from the data set (Kernohan et al. 2001).

We used 100% MCP estimates to compare estimates from this study with others in Oregon (Cross 1969, Foster 1992) and California (Gilman 1986) that used radio telemetry to relocate adult squirrels. Before making these comparisons, we assessed differences between study areas based on sex. Ninety-five percent FK estimates are available from studies in southern Washington (Klickitat County; Linders 2000, Vander Haegen pers. com.) and are the basis of comparison with this study. Linders (2000) used the reference bandwidth (h_{ref}) to produce her FK estimates. Unlike h_{LSCV}, use of h_{ref} assumes a bivariate normal distribution. Because h_{LSCV} and h_{ref} can often produce variable home-range estimates, we calculated additional FK estimates for this study using h_{ref} for comparability with Linders (2000).

Total home-range estimates reported for this study include all relocations for those animals with at least 30 fixes obtained over at least 6 months to maximize accuracy as well as the number of individuals included in analysis (Seaman et al. 1999). The fixes for 12 animals, 8 females and 4 males, met these requirements. Non-breeding home-range estimates include relocations collected July-January. We did not obtain enough relocations to make accurate breeding season (February-June) estimates because we could not replace collars chewed off during the winter until after snowmelt. We only used seasonal home-range estimates (95% FK_{LSCV} and 95% MCP) to explore general overlap trends and to assess site fidelity through visual inspection of plotted estimates. Additionally, we ran the built-in site fidelity test in Animal Movements that uses a Monte Carlo simulation to compare observed movements to a random set of movements. For this analysis, we used all locations for each animal and 1000 simulations. We made statistical comparisons between populations with Mann-Whitney tests and within populations with Wilcoxon Signed Ranks tests. We included an additional male in the overlap and site fidelity analysis for which we had 31 total locations and did not observe any overlap with the other collared animals. We did this in an effort to incorporate as many animals as possible into our analysis.

Nesting habits

We made comparisons of species, dbh, stand dominance, stand position, and connectivity between the 50 nest trees used for selection analysis and 112 nest trees sampled in Klickitat County (Linders 2000) using t-tests and chi-squared tests. We performed all statistical tests on SPSS (Version 11.0.0, 2001) software with $\alpha = 0.05$. We calculated variability as the standard error of the mean.

To identify the groups of variables that could be contributing to squirrels' selection of nest sites and individual nest trees at Black Canyon Creek we used logistic regression and the information theoretic approach (Anderson et al. 2000). The information theoretic approach combined with Akaike's Information Criteria (AIC) allows for comparisons of groups of variables based on biological knowledge rather than rejection of a potentially uninformative null hypothesis comparing only two variables (Anderson et al. 2000, Burnham and Anderson 2002). It favors models that not only fit the data well but that are parsimonious. Parsimonious models have an appropriate number of variables to balance bias and variance (Burnham and Anderson 2002). Logistic regression is suitable for this study because it does not assume that error terms are normally distributed and allows for analysis of data with a binary response variable (1 = selected, 0 = not selected/available; Hosmer and Lemeshow 2000). At

Black Canyon Creek, squirrel nests are rare. Additionally, the habitat preferences of this species in the absence of oak are unknown. Thus, systematic random sampling of suitable habitat was not feasible and we relied on radio telemetry to locate nests. As the majority of nests are clearly visible in trees, this study meets the assumptions of a case-control design (Hosmer and Lemeshow 2000, Keating and Cherry 2004). Interpretation of case-control habitat studies is limited to their particular data sets and should only be made in terms of odds ratios or habitat rankings, not a resource probability function spanning an animal's geographic distribution (Keating and Cherry 2004).

Using our field data, we compiled the variables previously identified as important to western gray squirrel nest-tree and habitat selection (Table 1 and Table 2). Then we developed *a priori* candidate models at two spatial scales, assessing squirrels' selection of a nest tree within the selected nest site and selection of nest sites within their home range (Table 3 and Table 4). The "KWA" models for nest-tree and nest-site selection include groups of variables that Linders (2000) noted as important to squirrels on the Klickitat Wildlife Area. The "WDFW" model includes tree species composition and distance to water, two variables noted in a WDFW (1993) report on the status of the western gray squirrel. Other models attempt to assess the importance of variables relating to various forest components (e.g. tree and ground cover characteristics), predator escape, and site placement.

We screened variables for collinearity with Pearson's correlations and scatter plots. We considered correlated variables to be those with a coefficient >0.7. We also

Table 1. Variables included in analysis of western gray squirrel nest-tree selection, Black Canyon Creek, Okanogan County, Washington.

Variable	Description	Reference
CBH	Crown-base height (m)	Foster 1992
Con	Connectivity: number of trees >12 cm dbh with branches ≤1 m away	Byrne 1979, Foster 1992, Halloran and Bekoff 1994, Linders 2000, Ryan and Carey 1995, Vander Haegen et al. 2005
DBH	Diameter at breast height (cm)	Linders 2000, Rodrick 1986, Vander Haegen et al. 2005
Dom	Stand dominance: dominant (1), subdominant (2), intermediate (3), overtopped (4)	Cross 1969, Gilman 1986, Foster 1992, Linders 2000
Site_ID	ID of site where tree occurs	used for stratification of analysis
Spp	Tree species: ponderosa pine (1), Douglas-fir (2), cottonwood (3)	Cross 1969, Gilman 1986, Foster 1992, Linders 2000
Stand_pos	Stand position: isolated (no other trees within 30 m; 1), separated (no other trees within 10 m; 2), marginal (on edge of a group of trees; 3), interior (surrounded by other trees; 4)	Linders 2000
TBV	Total Broom Volume (1-9), mistletoe rating of Parker and Mathiasen (2004)	Linders 2000
Tree_cond	% live canopy: 0% (1), 1-25% (2), 26-50% (3), 50-75% (4), >75% (5)	Foster 1992, Vander Haegen et al. 2005
Tree_ht	Tree height (m)	Byrne 1979, Foster 1992, Vander Haegen et al. 2005

Table 2. Variables included in analysis of western gray squirrel nest-site selection, Black Canyon Creek, Okanogan County, Washington.

Variable	Description	Reference
Asp†	Aspect: north (1), east (2), south (3), west (4)	Linders 2000
Can	Canopy cover (%) calculated from 28 Moosehorn coverscope readings	Rodrick 1986, Linders 2000
Con	Connectivity: average number of trees >12 cm dbh with branches ≤1 m away, calculated from 8 randomly selected trees	Byrne 1979, Foster 1992, Halloran and Bekoff 1994, Linders 2000, Ryan and Carey 1995, Vander Haegen et al. 2005
DW†	Distance (m) from nearest perennial water source	Foster 1992, Linders 2000, WDFW 1993
DR†	Distance (m) from nearest maintained road	Ryan and Carey 1995, WDFW 1993
Elev†	Elevation (m)	
Grndcov	Dominant ground cover: litter (1), vegetation (2), equal litter/vegetation (3)	Byrne 1979, Foster 1992, Ryan and Carey 1995, Vander Haegen et al. 2005
QDBH	Quadratic mean DBH (cm)	Byrne 1979, Linders 2000, Rodrick 1986, Vander Haegen et al. 2005
Shrubcov	Shrub cover: 0-1% (1), 2-5% (2), 6-25% (3), 26-50% (4), 51-75% (5), >75% (6)	Byrne 1979, Foster 1992, Ryan and Carey 1995, Vander Haegen et al. 2005
Squirrel	ID of animal's home range where nest/control site occurs	used for stratification of analysis
StandBA	Basal area (m^2/ha) of live trees	Byrne 1979, Linders 2000, Ryan and Carey 1995
Trees	Tree species composition (live trees only): ≥90% ponderosa pine (1), mixed conifer (2), mixed conifer/deciduous (3)	Byrne 1979, Cross 1969, Foster 1992, Linders 2000, Ryan and Carey 1995, Vander Haegen et al. 2005
Underspp	Number of understory species	Ryan and Carey 1995, Vander Haegen et al. 2005

† Estimated from GIS

Table 3. *A priori* candidate models used to examine western gray squirrel nest-tree selection, Black Canyon Creek, Okanogan County, Washington. Variables are defined in Table 1.

Model	Model Structure
KWA *(Klickitat Wildlife Area comparison)*	*Site_ID + Dom + DBH + Stand_pos + Con*
Pred *(predator escape)*	*Site_ID + Stand_pos + Con + TBV + Tree_cond*
Oregon *(Foster 1992)*	*Site_ID + DBH + Spp*
Treest *(tree structure)*	*Site_ID + TBV + CBH + Tree_cond + Tree_ht + Spp*

Table 4. *A priori* candidate models used to examine western gray squirrel nest-site selection, Black Canyon Creek, Okanogan County, Washington. Variables are defined in Table 2.

Model	Model Structure
Ground *(ground cover characteristics)*	*Squirrel* + *Shrubcov* + *Underspp* + *Grndcov*
KWA *(Klickitat Wildlife Area comparison)*	*Squirrel* + *Con* + *QDBH* + *Trees*
Pred *(predator escape)*	*Squirrel* + *Con* + *Shrubcov*
Stand *(stand characteristics)*	*Squirrel* + *QDBH* + *Trees* + *StandBA*
SP *(site placement)*	*Squirrel* + *Elev* + *Asp* + *DW* + *DR*
WDFW *(WA Dept. of Fish and Wildlife comparison)*	*Squirrel* + *Trees* + *DW*

inspected continuous variables for multicollinearity by calculating their individual variance inflation factors (VIF). Variables with a VIF score >10 are closely related and could cause difficulties in interpreting coefficients (Neter et al. 1996). Using the R software (packages 'Hmisc' and 'Design", Harrel 2001; R Development Core Team 2004), we first evaluated the goodness-of-fit of the full models with le Cessie-vanHouwelingen-Copas-Hosmer test (Harrell 2001). Then we calculated AIC values for all models and adjusted them for small sample size by determining their AIC_c values. After calculating the difference in AIC_c values (ΔAIC_c) we ranked the models in ascending order and used their Akaikie weights (w_i) to obtain the probability that each was the best model in the set (Burnham and Anderson 2002). We considered competing models to be those that are within two AIC_c units of the best model (Burnham and Anderson 2002). Upon determining the best model(s) from each model set, we performed a likelihood ratio test comparing it to a null model. As mentioned above, the number of nests associated with each squirrel varied. To account for this in our models, we stratified all models for site selection by a "squirrel" factor corresponding to the home range of the squirrel where the nest site occurs. We also used a "site" factor to stratify models for nest-tree selection that accounts for similarities within the site where the nest and control trees occur. These factors were nuisance variables that were costly in degrees of freedom. However, omitting the stratification factors were inappropriate because it would imply that unused sites or trees were randomly selected from the entire study area. To assess the potential meaning of the variables in the full models, we measured the relative importance (RIV) of each variable by summing the weights of each model in which they occurred (Burnham and Anderson 2002). We also compared AIC_c values for each variable run as a univariate model.

After determining the most important variables influencing squirrels' selection of nest sites and trees we used them to make pair-wise comparisons of natal and non-natal nests. For this analysis we used a t-test a chi-squared test.

Results

Trapping and radio telemetry

Between May 2003 and October 2004, we recorded 47 captures, trapping 10 females and 14 males. Of these 24 animals, we attached radio collars to nine females and nine males and obtained 1014 fixes between June 2003 and September 2004. In 50% (507) of the fixes we made visual locations and in 20% (207) we confirmed squirrels to be hidden in a nest. Of the remaining 30% (300), we estimated that 42% (126) were ≤10m and 58% (174) were ≤20m from the animal's actual location. We completed all tracking between 515 and 2044 h. Radio collars did not seem to increase mortality among squirrels as only three were depredated over the course of the study.

Interfix distance

Males moved further between fixes ($\bar{X}$ = 504.2 ± 23.6 m, range = 0-3,059 m, n = 5) than females ($\bar{X}$ = 257.6 ± 8.8 m, range = 0-1,172 m, n = 8; U = 64,990, P<0.001). All movements by males and females at Black Canyon creek were significantly longer than the distances Linders (pers. com.) measured for males and females in Klickitat County (Table 5).

The longest distance traveled by a male between fixes was 3,059 m during 5 days in May. The farthest ranging female traveled 1,172 m during 4 days in November. The largest distance covered in 24 hours was 2,139 m by a male in April. Loss of collars during the early winter prevented us from obtaining the quantity of fixes needed to observe movement fluctuations indicative of the start of the breeding season. While

Table 5. Comparison of interfix movements (m) from Okanogan County, Washington (North), versus Klickitat County, Washington (South). P-values from Mann-Whitney U-tests (α = 0.05).

	North Washington		South Washington			
	$\bar{X} \pm SE$	*n*	$\bar{X} \pm SE$	*n*	*U*	*P*
Females						
All	257.6 ± 8.8	8	185.9 ± 3.8[a]	16	455,710	<0.001
Breeding	157.0 ± 13.2	6	168.0 ± 6.4[a]	9	46,740	0.268
Non-breeding	290.7 ± 12.1	8	214.4 ± 5.6[a]	9	113,680	<0.001
Males						
All	504.2 ± 23.6	5	298.5 ± 9.0[a]	15	126,300	<0.001
Breeding	810.4 ± 66.6	5	346.2 ± 18.3[a]	15	10,055	<0.001
Non-breeding	391.7 ± 16.3	5	270.6 ± 9.4[a]	15	60,334	<0.001

[a] Linders (pers. com.)

it was not possible to pinpoint the onset of the breeding season with these data, the contrast in male movements between January and March indicate an upward trend beginning late in the winter (Figure 6). Females also show a slight decrease in movements during the same period typical of the breeding season when they become closely associated with a maternal nest. Because of a larger sample size, the end of the breeding season is more apparent. There is an increase in female movements and a corresponding decrease in male movements between June and July (Figure 6).

Male movements during both the breeding ($\bar{X}$ = 810.4 ± 66.6 m, range = 0-3,059 m) and non-breeding ($\bar{X}$ = 391.8 ± 16.3 m, range = 0-1,635 m) season, were significantly greater than female breeding ($\bar{X}$ = 157.0 ± 13.2 m, range = 0-802.1 m) and non-breeding ($\bar{X}$ = 290.7 ± 12.1 m, range = 0-1,089 m) movements (U_{breed} = 2,200, P<0.001, $U_{nonbreed}$ = 32,400, P<0.001). Male squirrels at Black Canyon Creek had significantly longer movements than males in Klickitat County during both the breeding and non-breeding season (Table 5). Female squirrels exhibited significantly longer movements at Black Canyon Creek during the non-breeding season but matched female movements in Klickitat County during the breeding season.

Home-range estimates

Of the 12 individuals used for home-range calculation, four females and three males had locations spanning 10-15 months. We tracked the remaining four females and one male for 6-7 months. The number of fixes used to calculate 100% MCP estimates ranged from 31 to 127. The adjusted data (i.e. only unique locations) used to

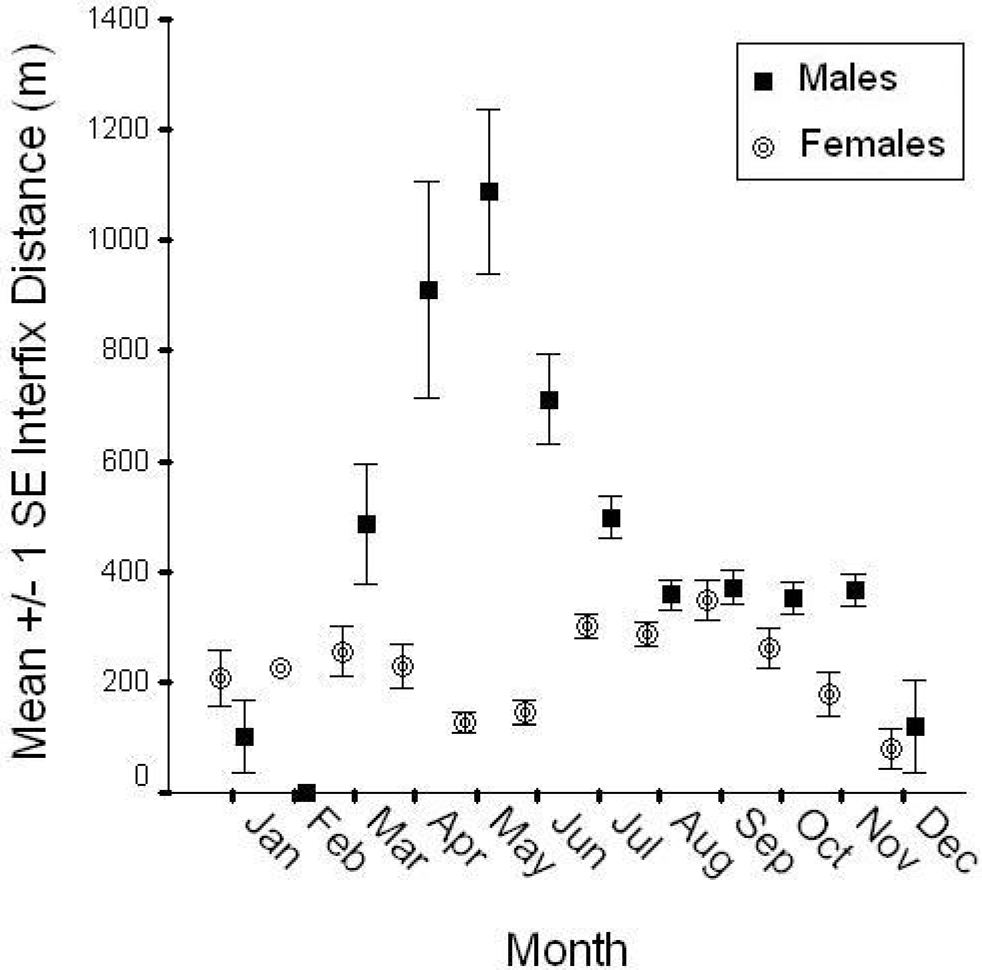


Figure 6. Plot of average monthly distance (m) traveled by male and breeding female western gray squirrels, Black Canyon Creek, Okanogan County, Washington.

calculate FK estimates ranged from 40 to 98 fixes. Males ($\bar{X}$ = 142.0 ± 15.0 ha, range = 103.3-175.3 ha, n = 4) had significantly larger total 95% FK home-range estimates than all females ($\bar{X}$ = 49.4 ± 7.0 ha, range = 17.7-77.9 ha, n = 8, U = 0.000, P<0.01). Non-breeding 95% FK home-range estimates averaged 43.2 ± 10.1 ha for females (range = 16.8-72.7 ha, n = 5) and 75.8 ± 10.8 ha for males (range = 63.4-97.2 ha, n = 3). These values are not statistically different (U = 2.0, P = 0.14). However, this could be the result of a Type II error caused by the small sample size.

Total and summer 100% MCP home-range estimates for males and females at Black Canyon Creek were significantly larger than those from Oregon and California (Table 6). We combined all estimates by sex from Oregon and California except total home-range estimates for males, which were significantly different between studies.

Male and female squirrels at Black Canyon Creek had significantly larger total 95% FK home-range estimates than those in Klickitat County regardless of the smoothing parameter used (Table 7). However, total 50% FK core estimates for females were not different.

The site fidelity test in Animal Movements for all animals rejected the null hypothesis that movement between fixes was random. In addition, visual inspection of home-range location determined no dramatic shift in home-range placement (Figure 7).

Overlap

Average total 95% FK home-range overlap for all squirrels was 16.0% ± 1.8 (n =13). Males ($\bar{X}$ = 25.1% ± 4.0, n = 5) did not differ significantly from females

Table 6. Comparison of total and summer 100% minimum convex polygon home-range estimates (ha) from Okanogan County, Washington, versus Oregon and California. P-values from Mann-Whitney U-tests (α = 0.05).

	North Washington		Oregon & California			
	$\bar{X} \pm SE$	*n*	$\bar{X} \pm SE$	*n*	*U*	*P*
Females						
Total	51.8 ± 9.5	8	9.1 ± 3.3[bc]	6	1.0	<0.01
Summer	35.5 ± 8.0	7	2.8 ± 0.5[bd]	7	0.0	<0.01
Males						
Total	255.5 ± 32.1	4	14.8 ± 2.8[b]	5	0.0	<0.05
			4.4 ± 0.5[c]	4	0.0	<0.05
Summer	85.7 ± 10.7	4	3.4 ± 0.4[bd]	11	0.0	<0.01

[b] Cross (1969), Oregon
[c] Foster (1992), Oregon
[d] Gilman (1986), California

Table 7. Comparison of total 95% and 50% fixed kernel home-range estimates (ha) from Okanogan County, Washington (North), versus Klickitat County, Washington (South). P-values from Mann-Whitney U-tests ($\alpha = 0.05$).

	North Washington		South Washington			
	$\bar{X} \pm SE$	*n*	$\bar{X} \pm SE$	*n*	*U*	*P*
Females						
Total (95%)	75.2 ± 11.1	8	21.9 ± 2.7[a]	12	1.0	<0.001
Total (95%)	49.4 ± 7.0	8	17.7 ± 1.5[e]	31	21	<0.001
Total (50%)	5.5 ± 0.8	8	4.1 ± 0.4[e]	31	74	0.08
Males						
Total (95%)	281.0 ± 25.6	4	73.9 ± 16.9[a]	9	4.0	<0.01

[a] Linders (H_{ref}; 2000)
[e] Vander Haegen (H_{LSCV}; pers. com.)

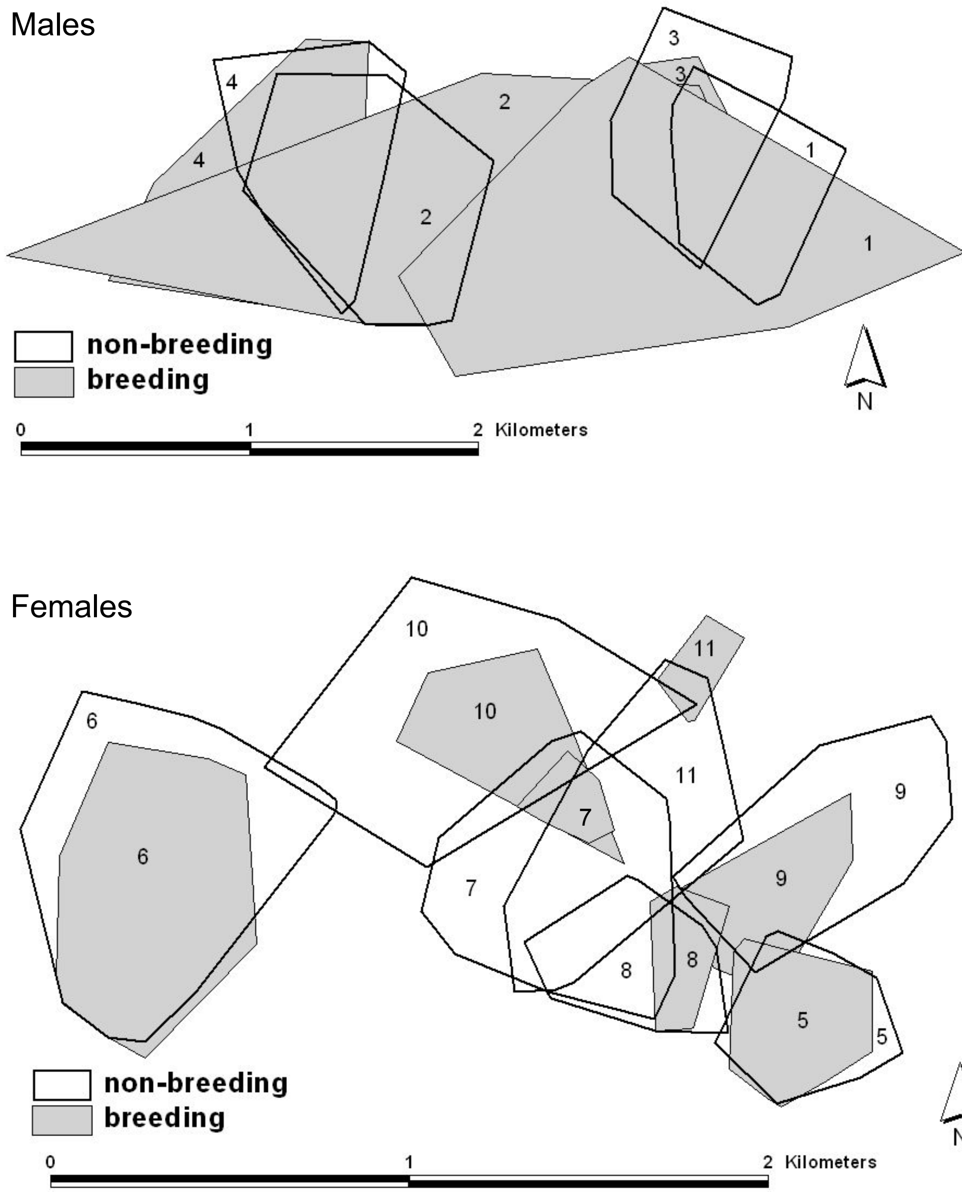


Figure 7. Orientation of male (top) and female (bottom) non-breeding and breeding 95% minimum convex polygon home ranges. Numbers represent labels for individual animals.

($\bar{X}$ =10.3% ± 1.4, *n* = 8) in their overlap of other squirrels (*U* = 2378.0, *P* = 0.056). Similarly, same sex overlap of males ($\bar{X}$ = 16.0% ± 5.4) was not significantly different from that of female overlap ($\bar{X}$ = 10.3% ± 1.8; *U* = 538, *P* = 0.78). Again, power to detect a statistical difference is low as sample sizes are small. During the breeding season, males overlapped all other squirrels ($\bar{X}$ = 63.9% ± 6.5, *n* = 4) significantly more than females ($\bar{X}$ = 6.7% ± 1.3, *n* = 7; *U* = 280, $P<0.001$). Additionally, male-male overlap during the breeding season ($\bar{X}$ = 49.8% ± 7.4, *n* = 4) was significantly larger than female-female overlap ($\bar{X}$ = 6.1% ± 1.7, *n* = 7; *U* = 17, $P<0.001$). Subsequent to the breeding season, males ($\bar{X}$ = 15.7% ± 3.2, *n* = 5) and females ($\bar{X}$ = 10.8% ± 1.6, *n* = 8) did not differ statistically in their non-breeding season overlap with all other squirrels (*U* = 2860, *P* = 0.92). In addition, male overlap with all other squirrels during the breeding season was significantly larger than their overlap during the non-breeding season (*Z* = -4.5, $P<0.001$). When we considered overlap of 95% MCP estimates we observed similar patterns.

Average overlap of total 50% FK core area estimates revealed that male core areas overlapped with other squirrels' core areas ($\bar{X}$ = 10.4% ± 2.9, *n* = 5) more than females ($\bar{X}$ = 1.4% ± 0.5, *n* = 8). Additionally, male-male core area overlap ($\bar{X}$ = 8.8% ± 4.4) was larger than female-female core area overlap ($\bar{X}$ = 0.2% ± 0.1). We did not however, detect a statistical difference between these estimates ($P_{mixedsex}$ = 0.079, $P_{samesex}$ = 0.076).

Total 95% MCP overlap of all individuals was significantly higher at Black Canyon Creek than Klickitat County, though marginally (Table 8). Separating overlap by sex for the two populations revealed that male overlap patterns were not significantly different. Again, the larger overlap between females at Black Canyon Creek was slightly significant.

Nest Use

Over the course of this study, we found squirrels in or associated with nests 25% (252/1014) of the time. We identified 64 nests as active. The majority of active nests were either shelter (78%; 50/64) or platform (20%; 13/64). One nest was in an alder cavity used by a female as a natal nest. Squirrels used 39% (25/64) of the nests once and 61% (39/64) two or more times. Most nests occurred in either ponderosa pine (81%; 52/64) or Douglas-fir (16%; 10/64). Furthermore, there was no difference in squirrels' use of ponderosa pine ($\bar{X} = 3.6 \pm 0.5$, range = 1-20, $n = 189$) and Douglas-fir ($\bar{X} = 4.7 \pm 1.8$, range 1-19, $n = 47$) for nesting ($U = 240$, $P = 0.66$). Platform and shelter nests occurred in pine and fir trees with equal frequency ($U = 230$, $P = 0.36$).

Natal nests comprised 17% (11/64) of the nests. The majority of natal nests were shelter nests (91%; 10/11) with only one female bearing young in a cavity. Thirty-five percent (88/252) of all the nest relocations were females at natal nests during the breeding season. Four of the six (67%) breeding females used more than one nest to rear young. Three used two nests and one female used three nests. The two females who did not move their young each had a litter of four and one was nesting in the

Table 8. Comparison of total 95% minimum convex polygon home-range overlap from Okanogan County, Washington (North), versus Klickitat County, Washington (South). P-values from Mann-Whitney U-tests ($\alpha = 0.05$).

	North Washington		South Washington			
	$\overline{X} \pm SE$	*n*	$\overline{X} \pm SE$	*n*	*U*	*P*
All	15.8% ± 2.1	13	11.0% ± 0.98 [a]	24	38,749	<0.05
Males (overlapping both sexes)	28.2% ± 4.5	5	18.3% ± 2.0 [a]	10	6,352.5	0.31
Females (overlapping Both sexes)	8.0% ± 1.3	8	5.9% ± 0.81 [a]	14	13,305	<0.05
Same sex Overlap						
Males	16.5% ± 5.4	5	15.1% ± 2.7 [a]	10	831.5	0.58
Females	7.0% ± 1.8	8	4.7% ± 1.1 [a]	14	4,301.5	<0.05

[a] Linders (2000)

cavity. Of the 10 shelter nests that were natal nests, 9 (90%) occurred in ponderosa pine trees and one was built in a Douglas-fir.

More than one squirrel used 25% (16/64) of the nests. Three pairs of squirrels used five of these “shared-use” nests at the same time. Two pairs used two nests each. One pair consisted of two males and the other was a male and a female. A male and an uncollared squirrel of unknown sex used the fifth nest. Every incidence of nest sharing occurred in the fall, outside of the breeding season.

The 12 squirrels included in home-range analysis used an average of 5.9 ± 1.0 (range 3-14) nests per squirrel. This is significantly less than the average number of nests used by squirrels in Linders’ (2000) Klickitat Co. study (14.3 ± 1.2, range 7-28, one sample test, $t = -8.6$, $P<0.001$). The number of nests used by males ($\bar{X} = 8.5 \pm 2.5$, range 3-14) and females ($\bar{X} = 8.6 \pm 0.5$, range 3-7) was not significantly different ($U = 8.50$, $P = 0.21$) nor was the number of nest locations for the two sexes ($\bar{X}_{males} = 21.2 \pm 5.6$; $\bar{X}_{females} = 18.6 \pm 2.5$; $U = 11$, $P = 0.46$).

Shelter nests were the most commonly used nests throughout the year and served as the dominant type of natal nest (Figure 8). The use of the cavity nest is attributable to one female with young. Platform use increased from 10% in the fall and spring to 24% in the warmer days of summer.

Nest and Nest-tree Characteristics

The mean height for 48 nests sampled at Black Canyon Creek was 11.8 ± 0.5 m.

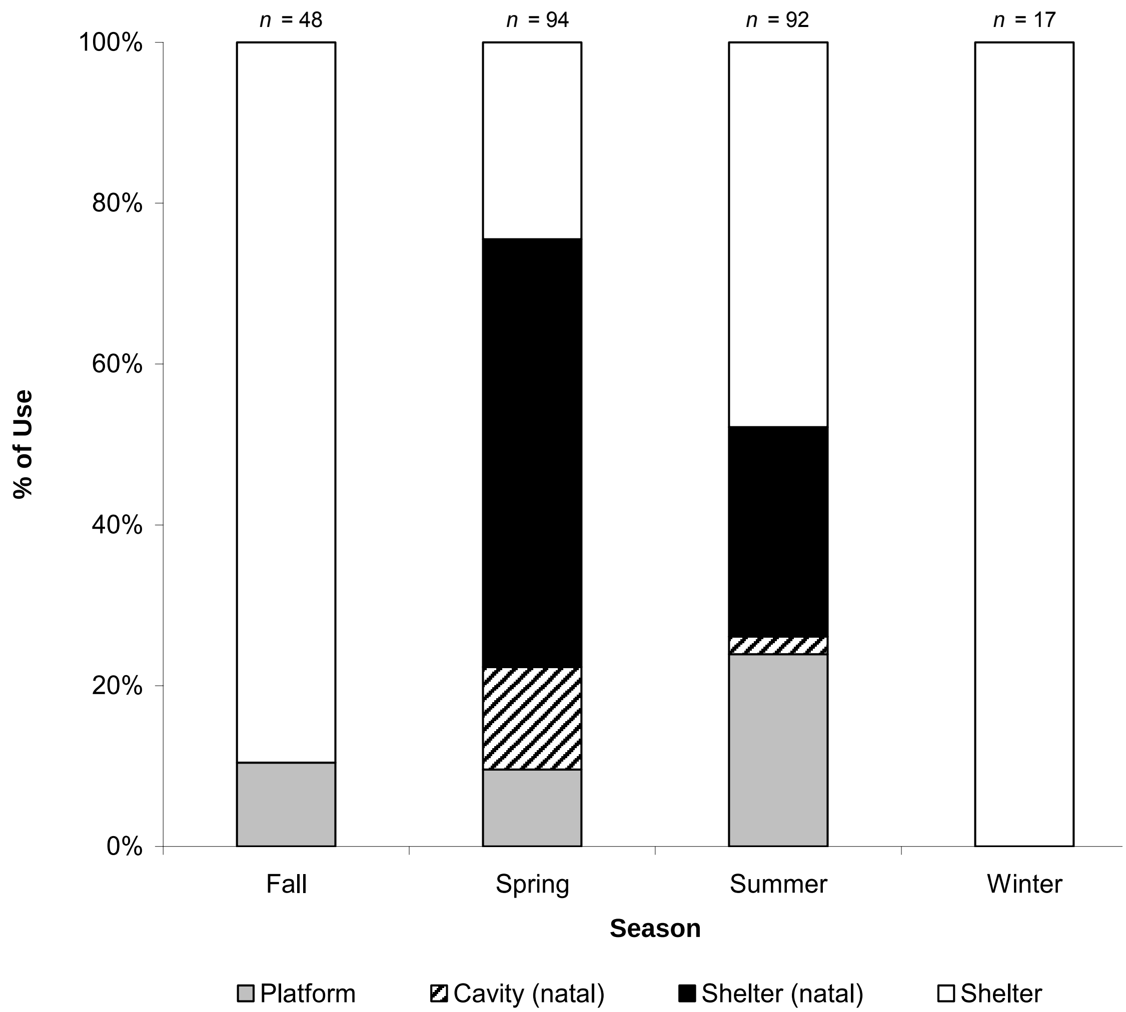


Figure 8. Proportion of western gray squirrel nest use by season by in Okanogan County, Washington, Spring 2003- Fall 2004. Sample size is number of nest relocations.

The mean ratio of nest height to tree height was 0.53 ± 0.03 (range: 0.20-0.92). Forty percent (19/48) of these nests occurred on the south side of the nest tree, 21% (10/48) were on the west side, 15% (7/48) were on the north side and 15% (7/48) were on the east side. Squirrels built five nests in the crotch of a tree and we labeled them as having no aspect. These values exclude the cavity nest and one shelter that was obscured by mistletoe. Proportions of tree species used for nesting by western gray squirrels in Okanogan and Klickitat Counties were not significantly different (Figure 9; $X^2 = 3.1$, $P = 0.21$). Most of the 50 nest trees sampled at Black Canyon Creek had dominant (12/50; 24%) or co-dominant crowns (34/50; 68%). Only four (8%) nest trees were in intermediate or overtopped trees. These proportions are not significantly different from those of nest trees in Klickitat County ($X^2 = 0.84$, $P = 0.66$). Similarly, nest trees used by the two populations were not significantly different in their distribution among stand position ($X^2 = 5.4$, $P = 0.07$) categories. Fifty-four percent of Black Canyon Creek nest trees (27/50) were interior and 40% (20/50) were in marginal trees on the edge of a stand. The *P*-value for the chi-squared test of stand position is close to the rejection level of 0.05. This is possibly because of the 19 trees in Klickitat Co. that were in the open/isolated category (Figure 9). According to Linders (2000), 16 of these 19 trees were associated with reproductive females (i.e. with young, pregnant, or lactating). We found no significant difference ($t = 1.63$, $P = 0.11$) in nest-tree dbh between this study ($\bar{X} = 45 \pm 1.8$ cm, range = 22-84, $n = 50$) and the findings for Klickitat County ($\bar{X} = 42$

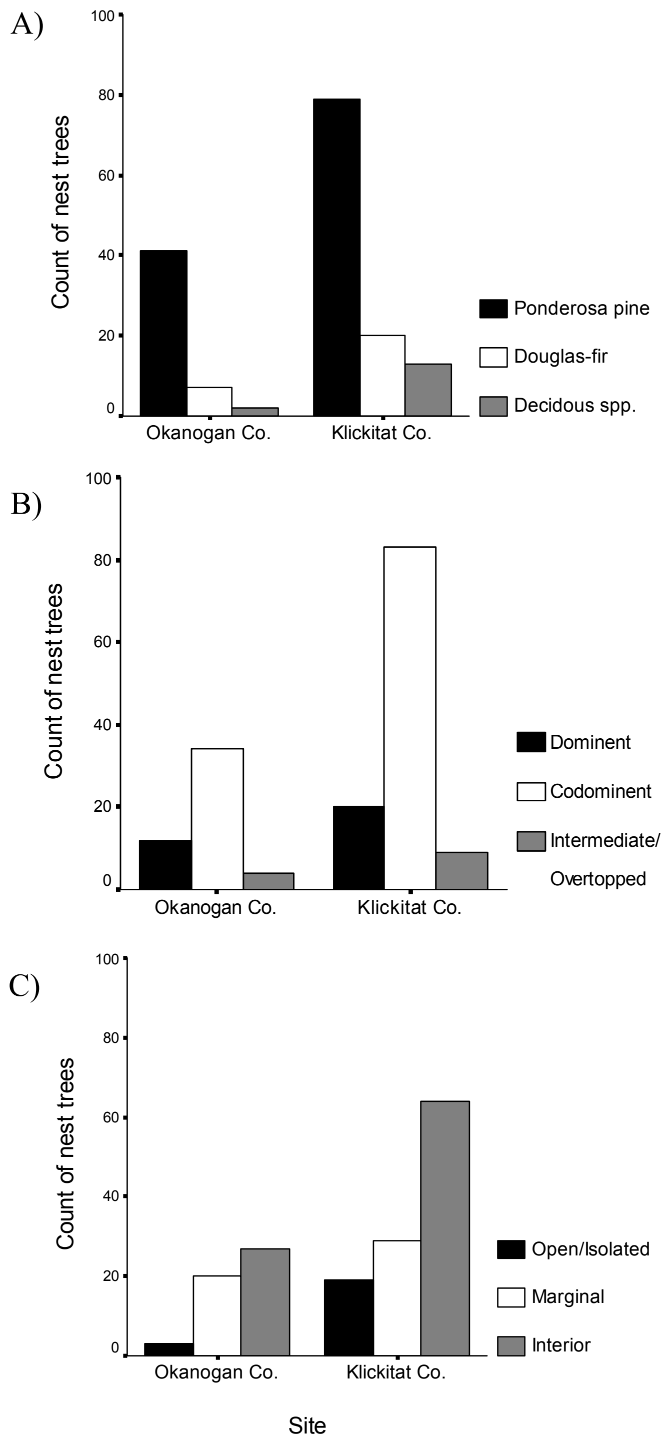


Figure 9. Distribution of western gray squirrel nest trees in Okanogan Co. and Klickitat Co., Washington by: A) Tree species, B) Stand dominance, and C) Stand position.

± 1.2 cm, range = 16-78, n = 112). However, the mean dbh for nest trees at Black Canyon Creek was significantly larger than the mean dbh of the 10.6 m radius plots where they occurred ($\bar{X}$ = 32 ± 1.1 cm, range = 19-51, n = 50, U = 412, P<0.001). The nest trees in Klickitat County did have significantly more connectivity ($\bar{X}$ = 4.1 ± 0.2 trees, range = 0-11, n = 111; t = -4.2, P<0.001), or number of trees with branches ≤1 m away, than those at Black Canyon Creek ($\bar{X}$ = 2.7 ± 0.2 trees, range = 0-9 cm, n = 50).

Nest-tree selection

We did not discover any significant correlations or multicollinearity among nest-tree variables. The goodness-of-fit for the full model did not reject the null hypothesis of no difference between fitted values and observed values (P = 0.064). This P-value is only slightly above the alpha level of 0.05 indicating the possibility of interactions between variables or an insufficient sample size. However, based on residuals and other diagnostics, the model seemed appropriate. The full model had a 65% likelihood of being the best model and the model describing tree structure (*Treest*) had a 35% likelihood of being the best model (Table 9). Both of these models are included in the confidence set as the sum of their weights is greater than 0.95 and therefore both have empirical support for being the best model (Burnham and Anderson 2002). In addition, the likelihood ratio tests determined that the residual deviances of both the full model and the model *Treest* were significantly lower than the deviances of the null model (P_{full}<0.001, P_{Treest}<0.001). Therefore, using these two models we

Table 9. Results of logistic regression analysis of western gray squirrel nest-tree selection Okanogan County, Washington. Models are defined in Table 3.

Model	[Log($\mathcal{L}$)]	K	AIC_c	ΔAIC_c	w_i
*Full**†	-86.21	65	325.61	0.00	0.65255
Treest†	-95.02	59	326.87	1.26	0.34744
Pred	-106.36	58	346.88	21.27	0.00002
Oregon	-135.95	52	390.29	64.68	0.00000
KWA	-134.35	55	394.91	69.30	0.00000

*goodness of fit: $p = 0.0636$

†In the 95% confidence set

calculated model-averaged (weighted) estimates for coefficients and standard errors (Table 10). The *post hoc* RIV calculations and AIC comparisons of univariate models identified the variable for mistletoe infection, total broom volume (TBV), as the highest-ranking variable (Table 11). The coefficients for the TBV variables give further evidence that it is a strong variable because the confidence intervals of their odds ratios do not include the number one. The TBV coefficients are positive meaning that, holding all other variables constant, the odds of a squirrel choosing a tree for nesting increase as mistletoe infection increases from the reference level of zero. Our case-control study design with stratification variables combined with low counts in the higher TBV categories are likely contributing to the unusually high coefficients and odd ratios for TBV (Table 10). The marginal odds ratios (MOR) for the TBV categories (MOR_{TBV1} = 9.0, MOR_{TBV2} = 13.9, MOR_{TBV3} = 24.3) give more conservative estimates and yet still emphasize TBV as an influential variable. Half (25/50) of our nest trees exhibited brooms associated with mistletoe infection compared to 7% (26/381) of the control trees (Figure 10, Table 12). The number one is not included in the odds ratio confidence intervals for dbh and connectivity thus they also are strongly influencing squirrels' nest-tree selection (Table 10). Nest trees at Black Canyon Creek had larger mean dbh and connectivity values than control trees (Table 12).

Nest-site selection

The only significant correlation that we discovered for the nest-site variables was between canopy cover (%) and stand basal area (m^2/ha, P = 0.87). Other studies

Table 10. Weighted coefficients incorporating the full model and the model *Treest* from logistic regression analysis describing western gray squirrel nest-tree selection Okanogan County, Washington. Odds ratios are calculated by exponentiation of the coefficient. The 95% confidence interval = $e^{(\beta \pm 1.96SE_{\beta})}$. Variables are defined in Table 1.

Variable	Coefficient (β)	Odds ratio	Std. error	95% C.I.
CBH	-0.0753	0.93	0.1285	0.72-1.19
Con	0.7043	2.02	0.2165	1.32-3.09‡
DBH	0.0834	1.09	0.0374	1.01-1.17‡
Dom2	-0.5602	0.57	1.1636	0.06-5.59
Dom3	-1.0785	0.34	1.9036	0.01-14.19
Spp2	-0.9812	0.37	0.8327	0.07-1.92
Spp3	1.8531	6.38	1.9014	0.15-265.05
Stand_pos3	-0.0347	0.97	1.4446	0.06-16.39
Stand_pos4	-0.5631	0.57	1.6518	0.02-14.51
TBV1	4.9042	134.86	1.0232	18.15-1,002.0‡
TBV2	7.4996	1807.30	1.7505	58.48-55,857.0‡
TBV3	10.7546	46847.0	2.2252	597.76-3,671,500.0‡
Tree_cond3	-1.0789	0.34	3.7742	0.00-554.80
Tree_cond4	-1.7398	0.18	3.8366	0.00-323.71
Tree_cond5	-2.3082	0.10	3.8308	0.00-181.28
Tree_ht	0.2313	1.26	0.1554	0.93-1.71

‡C.I. does not contain 1.

Table 11. *Post-hoc* results of logistic regression analysis using univariate models and relative importance values (RIV) of variables describing tree structure from the full model describing western gray squirrel nest-tree selection Okanogan County, Washington. Variables are defined in Table 1.

Model	[Log(*L*)]	K	AIC_c	ΔAIC_c	w_i	RIV
TBV	-111.94	52	342.26	0.00	1.0000	0.34745
DBH	-138.59	50	390.43	48.17	0.0000	0.00000
Tree_ht	-139.57	50	392.38	50.12	0.0000	0.34744
Dom	-142.54	51	400.88	58.62	0.0000	0.00000
CBH	-148.25	50	409.75	67.49	0.0000	0.34744
Con	-151.36	50	415.97	73.71	0.0000	0.00002
Spp	-150.42	51	416.64	74.38	0.0000	0.34744
Stand_pos	-152.04	51	419.90	77.64	0.0000	0.00002
Tree_cond	-152.45	52	423.30	81.04	0.0000	0.34745

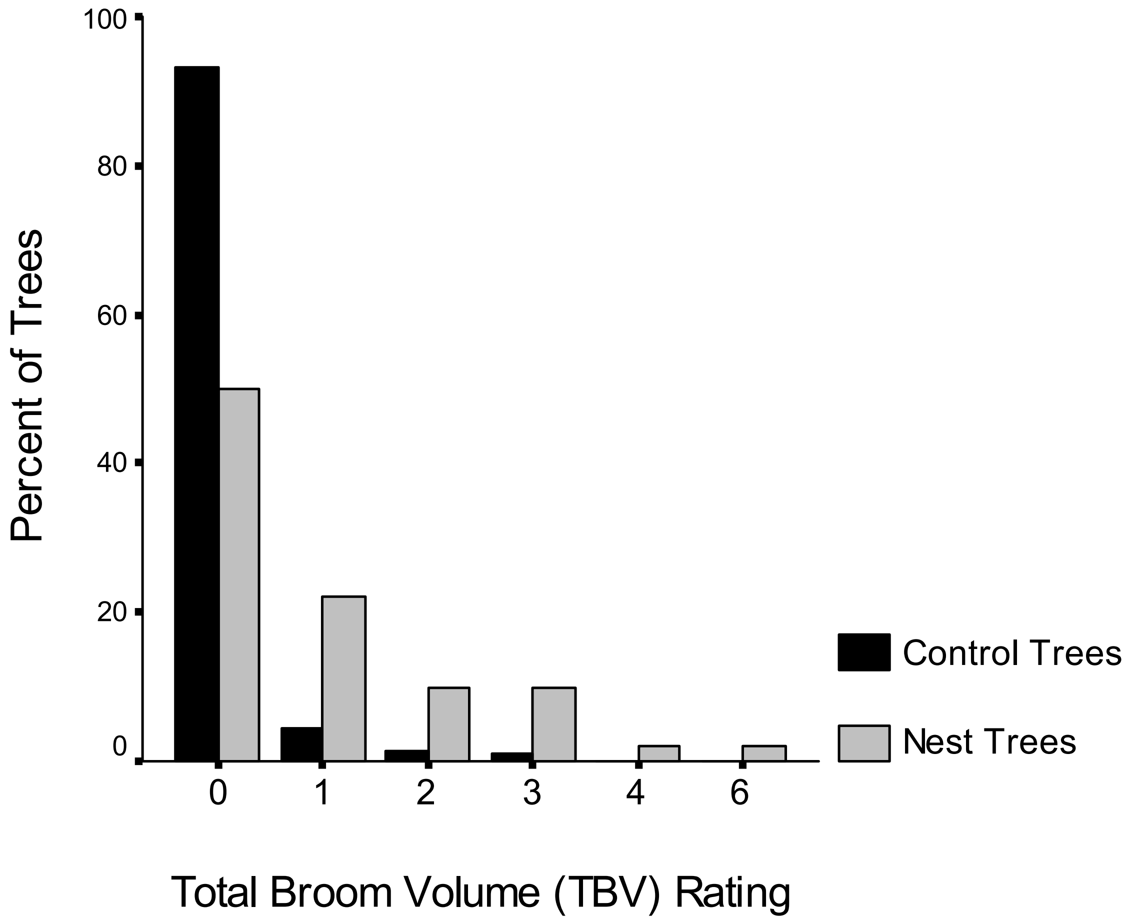


Figure 10. Percentage of western gray squirrel control and nest trees by Total Broom Volume (TBV) rating for mistletoe infection.

Table 12. Mean and standard error ($S_{\bar{X}}$) of continuous variables and counts of categorical variables for characteristics of selected and control nest trees of the western gray squirrel, Okanogan County, Washington.

Variable	Selected (n = 50)	Control (n = 387)
Crown base height (m)	5.9 (0.5)	4.7 (0.2)
Connectivity (count)	3 (range: 0-9)	2 (range: 0-8)
Diameter at breast height (cm)	45.5 (2.0)	37.5 (1.0)
Dominance		
Dominant	12	35
Co-dominant	34	247
Intermediate	4	105
Species		
Pine	41	297
Doug-fir	7	89
Deciduous	2	1
Stand position		
Separated	3	16
Marginal	20	191
Interior	27	180
Total Broom Volume		
No Brooms	25	361
Level 1	11	17
Level 2	5	5
Level 3	5	4
Level 4	1	0
Level 6	1	0
Tree condition (% live canopy)		
1-25%	2	2
26-50%	8	67
51-75%	16	118
>75%	24	200
Tree height (m)	23.0 (1.0)	20.0 (0.5)

have found that canopy cover is an important component of suitable squirrel habitat. However, during our time in the field, we did not observe squirrels limiting their movements to stands with high canopy closure and frequently individuals were willing to travel long distances on the ground. In addition, many nests are in trees that are too far from surrounding trees to allow arboreal travel. As stated above, nest trees at Black Canyon Creek have significantly less connectivity that those in Klickitat County. Also, of the 11 natal nests that we observed during this study, three (27%) of them had no connectivity with surrounding trees and three (27%) had connectivity with only one other tree. Therefore, we chose to exclude canopy cover from the analysis in favor of stand basal area. We did not detect any multicollinearity between continuous nest-site variables.

The goodness-of-fit test for the full model, with all nest-site variables, did not detect lack-of-fit (P = 0.27). Comparisons of the Akaikie weights of the model set, including the full model and all candidate models, distinguish the model *Stand* as having a 99.9% likelihood of being the best model (Table 13). The likelihood ratio test determined that the model *Stand* had a significantly lower residual deviance than the null model (P<0.001). The variables included in the model *Stand* (QDBH, Trees, StandBA) had equal RIV and were the highest ranked of all of the variables under consideration (Table 14). Comparisons of AIC values for the univariate models revealed stand basal area as the most influential variable in the model *Stand* with a weight of 0.999 (Table 14). In addition, the coefficient for stand basal area is significant

Table 13. Results of logistic regression analysis of western gray squirrel nest-site selection Okanogan County, Washington. Models are defined in Table 4.

Model	[Log($\mathcal{L}$)]	K	AIC_c	ΔAIC_c	w_i
Stand†	-40.96	19	129.43	0.00	0.999992
*Full**	-28.73	32	152.98	23.55	0.000008
KWA	-55.64	19	158.79	29.36	0.000000
WDFW	-60.91	18	166.26	36.83	0.000000
Ground	-57.49	22	172.11	42.68	0.000000
Pred	-62.97	20	176.57	47.14	0.000000
SP	-65.24	20	181.12	51.69	0.000000

*goodness of fit: p = 0.27
†In the 95% confidence set

Table 14. *Post-hoc* results of logistic regression analysis using univariate models and relative importance of variables from the best model (*Stand*) describing western gray squirrel nest-site selection Okanogan County, Washington. Variables are defined in Table 2.

Model	[Log($\mathcal{L}$)]	K	AIC_c	ΔAIC_c	w_i	R.I.V.
StandBA	129.61	16	136.16	0.00	0.999999	0.999992
Trees	156.32	17	163.78	27.62	0.000001	0.999992
QDBH	162.72	16	169.27	33.11	0.000000	0.999992

because the confidence interval of its odds ratio does not include the number one (Table 15). The 50 selected nest sites had an average basal area of 27 m^2/ha almost twice the mean of control sites (Table 16). Mean dbh (QDBH) is also influencing nest-site selection, as its coefficient is significant (Table 15). Squirrels selected nest sites with a mean dbh 4 cm larger than unselected control sites (Table 16). In addition, tree composition of 44% (22/50) of nest sites was mixed conifer or mixed conifer/deciduous compared to 12% of control sites (Table 16). The probability plots for the model *Stand* describe the shift in selection probability with changes in each of the variables (Figure 11). Of the sites that we studied, those with the highest mean dbh and the highest stand basal area had the highest probability of being nest sites. Tree species diversity had the greatest influence on selection probability at 25-35 cm dbh and at a basal area of 15-30 m^2/ha.

Natal nests

After determining that stand TBV and basal area were two important variables driving squirrels' selection of nest trees and sites, respectively, we used them to compare natal nests and non-natal nests. The mistletoe ratings for natal and non-natal nests were not significantly different ($X^2 = 2.3$, $P = 0.51$; Figure 12). However, stand basal area of natal nest sites ($\bar{X} = 19.6 \pm 3.2$ m^2/ha, $n = 11$) was significantly lower than that of non-natal nest sites ($\bar{X} = 29.4 \pm 1.9$ m^2/ha, $n = 39$, t = -2.5, $P<0.05$).

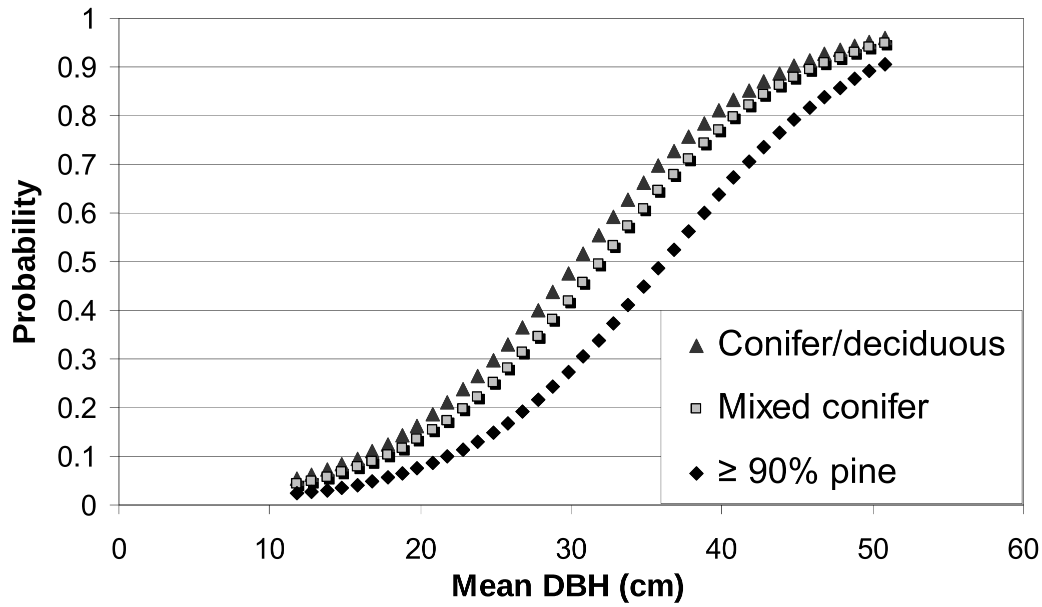
Table 15. Coefficients from logistic regression analysis the model (S*tand*) describing western gray squirrel nest-site selection Okanogan County, Washington. Odds ratios are calculated by exponentiation of the coefficient. The 95% confidence interval = $e^{(\beta \pm 1.96SE_{\beta})}$. Variables are defined in Table 2.

Variable	Coefficient (β)	Odds ratio	Std. error	95% C.I.
QDBH	0.15366	1.17	0.04865	1.06-1.28‡
Trees2	0.64953	1.91	0.79974	0.40-9.18
Trees3	0.88545	2.42	1.43057	0.15-40.0
StandBA	0.19223	1.21	0.04495	1.11-1.32‡

‡C.I. does not contain 1.

Table 16. Mean and standard error ($S_{\bar{X}}$) of continuous variables and counts of categorical variables for characteristics of selected and control nest sites of the western gray squirrel, Okanogan County, Washington.

Variable	Selected (n = 50)	Control (n = 50)
Aspect		
East	21	12
South	21	31
West	8	7
Canopy cover (%)	45 (3)	30 (2)
Connectivity (count)	2 (range: 0-5)	2 (range: 0-4)
Distance to water (m)	540 (50)	530 (50)
Distance to road (m)	430 (40)	430 (40)
Elevation (m)	760 (20)	760 (20)
Ground cover		
>50% litter	34	30
>50% vegetation	8	11
50/50 litter/veg.	8	9
QDBH (cm)	31.5 (1.0)	27.5 (1.0)
Shrub cover		
0-1%	13	5
2-5%	18	26
6-25%	13	11
26-50%	4	7
51-75%	2	1
Stand basal area (m^2/ha)	27.2 (1.7)	14.7 (1.1)
Tree species composition		
≥ 90% pine	28	44
Mixed conifer	16	5
Mixed conifer/deciduous	6	1
Understory species (count)	3 (range:1-7)	2 (range: 0-5)



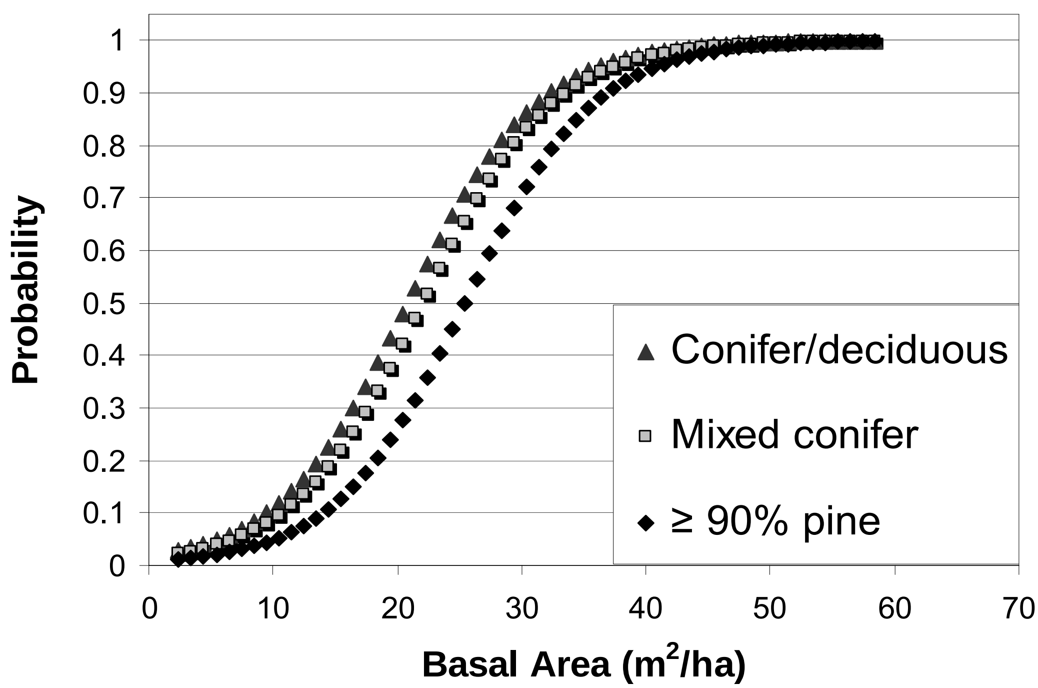


Figure 11. Western gray squirrel nest-site selection probability for the model *Stand* depicting changes in probability with changes in mean dbh and basal area at three different levels of site tree diversity.

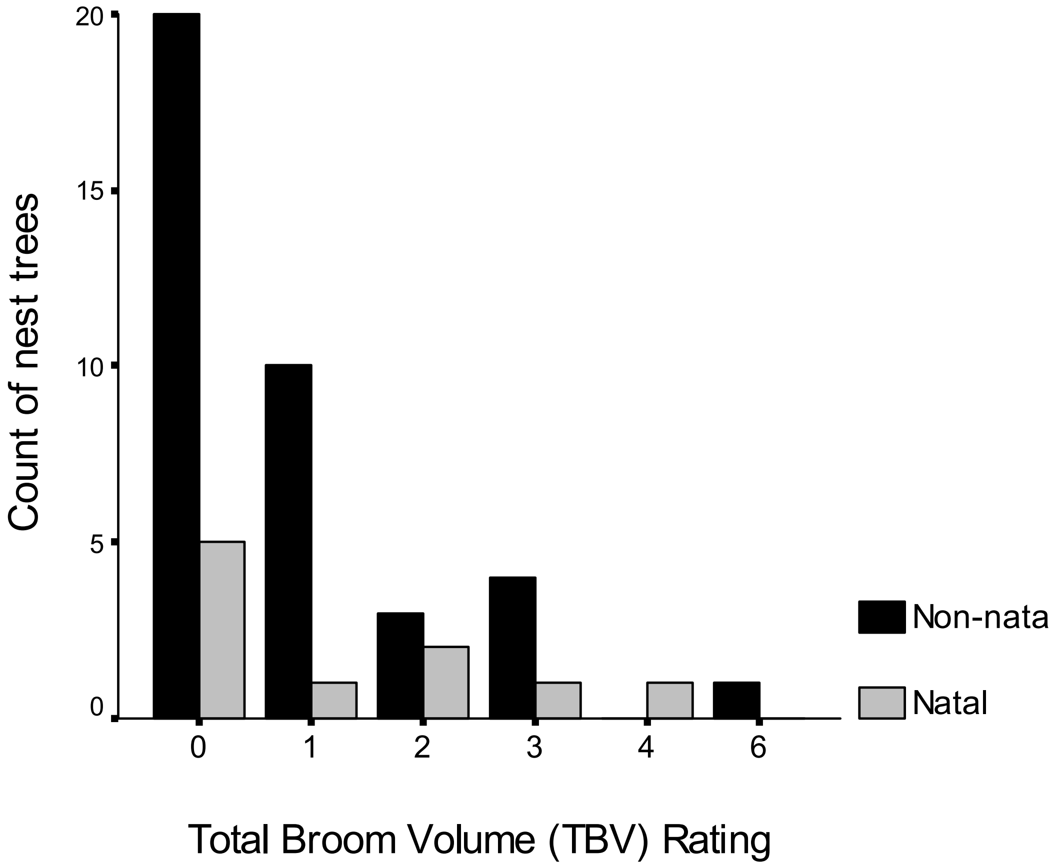


Figure 12. Distribution of western gray squirrel non-natal and natal nest trees by Total Broom Volume (TBV) rating for mistletoe infection.

Discussion

Movements

The large home-range and movement estimates found by this study can be used to make inferences about the quality of western gray squirrel habitat in Okanogan County, Washington. Don (1983) suggests an inverse relationship between home-range size and resource availability. Low resource availability contributes to low population density which Kenward (1985) cites as a primary driver of increased home-range size where individuals are forced to spread out to find mates. Both factors seem to be at work at the northern extent of the squirrel's distribution where individuals must travel long distances to meet both energetic and reproductive demands.

According to studies on the food habits of western gray squirrels in California (Stienecker and Browning 1970, Stienecker 1977) hypogeous fungi, acorns, and pine seeds are the top food items used by western gray squirrels. Foster (1992) determined that western gray squirrels in Oregon did not use acorns, but used the more abundant hypogeous fungi as their primary food source. Byrne (1979) also noted the exclusive use of hypogeous fungi when other food sources were in short supply. Lacking the oak component present throughout most of their range, squirrels at Black Canyon Creek are without acorns, an important food source, especially during the winter (Asserson 1974, Cross 1969, Gilman 1986, Ingles 1947, Linders 2000). Hypogeous fungi have a mutualistic relationship with ponderosa pine and rely on small mammals for their dispersal (Maser, Trappe, and Nussbaum 1978; Maser, Trappe, and Ure 1978). Surveys for hypogeous fungi in east-central Washington, measured average spring biomass in open Ponderosa pine forests, similar to those found at Black Canyon Creek, at 1.72 kg/ha (Lehmkuhl et al. 2004). The most common species encountered belongs to the genus *Rhizopogon* that Stienecker and Browning (1970) rank as the most important food item for the western gray squirrel. Thus, hypogeous fungi, which are palatable to squirrels, are almost certainly available at Black Canyon Creek yet we did not observe their presence nor confirm their consumption by squirrels. This is most likely attributable to this species' low tolerance for an approaching human while on the ground. Still, ponderosa pine seeds probably provide the richest source of food for this population. With the added security of vertical distance, we were able to observe individuals and occasionally groups foraging in pine trees. Squirrels started feeding on green cones during late spring (Linders 2000, pers. obs.). There was also sign that they were foraging for old seeds in the winter in the form of cone scales strewn on newly fallen snow. In addition, we speculate that squirrels at Black Canyon Creek could be using ponderosa pine cambium as a food source in the winter as well as the early spring. On many occasions, scattered at the base of various trees throughout the study site, we found the terminal ends of young branches that had been stripped of their bark. Other researchers have noted this behavior among western gray squirrels (Bowles 1921, Fritz 1932, Scheffer 1923, Mitchell 1950) and it is even more commonly observed among Abert squirrels, the western gray squirrel's closest relative (Keith 1965, Pederson et al. 1987). However, porcupines (*Erethizon dorsatum*) and red squirrels are also known to consume the bark of conifers (Dodge 1982, Elbroch 2003). Therefore, without direct behavioral observations of this behavior in western gray squirrels, we cannot rule out the possibility of another animal creating the debris that we observed. Still, there is some evidence from this study supporting this hypothesis including the small diameter of the branches on the trees that were stripped. They were not of sufficient strength to support an adult porcupine. In addition, we did not encounter any other sign of a porcupine (i.e. scat, quills, tracks) during the course of this study. Though red squirrels are present at Black Canyon Creek, we found the damaged trees upslope from the riparian areas where they are most common. Cambium is primarily fiber containing less than 10% of protein and fat making it a poor source of nutrients (Patton 1974). Thus, squirrels would have to consume increased volumes of cambium to meet their nutritional needs necessitating increased movements to find appropriate feeding trees. Though Douglas-fir may provide a supplemental source of mast (Cross 1969) we did not observe squirrels using them for forage as they did ponderosa pine. The red squirrel's stringent defense of Douglas-fir crops as well as its consumption of ponderosa seeds adds an element of competition that, when combined with western gray squirrels' potential reliance on a single mast producing species, further reduces the quality of habitat at Black Canyon Creek. Therefore, it is likely that squirrels travel increased distances to obtain food, resulting in large home-range estimates.

In addition to low resource availability, population density also seems to be having an immediate effect on squirrels' home-range size at Black Canyon Creek. The large interfix distances that we measured for males during the breeding season could be a result of low squirrel density. Female western gray squirrels are thought to be similar to females of other tree squirrel species that are only reproductive for one day during the breeding season (Thompson 1977). While there has been some speculation about whether this species can produce two litters in a year (Asserson 1974, Foster 1992) the movements and nesting behavior of females at Black Canyon Creek agree with the data from other studies supporting the production of only one litter per year (Cross 1969, Linders 2000). Thus, males must time their presence with females accordingly especially if the ratio of females to males is low (Steele and Koprowski 2001). Many observers have noted western gray squirrel breeding groups consisting of several males and one female (Cross 1969, Ingles 1947, Linders 2000). Therefore, if a male can cover large distances he will have a higher probability of finding a reproductive female. With low population density and fewer females, this distance will necessarily increase as well as overlap between males and other squirrels' home ranges (Linders et al. 2004, Wauters and Dhondt 1992, this study). Mean total home-range size for males is about twice that of mean non-breeding home-range size. This difference is most likely the result of the inclusion of breeding season locations in the total home-range estimate. This difference in male home-range size coupled with the significantly larger breeding male interfix movements lends support to other findings that population density is an important influence on squirrel movements (Farentinos 1979, Kenward 1985, Linders et al. 2004 Wauters and Dhondt 1998). Gurnell (1987) argues that population density is tied to food availability. He states that resource levels in the past influence birth rates and survivorship and therefore the present population density. Even though a rich food source seems to be lacking at Black Canyon Creek and squirrels there are moving long distances we did not observe any migration to a localized food supply in the winter or any other time of the year.

There is concern about Type II error caused by our small sample size, making it difficult to form conclusions about differences between home-range overlap at Black Canyon Creek and Klickitat County (Table 8). However, when considering the observations of Gilman (1986) and Ingles (1947), the Washington populations are probably overlapping less than those in California. This reinforces the idea posed by Linders et al. (2004) that squirrels in Washington could be partitioning pockets of habitat with relatively high concentrations of resources. In their review of ponderosa pine, Krannitz and Duralia (2004) note that individual trees are capable of high cone production across years. Female squirrels could be placing their home ranges around these trees for easy access during breeding periods when the demands of lactation are high and choosing to defend them, especially against other females. Female squirrels at Black Canyon Creek have 50% core areas of similar size to females in Klickitat County while their 95% probability contours are statistically larger (Table 7). The same pattern occurs in the comparison of female movement distances between the non-breeding and breeding seasons (Table 5). In addition, there is very little overlap between female total 50% FK core areas (Figure 13). These relatively small core areas and breeding movements could indicate that females are defending patchy resources to enhance breeding success. Furthermore, the low female overlap during the breeding season parallels the observed behavior of females in Klickitat County (Vander Haegen et al. 2005) as well as that of other squirrel species that tend to isolate themselves to a

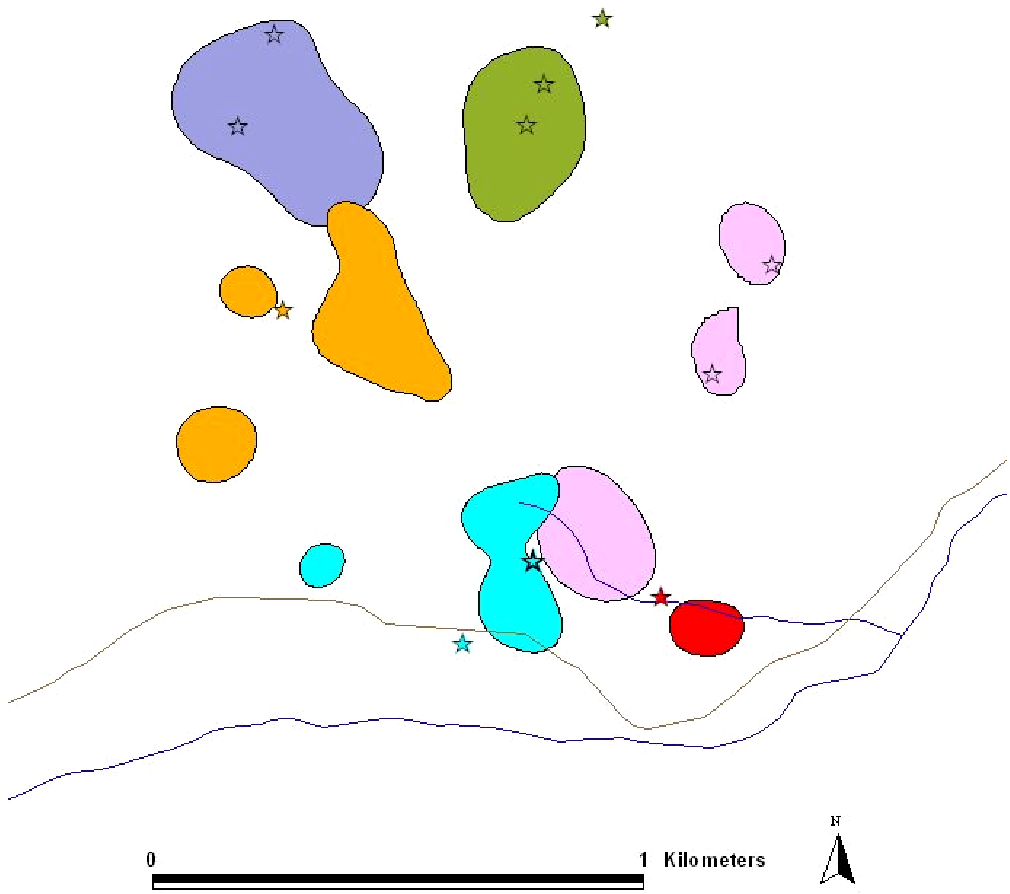


Figure 13. Female western gray squirrel total 50% fixed kernel core areas and respective natal nests (stars). Streams are in blue and roads are in brown.

specific nest site (Figure 7; Gurnell 1987, Wauters and Dhondt 1992). This behavior agrees with the idea of economic defendability outlined by Gurnell (1987) that an animal will invest energy in defending an area if available food supplies provide sufficient returns. Additional, long-term research on a larger number of animals is needed to explore this idea at Black Canyon Creek.

Nest use

Squirrels at Black Canyon Creek appear to exhibit nesting behaviors similar to those of other populations. We determined that 75% (48/64) of nests were used by only one radio-collared squirrel. In addition, most squirrels that shared nests separated their use temporally. These results are in concurrence with those of Cross (1969), Gilman (1986), and Linders (2000) for the western gray squirrel. Additionally, these studies found, as did ours, that squirrels used conifers most often as nest trees. However, given the relatively low occurrence of deciduous trees at Black Canyon Creek this finding is not surprising. With cavities largely unavailable to this population, they concentrated most of their use throughout the year on shelter nests that served not only as protective structures against the winter cold but also as natal nests (Figure 8). Presumably, cavity nests provide increased protection from predators and inclement weather; however, we did not observe any use of the one known squirrel cavity during the winter. One female used it exclusively as a natal nest in the spring and summer. In addition, squirrels used platform nests most often in the summer most likely in an effort to keep cool. This seasonal shift in nest use is consistent with that observed by Linders (2000). Squirrels at

Black Canyon Creek used fewer nests, on average, than squirrels in Klickitat County (Linders 2000). This could mean that there are fewer preferable nest sites for this northernmost population of western gray squirrels.

Tree squirrels are primarily solitary animals (Gurnell 1987). Therefore, nest sharing is observed infrequently, and being somewhat variable across species and habitats is not well understood. Some studies report that the majority of nesting pairs are of mixed sex occurring during the breeding season (Cross 1969, Linders 2000, Wauters and Dhondt 1990). Others report single sex pairs of males and females or only males gathering most commonly in the fall and winter to maintain warmth (Halloran and Beckoff 1994, Koprowski 1996). Linders (2000) was not certain of the causal factors behind the nest sharing that she observed among western gray squirrels in Klickitat County, but hypothesized that Notoedric mange, which can cause severe hair loss and death, played a role. During this study, we observed a male and a squirrel of unknown sex sharing a nest once and a pair of males and a male-female pair sharing a nest on more than one occasion. We suspect that, during our study, this behavior was a response to cold weather as all instances of nest sharing occurred in the months of October and November, outside of the breeding season, and there were no mange outbreaks. We should also note that this behavior might have been more frequent than we could observe with telemetry as most collars (7/10) were chewed off during the winter season. Given our collar design, a squirrel could not have chewed off its own collar. If squirrels were gathering frequently in the winter to maintain warmth, they were probably also grooming each other. This grooming behavior can involve mutual biting and chewing of the fur (Gurnell 1987) and could have resulted in the collar removal that we observed. Indeed, three of the squirrels that we observed engaging in nest sharing were among those that lost their collars over the winter.

Nest and nest-tree characteristics

On average, squirrels at Black Canyon Creek built nests about half way up nest trees with southern or western exposure. Halloran and Beckoff (1994) observed Abert squirrels placing their nests in the upper third of trees with the most exposure from the south or southeast. They found that squirrels were not positioning nests to maximize thermal exposure as over 60% of winter nest use occurred in north-facing nests. We did not explore this question, but it is of interest given that squirrels seem to be sharing nests in the colder months, possibly to aid in heat retention.

Western gray squirrel nest trees found during this study share many characteristics with trees in Klickitat County. The proportions of nest trees used by squirrels in Black Canyon Creek did not differ from those in Klickitat County in terms of species, stand dominance, stand position, or dbh. Thus, as Linders (2000) noted, dominant or co-dominant pines, ≥40 cm dbh, on the interior or the edge of a stand are the type of trees that western gray squirrels in Washington use the most for nesting. The tendency for squirrels to choose individual trees with a larger stem diameter than the mean diameter of the surrounding stand is similar to other squirrel populations (Byrne 1979, Halloran and Beckoff 1994, Linders 2000). However, the proximity of the trees surrounding nest trees varies between populations. Squirrels at Black Canyon Creek nest in trees with an average of 2.7 interlocking crowns versus 4.1 in Klickitat County. The mean connectivity of Abert squirrel nest trees (2.8 ± 1.2; Halloran and Beckoff 1994) is similar to that observed here. This is perhaps a result of a greater similarity in overall forest type between Black Canyon Creek and the predominantly pine stands of Colorado where trees are more dispersed throughout a stand.

Nest-tree selection

The full model, containing all of the variables describing squirrel nest-tree selection, was part of the 95% confidence set indicating a general weakness in our candidate models (Table 9). Though refinement of candidate models is needed, there is biological support for the variables that emerged as potentially important to western gray squirrel nest-tree selection: mistletoe infection, dbh and connectivity.

The variable describing mistletoe infection, TBV, received the most support as an influential variable with a very high relative importance (RIV) and a strong univariate model (Table 11). At Black Canyon Creek, the increased branching of mistletoe-infected trees seems to be attracting squirrels as nest trees. Although the odds of selection increase with increasing levels of infection, we only evaluated our data up to level 3 on the TBV scale as that was the highest level of infection among control trees. This equates to about 1/3 of a trees total volume (including the unfoliated portion of the stem) contorted into at least one broom (Parker and Mathiasen 2004). We cannot discuss the odds of selection beyond TBV level 3; however, 2 of our nest trees were rated at level 4 and level 6 indicating the possibility of selection above level 3 (Figure

10, Figure 12). Recognizing that mistletoe brooms can increase the "structural diversity" of a tree for many wildlife species, Garnett et al. (2004) inspected brooms of ponderosa pine in northern Arizona for evidence of specific wildlife species. They found significantly more use of broomed trees by wildlife than unbroomed trees. In addition, mammal use was the most common type of use of broomed trees (31 caching/foraging sites and 8 nest sites) and Abert squirrels were the most likely mammal to use a broom. They used 95% (39/41) of broomed trees that had mammal use.

The results of this study are similar to those of Halloran and Beckoff (1994) who determined that the dbh and connectivity of Abert squirrel nest trees were significantly greater than randomly selected control trees. They point out that larger trees are more likely to have branches substantial enough to support a nest and withstand adverse weather conditions, especially wind. In addition, increased connectivity to neighboring trees will increase the odds of nest-tree selection as it allows squirrels to travel horizontally through the canopy enhancing options for predator avoidance. It seems that there are some similarities between the nesting strategies of western gray squirrels at Black Canyon Creek and the Abert squirrel. While connectivity could be important to nest-tree selection, our comparison of this parameter between the nesting habitat at Black Canyon Creek and Klickitat County revealed that Black Canyon Creek is providing stands with lower connectivity. Thus, it is possible that some preferred habitat characteristics may not be available to the western gray squirrel in northern Washington.

Nest-site selection

Of the models we considered for squirrels' nest-site selection, the highest-ranking model contained the variables corresponding to basal area, dbh, and tree species diversity. This model, *Stand*, with a weight of 0.9999, is the only model in the 95% confidence set and therefore, has strong support for being the best model of the set (Table 13). Consideration of the regression coefficients for these variables reveals that they are positively correlated with squirrel nest-site selection at Black Canyon Creek (Table 15). Basal area seems to be an especially influential variable. Its AIC score as a univariate model distinguishes it from the other variables of the full model and its regression coefficient is significant (Table 15, Table 14).

The average basal area of nest sites at Black Canyon Creek (27 m^2/ha) is similar to the basal area measured at nest and core area plots for squirrels in Klickitat County, Washington (25.4 m^2/ha; Linders 2000). It also conforms to the value Ryan and Carey (1995) calculated for "high-use" stands in squirrel habitat on Ft. Lewis on the west side of the state. Thus, squirrels throughout Washington are selecting similar types of stands. However, the basal area measurements from studies in Washington are substantially lower than measurements from squirrel habitat in California (Byrne 1979, Hall 1980). Thus, it would seem that although the basal area of the stands at Black Canyon Creek is sufficient for supporting squirrels it may not be ideal.

Basal area is a function of the number of trees (i.e. density) as well as their size. Stands with equal basal area could consist of many, suppressed, small diameter trees or fewer, mature, large diameter trees. At Black Canyon Creek, tree diameter at selected sites is larger than the diameter at the control sites (Table 16) and an increase in mean dbh increases the odds of a squirrel selecting a site for nesting. During their experimental study of Kaibab squirrels in Arizona, Patton et al. (1985) observed a larger increase in squirrel density on control sites than treatment sites where basal area and average stem diameter decreased after timber harvest. Larger, more established trees tend to have higher mast production and provide more opportunities for nesting (Krannitz and Duralia 2004, Patton et al. 1985). Therefore, it would seem that given a choice between the two types of sites described above, squirrels would select the site with fewer large trees. Another variable potentially important to squirrels' habitat selection is the clustering of trees throughout a stand (Patton et al. 1985). Further inspection of the patchiness of a stand may help to add another level of detail to our understanding western gray squirrels' habitat selection strategies.

Western gray squirrels at Black Canyon Creek used nest sites farther from water than other population of squirrels (Foster 1992, Rodrick 1986, Ryan and Carey 1995). Nests with more than three squirrel relocations averaged 582 m from a perennial water source (range 20-1,230). Furthermore, our logistic regression analysis did not identify distance from water as an important variable. However, proximity to water can influence other variables that we determined as important to nest-site selection such as tree species diversity and stem diameter. Again, squirrels may prefer to nest in more mesic sites but are limited by intraspecific and interspecific competition especially from the red squirrel, which tends to inhabit sites with a stronger riparian component and higher tree species diversity (Koprowski 2005, pers. obs). While we did not study competition directly, we made several opportunistic observations of red squirrels chasing gray squirrels in what appeared to be an aggressive manner. In addition, during the year following our telemetry studies, we happened upon an owl at the opening of the cavity where one of our collared females had raised her young. We made this observation during the breeding season. Therefore, we suspect that that cavity, most likely a preferred nest type is not readily available to squirrels every year.

Natal nests

Though our sample of natal nests was small, their site basal area was significantly lower than that of non-natal sites. Furthermore, of the 19 nest trees Linders (2000) classified as open or isolated, 16 (84%) fit our definition of a natal nest. This agrees with our observations of natal nests as separated from stands with a greater riparian component and a denser tree structure. Perhaps these relatively remote sites allow females some protection from red squirrels and other nest predators. In addition, females placed there natal nests within or near their own core area and never within the core area of another female (Figure 13). Natal and non-natal nest trees were not statistically different in their TBV ranking. Even still, 6 of the 10 (60%) natal nests built in conifers had a TBV ranking of at least 1 and one nest was a level 4 (Figure 12). Female squirrels may also use these nests repetitively. In the breeding season following the one where we made our initial natal nest observations, we observed evidence of repeated use at two broomed nest trees. We found a new litter of three young at a natal tree with a level 2 TBV ranking and fresh material at another ranked at a level 4.

Mistletoe could provide the extra concealment that a female squirrel is likely seeking for her young and more opportunities for young squirrels to acclimate to arboreal travel as they emerge from the nest and begin to explore the nest tree itself. A larger sample of natal nests may reveal that squirrels are selecting trees with more mistletoe to rear their young.

Conclusions

Movements

Western gray squirrels at Black Canyon Creek exhibited larger movements and home ranges than squirrels in Oregon, California and Southern Washington. This is indicative of low quality habitat and low population density at the northern extent of their range where individuals are using more space searching for food and mates. This population has larger 100% MCP home-range estimates than those in Oregon and California. Both male and females have larger 95% FK home-range estimates than squirrels in Klickitat County however, female 50% core areas are not different. These relatively small core areas could indicate that females are partitioning patchy resources. Interfix movements of male squirrels in the Methow Valley were longer than female movements. Females in the Methow Valley had similar movements to females in Klickitat County during the breeding season, again possibly because of partitioning behavior. Otherwise, squirrels in the Methow Valley exhibited longer movements than squirrels in Klickitat County. Average monthly movements for males and females provide evidence of one breeding season that starts in the late winter and ends late in the summer. This agrees with previous observations of this species in Washington State. All animals tracked in the Methow Valley exhibited site fidelity. Despite their hypothesized reliance on food from human sources, squirrels did not move to a localized feeding source during the winter. With a small sample size, variation in home-range overlap was difficult to detect statistically. However, patterns of overlap indicated that males have a higher tendency than females to overlap other squirrels presumably a result of their breeding movements. Female core area overlap was especially limited and could be explored in relation to a hypothesis about resource partitioning.

Nest Use

Conifers are the most common type of tree at Black Canyon Creek and squirrels used them most frequently for nesting. Squirrels did not differ in their use of pine and fir for nest trees although from visual observations, pine is the most numerous species on the study site. Females reared young in shelter nests built in conifers. This may not be the preferred natal nest type as one female raised her litter in an alder cavity in a densely vegetated riparian area that differed substantially from other natal nest sites at Black Canyon Creek and in Klickitat County. Nest sharing occurred in the fall between one pair of males, one male and one female, and a male and a squirrel of unknown sex presumably in response to cold weather. Squirrels in the Black Canyon Creek used fewer nests per animal than squirrels in Klickitat County, which could indicate a lack of suitable nest sites or trees. However, males and females in Black Canyon Creek did not differ in the number of nests used or nest use frequency. Squirrels shifted their nest use in the summer season from shelter nests to platform nests, which provide increased ventilation.

Nest and nest-tree characteristics

On average, shelter and platform nests occurred half way up the nest tree with some southern exposure. Nest placement may aid in thermal exposure but this has yet to be explored thoroughly for this species. Nest trees in Black Canyon Creek tended to be dominant or co-dominant pines ≥40 cm dbh, with an interior or marginal stand position. Individual nest trees also had a larger stem diameter than the surrounding trees. Larger trees that are associated with other trees provide increased support for a nest and opportunities for arboreal travel. These characteristics are similar to nest trees of squirrels in Klickitat County. However, connectivity of nest trees in Black Canyon Creek was lower than the connectivity of nest trees in Klickitat County. This may be attributable to fundamental difference in forest structure.

Nest-tree and nest-site selection

The odds of a squirrel choosing a tree for nesting increased with increasing levels of mistletoe infection, dbh, and connectivity. Of the nest trees we sampled, 46% (23/50) had some level of deformation in their branches attributable to mistletoe infection, compared to 7% (26/387) of control trees. The average dbh of nest trees was 45.5 cm and that of control trees was 37.5 cm. Forty-eight percent (24/25) of nest trees had 3 or more interlocking crowns compared with 41% (157/387) of control trees. Larger trees with increased branching variation and connectivity may provide more opportunities for nesting cover and predator escape.

The odds of a squirrel choosing a site for nesting increased with basal area, dbh, and increasing tree species diversity. However, basal area and dbh received more statistical support. The average basal area for nest sites in the Methow Valley was 27 m^2/ha, almost twice the mean of control sites. This value is similar to those observed for western gray squirrel habitat in other parts of Washington but lower than habitat in California. Stands with large trees contributing to a large basal area may be related to increased opportunities for food and shelter. Though considered an important variable for other western gray squirrel populations, distance to water was not a strong influence on nest-site selection although it can influence other parameters such as dbh, and tree species diversity.

Natal nests

In the absence of oak cavities, the majority of females used stick nests to rear their young. However, the habit of cavity nesting still seems to be present in this population as one female did keep her litter in a cavity. Females established natal nests at sites that were either within or near their core areas and never within another female's core area. The majority of natal nests had some level of branching variation attributable to mistletoe infection, which may provide extra concealment for young squirrels. These natal sites also had a lower average basal area than non-natal nest sites. This may be a result of female squirrels choosing relatively remote sites to avoid other female gray squirrels as well as red squirrels, which occur in more densely forested riparian areas. Thus, there may be different variables driving selection of natal nests than those associated with non-natal nest selection.

Recommendations

The western gray squirrel in Black Canyon Creek and the Methow Valley occur in a habitat that, without an oak component, is relatively unique. Because squirrels are reproducing successfully here without obtaining resources directly from humans and because oak habitats in Washington are declining, squirrel conservation in the Methow Valley seems especially important. Given the results of this study, we make the following recommendations:

1) Because this was a short-term study on one localized population, we recommend expanding observation of squirrel movements and habitat selection to other sites in the Methow Valley and the North Cascades. Topics for study could include selection of natal nests, foraging behavior, and juvenile dispersal patterns.
2) Managers should consider a broad survey of the squirrel's distribution in the North Cascades to improve upon our current knowledge of its range and designate areas for more focused study. This is particularly important given its conservation status as a threatened species in Washington. Hair snares provide an efficient method to determine the presence/absence of squirrels in a variety of sites. Snares have been used to successfully monitor red squirrels (*Sciurus vulgaris*) in Britain and western gray squirrels on Ft. Lewis (Gurnell et al. 2003, Freed et al. 2005).
3) Long-term monitoring of squirrel abundance in the North Cascades should be implemented as part of a statewide management plan. Assessing population

trends over time will facilitate a coordinated recovery strategy for the three existing populations of western gray squirrels in Washington.

4) Current GIS layers should be improved to allow for squirrel management and opportunities for population modeling on a landscape scale. Detailed spatial data are needed for variables influencing squirrels' habitat use such as basal area, mean dbh, tree species composition, tree density, patchiness of stands, and mistletoe infection.

5) Of the sites we studied, those with the largest mean dbh and basal area as well as a relatively diverse assemblage of tree species were most likely to be nest sites. The probability of a site being a nest site increased the most between 25-35 cm mean dbh and 15-35 m^2/ha basal area. In addition to preserving existing stands of large trees, managers should give priority to increasing the mean dbh and basal area of mixed species stands that are below 35 cm dbh and 35 m^2/ha basal area.

6) The structure created by mistletoe deformations seems to be enhancing nesting opportunities for this species, perhaps filling a gap created by the lack of oak cavities for natal dens. Further study is needed to determine more specific mistletoe preferences and its contribution to squirrels' reproductive success. This is especially important as mistletoe is detrimental to tree health and managers will need to balance the needs of squirrels with those of the forest as a whole. While TBV is a valuable parameter for initial quantification of the level of mistletoe infection, another supplemental measure should be developed to

qualify a mistletoe broom's suitability as a squirrel nest. Important parameters to consider are the size of the broom and its location within the crown. In the interim, when managing for mistletoe, managers should consider leaving trees with brooms that are large enough to accommodate a nesting squirrel (at least 20 cm diameter) occurring in the upper half of the crown. This is particularly important if an infected tree is larger than 22 cm dbh (the minimum observed nest-tree dbh) and occurs in a stand with high selection probability as a nest site.

7) Current Forest Service guidelines allow individuals to cut trees for firewood that are within 200 ft. of a road and more than 300 ft. from a creek. Given the results of our study, squirrels were nesting in trees that could be taken for firewood. For example, one female established a natal nest in a tree within 20 ft. of Black Canyon Creek Road. Thus, we recommend that in areas where squirrel concentrations are high, firewood collection be limited to trees that are less than 20 cm dbh.

8) Prescribed burning has become an accepted strategy for managing fuel loads and improving forest health. Burning in the Methow Valley occurs in the spring and in the fall when the ground is relatively moist and fires are more controllable. Long-term results of prescribed burning could be beneficial to squirrels by promoting stands of mature, fire-adapted pine that provide nesting opportunities as well as seed and hypogeous fungi, two important food sources. In the short-term, however, burning during the breeding season could have negative effects on squirrels' reproduction, as females with young may be

unable to escape a fire. For this reason, prescribed burns should be scheduled during the fall, outside of the breeding season, unless it is clear than squirrels are not present.

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