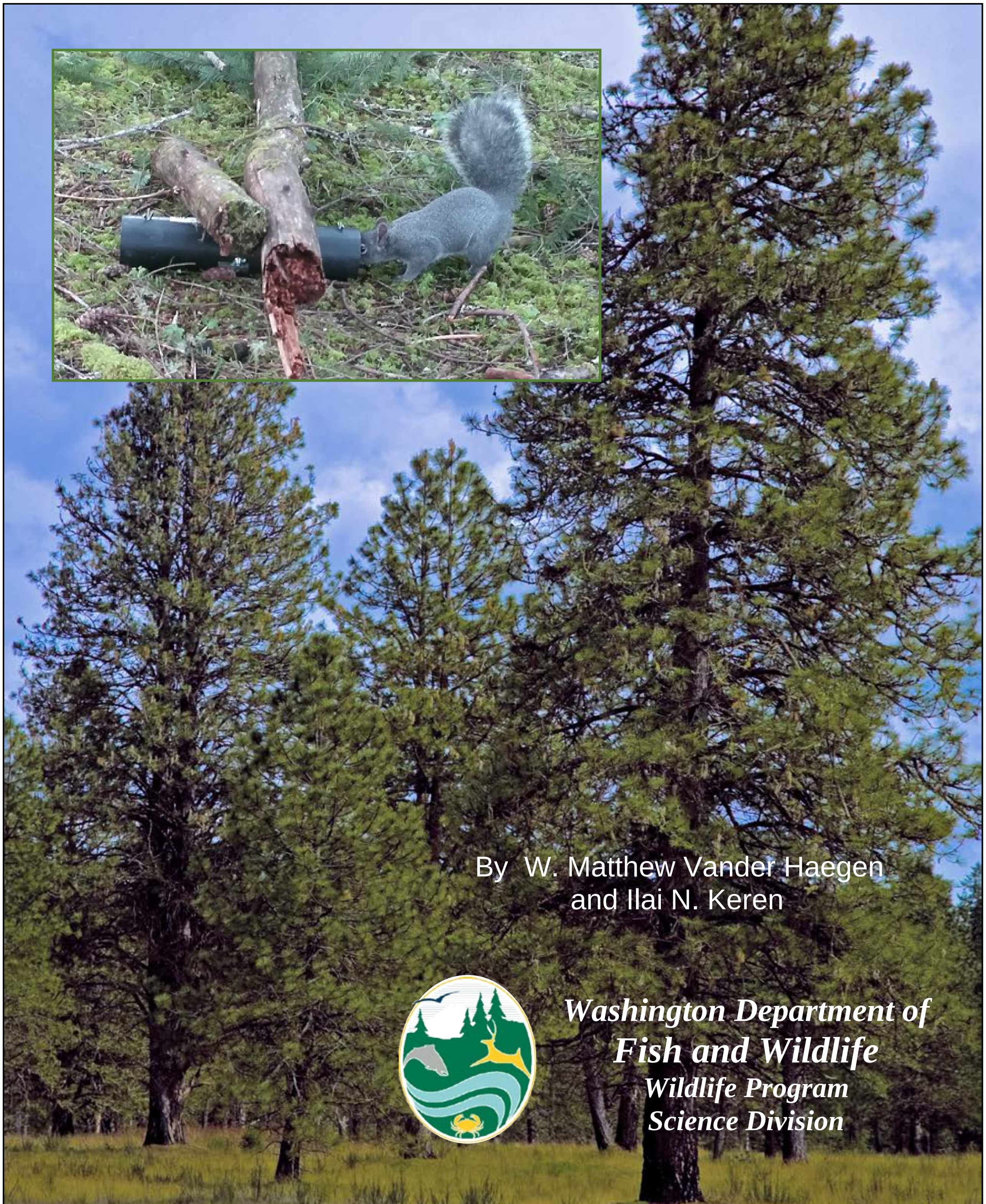
STATE OF WASHINGTON December 2021

Occupancy surveys for western gray squirrels in Washington



By W. Matthew Vander Haegen
and Ilai N. Keren

Washington Department of
Fish and Wildlife
Wildlife Program
Science Division

Final Report

Recommended Citation:

Vander Haegen, W. M. and I. N. Keren. 2021. Occupancy surveys for western gray squirrels in Washington. Final report. Washington Department of Fish and Wildlife, Olympia.

Cover photos by M. Vander Haegen: Ponderosa pine stand near Shaver Lake, Joint Base Lewis-McChord, Washington; western gray squirrel investigating hair-snag tube, Joint Base Lewis-McChord. Title page illustration by Darrell Pruett.

Occupancy Surveys for Western Gray Squirrels in Washington

W. Matthew Vander Haegen

and

Ilai N. Keren

28 December 2021

Final Report

Washington Department of Fish and Wildlife

Wildlife Program, Science Division

1111 Washington Street

Olympia, WA 98501

ACKNOWLEDGEMENTS

This project was possible only through the tremendous effort on the part of WDFW Regional staff and volunteers. We would like to acknowledge WDFW biologists Stefanie Bergh, Jeff Bernatowicz, Luke Burlingame, Emily Butler, Devon Comstock, Scott Fitkin, Jeff Heinlen, Todd Jacobson, Amber Johnson, Sue Van Leuven, Mary Linders, Will Moore, Graham Simon, Nick Steveson, Dave Volsen, and Carly Wickhem; staff from the Columbia Gorge National Scenic Area; and volunteers Bob Fischer, Anna Machowicz, and Sally Pfaff. We thank Todd Zuchowski and David Clouse from JBLM Fish and Wildlife, and Dennis Buckingham, Fayth Shuey, and the soldiers and interns from JBLM's Conservation Program for their support and outstanding work. We also thank Brian Cosentino for GIS support and Taylor Cotten and Mary Linders, WDFW Diversity Division, and Gary Bell, WDFW Habitat Program, for helpful suggestions and assistance. We thank the many landowners that allowed surveys to be conducted on their property and who assisted staff with access and coordinating placement of survey sites. Those landowners included: Brooks Memorial State Park, the Washington Department of Natural Resources, the Columbia Gorge National Scenic Area, USDA Forest Service, Conboy Lake National Wildlife Refuge, Columbia Land Trust, Western Pacific Timber Company, Hancock Timber Resource Group, Kreps Family Ranch, Horseshoe Bend Ranch, and the Sacred Earth Foundation. We thank Stefanie Bergh, Taylor Cotten, Scott Fitkin, Jeff Heinlen, Mary Linders, Melissa Merrick, and Robert Steidl for reviewing the manuscript.

Table of Contents

List of Figures

List of Tables

EXECUTIVE SUMMARY

The largest native tree squirrel in western North America, western gray squirrels (*Sciurus griseus*) occur along the west coast of the United States from Baja California to Washington State. The species is listed as threatened in Washington, largely due to habitat loss and a perceived reduction in population levels. Despite substantial study of the ecology of western gray squirrels in Washington, there has been limited systematic investigation of its occurrence and distribution. In 2018, Washington Department of Fish and Wildlife initiated a survey project to assess occupancy rates of western gray squirrels in the 3 primary population areas in Washington.

Three project areas were identified for occupancy surveys, each area representing current knowledge of the geographic core area for populations in the Puget Trough, the North Cascades, and the South Cascades. Geographic core here is defined as the spatial extent where past surveys and western gray squirrel observations suggest that suitable habitat occurs (or occurred in recent history) in sufficient acreage and distribution to support viable populations.

We used hair tubes to determine occupancy at survey sites and focused sampling within ecological systems that represent potential western gray squirrel habitat. The general approach was to survey along a 600m-long transect representative of the ecological system in the selected stand. Stands were selected using a geographic information system and various data layers including orthophotographs, topography, and ownership. Tubes were deployed between May and July and were checked at 2- to 4-week intervals. We used occupancy modeling on data pooled across years to derive a project-wide conditional detection probability (conditional on a squirrel being present) and to estimate occupancy for each project area.

Occupancy surveys spanning 3 years resulted in 138 sites deployed and checked across all 3 project areas. Eighteen sites were surveyed in the Puget Trough, 60 sites were surveyed in the North Cascades, and 60 sites were surveyed in the South Cascades. Conditional detection probability was high (0.91, SE = 0.03) indicating that squirrels generally were detected when present on a site. Modeled occupancy rate was 0.39 (SD = 0.12) for the Puget Trough, 0.27 (0.06) for the North Cascades, and 0.44 (0.07) for the South Cascades.

Surveys using hair tubes proved effective for documenting occupancy of western gray squirrels in Washington. An independent dataset from the South Cascades project area yielded a similar occupancy estimate based on nest surveys, providing support for our survey approach. Extant threats to habitat in all 3 population areas and recent habitat losses documented for the 2 Cascade populations make continued monitoring of these populations crucial for guiding management actions over the next few decades. Occupancy rates resulting from this survey can be considered a baseline, representing conditions extant during the survey period and providing values that can be compared with those from subsequent surveys using similar or comparable techniques.

INTRODUCTION

The largest native tree squirrel in western North America, western gray squirrels (*Sciurus griseus*) occur along the west coast of the United States from Baja California to Washington State (Carraway and Verts 1994). In Washington, they occur in 3 disjunct populations: 2 on the eastern slope of the Cascade mountains, and a third, smaller population in the southern Puget Trough (Linders and Stinson 2007). The North Cascades population represents the northernmost extent of the species' range and occurs in one of the few areas where the species can be found outside of the natural range of oaks (*Quercus* spp). The South Cascades population occurs along the Columbia River gorge and is believed to be the largest of the 3 populations (Linders and Stinson 2007). The Puget Trough population is likely the most threatened, currently limited to a 367-km^2 military base in an urbanizing landscape (Vander Haegen et al. 2018). The species is listed as threatened in Washington, largely due to habitat loss and a perceived reduction in population levels (Linders and Stinson 2007).

Numerous studies have identified canopy cover of trees and connectivity of tree crowns as key characteristics of suitable habitat both for western gray squirrels and for tree squirrels in general (Dodd et al. 2006, Lehmkuhl et al. 2006, Prather et al. 2006, Linders et al. 2010, Stuart et al. 2018). In the Puget Trough and the South Cascade populations, western gray squirrels use primarily oak/conifer communities (Linders and Stinson 2007, Johnston et al. 2020) whereas in the North Cascades their habitat is characterized by conifers and mixed coniferous/deciduous stands (Stuart et al. 2018). Low cover of shrubs in the understory and areas of open ground for foraging are common characteristics of western gray squirrel habitat in Washington (Linders et al. 2010, Johnston et al. 2020). Western gray squirrels depend on tree seeds for part of their diet, with Oregon oak (*Q. garryana*), ponderosa pine (*Pinus ponderosa*), and Douglas-fir (*Psuedotsuga menziesii*) providing important fall/winter foods in Washington (Linders and Stinson 2007, Johnston et al. 2019).

Despite substantial study of the ecology of western gray squirrels in Washington (e.g., Linders 2000, Stuart et al. 2018, Vander Haegen et al. 2018, Johnston et al. 2020), there has been limited systematic investigation of its occurrence and distribution. Previous survey efforts have generally been project-specific and were not designed to monitor trends in populations. Surveys for nests in Klickitat and Okanogan Counties in 1994-96 greatly increased the known area of squirrel distribution but evaluated a small portion of the suspected range (Rodrick 1999). Nest surveys conducted as part of forest practice applications in Klickitat County provided additional areas of known occurrence but also were limited in geographic area (Linders and Stinson 2007). Early surveys in the Puget Trough were primarily walking surveys focused on observing individual animals and were labor intensive (Ryan and Cary 1995, Bayrakci et al. 2001), whereas later surveys using hair tubes were more successful but were not systematic (Fimbel and Freed 2008). Hair tubes also have been used to identify occupied habitat in the Methow and Okanogan river valleys in the North Cascades (Yamamuro et al. 2011, WDFW unpublished data); like the surveys in the Puget Trough, they lacked any measure of detection probability and thus essentially were surveys for presence only. The largest dataset of western gray squirrel occurrences is housed in the Washington Department of Fish and Wildlife's Wildlife Species Data Management (WSDM) database. The database includes opportunistic observations as well as locations from most of the survey efforts mentioned above. WSDM data were used in developing population estimates for the species recovery plan (Linders and Stinson 20007); however, the lengthy temporal aspect of those data renders that effort not repeatable. As a state threatened species in Washington, there is building interest in monitoring western gray squirrel populations in known or presumed habitat in Washington using techniques that can be systematically repeated to track population trends.

Like many listed species, western gray squirrels are difficult to count in the field and so pose a dilemma for recovery goals based on population size. Many of the previous surveys in Washington were based on sign (primarily nests) that can indicate presence of the species on the site, but without some measure of detectability lack any certainty in confirming absence (MacKenzie et al. 2003). Moreover, there is uncertainty in discriminating nests of western gray squirrels from those of the eastern gray squirrel (*Sciurus carolinensis*), an introduced species that occurs to varying degrees in all 3 western gray squirrel population areas in Washington. Occupancy surveys provide information on where species occur on the landscape and make possible monitoring of species that are cryptic or difficult to count (Joseph et al. 2006). When paired with a detection probability, occupancy data can reliably estimate where species do and do not occur, allowing assessment of how prevalent a species is on the landscape (MacKenzie et al. 2003, MacKenzie and Royle 2005). The proportion of habitat occupied by a species changes with population size (Fretwell and Lukas 1970, Greene and Stamps 2001) and occupancy rates should increase as populations recover (Tempel and Gutierrez 2013). Repeated over time, such surveys can identify changes in occupancy level among surveyed stands.

Hair tubes have been used to detect presence of various small and meso-sized mammals in many ecological systems (see review in Bertolino et al. 2009). The method involves capturing hair from target species as they enter baited and appropriately sized plastic tubes equipped with a hair-capture device (e.g., 2-sided tape). Most published reports using these devices had determining presence of the species as the goal and did not consider detectability (e.g., Gurnell et al. 2004). Several studies have used data from hair tubes in an occupancy-modeling framework to examine occupancy rates; 3 studies of tree squirrels reported detection probabilities ranging from 0.1 to 0.6 (Mortelliti and Boitani 2008, Mortelliti et al. 2010, Amori et al. 2012). Although hair-tubes have been used to survey for presence of western gray squirrels in Washington, detection probabilities for this species have not previously been estimated.

From 2018 to 2020 we surveyed for western gray squirrels in the 3 primary population areas in Washington. We used hair tubes to document presence and used occupancy modeling to estimate conditional detection probability and occupancy rates. Our objective in the present survey was to establish occupancy rates for western gray squirrels in each of the 3 population areas that can serve as baseline measures for future surveys.

METHODS

Study Areas

We identified 3 project areas for occupancy surveys of western gray squirrels in Washington, each area representing current knowledge of the geographic core area for populations in the Puget Trough, the North Cascades, and the South Cascades (Fig. 1). Here, we define the geographic core as the area where past surveys, telemetry research, and western gray squirrel observations suggest that suitable habitat occurs (or occurred in recent history) in sufficient acreage and distribution to support viable populations. We used the potential range and habitat distribution maps created for Washington's State Wildlife Action Plan (SWAP; WDFW 2015) to define the initial areas for consideration. Distribution on these maps was delineated using watershed boundaries and the national Hydrologic Unit Code classification system (HUC, Level 12). In the SWAP process, individual HUCs were attributed based on known occurrence of western gray squirrels in the WSDM database. The specific spatial extents to include in the surveys were refined and reduced by dropping HUCs with few observations; also, survey areas did not extend to HUCs on the periphery of the geographic core areas as there was insufficient funding and staff time available. Moreover, it was judged that surveying peripheral areas with suspected low density of squirrels would provide little added information other than the ultimate spatial extent of the species range. Such surveys might be considered in the future.

We focused sampling within ecological systems that represent potential western gray squirrel habitat (Table 1). Ecological systems are defined under the NatureServe Ecological System Classification and were mapped at a spatial resolution of 30m (NatureServe, http://www.natureserve.org). In the large, eastern Washington project areas we used these systems to stratify sampling, allocating the number of sites for survey proportional to the spatial extent of each system within each survey HUC. Limited funding precluded surveying the entire east Cascades project areas, so we selected HUCs randomly within each project area for sampling. Based on simulations, we identified a sample size of 60 sites for each of the 2 eastern Washington project areas. All sampling locations in the North and South Cascades project areas were selected without consideration of current or historic use by western gray squirrels.

A different approach was needed for the Puget Trough where the targeted geographic core area was <10km^2 and selection of sites within a HUC framework was impractical. All surveys in this area were on Joint Base Lewis-McChord (JBLM), a 36,700-ha military base that provides habitat for most, if not all, of the Puget Trough western gray squirrel population (Linders and Stinson 2007). Surveys on JBLM focused on the eastern part of the Base where most of the squirrel population was believed to exist. Western gray squirrel habitat on JBLM, and in the Puget Trough as a whole, occurs in small patches associated with prairie edge habitat and oaks (Linders and Stinson 2007, Johnston et al. 2020). We selected 18 sites across the survey area that represented suitable habitat based on either previous use by squirrels (surveys or telemetry research) or based on vegetation type and structure determined from the Base vegetation map and LiDAR data layers (Johnston et al. 2020). Using this 2-tiered approach, sites surveyed in 2018 were in areas with a known history of past occupancy by western gray squirrels,

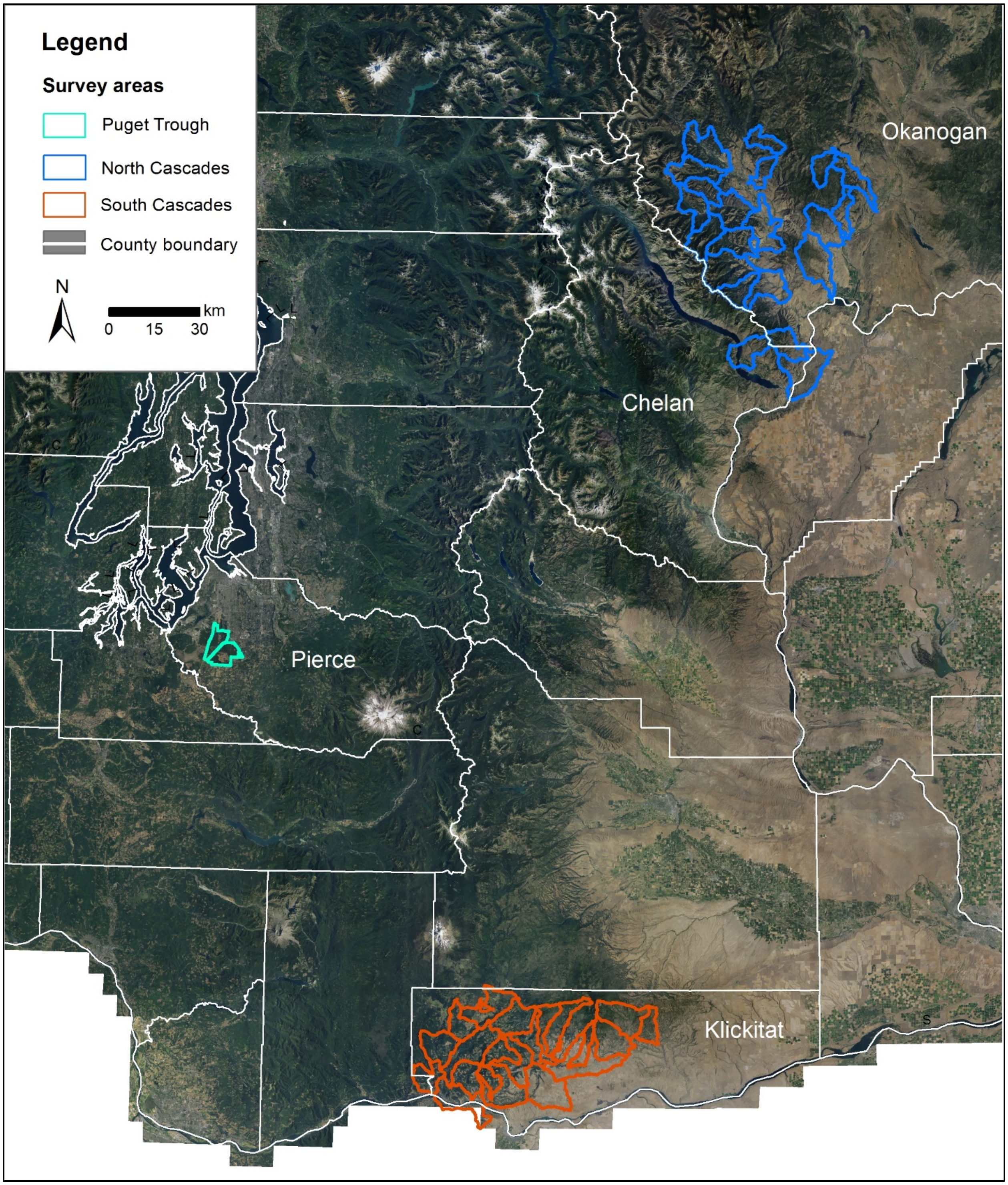


Figure 1. Survey areas for statewide western gray squirrel occupancy assessment, 2018-2020, delineated by Joint Base Lewis-McChord administrative boundaries in the South Puget Trough and by watershed units in the North Cascades and South Cascades.

whereas sites surveyed in subsequent years were in areas with unknown history of use. Suitable habitat surveyed on JBLM fell within 3 ecological systems (Table 1).

Table 1. Ecological systems defining potential habitat used to distribute survey sites for occupancy surveys of western gray squirrels in Washington, 2018-2020.

Ecological System	**Project area**[a]		
	PT	**NC**	**SC**
East Cascades Mesic Montane Mixed-Conifer Forest and Woodland		x	x
East Cascades Oak-Ponderosa Pine Forest and Woodland			x
Great Basin Foothill and Lower Montane Riparian Woodland and Shrubland			x
North Pacific Dry Douglas-fir-(Madrone) Forest and Woodland	x		
North Pacific Maritime Dry-Mesic Douglas-fir-Western Hemlock Forest	x		
North Pacific Oak Woodland	x		
Northern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest		x	x

[a] Project areas: PT=Puget Trough, NC=North Cascades, SC=South Cascades.

Candidate sites were walked before points were established to assess if they would likely meet criteria for vegetation structure and tree species. Desired stand characteristics were: 1) a conifer-dominated overstory of mature trees (primarily Douglas fir or ponderosa pine) or mixed stands of conifer and Oregon oak, with oak comprising <50% of the overstory; 2) tree canopy closure of ≥40% (averaged for the site); 3) large (≥16 in diameter breast height) conifer trees present in the stand; 4) shrub cover <50%; and 5) open ground ≥10%. Stand characteristics were estimated during preliminary scouting and later quantified at each point when tubes were deployed. Along riparian areas it was acceptable to have patches dominated by deciduous trees as long as ponderosa pine or Douglas fir also was present.

Surveys

We used hair tubes to determine occupancy at survey sites following protocols established in a pilot study (Vander Haegen and Keren 2018). The general approach was to survey along a 600m-long transect (hereafter, site) representative of the ecological system in the selected forest stand. Our goal was to maximize the likelihood of detecting ≥1 squirrel in occupied stands, so we chose a transect length approximately the diameter of a female home range and likely to intersect the use areas of ≥1 squirrel (Linders et al. 2004, Stuart 2012, Johnston 2013). Stands were selected using a geographic information system (ArcGIS ver. 10.7) and various data layers including orthophotographs, topography, and ownership. For the North and South Cascades project areas the goal was to include both public and private lands in rough approximation to their availability; surveys in the Puget Trough were all on U.S. Department of Defense land.

The sampling design was based on occupancy models and followed a removal design (MacKenzie and Royle 2005), wherein individual surveys concluded once a western gray squirrel was detected. We conducted a pilot study in 2017 and ran surveys on 13 sites known to recently support western gray squirrel, across all 3 project areas (Vander Haegen and Keren 2018). Using these data, we modeled detection probability with different array designs and sampling periods and determined that the design employed in the present survey would likely provide a conditional detection probability (conditional on a squirrel being present) of ≥94%.

Hair tubes were placed at 3 points along a transect, with points separated by 300m (Fig. 2). Four tubes comprised a sampling array at each point, with tubes positioned 35m from the point and at 90 degrees (Fig. 2). Tubes were baited with whole walnuts: 1 nut was glued in the tube to entice the squirrel to enter and 2 nuts were placed just outside each end of the tube to act as attractants. Several (2-3) nuts were tossed 3-4 m from the tube to act as additional attractants. The intent of the 4-tube array and associated walnut bait was to increase the likelihood that squirrels traversing their home range would encounter sufficient walnuts to recognize them as food and enter the tubes. Additionally, having multiple tubes at a point increased the likelihood that a squirrel would encounter an active, baited tube, in the event that non-target species removed nuts and/or left hair on some tapes (i.e., censoring). Tubes were held in place by downed limbs or rocks to prevent them from being moved by squirrels (Fig. 2).

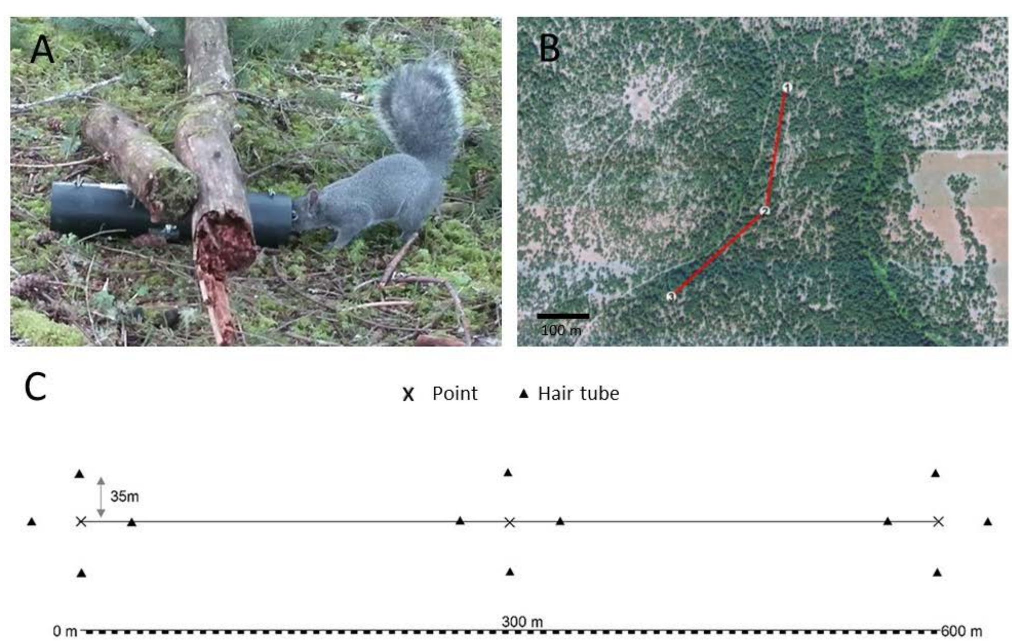


Figure 2. Survey site for western gray squirrels in Washington, illustrating A) western gray squirrel entering a hair tube, B) placement of a survey transect in a mixed conifer stand, and C) site schematic with 3 points spaced 300m apart, each with a detection array comprised of 4 tubes set 35m from a central point.

Tubes were deployed between May and July and checked at 2, 4, and 8 weeks after deployment. During each check, field staff examined each tape for the presence of hair, presence of the tube nut, presence of the bait placed immediately adjacent to the tube and noted if the tube had been moved. When hair was detected on a tape, the metal plate was removed and placed in a plastic bag labeled with the date and tube number. In all but the final checks, tubes were reset and rebaited with external nuts. Tubes where the tube nut was missing were replaced. Tubes were coded as "censored" when hair from non-target species was left on 1 or both tapes, when the tube nut was missing, or when the tube had been moved >3 m from where it was set. In the rare case when hair from both a western gray squirrel and a non-target species was identified at a tube, the point was recorded as positive for western gray squirrel.

Tubes were removed and the survey concluded after 8 weeks unless the site had suffered considerable censoring. Because censoring occurred to some extent on many sites, we set a minimum standard for a survey to be called successful. Successful sites had a minimum of 6 tubes active (i.e., not censored) on at least 2 checks. Most sites easily fit this standard; sites where only one of the first 3 checks met the standard were run an additional 4 weeks for a 4th check. Unsuccessful (i.e. censored) sites were surveyed again the following year; in cases where >75% of tubes were censored we selected an alternate site in the same HUC and ecological system.

Censoring of tubes occurred to a limited extent in all project areas but reached a disruptive level in the North Cascades in 2019 when the tube nut was removed by red squirrels (*Tamiasciurus hudsonicus*). Previously, only western gray squirrels, eastern gray squirrels, and California ground squirrels (*Otospermophilus beecheyi*) were documented to remove tube nuts, identification based on hair left in the tube. Smaller species commonly detected by hair tubes in Washington (e. g., red and Douglas squirrels [*Tamiasciurus douglasii*] and yellow pine chipmunks [*Neotamias amoenus*]) generally appear incapable of removing nuts glued inside the tubes, so what facilitated this change in 2019 is unknown. We fit each tube used in the North Cascades in 2020 with a small (25 cm^3) hardware cloth cage to secure walnut bait in the center of the tube. Cages were held in place by a bolt passed through the tube and secured with a wingnut. This replaced the glued nut previously used as bait.

We examined collected hair under a 10x hand lens or 20x stereoscope to determine if it came from a western gray squirrel. Hair samples were identified using characteristics such as length and color banding following Fimbel and Freed (2008). Reference samples were collected from all 3 study sites and included those of the more common, non-target species.

Tubes in the Puget Trough were deployed by WDFW Science Division staff and JBLM wildlife biologists and were checked by soldiers and interns working on JBLM conservation projects. Tubes in the North Cascades were deployed and checked by WDFW District and Diversity Division staff and 2 trained volunteers. Tubes in the South Cascades were deployed and checked by WDFW staff (District, Wildlife Area, Diversity Division, and Habitat Program) and by U.S. Forest Service staff.

Site Vegetation

We sampled vegetation characteristics at each point when the site was first established using plots of 35m and 10m radius centered on each point. We recorded the dominant and subdominant (if present) species of overstory tree occurring within the 35m plot. If a distinct understory of trees was present we recorded the dominant and subdominant (if present) species. Canopy cover of overstory trees was first estimated during site selection and later quantified using a Moosehorn cover scope, with readings taken at distances 10, 20, and 30m from the point in all 4 cardinal directions. We identified the dominant understory vegetation (young trees, shrubs, ferns, grasses/forbs, or litter [leaves and other dead vegetation]) within the 10m plot using ocular estimation. We defined open ground as ground covered with bare soil, rock, leaf litter, moss, grasses, or forbs. We recorded the proportion of open ground in the 10m plot using 4 bins (0-10, 11-30, 31-50 and >50%) and ocular estimation. We took photographs at each point center to document vegetation at the point for possible comparison with future conditions. We took digital images at eye level in each of the 4 cardinal directions and a 5th photograph pointing straight up at the canopy.

Analysis

We summarized annual tube visitation data by project area and calculated simple detection rates by dividing the number of sites positive for western gray squirrel by the number of sites surveyed (adjusted by subtracting the number of sites censored). These adjusted detection rates are sensitive to sample size and do not consider detection probability but provided an annual summary of positive vs. negative sites. We used occupancy modeling (MacKenzie et al. 2003) on data pooled across years to derive a project-wide conditional detection probability and to estimate occupancy for each project area.

To account for imperfect detection, we utilized a latent variable formulation in a hierarchical model of site occupancy (Royle and Kéry, 2007). For each occupied tube k (1-4) at point j (1-3) within site i (1-137) the probability of first detection (p) occurring on check x (1-3) out of v non-censored visits was given by the geometric series:

$$I(v \geq x)p(1-p)^{(x-1)}$$

where $I(v \geq x)$ is the identity function. Detection at the site level was then estimated as a series of Bernoulli trials down to the individual tube level, preserving both the spatial arrangement and removal design in our survey. We placed uniform (non-informative) Beta (1,1) priors on all detection and occupancy parameters in an MCMC model written in JAGS 4.2. (Plummer 2003). We retained every 10th of 10,000 iterations from 3 chains with independent starting values after discarding the first 5,000 as burn-in for a total of 1,500 independent draws from the joint posterior distribution of occupancy and detection. Visual inspection of trace and within-chain auto correlation plots as well as diagnostics such as R-hat ≤ 1.1 confirmed rapid convergence to a proper posterior distribution. JAGS code for the occupancy modeling is provided in the appendix.

We summarized vegetation characteristics at the site level by combining metrics measured at each of the 3 individual points. Canopy cover of overstory trees was the arithmetic mean of the 3 point values. For dominant understory and percent open ground, we selected the most common value among the 3 points to represent the site. In cases where all 3 values were unique, we selected the middle value for open ground (n = 15) and "Grasses/forbs" for dominant understory (n = 5); in all 5 cases, Grasses/forbs and Litter occurred as 2 of the 3 values and both represent open understory. We used Fisher's exact test to test for differences in vegetation values between occupied and unoccupied sites.

RESULTS

Positive Rates and Occupancy

Hair-tube surveys spanning 3 years resulted in 138 sites deployed and checked across all 3 project areas. Eighteen sites were surveyed in the Puget Trough, 60 sites were surveyed in the North Cascades, and 60 sites were surveyed in the South Cascades (Table 2). Combining all project areas, 32% of sites were positive for western gray squirrels. Forty-three positive determinations were based on hair collected at 1 or more points; we determined 1 site positive in the South Cascades based on active nests encountered during initial scouting for tube deployment. Of 43 positive sites surveyed with hair tubes, 44% were positive at only 1 point, 33% were positive at 2 points, and 23% were positive at 3 points. Censoring affected the number of sites used in annual calculations of positive rate (Table 2) and will be described below. Conditional detection probability (conditional on presence of ≥1 western gray squirrel on the site) was 0.97 (0.01 SE, 0.95-0.99 95% CI) at the point level and 0.91 (0.03 SE, 0.84-0.96) at the site level.

Adjusted positive rates for the Puget Trough ranged from 0.40 in 2018, when sites with known past use were surveyed, to 0.29 in 2019 when surveys focused on sites with unknown use (Table 2). The single site surveyed in 2020 was a replacement for a site that was repeatedly censored by black bear (*Ursus americanus)* visitation in previous years. Modeled occupancy rate, calculated using all sites across years, was 0.39 (0.12 SD) for the Puget Trough (Table 3, Fig. 3).

Adjusted positive rates for the North Cascades varied from 0.19 in 2018 and 2020, to 0.42 in 2019. Censoring rate in 2019 was unusually high (10 of 22 sites), a result of visits by red squirrels that removed the tube nut (Table 2). Modification of the tube to prevent removal of the tube nut allowed most censored sites to be resurveyed successfully in 2020. Modeled occupancy rate, calculated using all sites across years, was 0.27 (0.06 SD) for the North Cascades (Table 3, Fig. 4).

Adjusted positive rates for the South Cascades varied from 0.10 in 2018 to 0.80 in 2020 (Table 2). One site in 2019 was called positive based on active nests encountered during initial scouting for tube deployment. Censoring was not a significant issue, with 6 sites censored in 2018 due to movement of tubes by black bears and 1 site censored in 2019 after repeated visits by eastern gray squirrels. One site was positive for both western gray squirrels and eastern gray squirrels. Modeled occupancy rate, calculated using all sites across years, was 0.44 (0.07 SD) for the South Cascades (Table 3, Fig. 5).

Table 2. Results for western gray squirrel hair tube surveys in Washington, 2018-2020. Adjusted positive rate is the percentage of uncensored sites with a positive detection.

Area	Year	No. sites surveyed	No. sites censored	No. sites positive	Adjusted positive rate
Puget Trough	2018	11	1	4	0.40
Puget Trough	2019	7	0	2	0.29
Puget Trough	2020	1	0	0	0.00
North Cascades	2018	28	1	5	0.19
North Cascades	2019	22	10	5	0.42
North Cascades	2020	21	0	4	0.19
South Cascades	2018	35	6	3	0.10
South Cascades	2019	27	1	17	0.65
South Cascades	2020	5	0	4	0.80

Table 3. Cumulative results and modeled occupancy rate for sites surveyed for western gray squirrels in Washington using hair tubes, 2018-2020

	Sites (n)		Occupancy		
Area	Surveyed	Positive	Mean	Standard deviation	95% Credible interval
Puget trough	18	6	0.39	0.12	0.18—0.64
North Cascades	60	14	0.27	0.06	0.15—0.40
South Cascades	60	24	0.44	0.07	0.30—0.57

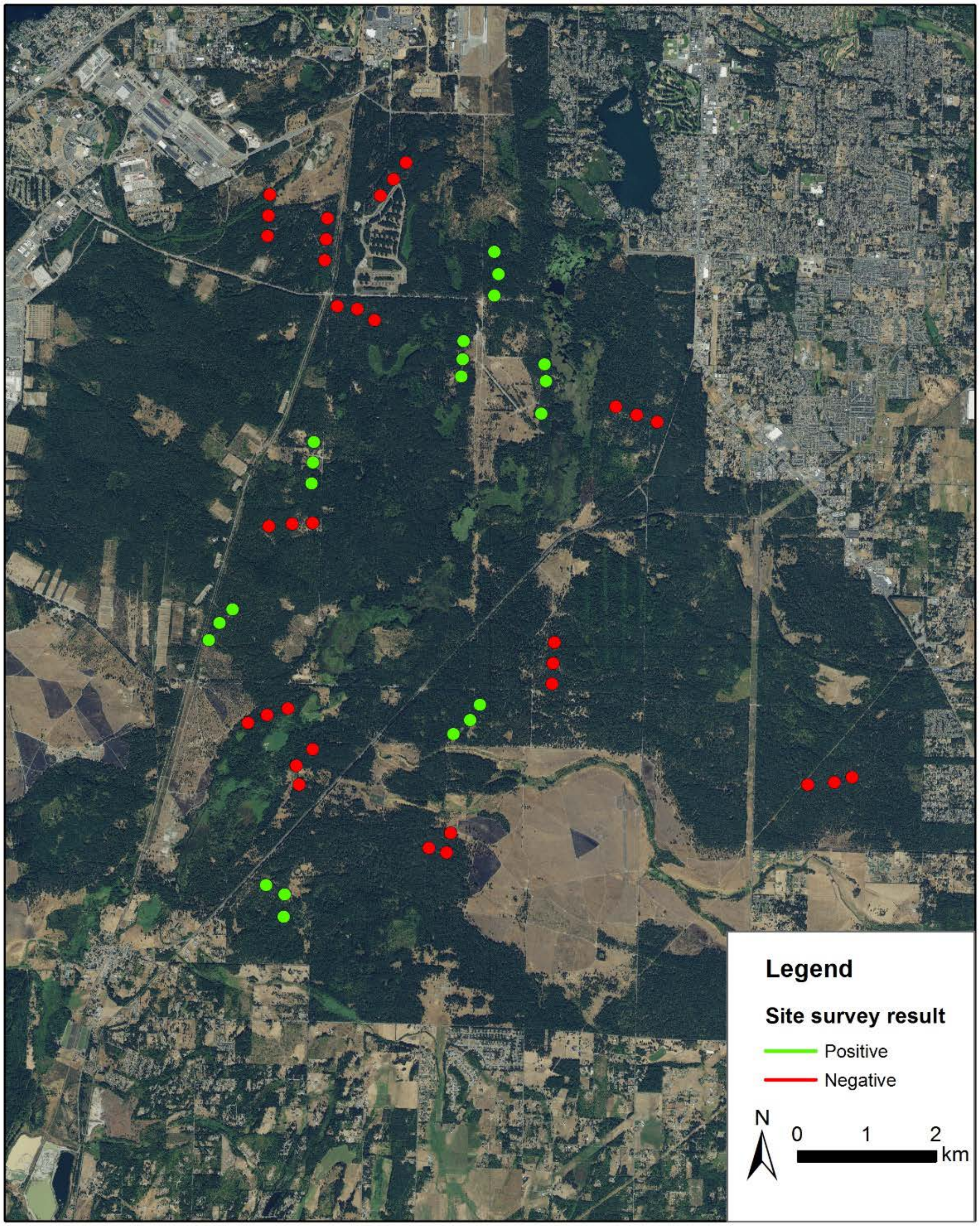


Figure 3. Survey sites labeled by result for Joint Base Lewis-McChord in the Puget Trough, statewide western gray squirrel survey, 2018-2020.

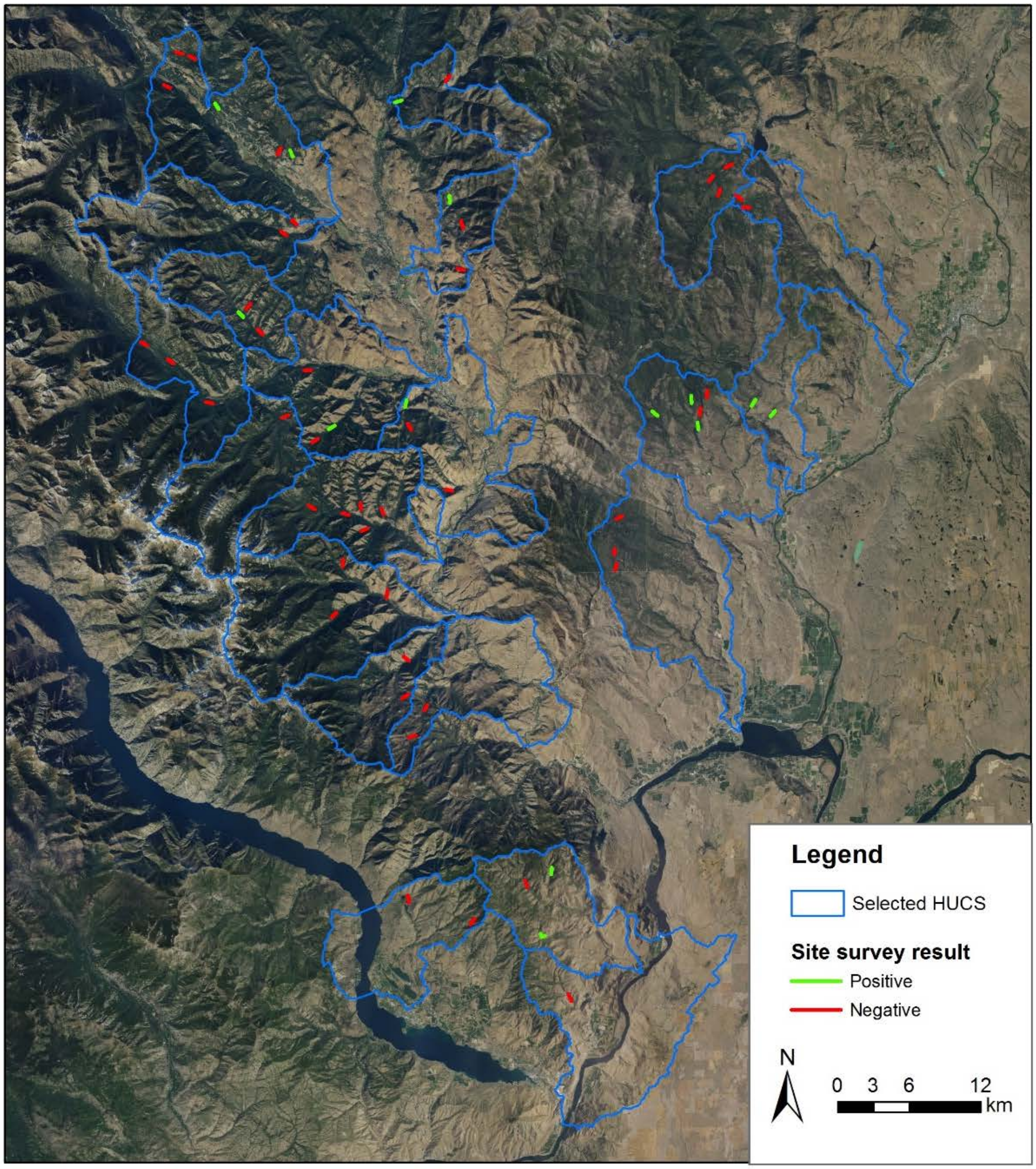


Figure 4. Survey watershed units (HUCs) and sites labeled by result for the North Cascades, statewide western gray squirrel survey, 2018-2020.

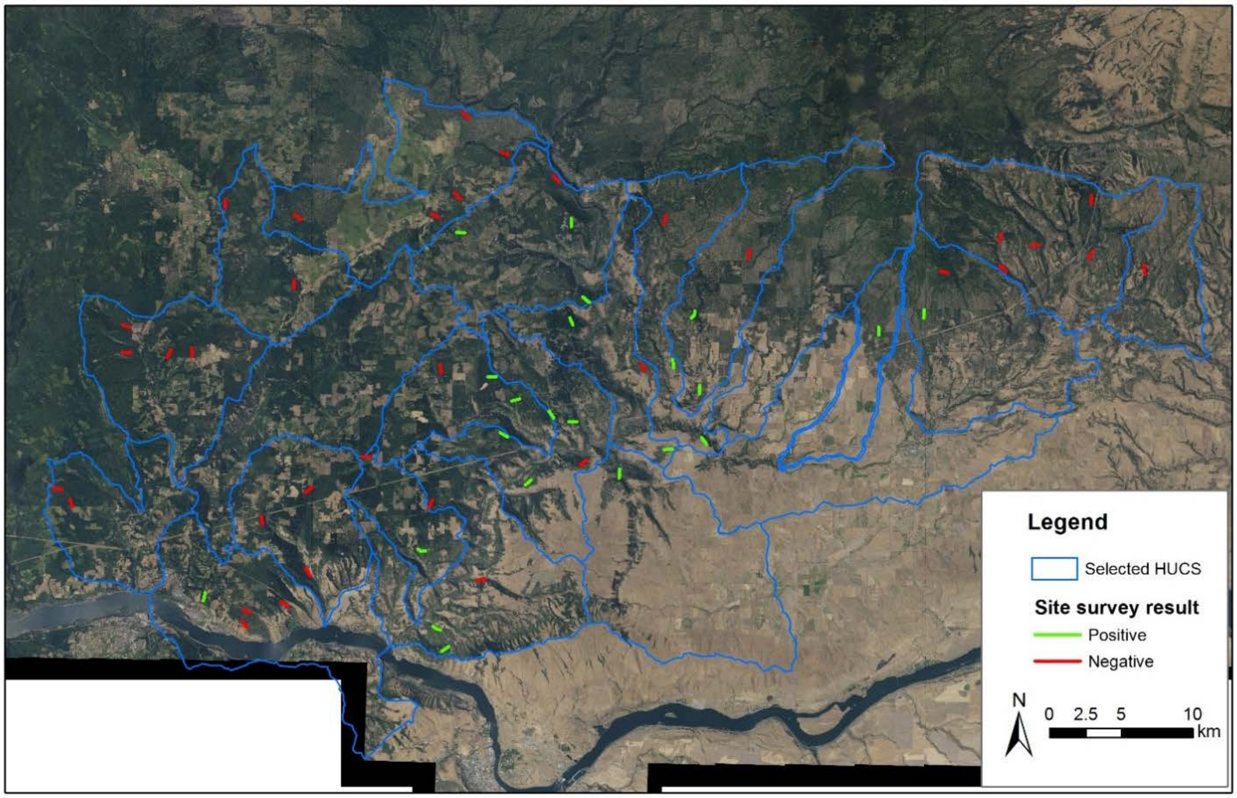


Figure 5. Survey watershed units (HUCs) and sites labeled by result for the South Cascade, statewide western gray squirrel survey, 2018-2020.

Habitat Characteristics of Survey Sites

Sites were selected to align with current knowledge of what represents suitable western gray squirrel habitat, although there was considerable variability in some parameters. The dominant overstory tree at points measured within sites was Douglas-fir (66%), followed by ponderosa pine (28%); all other species were < 3%. Most (93%) points in the Puget Trough had Douglas-fir overstories, whereas points in the North Cascades were dominated by Douglas-fir (52%) or ponderosa pine (48%) (Fig. 6). Most points in the South Cascades had Douglas-fir (70%) or ponderosa pine (17%) overstories, although 12 points were dominated by grand fir (7%), 2 points (4%) each were dominated by Oregon white oak and bigleaf maple (*Acer macrophyllum*), and 1 site was dominated by trembling aspen (*Populus tremuloides*) (1%) (Fig. 6). Considered at the site level, only 2 sites did not fit our criteria for suitable habitat based on overstory tree species; both sites were in the South Cascades and were dominated by grand fir and neither site was found positive for western gray squirrels.

Mean canopy cover of overstory trees for sites in the Puget Trough was 71% (SE = 2.0; range = 57-88), mean for the North Cascades was 45% (2.0; 22-75), and mean for the South Cascades was 64% (2.0;

18-95). While all sites in the Puget Trough were in the target range for canopy cover (≥40%), 22 sites in the North Cascades and 5 sites in the South Cascades had canopy cover <40% (Fig. 7). Canopy cover of sites positive for western gray squirrel aligned with overall distribution of canopy cover of sites at the project area scale, with the exception of the highest canopy cover classes in the Puget Trough (n = 4 sites) and the North Cascades (n = 10 sites) where we documented no positive sites (Fig. 7). Sites where mean canopy cover was below our intended minimum of 40% were mostly in the North Cascades (22 of 28 sites) and had a similar proportion positive for western gray squirrel compared to sites with >40% canopy cover (Fig. 7). Within the range of canopy cover values at our selected sites, canopy cover did not differ significantly between sites where western gray squirrels were present and sites where they were absent (Fig. 7).

Dominant understory was not in the set of selection criteria for establishing sites but was documented to inform future surveys. The dominant understory varied among the project areas and was largely Grasses/forbs or Shrubs in the Puget Trough, Grasses/forbs in the North Cascades, and Grasses/forbs or Shrubs in the South Cascades (Fig. 8). Dominant understory had a significant effect ($p = 0.006$) on occupancy only in the South Cascades where shrub-dominated understories had a negative effect (Fig. 8). No sites that were positive for western gray squirrel were dominated by ferns or young trees, but there were few such sites in our sample.

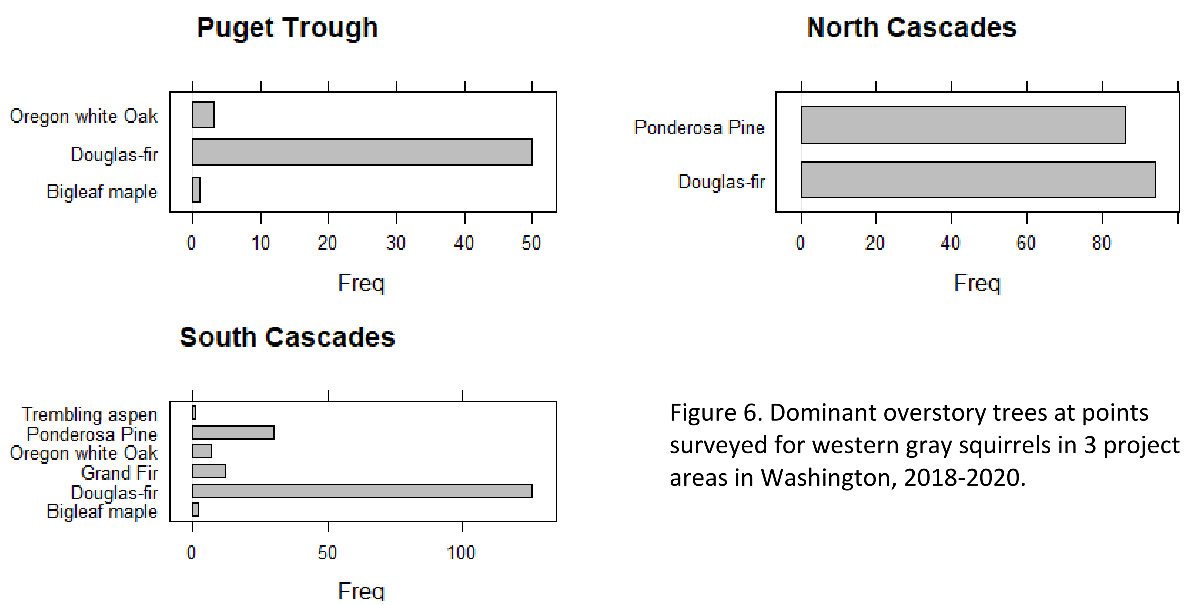


Figure 6. Dominant overstory trees at points surveyed for western gray squirrels in 3 project areas in Washington, 2018-2020.

The ground was largely open at sites in the 2 eastside Cascade project areas, with most sites characterized as >50% (Fig. 9). Sites in the Puget Trough were largely split between open (>50%) and more closed (0-10, 11-30), reflecting the difficulty in locating open sites in these westside systems (Fig. 9). Percent open ground had a significant effect ($p = 0.006$) on occupancy only in the South Cascades where open ground values ≤50% had a negative effect (Fig. 9).

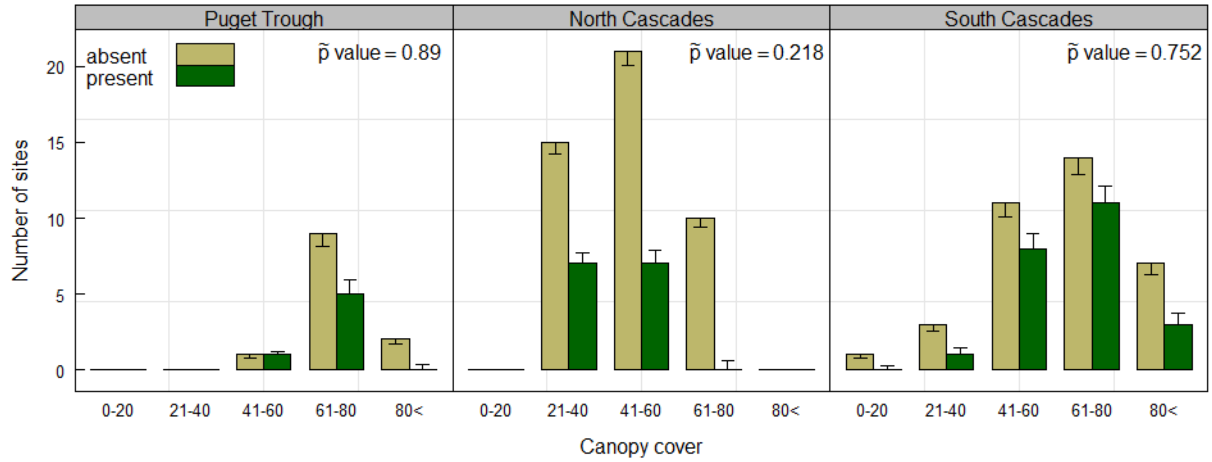


Figure 7. Tree canopy cover of sites surveyed for western gray squirrels in 3 project areas in Washington, 2018-2020. P value is from Fisher's exact test, comparing sites where squirrels were absent (not detected) to those where squirrels were present (detected).

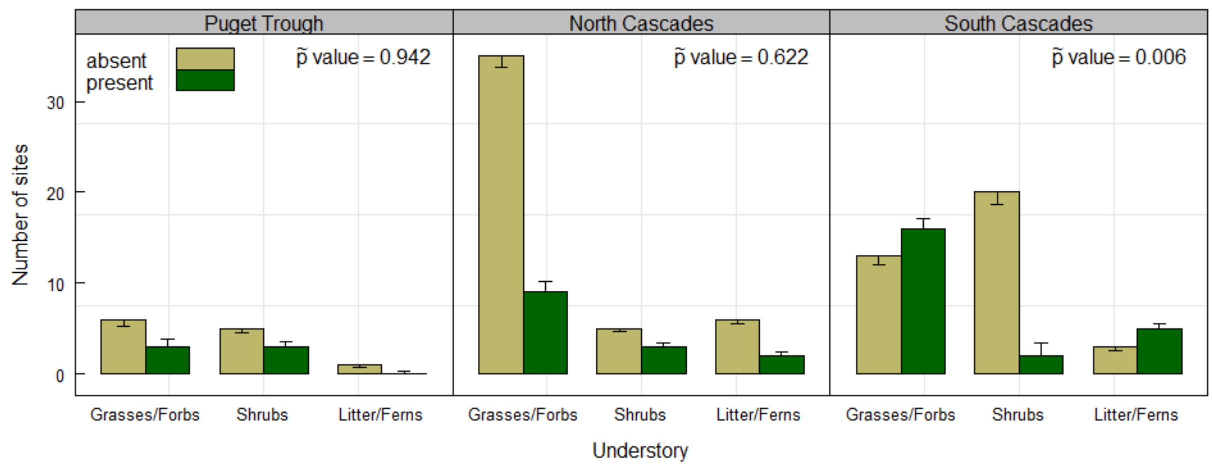


Figure 8. Understory composition of sites surveyed for western gray squirrels in 3 project areas in Washington, 2018-2020. P value is from Fisher's exact test, comparing sites where squirrels were absent (not detected) to those where squirrels were present (detected).

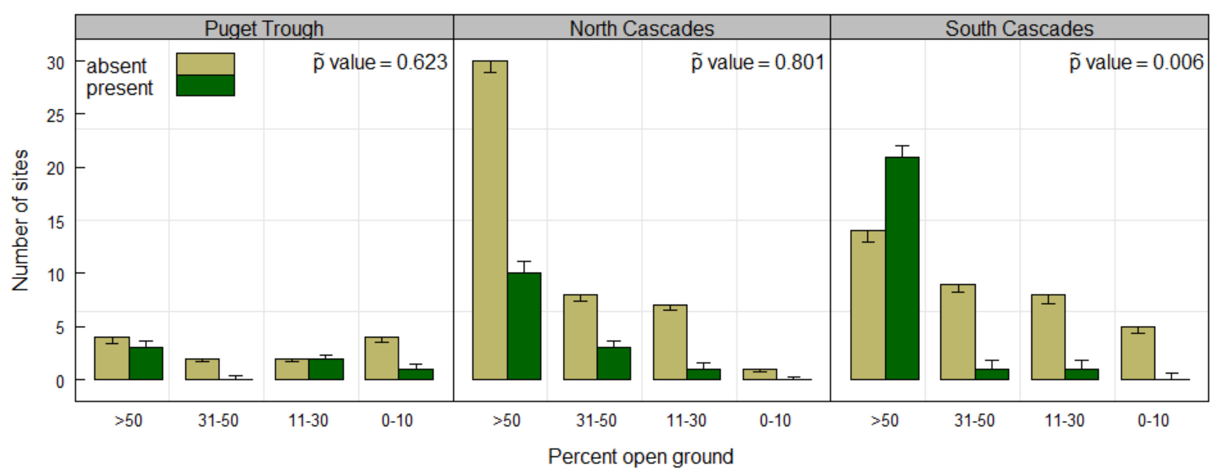


Figure 9. Percent open ground at sites surveyed for western gray squirrels in 3 project areas in Washington, 2018-2020. P value is from Fisher's exact test, comparing sites where squirrels were absent (not detected) to those where squirrels were present (detected).

DISCUSSION

Occupancy rates for western gray squirrels in Washington ranged from 0.27 to 0.44 among the 3 population areas studied. These rates derived from surveys in habitat judged to be suitable based on empirical studies in Washington and provide a baseline for comparison with results from future surveys. How these rates compare to historical occupancy rates, including those when the species was listed as threatened in 1993, is unknown. Several studies of other tree squirrel species provide occupancy estimates for comparison, although site suitability in terms of patch size or presence of competitors varied among survey sites. Occupancy of Eurasian red squirrels (*S. vulgaris*) in Italy varied from 0.32 to 0.41 and varied with patch size (Mortelliti et al. 2008) and presence of field mice (*Apodemus* sp.) (Mortelliti et al. 2010). In a study of eastern fox squirrels (*S. niger*) and eastern gray squirrels in Florida, Sovie et al. (2020) reported occupancy rates peaking in the 0.5 to 0.7 range, varying with presence of congenerics. That some apparently suitable habitat was found by our survey to be unoccupied is not surprising, as animal distributions, and the proportion of suitable habitat occupied, change with population size (Fretwell and Lukas 1970, Greene and Stamps 2001). We would expect a lower occupancy rate among these surveyed sites and similar sites within the project areas as populations decline and increasing occupancy rates as populations recover (Gaston et al. 2000, Tempel and Gutierrez 2013).

Underlying processes that affect detection in occupancy surveys include animal abundance, home range size, and animal movements within the home range over the course of the survey (Gaston et al. 2000, Steenweg et al. 2018). It has been suggested that results from occupancy surveys most closely align with animal abundance when sampling is conducted at the home range scale (MacKenzie and Nichols 2004, Noon et al. 2012) and may be optimal when the sampling cell (in our survey defined by the survey site) encompasses a single home range (Steenweg et al. 2018). The detection radius of our tube arrays was unknown but likely was in the range of 35 to 70m (up to twice the distance from the point to each tube) considering that squirrels use olfactory cues to locate food (Steele and Koprowski 2001). While each array in our sampling design might be considered a point, the 3 points that comprised our sampling sites worked in aggregate to sample a much larger area (Steenweg et al. 2018). With an overall length of 600m, our survey sites likely spanned an average female home range or the majority of a larger, male home range (Linders et al. 2004, Stuart 2012, Johnston 2013). Because male and female home ranges overlap (Linders et al. 2004) our survey sites potentially included ≥1 squirrel. Recognition of the walnut bait as food and willingness to enter the hair tubes were additional, behavioral processes necessary for detection. Previous live-trapping efforts and hair-tube surveys in Washington suggested that squirrels can take up to several weeks to begin consuming freely available walnuts (WDFW, unpublished data). By sampling over 8 weeks and visiting sites periodically to ensure that bait was available and tubes were operable we increased the likelihood that squirrels would enter the tubes and be detected during our surveys.

Occupancy surveys have inherent characteristics and assumptions that must be defined or considered in order to properly interpret their results (McKenzie et al. 2003). In the present survey we defined an occupied site as one where ≥1 western gray squirrel was present during the 8-week survey window. Under this definition, a survey site would be occupied if it intersected any squirrel home range in the forest stand, even though the site itself may have been visited only infrequently over the survey period. In our survey, inference of a positive site was to the forest stand that contained it; i.e., a positive site suggested the stand had ≥1 resident western gray squirrel. A key assumption stated in early papers on occupancy modeling is closure, or no change in occupied status over the span of the survey (McKenzie et al. 2003). Our survey approach met this assumption in that closure should apply to the forest stand that contained our survey site; western gray squirrels generally establish permanent home ranges that are the focus of their activities during their adult lives (Linders 2000, Vander Haegen et al. 2005). While we cannot exclude the possibility that a juvenile squirrel dispersing from its natal territory was detected as it passed through an otherwise unoccupied stand, we believe this to be unlikely given the lag between deploying walnut bait and first detections observed in previous live-trapping and hair-tube survey efforts. Moreover, the timing of our surveys likely preceded dispersal of most young from the female's home range (WDFW unpublished data).

Occupancy surveys can be most insightful when there is knowledge of the relationship between occupancy and abundance for the species being surveyed (Gaston et al. 2000). That relationship has not been examined for western gray squirrels, and the premise for our survey is based on the understanding that changes in occupancy most likely result from changes in abundance (Gaston and Blackburn 2003). Steenweg et al. (2018) used simulation modeling to examine the influence of various parameters on the occupancy/abundance relationship and found that surveys based on aggregate point data like those developed in our survey largely were insensitive to spatial scale but were affected by temporal scale. Surveys conducted over longer spans of time essentially integrate spatial use over time (Efford and Dawson 2012), with occupancy estimates increasing with longer survey periods (Steenweg et al. 2018). For future hair-tube surveys of western gray squirrels in Washington we recommend standardizing the survey period to 8 weeks to avoid this potential cause of variation.

Presence of western gray squirrels available to be detected in the forest stands we surveyed likely was influenced by habitat quality, so occupancy estimates also may have been influenced by habitat quality (Gaston et al. 2000, Tyre et al. 2001). While our criteria for site selection were based on extensive research in Washington and included what we identified as key habitat elements from these studies, there were unstudied metrics that may be of importance to the suitability of a site. Patch size, spatial context with other stand types and ages, and other landscape metrics that might influence occupancy have not been studied for western gray squirrels and were not considered in this study. Moreover, there are myriad unknown factors such as predator abundance, presence of competitors, and availability of various foods (e.g., hypogeous fungi) that were beyond the scope of this project. We can only base surveys on known relationships and we believe most surveyed stands were suitable habitat based on our criteria. Within the range of vegetation parameters measured on our survey sites, only dominant understory and percent open ground had measurable effects on occupancy, and these relationships appeared only in the South Cascades. The 2 sites in the South Cascades that had grand fir overstories did not fit our desired criteria for survey sites and may have been unsuitable habitat.

Although the occupancy rates documented for the 3 populations in this survey had a somewhat limited range, it is notable that occupancy in the North Cascades was considerably lower than in the South Cascades. Western gray squirrel habitat in the North Cascades may be more limited due to sharp elevation and vegetation gradients, with forests dissected by deep drainages, considerable grassland/shrubland communities, and steep slopes. These limitations on available habitat, combined with the lack of oaks as a food resource, may result in a more dispersed distribution. Currently, wildfire is the major factor affecting availability of habitat for western gray squirrels in the North Cascades (Vander Haegen et al. 2022). Under historic fire regimes in these communities we might expect a "shifting mosaic" (*sensu* Bormann and Likens 1979) of suitable habitat on the landscape, as low- to moderate-intensity wildfires reduce understory vegetation, with patches of more intense fire thinning or removing forest canopies, and as these stands regenerate over time to mature forest. These natural patterns have been interrupted by the increasing trend in large, stand replacing wildfires (Reilly et al. 2018, Prichard et al. 2020) that are removing forest canopy over extensive areas in the North Cascades and further fragmenting western gray squirrel habitat. This shift to larger, more severe fires likely is having a major influence on the distribution of western gray squirrels in the North Cascades.

In the South Cascades, timber harvest currently is having the greatest effect on availability of habitat for western gray squirrels (Vander Haegen et al. 2022). Repeated overstory thinning and complete overstory removal through clear-cutting has fragmented the landscape to a large degree, in some areas leaving riparian stringers as the only mature forest. In much of the industrial forests of eastern Klickitat County we found it difficult to located suitable remnant patches with sufficient canopy cover of large trees to meet our criteria as western gray squirrel habitat. The extent and spatial pattern of timber harvest on commercial timber lands likely is having a major influence on the distribution of western gray squirrels in the South Cascades.

The Puget Trough population is the most threatened of the 3 populations in Washington due to its small size and isolation (Linders and Stinson 2007, Vander Haegen et al. 2018). With a project area less than 10% the size of the 2 Cascade areas, surveys on JBLM examined occupancy at a much smaller scale. Despite the smaller scale and resulting closer proximity of survey sites, we found an occupancy rate similar to that in the Cascade populations, although the variance was greater due to smaller sample size. Sites surveyed on JBLM were not selected randomly but instead were based, in part, on knowledge of previously occupied areas. For this reason, the reported occupancy value should not be extended to other areas of the Base. Moreover, future surveys aimed at assessing change from the occupancy value presented here would be most valid if they resurveyed the same sites.

Similarity in the spatial patchiness of occupied sites between JBLM and the 2 Cascade areas can likely be attributed to the distribution of suitable habitat in the South Puget Trough, where habitat occurs in small patches (Johnston et al. 2020). Closely aligned with oak communities in these westside Douglas-fir systems, suitable habitat for western gray squirrels is naturally fragmented on JBLM (Johnston et al. 2020) which resulted in smaller sampled stands. Although conversion of forests to open areas for troop training and support infrastructure continues to fragment habitat on JBLM, the primary activity altering forest stands is timber harvest. Stand prescriptions currently employed on JBLM typically maintain a canopy of mature trees, including many of the larger trees in the stand, although it has yet to be determined if the canopy cover is sufficient or if the resulting understory is adequate for western gray squirrels.

This study represents the first assessment of occupancy for western gray squirrels in Washington and as such there are few data to draw upon for comparison. Washington Department of Fish and Wildlife Habitat Program has reviewed data on forest practice applications on non-federal lands annually since 2014 and has compiled a summary of applications that were flagged as including forest stands in potential western gray squirrel habitat in our South Cascades project area (reports on file with WDFW Habitat Program). For relevant applications, the results of nest surveys to ascertain presence of western gray squirrels was recorded. The number of applications identified in these summaries ranged from 56 to 112 annually and averaged 82. Surveys of 517 different sites over 6 years found positive indications of occupancy at 202 sites, yielding a naïve occupancy estimate of 39%. Although this naïve estimate did not account for detection probability (of nests), the fact that this independent dataset, collected during and just prior to our hair-tube survey and in the same general area, yielded a similar occupancy estimate (0.39 vs 0.44) provides support for our survey approach.

CONCLUSIONS

Surveys using hair tubes proved effective for documenting occupancy of western gray squirrels in Washington with a conditional detection probability of 0.91 (SE = 0.03). Occupancy rates ranged from 0.27 to 0.44 among the 3 population areas studied; how these rates compare to historical occupancy rates or those when the species was listed as threatened in 1993 is unknown. Occupancy rates resulting from this survey can be considered a baseline, representing conditions extant during the survey period and providing values that can be compared with those from subsequent surveys using similar or comparable techniques. Extant threats to habitat in all 3 population areas and recent habitat losses documented for the 2 Cascade populations make continued monitoring of these populations crucial for guiding management actions over the next few decades. Studies to establish the relationship between occupancy and abundance of western gray squirrels in Washington would allow additional insight to how the population is changing over time. We recommend that future occupancy surveys using hair tubes employ the described modification to secure bait in a wire cage to avoid theft by non-target species and that tubes be deployed for 8 weeks to ensure compatibility of results among surveys.

LITERATURE CITED

Amori, G., A. Mortelliti, G. Guidarelli, A. Schiavano, and L. Luiselli. 2012. Detectability of the European red squirrel (*Sciurus vulgaris*) in a Mediterranean area. Rendiconti Lincei-Scienze Fisiche E Naturali 23:203-206.

Bayrakci, R., A. B. Carey, and T. M. Wilson. 2001. Current status of the western gray squirrel population in the Puget Trough, Washington. Northwest Science 75:333-341.

Bertolino, S., L. Wauters, A. Pizzul, A. Molinari, P. Lurz, and G. Tosi. 2009. A general approach of using hair-tubes to monitor the European red squirrel: A method applicable at regional and national scales. Mammalian Biology 74:212-221.

Bormann, F. H., and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag, New York, USA

Boutin, S., L. A. Wauters, A. G. McAdam, M. M. Humphries, G. Tosi, and A. A. Dhondt. 2006. Anticipatory Reproduction and Population Growth in Seed Predators. Science 314:1928-1930.

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, Berkeley, USA.

Carraway, L. N., and B. J. Verts. 1994. Sciurus griseus. Mammalian Species 474:1-7.

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.

Efford, M. G., and D. K. Dawson. 2012. Occupancy in continuous habitat. Ecosphere 3:article32.

Fimbel, C., and S. Freed. 2008. Monitoring Western Gray Squirrels for Landscape Management in Western Washington. Northwest Science 82:299-308.

Fretwell, S. D., and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16-36.

Gaston, K. J., and T. M. Blackburn. 2003. Dispersal and the interspecific abundance-occupancy relationship in British birds. Global Ecology and Biogeography 12:373–379.

Gaston, K. J., T. M. Blackburn, J. J. D. Greenwood, R. D. Gregory, R. M. Quinn, and J. H. Lawton. 2000. Abundance–occupancy relationships. Journal of Applied Ecology 37:39-59.

Greene, C. M., and J. A. Stamps. 2001. Habitat selection at low population densities. Ecology 82:2091-2100.

Gurnell, J., P. W. W. Lurz, M. D. F. Shirley, S. Cartmel, P. J. Garson, L. Magris, and J. Steele. 2004. Monitoring red squirrels *Sciurus vulgaris* and grey squirrels *Sciurus carolinensis* in Britain. Mammal Review 34:51-74.

Hanski, I. 1991. Metapopulation dynamics: brief history and conceptual domain. Biological Journal of the Linnean Society 42:3-16.

Hunter, M. L., Jr. 1990. Wildlife, forests, and forestry: principles of managing forests for biological diversity. Prentice-Hall, Inc. Englewood Cliffs, N.J. 370pp.

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

Johnston, A. N., W. M. Vander Haegen, and S. D. West. 2020. Differential Resource Use between Native and Introduced Gray Squirrels. Journal of Wildlife Management 84:726-738.

Johnston, A. N., S. D. West, and W. M. Vander Haegen. 2019. Diets of native and introduced tree squirrels in Washington. Journal of Wildlife Management 83:1598-1606.

Joseph, L. N., S. A. Field, C. Wilcox, and H. P. Possingham. 2006. Presence-Absence versus Abundance Data for Monitoring Threatened Species. Conservation Biology 20:1679-1687.

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.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237–240.

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

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.

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.

Linders, M. J., and D. W. Stinson. 2007. Washington State Recovery Plan for the Western Gray Squirrel. Washington Department of Fish and Wildlife, Olympia. 128+ viii pp.

MacKenzie, D. I., and J. D. Nichols. 2004. Occupancy as a surrogate for abundance estimation. Animal Biodiversity and Conservation 27:461-467.

MacKenzie, D. I., and J. A. Royle. 2005. Designing occupancy studies: General advice and allocating survey effort. Journal of Applied Ecology 42:1105-1114.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200-2207.

McShea, W. J. 2000. The influence of acorn crops on annual variation in rodent and bird populations. Ecology 81:228-238.

Mortelliti, A., and L. Boitani. 2008. Inferring red squirrel (*Sciurus vulgaris*) absence with hair tubes surveys: a sampling protocol. European Journal of Wildlife Research 54:353-356.

Mortelliti, A., C. Cervone, G. Amori, and L. Boitani. 2010. The effect of non-target species in presence-absence distribution surveys: A case study with hair-tubes. Italian Journal of Zoology 77:211-215.

Noon, B. R., L. L. Bailey, T. D. Sisk, and K. S. McKelvey. 2012. Efficient species-level monitoring at the landscape scale. Conservation Biology 26:432-441.

Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing, 20–22 March 2003, Vienna, Austria.

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. 70:723-731.

Prichard, S. J., N. A. Povak, M. C. Kennedy, and D. W. Peterson. 2020. Fuel treatment effectiveness in the context of landform, vegetation, and large, wind-driven wildfires. Ecological Applications 30:e02104.

Reilly, M. J., M. Elia, T. A. Spies, M. J. Gregory, G. Sanesi, and R. Lafortezza. 2018. Cumulative effects of wildfires on forest dynamics in the eastern Cascade Mountains, USA. Ecological Applications 28:291-308.

Roderick, E. 1999. Western gray squirrel habitat mapping and surveys in Washington State, 1994-1996. Final Report to U. S. Fish and Wildlife Service, Partnerships for Wildlife Contract # P-1-D-2. Washington Department of Fish and Wildlife, Olympia.

Royle, J. A., and M. Kéry. 2007. A Bayesian state-space formulation of dynamic occupancy models. Ecology 88:1813-1823.

Ryan, L. A., and A. B. Carey. 1995. Distribution and habitat of the western gray squirrel (*Sciurus griseus*) on Ft. Lewis, Washington. Northwest Science 69:204-216.

Schmidt, K. A., and R. S. Ostfeld. 2008. Numerical and behavioral effects within a pulse-driven system: Consequences for shared prey. Ecology 89:635-646.

Sovie, A. R., D. U. Greene, and R. A. McCleery. 2020. Woody cover mediates fox and gray squirrel interactions. Frontiers in Ecology and Evolution 8:article239.

Steele, M. A., and J. L. Koprowski. 2001. North American tree squirrels. Smithsonian institution press, Washington, DC.

Steenweg, R., M. Hebblewhite, J. Whittington, P. Lukacs, and K. McKelvey. 2018. Sampling scales define occupancy and underlying occupancy–abundance relationships in animals. Ecology 99:172-183.

Stuart, K. D. 2012. Ecology and Conservation of the Western Gray Squirrel (*Sciurus griseus*) in the North Cascades, PhD Dissertation, University of Washington, Seattle.

Stuart, K. D., W. M. Vander Haegen, K. J. Jenkins, I. N. Keren, and S. D. West. 2018. Western gray squirrel resource selection related to fire fuel management. Journal of Wildlife Management 82:1478-1490.

Tempel, D. J., and R. J. Gutiérrez. 2013. Relation between Occupancy and Abundance for a Territorial Species, the California Spotted Owl. Conservation Biology 27:1087-1095.

Tyre, A. J., H. P. Possingham, and D. B. Lindenmayer. 2001. Inferring process from pattern: Can territory occupancy provide information about life history parameters? Ecological Applications 11:1722-1737.

Vander Haegen, M., and Keren, I. 2018. Pilot study for increasing the efficacy of hair-tube surveys for western gray squirrels in Washington. Final Report. Washington Department of Fish and Wildlife, Olympia.

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. 41pp.

Vander Haegen, W. M., G. R. Orth, A. N. Johnston, and M. J. Linders. 2018. Endemic diseases affect population dynamics of tree squirrels in contrasting landscapes. Journal of Wildlife Management 82:328-343.

Vander Haegen, M., B. Cosentino, I. Keren, M. Linders, and G. Bell. 2022. Assessment of habitat change for western gray squirrels in eastern Washington, 1993-2017. Draft Final Report (in prep). Washington Department of Fish and Wildlife, Olympia.

WDFW. 2015. Washington's State Wildlife Action Plan: 2015 update. Washington Department of Fish and Wildlife, Olympia.

Yamamuro, A.Y., K. Romain-Bondi, and P.H. Morrison. 2011. Western Gray Squirrel Distribution in the Upper Methow Valley, Washington. Report. Pacific Biodiversity Institute, Winthrop, Washington. 58 pp.

APPENDIX

JAGS code used for estimating occupancy of western gray squirrels using a latent variable approach in a removal design.

```
model{
   for(l in 1:n.area){
      psi[l] ~ dbeta(1,1)
   }
   theta ~ dbeta(1,1)
   phi ~ dbeta(1,1)
   p ~ dbeta(1,1)
   for(i in 1:n.site){
      Z.tr[i] ~ dbern(psi[area[i]])
   }
   for(j in 1:n.point){
      Z.pnt[j] ~ dbern(theta * Z.tr[site[j]])
   }
   for(k in 1:n.tube){
      Z.tb[k] ~ dbern(phi * Z.pnt[point[k]])
      fvisit[k] ~ dcat(xi[k,])
      xi[k , 1] <- 1 - Z.tb[k]  + Z.tb[k] * (1 - nvisit[k,1]*p - nvisit[k,2] * p * (1-p) - nvisit[k,3] * p * (1-p)^2)
      xi[k , 2] <- nvisit[k,1] * Z.tb[k] * p
      xi[k , 3] <- nvisit[k,2] * Z.tb[k] * p * (1-p)
      xi[k , 4] <- nvisit[k,3] * Z.tb[k] * p * (1-p)^2
   }
}
```