The Journal of Wildlife Management 82(7):1478–1490; 2018; DOI: 10.1002/jwmg.21499

Research Article

Western Gray Squirrel Resource Selection Related to Fire Fuel Management

KATHRYN D. STUART,[1] *Wildlife Science Group, School of Environmental and Forest Sciences, University of Washington, Box 352100, Seattle, WA 98195, USA*

W. MATTHEW VANDER HAEGEN, *Washington Department of Fish and Wildlife, 600 Capitol Way N, Olympia, WA 98501, USA*

KURT J. JENKINS, *U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, 600 East Park Avenue, Port Angeles, WA 98362, USA*

ILAI N. KEREN, *Washington Department of Fish and Wildlife, 600 Capitol Way N, Olympia, WA 98501, USA*

STEPHEN D. WEST, *Wildlife Science Group, School of Environmental and Forest Sciences, University of Washington, Box 352100, Seattle, WA 98195, USA*

ABSTRACT One of 3 populations of the state-threatened western gray squirrel (*Sciurus griseus*) in Washington occurs in the northern Cascade Range (i.e., North Cascades), where long-term fire suppression has increased the risk of catastrophic wildfire. Land management agencies throughout this region have implemented fire fuel reduction programs that alter squirrel habitat and may affect their populations. From April 2008 to September 2011, we investigated resource selection of 38 radio-collared western gray squirrels at 2 study sites in the North Cascades following fire fuel management activities including mechanical thinning and prescribed burning. We developed conditional logistic models to examine resource selection at 3 spatial scales: nest trees, nest sites, and core areas within home ranges. The odds of a squirrel selecting a tree for nesting increased with dwarf mistletoe (*Arceuthobium* spp.) presence, greater number of surrounding trees with interlocking branches, and tree size. Squirrels selected nest sites that had greater canopy cover, tree connectivity, and presence of dwarf mistletoe than available, unused sites. Core-use areas within home ranges had greater canopy cover, a greater number of tree species, and trees with higher live crowns compared to low-use areas. Our results indicate that fire fuel treatments may negatively affect western gray squirrel habitat across multiple spatial scales. Most variables that were positively related to habitat selection are specifically targeted for reduction in fire fuel management plans and were lower in sampled treated areas compared to untreated areas within the study sites. Key considerations in designing fuel reduction programs that benefit both squirrel habitat conservation and fire fuel management include maintaining forest patches with suitable canopy cover and connectivity, retaining large trees of a mix of species, and allowing for mistletoe infection at a reduced rate.

KEY WORDS Cascades Range, fuels management, resource selection, *Sciurus griseus*, threatened species, Washington, western gray squirrel, wildfire.

Wildlife populations are influenced by natural disturbances. On the eastern slopes of the northern Cascade Range (i.e., North Cascades), Washington, USA, wildfire is the dominant natural disturbance that has shaped the landscape (Wright and Heinselman 1973). In response to several large-scale, high-intensity forest fires in the early 1900s, natural resource managers enforced a policy of fire suppression from 1910 until the late 1960s that excluded and quickly contained all forest fires when possible (Pyne 1982). The absence of wildfire significantly changed the structure of forest stands in many areas of the North Cascades; species composition changed from ponderosa pine (*Pinus ponderosa*) dominant to mixed conifer or Douglas-fir (*Pseudotsuga menziesii*) dominant, tree density increased and tree diameters decreased, dead woody debris accumulated, and forest diseases became more prevalent, particularly dwarf mistletoe infection (*Arceuthobium douglasii* in Douglas fir and *A. campylopodum* in ponderosa pine; Wright and Agee 2004). Dwarf mistletoe derives water and nutrients from host trees, which respond to the higher demand for photosynthesis with increased branching. These distorted structures, known as mistletoe brooms, may provide a fuel ladder, drawing flames higher into the canopy and increasing fire intensity and spread (Hadfield et al. 2000, Beatty and Mathiasen 2003). An increase in fuels has facilitated an increase in the intensity, scale, and frequency of wildfires in recent years (Everett et al. 2000, Brown et al. 2004, Hessburg et al. 2005).

Over the last 2 decades, land managers in the North Cascades have implemented silvicultural practices designed

Received: 18 April 2017; Accepted: 20 April 2018

[1]*E-mail: kshipe@u.washington.edu*

to restore natural fire regimes and forest structure and reduce the probability of high-intensity stand-replacing wildfire by reducing the accumulation of fuels and increasing tree vigor and resistance to fire. Fire fuel reduction treatments practiced throughout the region include prescribed burning, mechanical thinning, and removal of mistletoe brooms and ladder fuels. Common management goals are to protect human life and property, maintain late-successional forest structure and wildlife habitat, and restore natural fire regimes (U.S. Department of the Interior National Park Service [USDI] 1995; U.S. Department of Agriculture [USDA] Okanogan-Wenatchee National Forest 2000, 2012). Because fire fuel treatments modify stand structure and composition, they also have the potential to affect habitats and resource selection patterns of threatened populations of forest wildlife including the western gray squirrel (*Sciurus griseus*).

The Washington Department of Fish and Wildlife (WDFW) listed the western gray squirrel as a threatened species in 1993 (Linders and Stinson 2007). Populations of western gray squirrels have declined in range and number and now are limited to 3 geographically isolated areas in Washington: the southern Puget Trough in western Washington, the southern Cascades Range, and the North Cascades (Fig. 1). Causes for decline over the past century

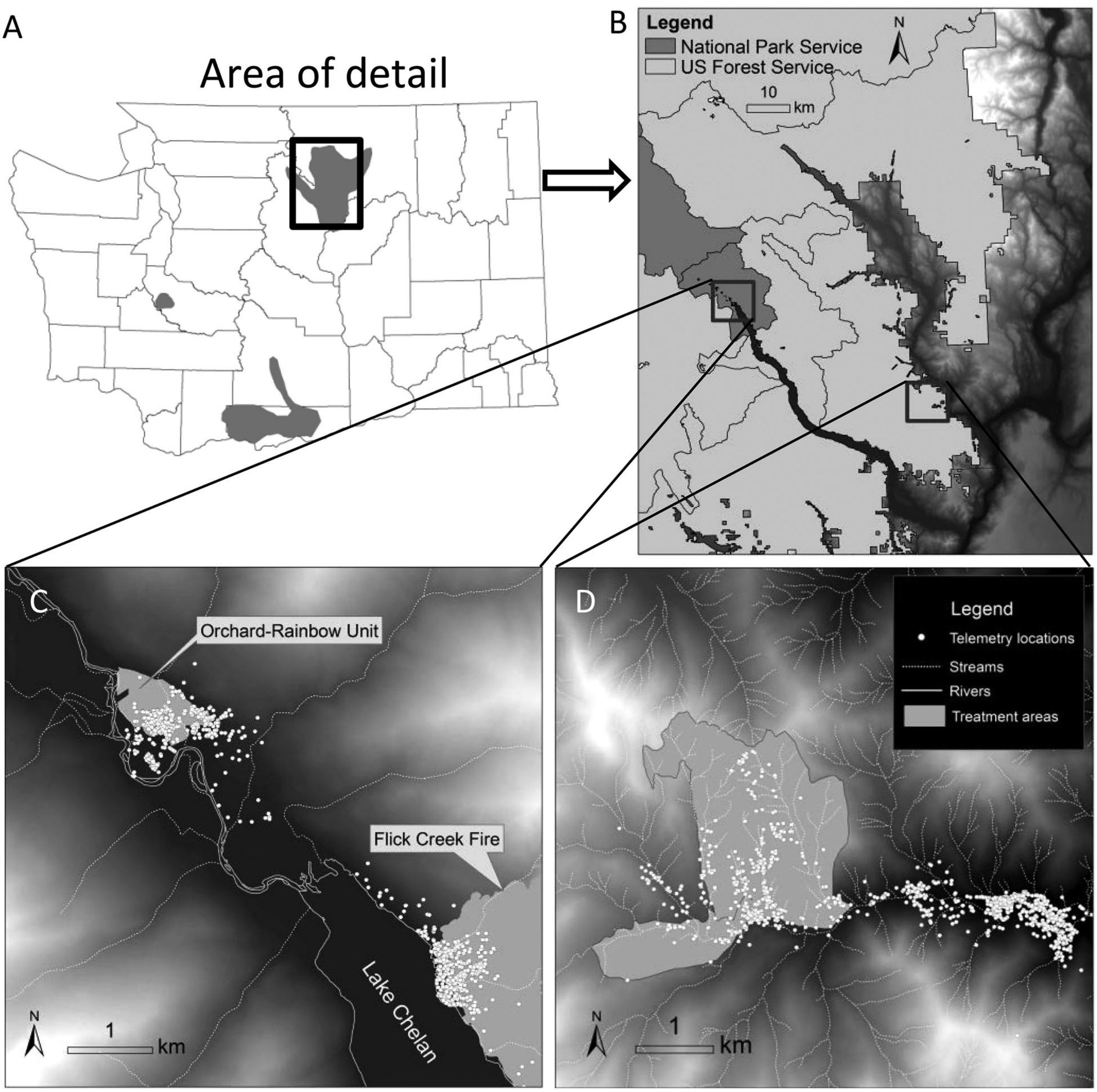

Figure 1. Study sites for research (Apr 2008–Aug 2011) on effects of fire fuel treatments on resource use by western gray squirrels were in the northernmost of 3 populations (indicated by shaded polygons) in Washington, USA (A; unshaded polygons depict county boundaries). Study sites were located in the North Cascades Recovery Area for the species (Linders and Stinson 2007), an area comprised mostly of federal lands (B). The Stehekin study area (C) was located at the northern end of Lake Chelan and had 2 treatment areas; the Squaw Creek study area (D) was located in the lower Methow River valley. We created the background layer for panels B–D from a digital elevation model with increasing elevation represented along a gradient from black (low elevation) to white (high elevation).

include habitat loss, predation, disease, vehicle strikes, overhunting, and potential competition with introduced squirrels (Linders and Stinson 2007). Wildfire is a clear threat to western gray squirrel habitat in the 2 Cascade populations (Linders and Stinson 2007); in 2014 and 2015 >310,000 ha of forest burned in the North Cascades alone (Northwest Interagency Coordination Center 2014, 2015). Without active management there is substantial risk of wildfire eliminating suitable habitat for decades or longer; however, fire fuel reduction treatments have also been identified as a potential threat to tree squirrel habitat in dry forests of the North Cascades because they have the potential to reduce canopy cover, simplify species composition, and alter availability of some foods (Lehmkuhl et al. 2004). The North Cascades Recovery Area for western gray squirrels in Washington is made up largely of federal lands (Fig. 1; Linders and Stinson 2007); management actions applied to these extensive ownerships could have significant influence on the extent of suitable habitat on the landscape for critical activities including nesting.

Western gray squirrels build nests out of tree branches and other vegetation for shelter, resting, and reproduction. Nests used for resting are typically flat platforms, whereas natal nests and nests used during winter are generally spherical shelter nests (dreys). Cavities in the boles of trees also are used frequently for natal nests (Ingles 1947, Cross 1969, Gilman 1986) but may be less available in the North Cascades than in other regions (Gregory et al. 2010). Prior studies in the North Cascades indicated that western gray squirrels prefer to nest in large-diameter trees that have well-connected canopies and dwarf mistletoe deformations (Hamer et al. 2005, Gregory et al. 2010). Fire fuel reduction treatments decrease tree density, which allows remaining trees to increase in diameter over time, thus providing future nest trees. Reduced canopy connectivity in the years following treatment and removal of dwarf mistletoe brooms, however, could decrease availability of preferred nest trees for western gray squirrels. Previous research indicated that western gray squirrels nested predominantly in mistletoe brooms in the North Cascades and mistletoe presence was the dominant predictive variable for nest tree selection (Gregory et al. 2010). Structure of forest stands also may influence population dynamics of tree squirrels; recruitment of tassel-eared squirrels (*Sciurus aberti*) in ponderosa pine forests in Arizona was strongly and positively correlated with the number of interlocking canopy trees in the stand (Dodd et al. 2003).

Food resources for squirrels also may be altered by wildfire and fuel treatments. Western gray squirrels consume hypogeous fungi (truffles and false truffles), pine nuts, acorns, seeds, green vegetation, fruit, and insects (Cross 1969, Stienecker and Browning 1970, Byrne 1979). Low-intensity prescribed burning also removes understory features such as surface litter, log cover, and herbaceous plant and shrub cover all of which correlate strongly with growth of hypogeous fungi (Trappe et al. 2009). Lower truffle diversity has been documented in thinned versus legacy forests (Carey et al. 2002), and lower species richness and biomass of truffles has been linked to simplification of stand composition and structure, a common management goal of fire fuel reductions (Lehmkuhl et al. 2004). Removal of mast-producing shrubs also could reduce a supplemental food resource. Prescriptions that reduce basal area and stem density of stands, however, may increase seed production in ponderosa pine (Krannitz and Duralia 2004), providing increased food resources in cone production years. In Arizona, tassel-eared squirrels exploited cone crops in areas where cone production appeared to have been promoted through forest thinning (Dodd et al. 2003).

Fire fuel reduction treatments also may increase vulnerability of squirrels to predation. Known or suspected predators of the western gray squirrel in Washington include the northern goshawk (*Accipiter gentilis*), red-tailed hawk (*Buteo jamaicensis*), golden eagle (*Aquila chrysaetos*), great horned owl (*Bubo virginianus*), weasels (*Mustela* spp.), martens (*Martes americana*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*; Carraway and Verts 1994, Vander Haegen et al. 2013). Removal of mistletoe brooms and reduced canopy cover associated with fire fuel reduction treatments could make squirrels more visible to predators in fire-fuel-treated areas. Decreased connectivity of canopy trees impedes traveling and foraging by flying squirrels (*Glaucomys sabrinus*; Carey 2000, 2001) and could similarly restrict arboreal travel by western gray squirrels. Removal of ladder fuels leading to an increase in the average height to the lowest live crown also could increase vulnerability to predation for squirrels climbing trees.

The purpose of this study was to investigate multiscalar habitat relationships of western gray squirrels to define habitat needs of the species in landscapes managed for fire fuel reduction and provide information needed to integrate wildlife habitat conservation and fire fuel management objectives. Our objectives were to identify patterns of western gray squirrel nest tree and nest site selection in landscapes that had been mechanically thinned and or burned by prescription or wildfire within the past 5 years, and evaluate differences in habitat characteristics between western gray squirrel core- and low-use areas in fire-fuel-treated landscapes. We predicted that nest tree and nest site characteristics would be similar to those documented in other parts of the species' range and that fuel reduction treatments would be detrimental to squirrel habitat in the short term by reducing trees and structures used for nesting security such as canopy cover, mistletoe brooms, and canopy connectivity. We predicted core area characteristics would be different from nest tree and nest site characteristics and would include additional variables more descriptive of foraging needs or security from predators.

STUDY AREA

We studied resource selection by western gray squirrels at 2 study sites in the North Cascades in north-central Washington State, USA: the Stehekin Valley (i.e., Stehekin), part of the Lake Chelan National Recreation Area of the North Cascades National Park Service Complex, and the Squaw Creek drainage (i.e., Squaw Creek) in the Methow

Valley, part of the Okanogan-Wenatchee National Forest from April 2008–August 2011 (Fig. 1). Both study sites were dominated by mixed conifer and deciduous forests composed primarily of Douglas-fir and ponderosa pine, with lesser amounts of lodgepole pine (*Pinus contorta*), black cottonwood (*Populus trichocarpa*), bigleaf maple (*Acer macrophyllum*), and trembling aspen (*Populus tremuloides*). Other dominant fauna included the red squirrel (*Tamiasciurus hudsonicus*), Douglas squirrel (*Tamiasciurus douglasii*), yellow-pine chipmunk (*Tamias amoenus*), marten, bobcat, coyote, northern goshawk, great horned owl, mule deer (*Odocoileus hemionus*), and black bear (*Ursus americanus*).

Elevations ranged from 348 m to 1,060 m. Summers were hot and dry and winters were cool and wet with temperatures ranging from -20°C to 40°C and average annual precipitation of 50 cm (2005–2010 National Climatic Data Center National Oceanic and Atmospheric Administration Climatological Data). Fire fuel management, involving stand thinning and prescribed fire, was a high priority of land management agencies at both sites (USDI 1995; USDA Okanogan-Wenatchee National Forest 2000, 2012).

Each study site included areas treated for fire fuel reduction (Fig. 1). The Orchard-Rainbow Unit in Stehekin (48-ha) was thinned and burned under a step-wise prescription across small spatial scales (~3–10 ha) at approximate 2-year intervals starting in 1993 as part of the Lake Chelan National Recreation Area Fire Fuel Reduction Area. The entire unit received light thinning between 2009 and 2012 and 2 sub-units received large-diameter thinning in 2001. Prescribed burns in this area all were low-intensity fires (USDI 2017). The Stehekin study area also included an approximately 690-ha area that was repeatedly thinned for fuel reduction and hazard tree removal starting in 1995 and naturally burned at mostly (44%) moderate intensity in the Flick Creek fire of 2006 (U.S. Geological Survey [USGS] 2017). Within the Squaw Creek study area, the 558-ha East Douglas unit of the Hungry Hunter Ecosystem Management Project was prescribe-burned at low intensity and several sub-units also were thinned as part of a timber sale from 2006 to 2008 (M. M. Trebon, U. S. Forest Service, personal communication; Figs. 1 and 2). Management objectives for treatment areas at both study sites were to reduce stand density (number of trees/acre), alter species composition towards more fire-tolerant species (i.e., ponderosa pine), reduce fuel loads, and reduce susceptibility to insects and disease, including removal or pruning of mistletoe-infected trees (USDI 1995; USDA Okanogan-Wenatchee National Forest 2000, 2012).

Analysis areas for both Stehekin and Squaw Creek were delineated by a 500-m buffer around all telemetry locations of radio-collared squirrels, consistent with methods used in previous studies (Gregory 2005). In Stehekin, we limited the 500-m buffer to the northwestern and northeastern side of Lake Chelan because there were no records of western gray squirrels on the south side of Lake Chelan within the study area extent (WDFW Wildlife System Data Management database). The Stehekin study area was 3,468 ha; Squaw Creek was 5,773 ha. Fire fuel treatment areas covered 37.4% and 17.8% of the Stehekin and Squaw Creek study areas, respectively.

METHODS

Between April 2008 and September 2011, we trapped squirrels using wire mesh $15 \times 15 \times 48$-cm live traps (Tomahawk Live Trap, Hazelhurst, WI, USA). We spaced traps between 50 m and 80 m apart along transects near and between areas where squirrels or signs of their presence were observed (e.g., observations by study area residents, foraging remains, presence of nests). Each transect generally included 10–15 traps. We focused trapping in treated areas to address study objectives but also placed transects in adjacent untreated control areas. We placed 4–7 transects in treated and untreated areas at each study site. Trapping sessions of 3 to 6 days occurred every 1 to 3 months at each study area. We baited traps with whole English walnuts and wired them open for a pre-baiting period. Trapping began when bait was missing from approximately half of the traps, which took 1 to 4 weeks of pre-baiting on average. We opened traps just prior to sunrise and checked them every 2 hours. Trapping records showed high site fidelity of squirrels, and the proportion of recaptures to new captures suggested we had trapped most squirrels at each site during the study.

We processed captured animals in a handling bag (Koprowski 2002) modified with an additional ventral opening. We weighed, sexed, and marked squirrels with uniquely numbered ear tags (model 1005-3, National Band and Tag, Newport, KY, USA) and fitted most with radio-collars (model SC-2C, Holohil Systems, Carp, Ontario, Canada). Radio-collars weighed approximately 15 g and consisted of a metal cable protected with a thick plastic coating and covered with plastic tubing to prevent abrasion to the squirrel. We only fit squirrels weighing $\geq$600 g with radio-collars. All methods followed recommendations of the American Society of Mammalogists (Sikes et al. 2016) and were approved by the University of Washington Institutional Animal Care and Use Committee (IACUC; protocol number 2479-29).

We located radio-collared squirrels with ground-based homing techniques (White and Garrott 1990) using 2-element, hand-held directional antennas and portable receivers (Telonics, Mesa, AZ, USA). We assessed activity of each squirrel based on the consistency of its telemetry signal prior to homing in on its location; changes in amplitude indicated active squirrels, whereas consistent amplitude for 3 minutes indicated inactive squirrels (G. R. Orth, WDFW, personal communication). We discontinued tracking if signal strength decreased abruptly >1 time during pursuit, indicating the animal was running from the observer and movements were being influenced. We tracked squirrels to the tree or location on the ground and confirmed locations visually when possible. When tracking an inactive squirrel to a tree, we visually searched the tree for nests with binoculars. We recorded Universal Transverse Mercator (UTM; North American Datum 1983) coordinates on hand-held global positioning system units and plotted them using a geographic information system (GIS: Environmental Systems Research Institute, Redlands, CA, USA).

We located squirrels on average 3–6 days/week, 1–3 times each day. To ensure independence between observations (White and Garrott 1990, Swihart and Slade 1997, Otis and White 1999), we spaced relocations across the diurnal period with a minimum separation of 2 hours between fixes, a period adequate for a squirrel to traverse its home range (Linders et al. 2004). We located all squirrels with approximately equal frequency.

Habitat Sampling

We examined resource selection by western gray squirrels at nest trees, nest sites, and core areas within the home range. Nest trees contained nests that we documented as used by a radio-collared squirrel >1 time (to increase representation of nests used by squirrels repetitively); we defined nest sites as that portion of the stand within 25.25 m (0.2 ha) of a nest tree (Gregory et al. 2010). We calculated home ranges of squirrels that had a minimum of 30 locations using a 99% fixed-kernel estimator (Worten 1989) and Hawth's Analysis Tools for GIS (Beyer 2004). We used the bivariate plug-in smoothing parameter calculated with package ks (Duong 2012) in R version 2.7.2 (R Development Core Team 2011). We removed repeated observations in the same nest to reduce spatial autocorrelation. We defined core areas as the region within the 25% fixed-kernel contour and low-use areas as the region between the 75% and 99% fixed-kernel contours. We selected these contours to maximize potential differences in squirrel habitat use while allowing adequate space for habitat plots and for consistency with concurrent research studies (Johnston 2013). We examined core area selection only for females because they provide potentially more useful information on habitat selection. Females have smaller home ranges than males and exhibit territoriality; the larger home ranges of males overlap and contain more habitat of potentially lower quality (Linders et al. 2004, Gregory 2005, Vander Haegen et al. 2005).

Nest tree selection.—Within a 0.2-ha plot centered around the nest tree, we randomly selected 8 non-nest trees for comparison using the procedure described by Skalski (1987), which corrects for bias toward the center of circular plots. Eight random trees per nest provided variability consistent with previous study (Gregory et al. 2010). We required non-nest trees to be ≥20 cm diameter at breast height (DBH), the minimum DBH of nest trees documented in the North Cascades (Gregory et al. 2010). For each nest tree and random tree, we measured DBH, height, and height to lowest live crown (LLC). We recorded tree species, which we reduced to 3 categories representing the most abundant species across sites (Douglas-fir, ponderosa pine, and other) and whether mistletoe brooms were present or absent. We categorized tree condition based on percent live canopy: 0–50% live, 51–75% live, or >75% live. We also categorized trees by relative height: taller than, equal to, or shorter than surrounding trees within the stand. We measured connectivity by counting the number of trees surrounding the focal tree with branches ≤1 m away, which is the estimated maximum distance a squirrel can jump between trees (Linders 2000). Whenever possible, we kept habitat measurements consistent with Gregory et al. (2010) to facilitate comparison. For each nest we recorded the type (drey, platform, or cavity), the aspect of the nest in relation to the tree trunk, the height of the nest from the ground, and the ratio of nest height to tree height. We measured all heights using an electronic clinometer (HEC, Haglöf, Sweden).

Nest site selection.—We compared habitat characteristics of used nest sites with available unused sites at a 1:1 ratio within the home range (99% fixed kernel) of the squirrel that used the nest most frequently. We centered nest site plots (0.2 ha) around nest trees as described above and centered unused plots around the tree (≥20 cm DBH; Gregory et al. 2010) that was closest to randomly generated coordinates within the squirrel's home range. Because the largest sampling area for vegetation was a 25-m radius circle, we required all unused nest sites be ≥50 m from nest trees. We averaged tree characteristics within plots to represent average tree conditions for the site (i.e., average tree height, average lowest live crown, average connectivity). We estimated average tree diameter as the quadratic mean diameter (QDBH). In a 0.04-ha plot nested within the 0.2-ha plot used for tree measurements (Gregory et al. 2010), we measured DBH, presence and absence of mistletoe, condition (live or dead), and species of all trees ≥5 cm DBH and from these data calculated basal area (m^2/ha) and the percent of mistletoe infection and live trees within stands. We summarized tree species composition at the site as ≥90% single-species conifer (ponderosa pine or Douglas-fir) or other mixture (e.g., mixed conifer, mixed conifer deciduous). Prior to analysis we reduced percent mistletoe and live trees to binary presence and absence variables to better fit their distributions and account for asymmetry in the data. We classified sites with mistletoe as 1 and sites without mistletoe as 0. We classified sites with and without 100% live trees as 1 and 0, respectively. We also tallied all coarse woody debris with ≥10-cm diameter in decay classes 1 and 2 following Maser et al. (1979). We estimated canopy cover using a spherical densitometer (Geographic Resource Solutions, Arcata, CA, USA) at 8 evenly spaced points along the plot radius including the 4 cardinal directions and northwest, northeast, southwest, and southeast. In a 0.01-ha plot nested within the 2 larger plots (Gregory et al. 2010), we used ocular estimation to categorize shrub cover (0%, >0–1%, 2–5%, 6–25%, 26–50%, 51–75%, >75%) and ground cover (>50% litter, >50% vegetation, or litter = vegetation). We also tallied the number of tree and shrub species within each 0.01-ha plot. We trained observers using known cover classes to enhance consistency.

Core area selection.—At the scale of the squirrel home range, we randomly selected 9 plots per squirrel for vegetation sampling: 3 in core and 6 in low-use areas on average. Vegetation sampling methods for core and low-use areas followed the same protocol as for nest sites. We sampled more habitat plots in low-use areas because of the larger area and potential greater variability on the range perimeter. We combined core and low-use areas with a high degree (>50%) of overlap between squirrels and randomly selected habitat plots from pooled kernels. To account for repeated use of some vegetation plots to represent >1 individual squirrel, we employed a bootstrap procedure (described below). Because we removed repeated observations of squirrels in the same nest prior to home range calculation, core area analysis was more representative of squirrel habitat requirements including foraging and security from predators.

Statistical Analysis

To identify variables associated with western gray squirrel nest tree, nest site, and core area selection we fit conditional logistic regression models with package survival (Therneau 2015) in R version 3.1.3 (R Development Core Team 2011) and evaluated them using an information-theoretic approach (Burnham and Anderson 2002). Conditional logistic regression takes into account the matched case-control structure of our habitat sampling (Hosmer and Lemeshow 2015); we stratified matched nest and available trees by nest site, we stratified matched nest and available sites and core and low-use areas by squirrel home range.

To derive appropriate estimates of regression and variance parameters for core area models, we composed a hierarchical, non-parametric bootstrap routine (Efron 1979, Efron and Tibshirani, 1993). We strategically re-sampled the data with and without replacement at different levels to replicate the complex hierarchical dependencies (Ren et al. 2010). At every iteration we randomly sampled 85 core area plots (cases), with replacement, and then randomly sampled an individual squirrel, without replacement, conditional on each case (because some plots were attributed to >1 squirrel). Then, conditional on each squirrel, we randomly sampled a low-use-area plot (control) for a final boot sample of 170 balanced, matched case-control plots with no missing data or overlap. The first step in our routine retained the original contribution of individual females to the model via the proportions of available cases in the sample, whereas steps 2 and 3 ensured there was no ambiguity in the assignment of a plot to case, control, or strata with a boot sample size the same as the original. Preliminary trials indicated we achieved convergence with 1,200 iterations.

We created sets of *a priori* candidate models for nest tree, nest site, and core area analyses (Tables 1–3) based on previous work in the North Cascades (Gregory 2005, Hamer et al. 2005, Gregory et al. 2010), observations from a pilot study conducted in 2008, and variables of interest to natural resource managers. Model sets were similar across all scales to facilitate comparisons. At each scale, we included a model set based on the highest ranked models describing nest tree and nest site selection in the North Cascades (Gregory et al. 2010). We also included fuel treatment and wildfire effects model sets based on observed differences at sampled fire-fuel-treated and untreated stands within our study areas (Stuart 2012; Table S1, available online in Supporting Information), and variables that were explicitly targeted in management objectives for treatment areas. We evaluated a global model including all predictor variables at each scale. Base models for comparison at the scale of the nest tree described tree structure. Additional model sets at the scale of the nest site and core area included variables that influence the ability of a stand to produce tree seeds, truffles, and shrub-based foods (foraging; Krannitz and Duralia 2004, Lehmkuhl et al. 2004, Trappe et al. 2009), and variables related to concealment from avian predators and facilitation of escape from mammalian predators hunting squirrels on the ground (predator avoidance and security; Johnston 2013).

We screened for collinearity between predictor variables using correlation coefficients for continuous predictor pairs,

Table 1. *A priori* models used to compare nest trees used by western gray squirrels ($n = 100$) to available unused trees ($n = 796$) within nest sites (0.02 ha; $n = 100$) in Chelan and Okanogan counties, Washington, USA (Apr 2008–Aug 2011). We present the log likelihood (Log(L)), number of parameters (K), difference in Akaike's Information Criterion values corrected for small sample size (ΔAIC_c), and Akaike weights (w_i) are listed. We derived test values with conditional logistic regression.

Model[a]	Model set	Log(L)	K	ΔAIC_c	w_i
3. Connect+DBH+mist	Gregory et al. (2010)	−159.346	3	0.00	0.690
5. Cond+connect	Fuel treatment and wildfire effects	−161.339	2	1.98	0.256
6. Connect+DBH+LLC+mist	Fuel treatment and wildfire effects	−161.112	4	5.53	0.043
16. Cond+connect+DBH+LLC+mist+RHt+Spp	Global	−159.653	7	8.61	0.009
1. Cond+DBH+mist+Spp	Gregory et al. (2010)	−165.773	4	14.85	0.000
2. Cond+DBH+LLC+mist+Spp	Gregory et al. (2010)	−165.195	5	15.70	0.000
4. Mist	Gregory et al. (2010)	−170.824	1	18.95	0.000
11. Cond+connect+DBH+RHt+Spp	Tree relative to stand	−198.635	5	82.58	0.000
12. Cond+connect+DBH+LLC+RHt+Spp	Tree relative to stand	−198.562	6	84.43	0.000
8. Cond+DBH+Spp	Tree structure	−202.542	3	86.39	0.000
9. Cond+DBH+LLC+Spp	Tree structure	−202.457	4	88.22	0.000
15. Connect+Rht	Tree relative to stand	−205.253	2	89.81	0.000
13. Cond+connect+RHt+Spp	Tree relative to stand	−204.052	4	91.41	0.000
14. Cond+connect+LLC+RHt+Spp	Tree relative to stand	−203.959	5	93.22	0.000
7. Cond+connect+DBH+LLC+mist	Fuel treatment and wildfire effects	−208.853	5	103.01	0.000
10. Cond+LLC+Spp	Tree structure	−214.311	3	109.93	0.000

[a] Variables: cond, tree condition; connect, connectivity; DBH, diameter at breast height; LLC, lowest live crown; mist, mistletoe presence; RHt, relative tree height; Spp, tree species.

Table 2. *A priori* models used to compare nest sites (0.02 ha) used by western gray squirrels ($n = 100$) to available unused nest sites ($n = 100$) within home ranges ($n = 35$) in Chelan and Okanogan counties, Washington, USA (Apr 2008–Aug 2011). We present the log likelihood (Log(L)), number of parameters (K), difference in Akaike's Information Criterion values corrected for small sample size (ΔAIC_c), and Akaike weights (w_i). We derived test values with conditional logistic regression.

Model[a]	Model set	Log(L)	K	ΔAIC_c	w_i
13. CC+connect+mist	Predator avoidance and security	−71.928	3	0.00	0.587
3. Connect+mist+QDBH	Nest tree comparison	−72.887	3	1.92	0.225
11. BA+CC+connect+CWD+LLC+mist+QDBH	Fuel treatment and wildfire effects	−69.176	7	2.65	0.156
12. BA+CC+connect+CWD+live+LLC+mist	Fuel treatment and wildfire effects	−71.529	7	7.28	0.015
15. BA+CC+CntVeg+connect+CWD+GCov+live +LLC+mist +QDBH+shrub+tree	Global	−66.394	12	7.35	0.014
2. BA+mist+QDBH+tree	Gregory et al. (2010)	−77.516	4	13.20	0.001
5. Live+LLC+mist+QDBH+tree	Nest tree comparison	−77.418	5	15.03	0.000
4. Live+mist+QDBH+tree	Nest tree comparison	−78.924	4	16.01	0.000
9. BA+CC+connect+live	Fuel treatment and wildfire effects	−88.322	4	34.90	0.000
10. BA+CC+CntVeg+connect+CWD+live+shrub	Fuel treatment and wildfire effects	−87.746	7	39.68	0.000
1. BA+QDBH+tree	Gregory et al. (2010)	−93.588	3	43.32	0.000
14. Connect+CWD+GCov+LLC+shrub	Predator avoidance and security	−92.928	5	46.07	0.000
6. Live+QDBH+tree	Foraging	−95.377	3	46.90	0.000
8. CntVeg+CWD+GCov+live+QDBH+shrub+tree	Foraging	−95.161	7	54.62	0.000
7. CntVeg+CWD+GCov+shrub	Foraging	−98.824	4	55.84	0.000

[a] Variables: BA, basal area; CC, canopy cover; CntVeg, count of tree and shrub species; connect, average connectivity; CWD, coarse woody debris; GCov, vegetative cover; live, live trees; LLC, average lowest live crown; mist, mistletoe presence; QDBH, quadratic mean diameter; shrub, shrub cover; tree, tree species.

contingency tables with chi-square tests for categorical predictor pairs, and 1-way analysis of variance (ANOVA) with F-tests for continuous-categorical pairs. We removed tree height from the analyses because of collinearity ($r \geq 0.6$; $P \leq 0.001$) with LLC and QDBH.

We calculated Akaike's Information Criterion (AIC) values for all *a priori* models with the second-order bias adjustment for small sample size (AIC_c). We ranked the models by AIC_c values, calculated the differences (ΔAIC_c), and used their weights (w_i) to obtain the probability that each model was the best in the set. We considered models within 4 AIC_c units of the best model as competitive (Burnham and Anderson 2002) following Gregory et al. (2010). We averaged coefficients across all models and we derived odds ratios for parameter estimates. We evaluated the strength of predictor variables by examining parameter estimates and considered 95% confidence intervals that did not include zero to indicate a significant effect (Agresti 1990). In addition, we evaluated the relative importance of predictors by summing the weights of each model in which they were included to obtain their cumulative weight (Burnham and Anderson 2002).

In our examination of nest sites and core-use areas, we sampled 186 plots in untreated areas and 166 plots in treated areas. We compared characteristics between untreated and treated sites with 2 sample t-tests, Wilcoxon rank sum tests, and chi-square tests as appropriate (Table S1).

RESULTS

We captured 61 squirrels from 2008 to 2011: 24 in Stehekin and 37 at Squaw Creek. We collared 12 females and 10 males in Stehekin and 12 females and 12 males at Squaw Creek. Of

Table 3. *A priori* models used to compare core areas (upper 25% fixed-kernel contour; $n = 161$), and low-use areas (75–99% fixed-kernel contour; $n = 248$) within home ranges ($n = 37$) of western gray squirrels in Chelan and Okanogan counties, Washington, USA (Apr 2008–Aug 2011). We present the log likelihood Log(L), number of parameters (K), difference in Akaike's Information Criterion values corrected for small sample size (ΔAIC_c), and Akaike weights (w_i). We derived test values with conditional logistic regression.

Model[a]	Model set	Log(L)	K	ΔAIC_c	w_i
15. BA+CC+CntVeg+connect+CWD+GCov+live+ LLC+mist +QDBH+shrub+tree	Global	−67.797	12	0.00	0.807
12. BA+CC+connect+CWD+live+LLC+mist	Fuel treatment and wildfire effects	−75.099	7	4.61	0.081
11. BA+CC+connect+CWD+LLC+mist+QDBH	Fuel treatment and wildfire effects	−75.226	7	4.86	0.071
5. Live+LLC+mist+QDBH+tree	Nest tree comparison	−78.652	5	7.71	0.017
9. BA+CC+connect+live	Fuel treatment and wildfire effects	−80.116	4	8.64	0.011
10. BA+CC+CntVeg+connect+CWD+live+shrub	Fuel treatment and wildfire effects	−77.262	7	8.93	0.009
13. CC+connect+mist	Predator avoidance and security	−82.490	3	11.39	0.003
14. Connect+CWD+GCov+LLC+shrub	Predator avoidance and security	−81.065	5	12.54	0.002
1. BA+QDBH+tree	Gregory et al. (2010)	−85.393	3	17.19	0.000
2. BA+mist+QDBH+tree	Gregory et al. (2010)	−84.400	4	17.21	0.000
3. Connect+mist+QDBH	Nest tree comparison	−86.692	3	19.80	0.000
6. Live+QDBH+tree	Foraging	−87.128	3	20.66	0.000
4. Live+mist+QDBH+tree	Nest tree comparison	−86.138	4	20.68	0.000
8. CntVeg+CWD+GCov+live+QDBH+shrub+tree	Foraging	−83.990	7	22.39	0.000
7. CntVeg+CWD+GCov+shrub	Foraging	−91.250	4	30.91	0.000

[a] Variables: BA, basal area; CC, canopy cover; CntVeg, count of tree and shrub species; connect, average connectivity; CWD, coarse woody debris; GCov, vegetative cover; live, live trees; LLC, average lowest live crown; mist, mistletoe presence; QDBH, quadratic mean diameter; shrub, shrub cover; tree, tree species.

those, we accumulated >30 telemetry locations for 12 females and 5 males in Stehekin, and 11 females and 10 males in Squaw Creek, and used this data for resource selection analyses. We collected 1,690 locations of collared squirrels in Stehekin and 2,124 at Squaw Creek. We visually confirmed 22% of the locations in Stehekin and 44% at Squaw Creek. We identified another 57% percent of locations in Stehekin and 37% of locations at Squaw Creek to a single tree allowing accuracy within 5 m for 92% of locations at both study areas. The number of fixes used to calculate home range sizes ranged from 30 to 192. We tracked squirrels on average for 6 months (range = 3–17 months).

Nest Tree Selection

We located 54 nests in Stehekin and 118 nests at Squaw Creek. Twenty-five percent of all squirrel telemetry locations were at nests (Stehekin: 22%, $n = 409$; Squaw Creek: 29%, $n = 624$). We located squirrels in 68% of the nests >1 time (Stehekin: 72%; Squaw Creek: 63%). Individual nests were used by 2 ± 0.1 (SE) radio-collared squirrels on average (range = 1–9). Almost all nests were dreys or platforms (Stehekin: 76% drey, 22% platform, Squaw Creek: 80% drey, 19% platform). We identified only 1 cavity nest at each site; we did not observe juvenile squirrels at either nest to document these as natal dens. We positively identified 2 natal shelter nests (1 at each site) by presence of juvenile squirrels. In Stehekin 13% of the nests were located on the north side of the tree, 18% on the east side, 44% on the south side, and 24% on the west side. At Squaw Creek 19% of nests were on the north side of the tree, 25% on the east side, 38% on the south side, and 18% on the west side. Mean nest height was 18.2 ± 0.93 m in Stehekin and 14.5 ± 0.49 m at Squaw Creek. At both study sites most nests were located approximately halfway up the tree; nest-height-to-tree-height ratio was 0.50 ± 0.02 (range = 0.16–1) in Stehekin and 0.57 ± 0.01 (range = 0.21–0.84) at Squaw Creek. In Stehekin, we found most nests in Douglas-fir (77%) and ponderosa pine trees (20%); at Squaw Creek we found the same number of nests in Douglas-fir and ponderosa pine (each 42%). The 2 cavity nests were in a bigleaf maple and lodgepole pine in Stehekin and Squaw Creek, respectively. Both natal shelter nests were in Douglas-fir trees. We found 56% and 30% of nests in dwarf mistletoe brooms in Stehekin and Squaw Creek, respectively. Forty-seven percent of nest trees in Stehekin and 30% of nest trees at Squaw Creek had scorch marks showing evidence of recent wild or prescribed fire. We found 8 shelter nests in dead snags.

We measured habitat characteristics of 100 randomly selected nest trees and 796 available trees within 45 nest sites in Stehekin and 55 nest sites at Squaw Creek (see Table S2, available online in Supporting Information). The model with the greatest support was composed of the same variables that comprised the most highly supported model describing nest tree selection in the Black Canyon Creek drainage of the Methow Valley (Gregory et al. 2010). Nest trees, compared to available trees, were more likely to have dwarf mistletoe infection, greater connectivity, and larger DBH (Table 1). This model's weight was 2.7 times greater than the next best model, which described observed differences between fire-fuel-treated and untreated areas. Model-averaged coefficients in the best model were all significantly different from zero. The variables in the best model also were the strongest predictors of squirrel nest tree selection based on odds ratios (Table 4). Connectivity had the highest cumulative weight across all models (0.999), followed by mistletoe and DBH (both 0.744).

Nest Site Selection

Sixty-two percent of nest sites in Stehekin and 36% of nest sites at Squaw Creek occurred in areas where fuels had been treated or had burned in wildfire within the past 5 years. Three of 14 models of nest site selection were competitive (within 4 AIC_c units; Table 2; for habitat characteristics of used and available nest sites see Table S3, available online in Supporting Information). The highest-ranked model included canopy cover, connectivity, and mistletoe presence; all were greater at nest sites compared to available sites (Table 5). This model's weight was 2.6 times greater than the next best model. The 2 competing models also ranked highly for nest tree selection and core area selection (see below), providing additional evidence of the importance of these models and variables across scales of resource selection. Cumulative weights of model-averaged coefficients were 1.0, 0.999, and 0.773 for mistletoe presence, canopy connectivity, and canopy cover, respectively.

Core Area Selection

We used data from 103 core-area plots and 138 low-use plots (Stehekin: 63, 87; Squaw Creek: 40, 51) within the home

Table 4. Coefficients, 95% confidence intervals, and odds ratios for explanatory variables of western gray squirrel nest tree selection in Chelan and Okanogan County, Washington, USA (Apr 2008–Aug 2011) based on model-averaged coefficients.

Variable	Estimate	LCI	UCI	Odds ratio
Condition >75% live crown	−0.043	−1.459	1.373	0.958
Condition 50–75% live crown	−0.778	−1.797	0.240	0.459
Connectivity[a]	0.235	0.084	0.387	1.266
DBH[a]	0.020	0.007	0.034	1.021
Lowest live crown	0.005	−0.043	0.053	1.005
Mistletoe[a]	3.234	2.320	4.149	25.390
Relative height equal	−0.306	−0.908	0.296	0.737
Relative height shorter	−0.912	−1.867	0.043	0.402
Species other	−0.452	−1.230	0.326	0.636
Species ponderosa pine	−0.322	−0.953	0.309	0.725

[a] Significant result (i.e., CI does not include 0).

Table 5. Coefficients, 95% confidence intervals, and odds ratios for explanatory variables of western gray squirrel nest site selection in Chelan and Okanogan County, Washington, USA (Apr 2008–Aug 2011) based on model-averaged coefficients.

Variable	Estimate	LCI	UCI	Odds ratio
Basal area	−0.178	−0.850	0.494	0.837
Canopy cover[a]	2.212	0.371	4.053	9.136
Coarse woody debris	0.027	−0.072	0.126	1.027
Connectivity[a] (average)	0.393	0.065	0.722	1.482
Count understory species	−0.030	−0.281	0.221	0.970
Ground cover >50% vegetation	−0.519	−1.473	0.436	0.595
Ground cover litter = vegetation	−1.047	−2.349	0.254	0.351
Live canopy	0.095	−0.708	0.898	1.100
Lowest live crown (average)	−0.018	−0.139	0.103	0.982
Mistletoe[a]	2.381	1.445	3.318	10.818
QDBH[b]	0.033	−0.001	0.067	1.034
Shrub cover	0.000	−0.082	0.083	1.000
Trees	−0.753	−1.665	0.159	0.471

[a] Significant result (i.e., CI does not include 0).
[b] quadratic mean diameter.

ranges of 23 squirrels (Stehekin: 12, Squaw Creek 11) to analyze core area selection (for habitat characteristics of high- and low-use plots see Table S4, available online in Supporting Information). Of the candidate models only the fuel treatment and wildfire effects models had support with ΔAIC_c values <5, just outside the best model set (Table 3). Core areas were more likely to have greater canopy cover, higher average lowest live crown, and be located in mixed-conifer or mixed-conifer and deciduous rather than single-species conifer stands (Table 6). Because the global model ranked highest, cumulative weights of all model-averaged coefficients were high (range = 0.772–0.983).

Sixteen squirrels in Stehekin (11 female, 5 male), and 10 squirrels at Squaw Creek (4 female, 6 male) had home ranges encompassing fire-fuel-treated and untreated areas. All squirrels spent at least part of their time outside treated areas. In Stehekin, 1 female squirrel's home range was completely outside of fire-fuel-treated and burned areas; at Squaw Creek 6 females and 4 males had home ranges outside of the fire-fuel-treated area. Use of treated and untreated areas by squirrels provided an opportunity to compare stand characteristics between treated and untreated areas, recognizing that the comparison is constrained to those portions of treated stands used by squirrels.

Four females made extensive use of the fire fuel treatment areas in the Squaw Creek study area; however, only 1.4% of 280 telemetry locations for these 4 females occurred within thinning-treatment boundaries and no core areas (25% utilization distribution) intersected the thinning units (Fig. 2). Four females made extensive use of the Orchard-Rainbow fire fuel treatment area in Stehekin and 3 of these females also used the forest thinning units extensively. Of 389 telemetry locations used for these 4 females in Stehekin, 42% occurred within thinning treatment boundaries and core areas for 3 of 4 females intersected the thinning units (Fig. 2). Most telemetry locations and all core areas intersecting thinning units in Stehekin were in areas that received less thinning. Canopy cover and connectivity were lower in treated than untreated areas at both Squaw Creek-East Douglas ($P \leq 0.001$ for both variables), and the Orchard-Rainbow Unit in Stehekin ($P = 0.004$ and $P = 0.002$ for canopy cover and connectivity, respectively; Table S1).

Table 6. Coefficients, 95% confidence intervals, and odds ratios for explanatory variables of western gray squirrel core area selection in Chelan and Okanogan County, Washington, USA (Apr 2008–Aug 2011) based on model-averaged coefficients.

Variable	Estimate	LCI	UCI	Odds ratio
Basal area	−0.250	−1.293	0.756	0.779
Canopy cover[a]	3.670	1.162	6.760	39.252
Coarse woody debris	−0.049	−0.255	0.137	0.952
Connectivity (average)	0.195	−0.324	0.806	1.215
Count understory species	0.016	−0.277	0.327	1.016
Ground cover >50% vegetation	0.569	−0.409	1.695	1.766
Ground cover litter = vegetation	0.354	−1.097	2.034	1.425
Live canopy	−1.441	−4.538	1.435	0.237
Lowest live crown (average)[a]	0.135	0.004	0.300	1.145
Mistletoe	−0.305	−1.367	0.715	0.737
QDBH[b]	0.026	−0.014	0.065	1.026
Shrub cover	−0.007	−0.037	0.026	0.993
Trees[a]	−0.927	−1.884	−0.042	0.396

[a] Significant result (i.e., CI does not include 0).
[b] quadratic mean diameter.

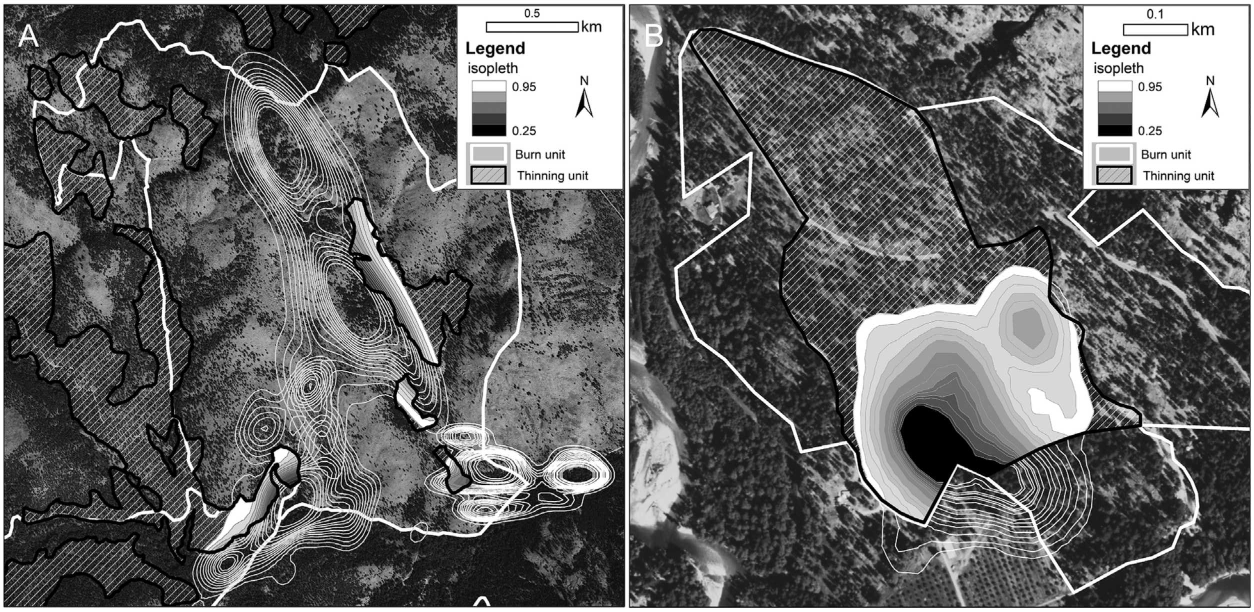

Figure 2. Intersection of fixed-kernel isopleths for representative female western gray squirrels with polygons depicting forest stands thinned as part of fire fuel treatments in (A) Squaw Creek (3 females shown), and (B) Stehekin Valley (1 female shown), Washington, USA, (Apr 2008–Aug 2011). Images show fixed-kernel isopleths and area of intersection with thinned stands, grading from low-use areas (95% isopleth) to core-use areas (25% isopleth), within larger units treated with prescribed burns.

Thinning treatments resulted in significantly lower canopy cover and connectivity at Squaw Creek than at the Orchard-Rainbow unit in Stehekin ($P \leq 0.001$ for both variables), which is reflected by differential squirrel use of thinned areas between study sites. Average canopy cover at sites we sampled in treated areas at Squaw Creek was $45 \pm 0.0\%$ with average connectivity of 1.5 ± 0.1 trees compared to $65 \pm 0.0\%$ and 3.0 ± 0.1 trees in Stehekin-Orchard-Rainbow unit (Table S1).

DISCUSSION

This is the first study to directly relate western gray squirrel habitat use to fire fuel reduction treatments and builds upon prior research on western gray squirrels in the North Cascades (Gregory 2005, Hamer et al. 2005, Gregory et al. 2010) by expanding the geographic range of inference and scale of resource selection. Our results indicate that fire fuel treatments reduce availability of habitat suitable to western gray squirrels across multiple spatial scales. Most variables that were positively related to habitat selection (canopy cover, canopy connectivity, mistletoe presence) are specifically targeted for reduction in fire fuel management plans, and many were lower in sampled, treated areas compared to untreated areas. The only variables expected to be affected through fire fuel reduction treatments in a positive way for western gray squirrels were tree diameter (QDBH) and lowest live crown (LLC) because thinning treatments generally remove smaller diameter trees (USDI 1995; USDA Okanogan-Wenatchee National Forest 2000, 2012) and ladder fuel removal increases average LLC. Likely changes to stand structure from fire fuel treatments, including a less complex and more open canopy, lower diversity in canopy tree species, reduced availability of mistletoe brooms, and a drier microclimate resulting in lower biomass and diversity of truffles, represented lower quality habitat for flying squirrels (lower density and recruitment) in the eastern Washington Cascades (Lehmkuhl et al. 2004, 2006). Our results suggest that similar changes resulting from fuel treatments also would decrease habitat quality for western gray squirrels.

Nest tree characteristics and selection by western gray squirrels at our 2 study sites in the North Cascades aligned with patterns observed previously in the Black Canyon Creek drainage of the Methow Valley (Gregory et al. 2010). Our study strengthens conclusions that dwarf mistletoe presence, canopy connectivity, and tree diameter have a strongly positive influence on western gray squirrel nest tree selection in the North Cascades. Trees with greater connectivity and DBH were selected by western gray squirrels for nesting throughout their range in Washington (Linders 2000, Gregory et al. 2010, Johnston 2013). Mistletoe presence was the dominant predictor variable whenever included in a model and mistletoe brooms were present in a higher proportion of nest trees than in available trees, consistent with Gregory et al. (2010). Mistletoe brooms appear to function as alternatives to cavities for denning in an area where suitable cavities are scarce (Gregory et al. 2010), as was previously concluded for flying squirrels in the North Cascades (Lehmkuhl et al. 2006). Mistletoe brooms frequently are used by wildlife for nesting, foraging, and resting and also could be used as hiding places from predators. Trees with mistletoe brooms were used more frequently by small mammals than trees without brooms in northeast Oregon (Parks et al. 1999) and northern Arizona (Garnett et al. 2004).

Bull et al. (2004) suggested that the type of mistletoe reduction treatment affects wildlife and that retaining patches of mistletoe-infected trees within treated stands may help maintain sufficient nesting and resting habitat for arboreal squirrels. Our results suggest an additional pruning strategy for mistletoe removal within individual trees that could reduce negative effects to squirrel habitat. Of the 66 mistletoe brooms we identified as containing a western gray squirrel nest across both study sites, only 10 (15%) were located in the bottom third of the tree. Limiting removal of mistletoe brooms to the lower third of the tree could accomplish both ladder fuel removal and retention of nesting and resting structures for western gray squirrels and other wildlife species.

Most of the same parameters that best described nest tree selection also were influential at the scale of the nest site, including stand mistletoe presence (a new variable measured with this study), and canopy connectivity. Canopy connectivity was the top discriminating variable for western gray squirrel nest site selection in the southern Puget Trough (Johnston 2013) indicating that this habitat feature is important for western gray squirrels through much of their range in Washington. The number of interlocking canopy trees also was a positive predictor of density, juvenile recruitment, and survival of tassel-eared squirrels in north-central Arizona (Dodd et al. 2006). Canopy cover was a strong predictor variable for both nest sites and core areas at our study sites and has been correlated with population density of northern flying squirrels in the North Cascades (Lehmkuhl et al. 2006). Fox squirrels (*Sciurus niger*) also were more likely to occur in areas with higher canopy cover in Florida (Greene and McCleery 2017). In Arizona, Mexican fox squirrels (*Sciurus nayaritensis chiricahuae*) fed more in forests with closed canopy cover and placed home ranges in areas with larger trees than random sites (Doumas and Koprowski 2013). Our second-ranked model for nest site selection was identical to our highest-ranked model for nest tree selection, indicating that squirrels may select nest sites that contain many potential nest trees. This is consistent with observations of spatial clustering of western gray squirrel nests at our study sites and in other areas (Linders 2000, Gregory et al. 2010, Johnston 2013). Squirrels with access to multiple nests within their home range may expend less energy while also reducing exposure to parasites and predation risk. The combination of variables related to concealment from avian predators fit patterns of nest site selection best. Twenty-five percent and 40% of observed mortalities of radio-collared squirrels at Stehekin and Squaw Creek, respectively, were attributed to avian predation (Stuart 2012). Avian predation was determined to be the likely proximate cause of death for ≥25% of 81 documented mortalities of radio-collared western gray squirrels in the South Cascades (Vander Haegen et al. 2013).

Modeling results of core area analyses did not entirely fit our predictions; some influential parameters for nest tree and nest site selection (canopy cover) also were significant at this scale. However, the high ranking of the global model likely reflects the broader resource needs of western gray squirrels, including foraging, predator escape, and nesting. Although parameters consistent with security from avian predators (canopy cover, connectivity, and mistletoe presence) were included in the fire fuel treatment models that had some support, the global model added the significant variable describing tree species composition. Greater number of tree species on a site likely would provide a greater diversity of foods for squirrels including tree seeds and hypogeous fungi (Lehmkuhl et al. 2004, Trappe et al. 2009).

Large-scale wildfires have occurred with increasing frequency in dry forest landscapes in the North Cascades over the last 2 decades (Everett et al. 2000, Hessburg et al. 2005) and fire fuel reduction will continue to be an important tool to reduce the frequency or extent of stand-replacing wildfires. Our retrospective study lacked the power of an experimental approach but identified stand characteristics important to western gray squirrels that can be incorporated into future adaptive management studies of fire fuel treatments (Lehmkuhl et al. 2006). Our results corroborate the general consensus across regions and species for the importance of maintaining canopy cover, tree connectivity, and large trees for arboreal squirrels (Dodd et al. 2006, Lehmkuhl et al. 2006, Prather et al. 2006, Linders et al. 2010). Size and density of patches required to maintain habitat for western gray squirrels and other sciurids on the landscape has not been well quantified and will vary with the scale considered; estimates range from 25% of a female's home range (2 patches >2.5 ha for every 20 ha; Linders et al. 2010) to a patch size of 160 ha representing use areas for multiple animals (Prather et al. 2006). In both of these scenarios, the managed forest matrix would need to maintain suitable tree density to provide secondary foraging habitat and connectivity among patches (Lehmkuhl et al. 2006, Linders et al. 2010). Retaining large (>40 cm DBH) overstory trees in more heavily thinned stands within the matrix would preserve some foraging benefits and may promote use by squirrels as the stand vegetation responds to the treatment (Prather et al. 2006).

Current thought on restoration in fire-frequent forests like those in the North Cascades includes structural and spatial components, recognizing the need to consider historical patterns of patchiness and the range of natural variation (Allen et al. 2002, Wright and Agee 2004, Larson and Churchill 2012). Incorporating spatial patchiness in forest restoration projects may be critical for attaining resiliency to future fires (Churchill et al. 2013) and could increase the value of these restored forests to tree squirrels. Additional research examining resource selection before and after fire fuel reduction treatments could better evaluate response by western gray squirrels to various patch sizes within the range indicated above. An effective experimental design would overlay randomly assigned treatments on stands within existing squirrel home ranges in a before-after-control-impact design (Bernstein and Zalinksi 1983). It also would be valuable to monitor resource selection beyond 5 years post-treatment to evaluate longer term effects of thinning and prescribed burning on squirrel habitat, particularly food resources, as understory features and stand structure changes over time.

MANAGEMENT IMPLICATIONS

Fire fuel reduction treatments are essential for preventing large-scale stand-replacing wildfires, restoring natural ecological processes, and protecting lives and habitats of humans and wildlife. Fire fuel reduction treatments will benefit squirrels when they help achieve these goals while also retaining stands with suitable habitat structure on the landscape. Key considerations in designing fuel reduction programs that benefit tree squirrel habitat conservation and fire fuel management include maintaining forest patches with suitable canopy cover and connectivity, retaining large trees of a mix of species, and allowing for mistletoe infection at a reduced rate. Our results support a growing body of literature based on multiple species of tree squirrels that preserving patches of forest with these characteristics could provide habitat for western gray squirrels (and other tree squirrels) while reducing overall fire risk across the landscape.

ACKNOWLEDGMENTS

We thank R. C. Kuntz, D. Rains, B. Rains, J. Rohrer, D. P. Volsen, A. Zink, National Park Service staff in Stehekin, and the Washington Department of Fish and Wildlife for logistical support, field housing, and transportation. We thank private landowners for access to their lands for research. Valuable field help was provided by R. E. Agbalog, A. M. England, D. J. Farrar, A. N. Johnston, K. M. Kranzler, A. M. Lee, K. E. Lorberau, M. McDonald, G. R. Orth, C. C. Shipe, K. C. Shipe, C. R. Shores, M. S. Stacey, and C. Stackhouse. We thank J. F. Lehmkuhl for providing peer review of the manuscript. Funding was provided by the United States Geological Survey (Natural Resources Preservation Program), the University of Washington, the Washington Chapter of the Wildlife Society, the Washington Department of Fish and Wildlife Aquatic Lands Enhancement Account, and Seattle City Light's Skagit Wildlife Research Grant. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. Data for this study is available in Stuart and Jenkins (2017).

LITERATURE CITED

Agresti, A. 1990. Categorical data analysis. Wiley and Sons, New York, New York, USA.

Allen, C. D., M. Savage, D. A. Falk, K. F. Suckling, T. W. Swetnam, T. Schulke, P. B. Stacey, P. Morgan, M. Hoffman, and J. T. Klingel. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. Ecological Applications 12:1418–1433.

Beatty, J. S., and R. L. Mathiasen. 2003. Dwarf mistletoes of ponderosa pine. USDA Forest Service, University of Minnesota, Minneapolis, Minnesota, USA.

Bernstein, B. B., and J. Zalinksi. 1983. An optimum sampling design and power tests for environmental biologists. Journal of Environmental Management 16:35–43.

Beyer, H. L. 2004. Hawth's Analysis Tools for ArcGIS. http://www.spatialecology.com/htools. Accessed 10 Jan 2009.

Brown, R. T., J. K. Agee, and J. F. Franklin. 2004. Forest restoration and fire: principles in the context of place. Conservation Biology 18:903–912.

Bull, E. L., T. W. Heater, and A. Youngblood. 2004. Arboreal squirrel response to silvicultural treatments for dwarf mistletoe control in northeastern Oregon. Western Journal of American Forestry 19:133–141.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodal inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.

Byrne, S. 1979. The distribution and ecology of the non-native tree squirrels *Sciurus carolinensis* and *Sciurus niger* in northern California. Dissertation, University of California, Berkley, USA.

Carey, A. B. 2000. Effects of new forest management strategies on squirrel populations. Ecological Applications 10:248–257.

Carey, A. B. 2001. Experimental manipulation of spatial heterogeneity in Douglas-fir forests: effects on squirrels. Forest Ecology and Management 152:13–20.

Carey, A. B., W. Colgan, III., J. M. Trappe, and R. Molina. 2002. Effects of forest management on truffle abundance and squirrel diets. Northwest Science 76:148–157.

Carraway, L. N., and B. J. Verts. 1994. *Sciurus griseus*. Mammalian Species Account No. 474:1–7.

Churchill, D. J., A. J. Larson, M. C. Dahlgreen, J. F. Franklin, P. F. Hessburg, and J. A. Lutz. 2013. Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. Forest Ecology and Management 291:442–457.

Cross, S. P. 1969. Behavioral aspects of western gray squirrel ecology. Dissertation, University of Arizona, Tucson, USA.

Dodd, N. L., R. E. Schweinsburg, and S. Boe. 2006. Landscape-scale forest habitat relationships to tassel-eared squirrel populations: implications for ponderosa pine forest restoration. Restoration Ecology 14:537–547.

Dodd, N. L., J. S. States, and S. S. Rosenstock. 2003. Tassel-eared squirrel population, habitat condition, and dietary relationships in north-central Arizona. Journal of Wildlife Management 67:622–633.

Doumas, S. L., and J. L. Koprowski. 2013. Return of fire as a restoration tool: long-term effects of burn severity on habitat use by Mexican fox squirrels. Restoration Ecology 21:133–139.

Duong, T. 2012. ks: Kernel smoothing. R package version 1.8.6. http://CRAN.R-project.org/package=ks. Accessed 21 Sep 2011.

Efron, B. 1979. Bootstrap methods: another look at the jackknife. Annals of Statistics 7:1–26.

Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman & Hall, New York, New York, USA.

Everett, R. L., R. Schellhaas, D. Keenum, D. Spurbeck, and P. Ohlson. 2000. Fire history in the ponderosa pine and Douglas-fir forests on the east slopes of the Washington Cascades. Forest Ecology and Management 129:207–225.

Garnett, G. N., R. L. Mathiasen, and C. L. Chambers. 2004. A comparison of wildlife use in broomed and unbroomed ponderosa pine trees in northern Arizona. Western Journal of Applied Forestry 19:42–46.

Gilman, K. N. 1986. The western gray squirrel (*Sciuris griseus*), its summer home range, activity times, and habitat usage in northern California. Thesis, California State University, Sacramento, California, USA.

Greene, D. U., and R. A. McCleery. 2017. Multi-scale responses of fox squirrels to land-use changes in Florida: utilization mimics historic pine savannas. Forest Ecology and Management 391:42–51.

Gregory, S. C. 2005. Seasonal movements and nest site selection of the western gray squirrel (*Sciurus griseus*) in the Methow River watershed. Thesis, University of Washington, Seattle, USA.

Gregory, S. C., W. M. Vander Haegen, W. Y. Chang, and S. D. West. 2010. Nest site selection by western gray squirrels at their northern range terminus. Journal of Wildlife Management 74:18–25.

Hadfield, J. S., R. L. Mathiasen, and F. G. Hawksworth. 2000. Douglas-fir dwarf mistletoe. USDA Forest Service, University of Minnesota, Minneapolis, Minnesota, USA.

Hamer T., N. Denis, and J. Harmon. 2005. Distribution and habitat characteristics of western gray squirrel nest sites in the Stehekin River Valley, North Cascades National Park. Hamer Environmental, Mount Vernon, Washington, USA.

Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. Forest Ecology and Management 211:117–139.

Hosmer, D. W., and S. Lemeshow. 2015. Applied logistic regression. Third edition. Wiley and Sons, New York, New York, USA.

Ingles, L. G. 1947. Ecology and life history of the California gray squirrel. California Fish and Game Bulletin 33:139–157.

Johnston, A. N. 2013. Eastern gray squirrel ecology and interactions with western gray squirrels. Dissertation, University of Washington, Seattle, USA.

Koprowski, J. L. 2002. Handling tree squirrels with a safe and efficient restraint. Wildlife Society Bulletin 30:101–103.

Krannitz, P. G., and T. E. Duralia. 2004. Cone and seed production in *Pinus ponderosa*: a review. Western North American Naturalist 64:208–218.

Larson, A. J., and D. Churchill. 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. Forest Ecology and Management 267:74–92.

Lehmkuhl, J. F., L. Gould, E. Cazares, and D. Hosford. 2004. Truffle abundance and mycophagy by northern flying squirrels in eastern Washington forests. Forest Ecology and Management 200:49–65.

Lehmkuhl, J. F., K. D. Kistler, J. S. Begley, and J. Boulanger. 2006. Demography of northern flying squirrels informs ecosystem management of western interior forests. Ecological Applications 16:584–600.

Linders, M. J. 2000. Spatial ecology of the western gray squirrel (*Sciurus griseus*) in Washington: the interaction of season, habitat and home range. Thesis, University of Washington, Seattle, USA.

Linders, M. J., and D. W. Stinson. 2007. Washington state recovery plan for the western gray squirrel. Washington Department of Fish and Wildlife, Olympia, USA.

Linders, M. J., W. M. Vander Haegen, J. M. Azerrad, R. Dobson, and T. Labbe. 2010. Management recommendations for Washington's priority species: western gray squirrel. Washington Department of Fish and Wildlife, Olympia, USA.

Linders, M. J., S. D. West, and W. M. Vander Haegen. 2004. Seasonal variability in the use of space by western gray squirrels in southcentral Washington. Journal of Mammalogy 85:511–516.

Maser, C., R. G. Anderson, K. Cromack Jr., J. T. Williams, and R. E. Martin. 1979. Dead and down woody material. Pages 78–95 *in* J. W. Thomas, editor. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. USDA Forest Service Agricultural Handbook No. 553, Washington, D.C., USA.

Northwest Interagency Coordination Center. 2014. Northwest annual fire report, 2014. http://gacc.nifc.gov/nwcc. Accessed 18 Sep 2015.

Northwest Interagency Coordination Center. 2015. Northwest annual fire report, 2015. http://gacc.nifc.gov/nwcc. Accessed 18 Sep 2015.

Otis, D. L., and G. C. White. 1999. Autocorrelation of location estimates and the analysis of radiotracking data. Journal of Wildlife Management 63:1039–1044.

Parks, C. G., E. L. Bull, R. O. Tinnin, J. F. Shepherd, and A. K. Blumton. 1999. Wildlife use of dwarf mistletoe brooms in Douglas-fir in northeast Oregon. Western Journal of Applied Forestry 14:100–105.

Prather, J. W., N. L. Dodd, B. G. Dickson, H. M. Hampton, Y. Xu, E. N. Aumack, and T. D. Sisk. 2006. Landscape models to predict the influence of forest structure on tassel-eared squirrel populations. Journal of Wildlife Management 70:723–731.

Pyne, S. J. 1982. Fire in America: a cultural history of wildland and rural fire. Princeton University, Princeton, New Jersey, USA.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ren, S., H. Lai, W. Tong, M. Aminzadeh, X. Hou, and S. Lai. 2010. Nonparametric bootstrapping for hierarchical data. Journal of Applied Statistics 37:1487–1498.

Sikes, R. S., and the Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Skalski, J. R. 1987. Selecting a random sample of points in circular field plots. Ecology 68:749.

Stienecker, W. E., and B. M. Browning. 1970. Food habits of the western gray squirrel. California Fish and Game Bulletin 56:36–48.

Stuart, K. D. 2012. Ecology and conservation of the western gray squirrel (*Sciurus griseus*) in the North Cascades. Dissertation, University of Washington, Seattle, USA.

Stuart, K. D. and K. J. Jenkins. 2017. Habitat use, diet, movement, and vegetation use by western gray squirrels (*Sciurus griseus*) in the North Cascades Range, USA, 2008-2011: U.S. Geological Survey Data Release, https://doi.org/10.5066/F7ZG6QQH

Swihart, R. K., and N. A. Slade. 1997. On testing for independence of animal movements. Journal of Agricultural, Biological and Environmental Statistics 2:48–63.

Therneau, T. 2015. A package for survival analysis in S. R package version 2.37-7. http://CRAN.R-project.org/package=survival. Accessed 12 Jan 2015.

Trappe, J. M., R. Molina, D. Luoma, E. Cázares, D. Pilz, J. E. Smith, M. A. Castellano, S. L. Miller, and M. J. Trappe. 2009. Diversity, ecology, and conservation of truffle fungi in forests of the Pacific Northwest. United States Department of Agriculture Forest Service Pacific Northwest Research Station, Portland, Oregon, USA.

United States Department of Agriculture [USDA] Okanogan-Wenatchee National Forest. 2000. Strategy for management of dry forest vegetation. USDA, Wenatchee, Washington, USA.

United States Department of Agriculture [USDA] Okanogan-Wenatchee National Forest. 2012. Restoration strategy: adaptive ecosystem management to restore landscape resiliency. USDA, Wenatchee, Washington, USA.

United States Department of the Interior [USDI] National Park Service. 1995. Lake Chelan National Recreation Area forest fuel reduction/firewood management plan. USDI, Stehekin, Washington, USA.

United States Department of the Interior [USDI] National Park Service. 2017. Environmental assessment fire management program, North Cascades National Park Service Complex. USDI, Marblemount, Washington, USA.

United States Geological Survey [USGS]. 2017. National burn severity mapping project: fire request: Flick Creek. https://burnseverity.cr.usgs.gov/burn-show.php?intID=322. Accessed 28 Nov 2017.

Vander Haegen, W. M., G. R. Orth, and L. M. Aker. 2005. Ecology of the western gray squirrel in south-central Washington. Progress Report. Washington Department of Fish and Wildlife, Olympia, USA.

Vander Haegen, W. M., G. R. Orth, and M. J. Linders. 2013. Survival and causes of mortality in a northern population of western gray squirrels. Journal of Wildlife Management 77:1249–1257.

White, G. C., and R. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, New York, New York, USA.

Worten, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

Wright, C. S., and J. K. Agee. 2004. Fire and vegetation history in the eastern cascade mountains, Washington. Ecological Applications 14:443–459.

Wright, H. E., and M. L. Heinselman. 1973. The ecological role of fire in natural conifer forests of western and northern North America: introduction. Quaternary Research 3:319–328.

Associate Editor: Jamie Sanderlin.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.