




## Research Article

# Differential Resource Use between Native and Introduced Gray Squirrels

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**ABSTRACT** Differences in habitat requirements and the spatial distribution of habitat for native and introduced species can determine outcomes of biological invasions. Introduced eastern gray squirrels (*Sciurus carolinensis*) have displaced native red squirrels (*S. vulgaris*) in Europe and have been implicated as a contributing factor to the decline of western gray squirrels (*S. griseus*) in North America. Eastern and western gray squirrels are associated with oak (*Quercus* spp.), but little is known about how these species interact. From April 2007 to April 2012, we radio-tracked sympatric eastern and western gray squirrels in western Washington to compare habitat use and evaluate competitive interactions. We developed resource utilization functions for each species and evaluated distribution of habitat on Joint Base Lewis-McChord, Washington, USA. Both species shared affinity for closed canopy forests and oaks; however, important differences in relationships with riparian areas and shrub cover resulted in low overlap in habitat distribution, which likely limited potential competitive interactions. Eastern gray squirrels appeared restricted to areas around wetlands likely because they supported the deciduous tree species that comprise habitat for this species in its native range. Use by western gray squirrels, but not eastern gray squirrels, significantly decreased with increasing shrub cover. Forestry practices that promote mixed oak-conifer with little shrub cover in uplands can benefit western gray squirrels and minimize interactions with eastern gray squirrels. © 2020 The Wildlife Society.

**KEY WORDS** competition, eastern gray squirrel, invasive species, resource utilization function, *Sciurus carolinensis*, *Sciurus griseus*, western gray squirrel.

Biological invasion by non-native species is a primary factor influencing losses in biodiversity, second only to habitat loss (Bellard et al. 2016). Mechanisms of displacement of native species by introduced species, such as predator-prey interactions, disease, habitat loss, and competition (Doherty et al. 2016, Gao and Reitz 2017, Young et al. 2017), can be mediated by niche similarity (Tilman 2004, Meszén et al. 2006). Accordingly, assessments of niche breadth, partitioning, and overlap are important steps in understanding the vulnerability of native species to threats from introduced species. Habitat is a fundamental component of the niche that can dictate outcomes of species interactions because similarity in habitat requirements and the juxtaposition of habitats influences interaction frequency (Schoener 1974). Niche theory suggests that coexistence among similar species may be achieved through differential habitat use (Hutchinson 1957, Hardin 1960, Keddy 2001), but habitat

requirements and the degree of differentiation necessary for coexistence are often unknown.

Outcomes of biological invasions can be influenced by the spatial distribution of areas suitable to interacting species (Tilman 1994, Stewart-Koster et al. 2015). For example, invasive barred owls (*Strix varia*) occupy a broad range of forest types that include old growth forests required by spotted owls (*S. occidentalis*; Hamer et al. 2007). This can provide a competitive advantage by allowing barred owls to outnumber spotted owls and infiltrate spotted owl territories across a wide range of landscapes (Dugger et al. 2016). In some cases, the spatial distribution of habitat can create refugia from competitors (Durant 1998, Paul and Post 2001). Competition between bull trout (*Salvelinus confluentus*) and introduced brook trout (*S. fontinalis*), for example, is concentrated in stream reaches with moderate temperatures that can support both species, whereas the coldest stream reaches are suitable only for bull trout (Rodtka and Volpe 2007). Mapping the spatial distribution of habitat for native and introduced species can provide important insights on habitat amount, distribution, and connectivity that influence interactions and population dynamics of species (Stevenson-Holt et al. 2014, Alakoski et al. 2019). Habitat suitability maps also enable identification of areas with species overlap to help managers

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prioritize treatments to recover native species. Recent advances in remote sensing, such as light detection and ranging (LiDAR), are improving the ability to characterize land-surface features and map habitat suitability at high spatial resolutions, especially for species that select resources at fine spatial scales (Johnston and Moskal 2017). This allows unprecedented assessment of resource partitioning and improved understanding of species interactions for species with small home ranges.

Eastern gray squirrels (*Sciurus carolinensis*) have been introduced to many regions across the globe and have replaced Eurasian red squirrels (*S. vulgaris*) in Europe through disease and competition (Wauters et al. 2005, Shuttleworth et al. 2016). Little is known about how eastern gray squirrels interact with native tree squirrels in western North America, where introduced eastern gray squirrels occupy some areas held previously by native western gray squirrels (*S. griseus*; Johnston 2013). Western gray squirrels were listed as a threatened species by the state of Washington in 1993, where habitat loss and competition with introduced squirrels are postulated reasons for population declines (Linders and Stinson 2007). Previous researchers have described habitat associations of western gray squirrels in the Cascade Mountains in some detail (Linders 2000, Gregory et al. 2010, Stuart et al. 2018), but only broad associations have been described for this species in western Washington (Ryan and Carey 1995, Bayrakçi et al. 2001, Fimbel and Freed 2008). Most remaining habitat in western Washington for western gray squirrels occurs in areas subject to timber harvest or expanding urban development. In contrast, habitat selection by eastern gray squirrels in western North America is poorly understood (Byrne 1979, Gonzales et al. 2008, Jessen et al. 2018), especially in undeveloped areas (Johnston 2013). Byrne (1979) reported strong affiliations of eastern gray squirrels with riparian areas and woodlands in California, USA, whereas western gray squirrels were in upland, conifer forests. Western gray squirrels commonly inhabit conifer-oak (*Quercus* spp.) forests and have not been reported to have strong riparian affiliations in Washington (Linders 2000, Gregory et al. 2010, Stuart et al. 2018). Such habitat differences between species may be important to interspecies interactions. Detailed habitat assessments are important for habitat management for western gray squirrels and to evaluate similarity in habitat requirements with eastern gray squirrels.

In western Washington, western gray squirrels exist as a small, isolated population that largely resides in undeveloped forests and woodlands on Joint Base Lewis-McChord (i.e., the Base), a military reservation near Tacoma, Washington. The distribution of western gray squirrels in Washington has decreased over the past century with increasing habitat loss from anthropogenic activities (Linders and Stinson 2007). Intensive efforts to study and recover western gray squirrels on the Base began in 2007 because of increasing evidence that this population was vulnerable to extirpation (Ryan and Carey 1995, Bayrakçi et al. 2001, Fimbel and Freed 2008). From 2007–2012, biologists augmented the population by releasing western

gray squirrels translocated from other populations in Washington and Oregon, USA, and monitored their movements alongside resident squirrels with radio-telemetry to investigate squirrel ecology and evaluate augmentation success (Vander Haegen and Orth 2011, Vander Haegen et al. 2018). Concurrently, Johnston (2013) radio-tracked eastern gray squirrels and experimentally removed some individuals to evaluate competitive interactions with western gray squirrels based on spatial partitioning, resource use, fitness correlates, diet (Johnston et al. 2019), and behavior. In the present study, no translocated females had spatiotemporal overlap with radio-tracked eastern gray squirrels and only 1 translocated female had spatiotemporal overlap with a resident, female western gray squirrel used in our analysis. Few translocated males overlapped with resident, female western gray squirrels used in our analysis.

Eastern gray squirrels were introduced to Seattle, Washington in 1925 and spread throughout urban areas around Puget Sound (Dalquest 1948). Eastern gray squirrels occur on developed portions of the Base since at least the early 1980s, but little is known about the population status in undeveloped areas on the Base. Smaller in size than western gray squirrels, eastern gray squirrels had smaller home ranges than western gray squirrels (7.7 vs. 35.2 ha) and occurred at greater density than western gray squirrels (0.11 vs. 0.032/ha) on the Base (Johnston 2013). Ryan and Carey (1995) reported that eastern gray squirrels were common in the housing areas on the Base in 1992–1993 but did not observe this species elsewhere on the Base. Bayrakçi et al. (2001) observed eastern gray squirrels in undeveloped areas on the Base in 1998–1999 but only within 1 km of residential areas. Fimbel and Freed (2008) used hair snags to detect eastern gray squirrels in many undeveloped areas on the Base from 2004–2007 and suggested that invasion of these areas was recent. Previous researchers may have failed to detect eastern gray squirrels in undeveloped forests on the Base because of their obscurity and occupancy of densely vegetated bottomlands (Johnston 2013). Experimental removals of eastern gray squirrels on the Base from 2009–2011 revealed that many eastern gray squirrels could invade removal sites about 1 year after trapping (Johnston 2013), which suggests that eastern gray squirrels could have saturated available habitat within interior portions of the Base by the time of this study.

Johnston (2013) did not detect strong effects of competition from eastern gray squirrels on western gray squirrels based on changes in spatial partitioning and fitness correlates following experimental removals of eastern gray squirrels. Although females of both species excluded other conspecific females from their high-use areas, competitive exclusion from preferred habitat was not apparent between species. Annual survival of female western gray squirrels on the Base (0.62) was comparable to that measured for a much larger population in southern Washington (0.64; Vander Haegen et al. 2018). In contrast, annual productivity of female western gray squirrels on the Base (0.94 female young/breeding age female) was lower than for females in southern Washington (1.3; Vander Haegen et al. 2018).

We evaluated resource use by gray squirrels on the Base to identify habitat associations and compare habitat distribution between species. Our main objective was to determine whether differences in resource use could influence interspecies interactions and potentially limit negative effects of an introduced species on a native congener. We predicted that shared dependence on oaks would result in high overlap in habitat distribution between the 2 species.

## STUDY AREA

We studied gray squirrels from April 2007 to April 2012 on Joint Base Lewis-McChord, a military reservation near Tacoma, Washington. The Base covered 35,000 ha, most of which was set aside as managed forests, prairies, and woodlands for use as training areas for military personnel. Elevation ranged from 120 m to 160 m, and terrain was mostly flat. Most precipitation fell as rain and occurred from October through March. Average precipitation in February and August from 1981 to 2010 was 14 cm and 2.5 cm, respectively (Daly et al. 2008). Average minimum temperature in February was 0°C, and average maximum temperature in August was 26°C. Historically, much of this region was maintained as prairie and oak woodlands through burning practices of Native Americans (Norton 1979). Over the past century, fire exclusion has allowed succession to proceed and at the time of this study, most of the Base was densely forested by young or mature (20–80 yrs) Douglas-fir (*Pseudotsuga menziesii*). Prairie remnants, Oregon white oak (*Quercus garryana*) woodlands, and ponderosa pines (*Pinus ponderosa*) were sparsely distributed throughout the Base. Riparian areas supported Oregon white oak, Oregon ash (*Fraxinus latifolia*), bigleaf maple (*Acer macrophyllum*), black cottonwood (*Populus trichocarpa*), red alder (*Alnus rubra*), and western red cedar (*Thuja plicata*). Common shrubs included snowberry (*Symphoricarpos albus*), beaked hazelnut (*Corylus cornuta*), Indian plum (*Oemleria cerasiformis*), and ocean spray (*Holodiscus discolor*). Sciurids on the Base included Douglas' squirrels (*Tamiasciurus douglasii*), northern flying squirrels (*Glaucomys sabrinus*), and Townsend's chipmunks (*Tamias townsendii*). Potential predators of tree squirrels included coyotes (*Canis latrans*), bobcats (*Lynx rufus*), cougars (*Puma concolor*), red-tailed hawks (*Buteo jamaicensis*), great horned owls (*Bubo virginianus*), and barred owls (*Strix varia*).

Eastern gray squirrels occupied developed and undeveloped portions of the Base, whereas western gray squirrels were only in undeveloped forests and woodlands (Johnston 2013). Much of the Base was surrounded by urban or agricultural areas that supported eastern gray squirrels but not western gray squirrels. In 2006, biologists removed 31 eastern gray squirrels from a 4,000-ha area on the Base to evaluate whether reducing the eastern gray squirrel population was a viable option for conservation of western gray squirrels (C. Fimbel, The Nature Conservancy, unpublished data). Some of these squirrels were trapped from areas that we subsequently included in our study; however, our subsequent trapping suggested that eastern gray squirrels had returned in numbers similar to what

existed before the removals. Johnston (2013) experimentally removed an additional 33 eastern gray squirrels from 3 sites in this study by trapping each site every 3–4 months from September 2009 to December 2011.

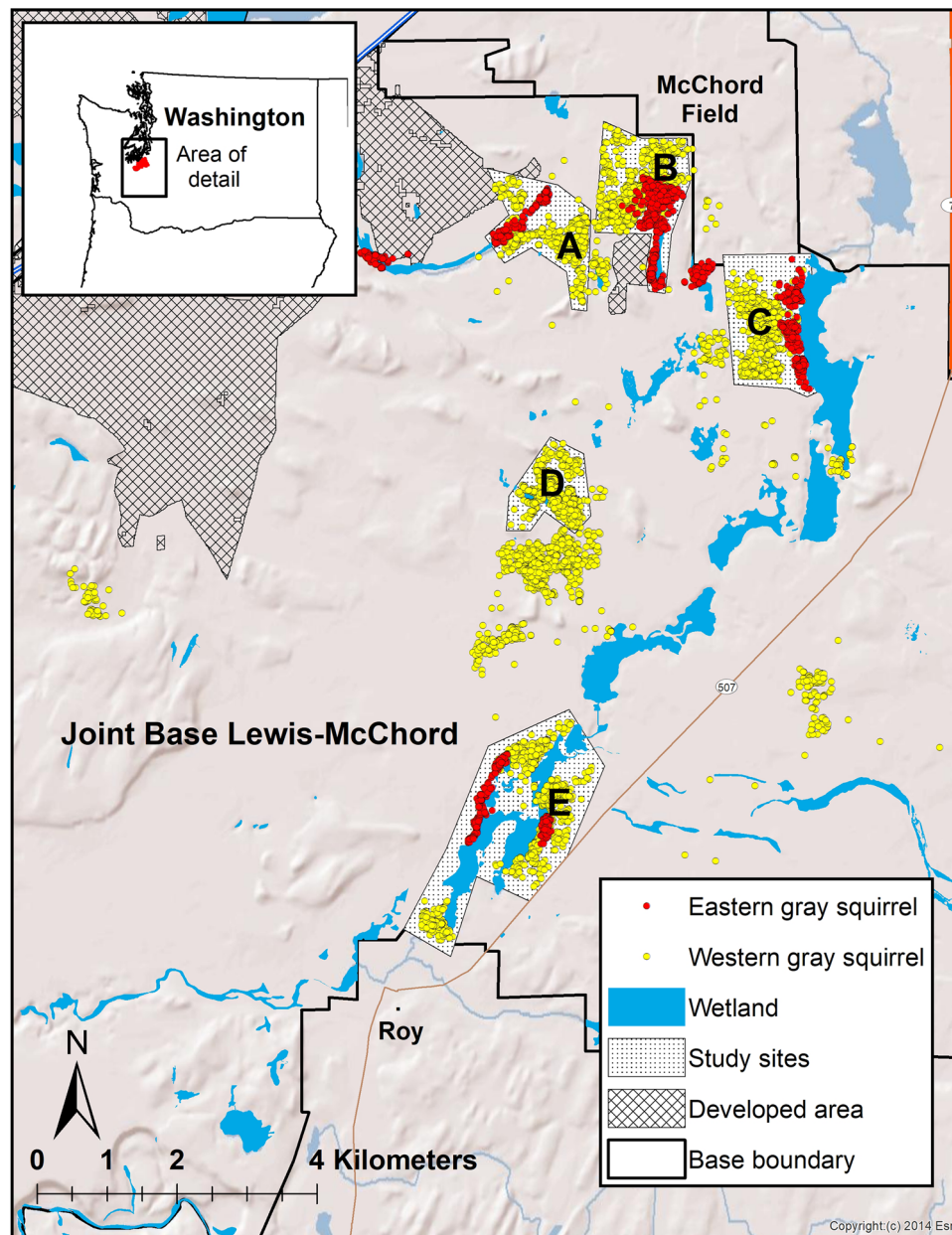
## METHODS

### Field Methods

We radio-tracked sympatric eastern and western gray squirrels in undeveloped forests on the Base from April 2007 to April 2012. We placed box traps (models 105 and 106, Tomahawk Live Traps, Hazelhurst, WI, USA), baited with whole walnuts, 50–100 m apart along transects in areas of forest cover and trapped squirrels for 3–7 days every 3–5 months. Transect length and configuration varied by site according to forest distribution; <100 traps were adequate to saturate most sites with traps. Our trapping efforts included intensive grid trapping of 2 sites in 2008 that informed transect configuration and length of trapping sessions for monitoring most or all squirrels in an area. Also, we conducted extensive exploratory trapping elsewhere on the Base to identify study sites. Site selection was guided by previous hair-snag surveys (Fimbel and Freed 2008) that showed western gray squirrels were most abundant on the eastern portion of the Base and that both species occurred in some areas. The limited number of sites known to support both species prevented random selection of sites. Our goal was to capture most, if not all, squirrels within each of 5 sites on the Base that were sufficiently separated such that female squirrels did not move between sites (Fig. 1). Males occasionally moved between sites during the breeding season. We radio-tracked both squirrel species at 5 sites that were units in experimental removals of eastern gray squirrels (Johnston 2013). We tracked western gray squirrels at additional sites on the Base but were unable to capture eastern gray squirrels in these areas, suggesting that they were absent.

We restrained squirrels in a cloth-handling cone (Koprowski 2002) to assess their condition and attach radio-collars. We equipped all squirrels with ear-tags (number 1005, National Band and Tag, Newport, KY, USA) and attached radio-collars (model SC-2, 15 g, 18-month battery, Holohil Systems, Carp, Ontario, Canada) to a subset of adult and sub-adult squirrels. We tracked all female squirrels and several males year-round within each site. We used radio-telemetry to home in on each squirrel until we saw the squirrel or pinpointed its location to within 10 m based on the radio signal. We used a global positioning system (GPS) unit (Trimble Navigation Limited, Westminster, CO, USA) to record 3 locations/week for each squirrel ( $\leq 1$  location/day) until death or the end of the study in April 2012. We followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) for trapping, handling, and tracking squirrels; this project was approved by the Institutional Animal Care and Use Committee at the University of Washington (protocol 2479-28).

We captured 72 female and 73 male western gray squirrels on the Base. Of these squirrels, we equipped 64 female and 28 male squirrels with radio-collars and collected >50



**Figure 1.** Study sites (7 South [A], Ammo Storage [B], Spanaway Marsh [C], Lake de Balon [D], Shaver Lake [E]) and telemetry locations for female gray squirrels (40 western gray squirrels, 16 eastern gray squirrels) included in habitat analyses with resource utilization functions on Joint Base Lewis-McChord, Washington, USA, 2007–2012 (Esri 2014). Telemetry locations among individuals are combined within species by color (i.e., red = eastern gray squirrel, yellow = western gray squirrel). Polygons for study sites identify areas of intensive trapping and monitoring of gray squirrels for investigations of competitive interactions with experimental removals of eastern gray squirrels. Following a pre-treatment tracking period, Johnston (2013) removed eastern gray squirrels from Spanaway, Shaver Lake, and de Balon. No locations for eastern gray squirrels are shown for de Balon because we captured and tracked only males at that site. We trapped and monitored squirrels in areas outside of the polygons frequently but did not detect both species in those areas to warrant their inclusion in removal efforts.

locations on 43 female and 15 male western gray squirrels. Tracking periods for female western gray squirrels included in the habitat analysis ranged from 6 to 50 months, and number of relocations ranged from 55 to 430. We also captured 31 female and 70 male eastern gray squirrels. We equipped 20 female and 17 male eastern gray squirrels with radio-collars and collected >50 locations on 16 female and 8 male squirrels. Tracking periods for female eastern gray squirrels included in the habitat analysis ranged from 5 to 49 months, and number of relocations ranged from 55 to 322.

### Habitat Data

We developed geographic information system (GIS) layers that described canopy height, canopy height variability, canopy cover, and shrub cover at 20-m resolution (Table 1) based on LiDAR data acquired with an Optec-Gemini Airborne Laser Mapping system in June and July 2010. This scanner recorded up to 4 returns per pulse with an average density of about 6 points/m<sup>2</sup>. We resampled a LiDAR-derived model of canopy height from 2.5-m to 20-m resolution by assigning the cell value as the maximum

**Table 1.** Predictors in resource utilization functions for gray squirrels on Joint Base Lewis-McChord, Washington, USA, 2007–2012.

Predictor <sup>a</sup>	Description
Canopy cover (%)	Proportion of all light detection and ranging (LiDAR) returns >3 m.
Canopy height (m)	Max. height from a canopy height model with 2.5-m resolution.
Canopy height variability	Standard deviation of heights from a canopy height model with 2.5-m resolution.
Shrub cover (%)	Proportion of all LiDAR returns <3 m with heights 1–3 m.
Distance to oak (m)	Euclidean distance to nearest oak based on land cover maps.
Distance to wetland (m)	Euclidean distance to nearest wetland based on maps.

<sup>a</sup> Predictors represented measures of canopy structure and shrub cover calculated over 20-m cells. Percentages were expressed as proportions with maximum range of 0–1 in the analysis.

height value of the 64 2.5-m cells encompassed by the new 20-m cell. We used the heights of the 64 2.5-m cells that fell within each 20-m cell to calculate the standard deviations of canopy height. We calculated tree canopy cover as the proportion of returns >3 m within each 20-m cell. Shrub cover was the proportion of all returns <3 m that occurred between 1 m and 3 m above the ground and had good correlation ( $R^2 = 0.67$ ,  $n = 211$ ) with shrub cover measured at ground plots (Johnston 2013). We used National Wetlands Inventory data layers to represent wetlands on the Base. Our data layer of oak woodlands combined mapping from aerial photography and field reconnaissance in 2003 (Chappell et al. 2003) and more recent data created through a fusion of LiDAR and high-resolution satellite imagery by researchers on the Base in 2007 (Chastain 2007). We edited this data layer to correct errors of omission and commission that we identified through field reconnaissance.

### Statistical Methods

We evaluated resource use by squirrels within their home ranges and mapped predicted use for the entire Base with a resource utilization function (RUF; Marzluff et al. 2004), which is a form of multiple regression that relates animal use to mapped resources and accounts for spatial autocorrelation inherent in habitat analyses based on animal tracking. The response variable is a continuous measure of use based on the utilization distribution (Kernohan et al. 2001) that is estimated from the spatial configuration of telemetry locations. All areas within an animal's home range (i.e., utilization distribution) are considered available to that animal. The RUF evaluates habitat relationships based on the measures of use and resources sampled across a grid of points that covers the home range. A Matern model (Handcock and Stein 1993) accounts for spatial autocorrelation among cell values for the regression based on the range of spatial dependence and smoothness of the utilization distribution surface. We developed a RUF for each squirrel using mapped resources, including LiDAR-based metrics of forest structure (Table 1), and then averaged predictor coefficients across RUFs to develop population RUFs for each species.

For each squirrel, we estimated fixed-kernel densities and utilization distributions (Kertson and Marzluff 2011) at 20-m resolution with the Geospatial Modeling Environment (Beyer 2012) and ArcGIS 10.0 (Esri, Redlands, CA, USA). We excluded repeat observations of squirrels within nests to avoid biasing measurements of use toward nest sites. We used the bi-variate plug-in from the KS package (Duong 2007) in R (R Development Core Team 2011) to estimate the smoothing parameter for each squirrel in the calculations of kernel density (Wand and Jones 1995, Wand 2006) because the plug-in was expected to work well based on the spatial configuration of squirrel locations (Gitzen et al. 2006). Squirrel locations often were distributed without excessive clustering or isolated groups. The height of the utilization distribution for each cell represented the relative use by the squirrel within its home range. We then converted the utilization distribution to a percent volume polygon, where contours identified 1–99 percentiles for probabilities of use by each squirrel. We created sampling grids with points that were spaced 20 m apart and centered on the cells of the rasters for habitat variables derived from LiDAR. We measured distance to the nearest oak stand and wetland for each sampling point to test associations with these habitat features. We extracted the values of squirrel use and habitat variables at each sampling point to develop RUFs with the *ruf.fit* package in R (Handcock 2011). We used the estimate of the smoothing parameter from the bi-variate plug-in (Wand 2006) for each squirrel as the starting point for estimating the range of spatial dependence in the Matern model. For the smoothing estimate, we used 1.5 derivatives as the algorithm's starting point for all squirrels.

We limited our analysis to female squirrels because males use habitat differently and because of low sample sizes for males. Females often occupied their high-use areas exclusive to other adult females, whereas males had high overlap with home ranges of other squirrels of both sexes (Johnston 2013). Habitat use by males was influenced by breeding activities that included frequent, long-distance movements in pursuit of females throughout the breeding season. This led to larger and more dynamic home ranges that were determined by the distribution of females across the landscape. Brief visits by males to high-quality habitat within female home ranges for mating purposes can mislead habitat analyses that are based on resource use. In addition, several males used areas beyond the extent of mapped resources, which would have limited our habitat analyses for males to 10 western gray squirrels and 5 eastern gray squirrels.

We created RUFs for 40 western gray squirrels and 16 eastern gray squirrels comprising all female squirrels that met our analysis criteria of >50 telemetry locations, excluding repeat use of nests, and home ranges within the extent of mapped resources. We excluded 3 of 43 female western gray squirrels with >50 locations from the analysis because 2 females used areas beyond the extent of mapped resources and 1 female had high overlap with a female that subsequently occupied the area. We randomly selected 5 squirrels from each species to screen variables for correlation and evaluate model fit. We retained all variables for

model building because none were consistently correlated ( $r > 0.7$ ) across squirrels. We evaluated the need for transformations and quadratic terms by examining residual plots from univariate RUFs for these squirrels. In all cases, the response variable was right-skewed because there were more low-use cells than high-use cells within the utilization distributions (Johnston 2013). Log transformation of the response normalized the response variable and residuals from RUFs. No quadratic terms or transformations of predictor variables were necessary. We examined residual plots from a rich model for each squirrel to ensure assumptions of multiple regression were met before proceeding with model building. We first created RUFs for each squirrel with all predictor variables and followed backwards selection (Ramsey and Schafer 2002) based on  $t$ -tests of coefficients (Marzluff et al. 2004) to determine which variables should be retained ( $\alpha = 0.1$ ) for final population models and mapping purposes. We created population RUFs for each species by averaging coefficient estimates across squirrels. For each squirrel species, we identified important habitat characteristics by ranking the standardized coefficients of the population RUF based on their magnitudes.

We evaluated model performance of final population RUFs for each species with  $k$ -fold cross validation (Boyce et al. 2002, Long et al. 2009). For each squirrel, we predicted its use with a population RUF created from the RUFs of all other conspecific squirrels. Then, we sorted the predicted values from lowest to highest and divided the data into 8 bins with equal numbers of observations. We summed the values of observed and predicted values within each bin and used simple linear regression to regress observed sums on predicted sums. High positive coefficients of determination and significantly positive slopes indicated good model fit. We reported average coefficients of variation and the number of squirrels with positive and negative slopes. In our calculations of the averages, we applied a negative sign to coefficients of variation when the slope was negative to account for poor model fit.

We used the final population RUF with unstandardized coefficients for each species to map their relative probabilities of use for the entire Base. We back-transformed the mapped probabilities to the original scale and reclassified

them as high-use or low-use based on a threshold value that corresponded to areas of 50% probability of use by individuals for which the model had a significant positive slope for regression of observed and predicted values. This threshold was the average of predicted values across areas of 45% to 55% probabilities of use from the percent volume polygons that were derived from utilization distributions of selected squirrels. Finally, we calculated the percent of high-use areas for western gray squirrels overlapped by high-use areas for eastern gray squirrels.

## RESULTS

Population RUFs indicated that use by eastern and western gray squirrels increased with oak proximity, canopy cover, and canopy height (Tables 2 and 3). Distance to oaks was the most important predictor for western gray squirrels, but the positive relationship of eastern gray squirrels with oaks was suggested only after backwards selection in the final population RUF ( $P = 0.055$ ). Evidence for a positive relationship of eastern gray squirrels with canopy height also was marginal in the population RUF with all predictors ( $P = 0.064$ ), and this predictor was included only in the final population RUF for western gray squirrels. Wetland proximity was the most important predictor of use by eastern gray squirrels because this species was strongly tied to riparian areas around wetlands. In contrast, western gray squirrels had no significant relationship with distance to wetlands. Canopy cover was the second most important predictor of use for both eastern and western gray squirrels. Unlike eastern gray squirrels, use by western gray squirrels decreased significantly with increasing shrub cover. The standard deviation of canopy height poorly explained use by gray squirrels (eastern  $P = 0.091$ , western  $P = 0.613$ ). With few exceptions, top predictors were consistent in the direction of correlation with use across squirrels.

Cross validation indicated that RUFs performed well for eastern and western gray squirrels (Table 4). The averaged coefficients of variation were high for both species despite a few squirrels that had negative relationships between observed and predicted values of use. Relationships between observed and predicted probabilities of use were positive ( $P < 0.05$ ) for most squirrels. Some negative relationships

**Table 2.** Means and 95% confidence intervals for standardized coefficients of resource utilization functions with all predictors, ranked from most (rank = 1) to least important for individual eastern and western gray squirrels on Joint Base Lewis-McChord, Washington, USA, 2007–2012.

Predictor <sup>a</sup>	Eastern gray squirrel				Western gray squirrel			
	$\bar{x}$	Lower CI	Upper CI	Rank	$\bar{x}$	Lower CI	Upper CI	Rank
Canopy cover (%)	0.1202***	0.0405	0.1999	2	0.0474****	0.0317	0.0631	2
Canopy height (m)	0.0714*	-0.0047	0.1475	4	0.0324**	0.0035	0.0613	3
SD canopy height	-0.0263*	-0.0573	0.0048	5	-0.0026	-0.0128	0.0077	6
Shrub cover (%)	-0.0025	-0.0334	0.0284	6	-0.0137**	-0.0265	-0.0010	4
Distance to oak (m)	-0.0875	-0.2495	0.0745	3	-0.2121****	-0.3236	-0.1005	1
Distance to wetland (m)	-0.3004***	-0.4809	-0.1199	1	-0.0100	-0.1539	0.1338	5

<sup>a</sup> Percentages were expressed as proportions with maximum range of 0–1 in the analysis.

\*  $P < 0.10$ .

\*\*  $P < 0.05$ .

\*\*\*  $P < 0.01$ .

\*\*\*\*  $P < 0.001$ .

**Table 3.** Means and 95% confidence intervals for unstandardized coefficients of variables included in final resource utilization functions for eastern and western gray squirrels on Joint Base Lewis-McChord, Washington, USA, 2007–2012.

Predictor <sup>a</sup>	Eastern gray squirrel			Western gray squirrel		
	$\bar{x}$	Lower CI	Upper CI	$\bar{x}$	Lower CI	Upper CI
Canopy cover (%)	0.5966****	0.3074	0.8858	0.1969****	0.1302	0.2636
Canopy height (m)				0.0017**	0.0001	0.0034
Shrub cover (%)				-0.1543**	-0.2964	-0.0122
Distance to oak (m)	-0.0066*	-0.0133	0.0002	-0.0027****	-0.0042	-0.0013
Distance to wetland (m)	-0.0086***	-0.0132	-0.0040			

<sup>a</sup> Percentages were expressed as proportions with maximum range of 0–1 in the analysis.

\*  $P < 0.10$ .

\*\*  $P < 0.05$ .

\*\*\*  $P < 0.01$ .

\*\*\*\*  $P < 0.001$ .

occurred for squirrels that did not follow the expected relationship with distance to wetlands or oaks. The population RUF poorly predicted use by 2 eastern gray squirrels that had core areas in low-lying areas with riparian vegetation but that did not have standing water and were not mapped as wetlands. Such areas were rare on our study sites. A third eastern gray squirrel was located alongside a wetland but had enough space between her core area and the wetland edge such that use increased with distance to wetland. Similarly, poor predictions occurred for some western gray squirrels that had core areas far from oaks but moved into areas with oaks seasonally when acorns were available.

Maps of predicted probabilities of use by eastern and western gray squirrels indicated that high-use probabilities for western gray squirrels covered substantially more area on the Base than those of eastern gray squirrels (4,591 vs. 300 ha, respectively; Fig. 2). Predicted probabilities for eastern gray squirrels were highest in riparian areas, and areas away from wetlands were predicted to have little or no use. In contrast, predicted habitat for western gray squirrels was limited by the distribution of oaks rather than wetlands. The proportion of high-use areas predicted for western gray squirrels that overlapped with high-use areas of eastern gray squirrels was 6.1% (Fig. 3).

## DISCUSSION

Habitats used by eastern and western gray squirrels differed in important ways based on riparian affiliations, forest composition, and shrub cover, which led to low spatial overlap between species (Johnston 2013). Fine-scale spatial partitioning between eastern and western gray squirrels occurred where

riparian areas with abundant shrubs and deciduous trees transitioned to upland areas dominated by conifers with little shrub cover. Interspecies avoidance may have occurred in these transitional areas, but areas suitable for both species were rare on the Base, according to relative probabilities of use predicted by RUFs. These results have important management implications for squirrel conservation and depend on an assumption that the differences in resource use reflect dissimilarities in habitat preference between squirrel species rather than competitive interactions (Rosenzweig 1991).

Resource use by species that share habitat requirements can be influenced by interference competition, whereby 1 species excludes another from its preferred habitat. The severity of competition and effect on resource use also depends on many factors including competitor abundances, spatiotemporal heterogeneity of resources, and similarity in preferred habitats (Wiens 1977, Chesson 2000). Competing species with different preferred habitats should occupy their preferred habitat until density of the species reduces habitat quality to a level that leads some individuals to use habitats of secondary preference (Morris 1988). Occupancy of high-use areas by female gray squirrels exclusive of other conspecific females was evident on the Base (Johnston 2013) and suggests that interference competition could explain some differences in resource use. We suggest, however, that eastern and western gray squirrels also differ in their preferred habitats based on our observations, experimental removals of eastern gray squirrels (Johnston 2013), and habitat associations of these squirrels reported elsewhere (Byrne 1979, Linders 2000, Gregory et al. 2010, Stuart et al. 2018).

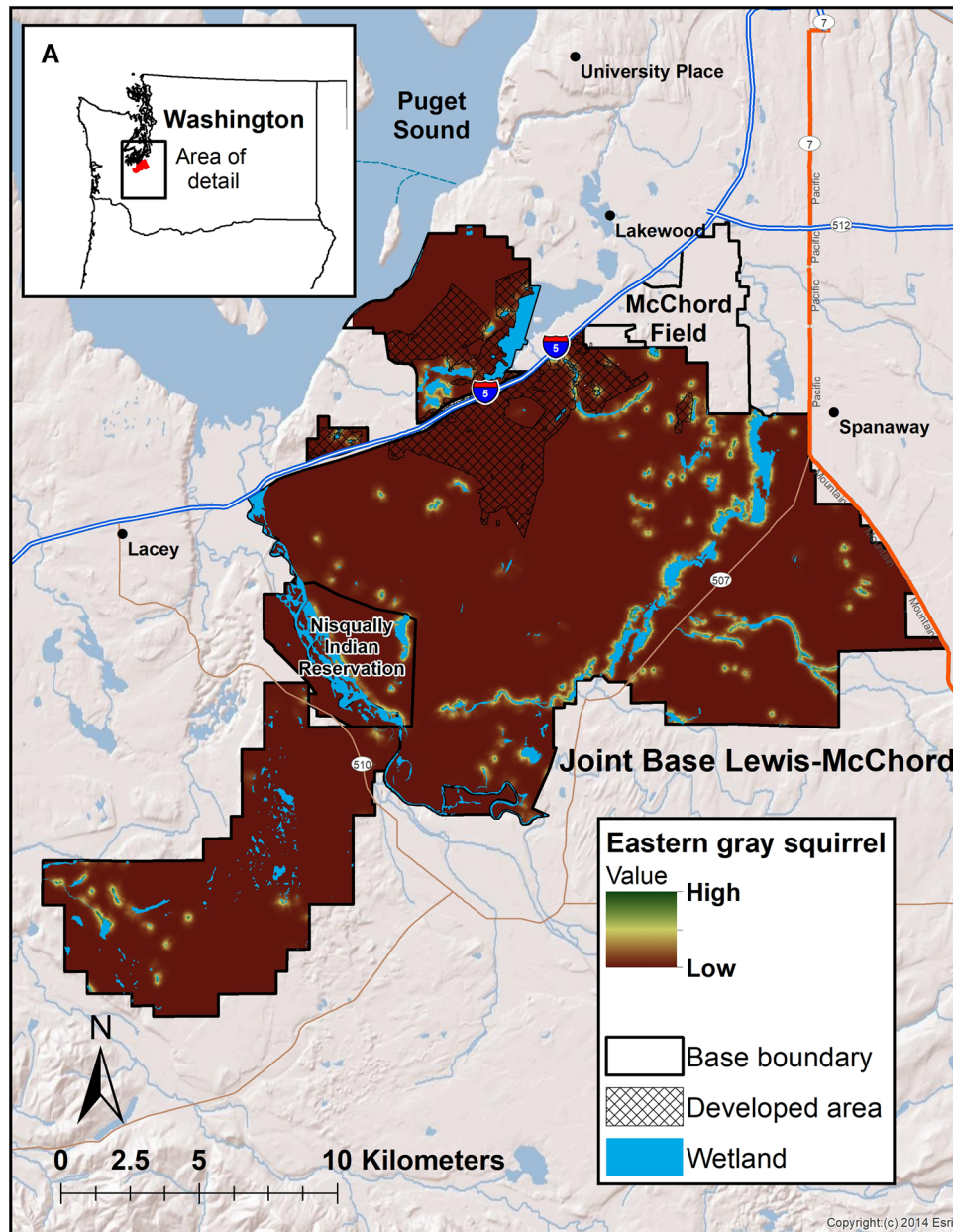
High abundances of an invasive species may be required to exclude native species from preferred habitats, especially when native species are superior in 1-on-1 encounters (Persson 1985) or native species occupy habitats secondary in preference for invasive species (Rosenzweig 1981). Both conditions may apply to eastern and western gray squirrels. Western gray squirrels might dominate eastern gray squirrels in 1-on-1 encounters because they average 148 g heavier than eastern gray squirrels (Johnston 2013), but outcomes remain poorly understood because we observed only 9 close encounters in 5 years of radio-tracking. Two or more eastern gray squirrels vocalized at a western gray squirrel on 4 encounters, and an eastern gray squirrel fled as a western

**Table 4.** Cross-validation results for resource utilization functions for eastern ( $n = 16$ ) and western ( $n = 40$ ) gray squirrels on Joint Base Lewis-McChord, Washington, USA, 2007–2012. We averaged coefficients of determination ( $R^2$ ) and  $t$ -statistics over all squirrels, whereas we tallied the number of positive (POS) and negative (NEG) slopes and the number of significant (sig;  $\alpha = 0.05$ ) slopes (ratio of positive to negative slopes = P:N).

RUF model	$R^2$	$t$	POS	NEG	POS (sig)	NEG (sig)	P:N	P:N (sig)
Eastern gray squirrel	0.64	4.6	13	3	13	0	4.3	
Western gray squirrel	0.42	3.7	31	9	24	5	3.4	4.8

gray squirrel approached within the same tree in another encounter. The other 4 interactions were non-agonistic, as these species foraged within 25 m of each other. It was unclear whether eastern gray squirrels had saturated their preferred habitats partly because of uncertainty about their invasion status in undeveloped areas of the Base. Low densities of eastern gray squirrels on the Base (Johnston 2013) relative to densities reported in their native range (Barkalow et al. 1970, Doebel and McGinnes 1974) were likely due to patchy distribution and low-quality of habitat. Eastern gray squirrels had similar litter sizes to those in their native range (Brown and Yeager 1945, Nixon et al. 1975), but fecundity, an indicator of habitat quality, was low

because many squirrels failed to reproduce and none had >1 litter/year (Nixon and McClain 1975, Johnston 2013). We did not find eastern gray squirrels away from wetlands despite extensive trapping for 5 years that included many upland areas unoccupied by western gray squirrels. Radio-tagged eastern gray squirrels did not inhabit former territories of western gray squirrels and vice versa. These observations were consistent with those from 1–2 years of monitoring western gray squirrels after removals of eastern gray squirrels (Johnston 2013). Translocated western gray squirrels had little or no influence on our measures of resource use based on low spatiotemporal overlap with squirrels in our analysis.



**Figure 2.** Relative probabilities of use by eastern (A) and western (B) gray squirrels, as predicted by resource utilization functions, on Joint-Base Lewis McChord, Washington, USA, 2007–2012 (Esri 2014). Predictions are stretched by minimum to maximum values. Predictions for McChord Field (former McChord Airforce Base) are not available.



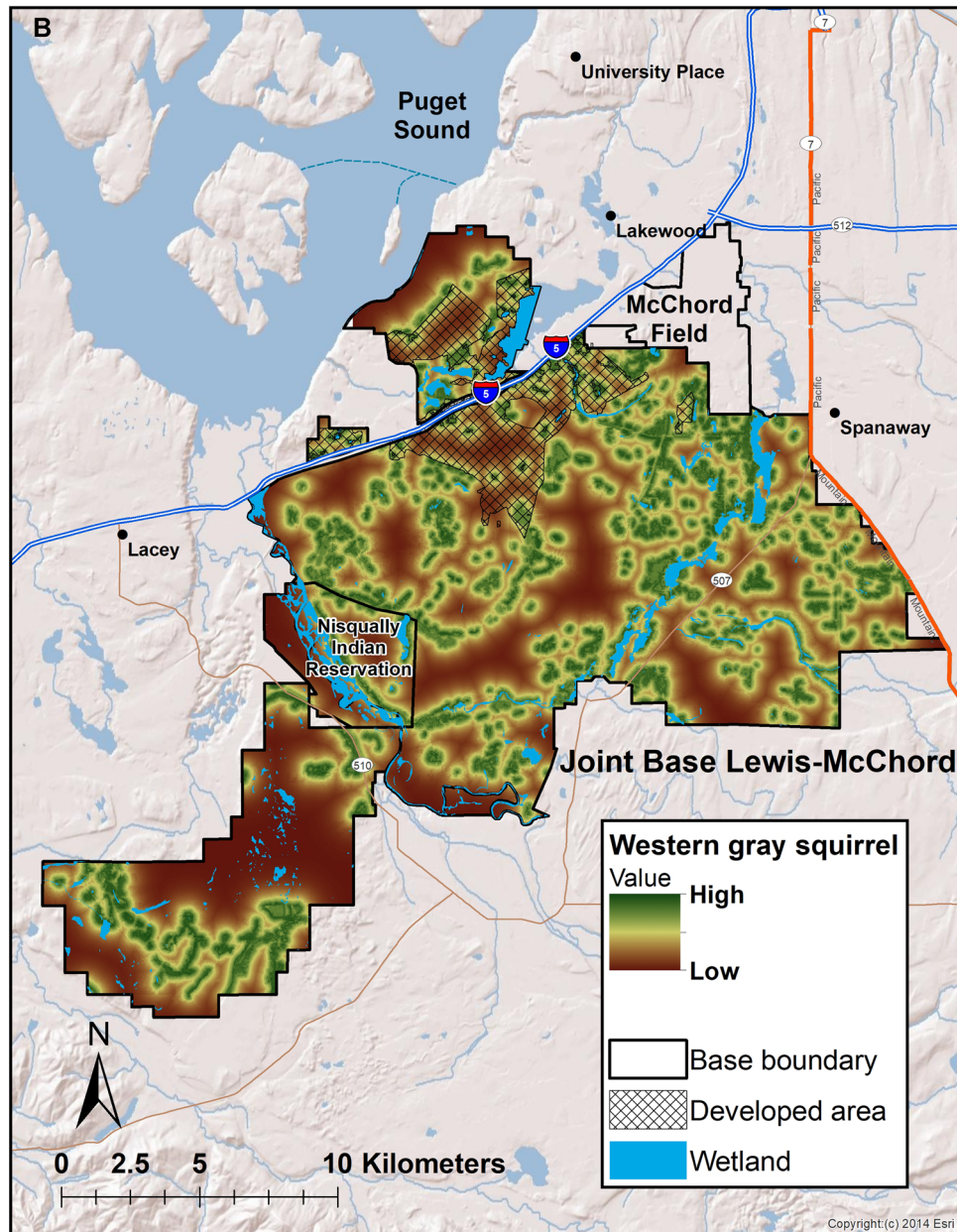


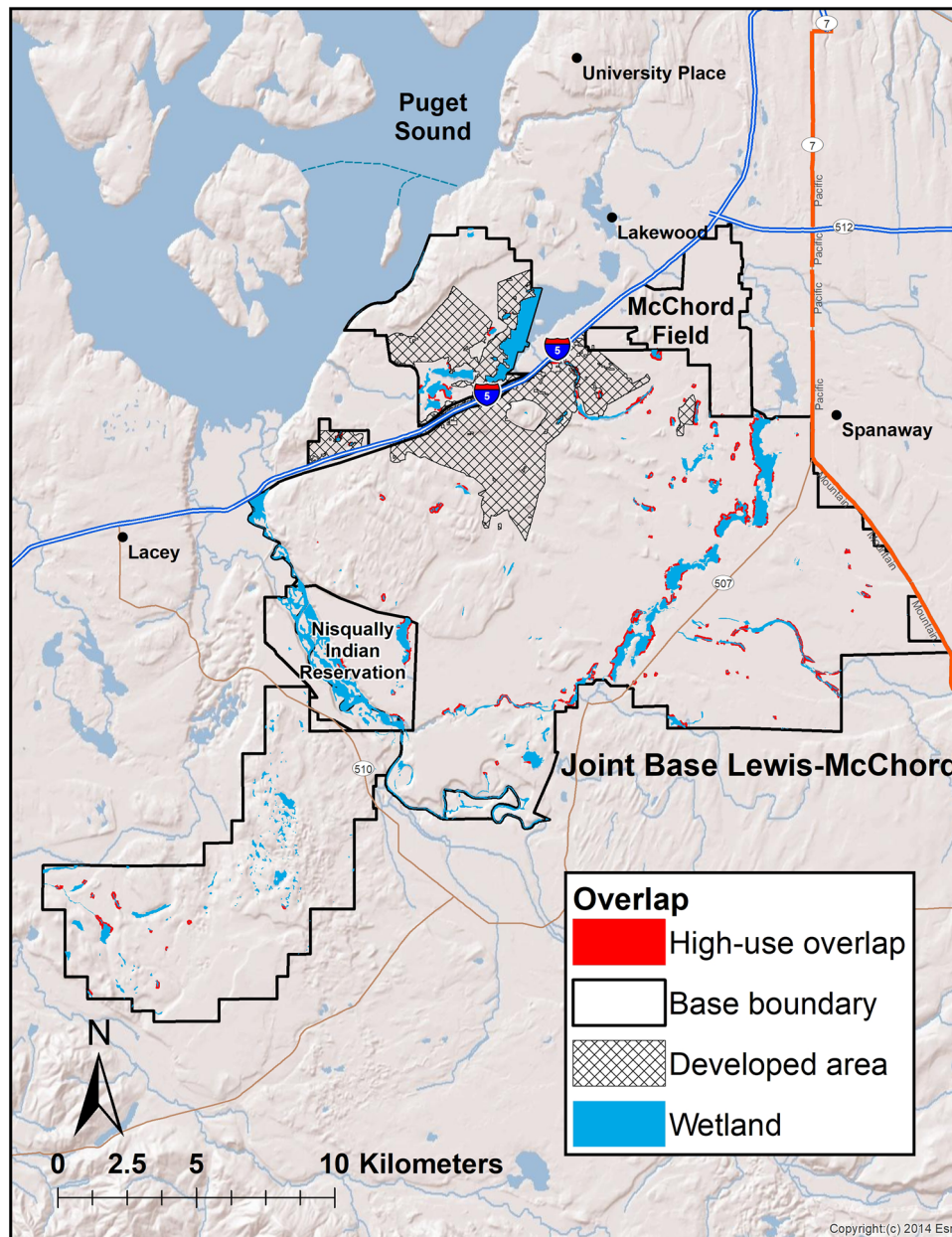
Figure 2. Continued.

Oak mast fluctuated prior to and during this study, which suggests that gray squirrels had experienced food shortages that could lead to competition. Oak masts failed and peaked every 2–4 years following productivity patterns typical of Oregon white oak (Peter and Harrington 2002, Devine and Harrington 2006), and a severe mast failure occurred in 2010, according to annual surveys (Peter and Harrington 2009) on the Base (D. H. Peter, U.S. Department of Agriculture Forest Service, unpublished data). Conifer mast failed the same year based on similar surveys of both Douglas-fir and ponderosa pine on our study area (Vander Haegen and Orth 2011). During these mast failures, squirrels sought alternative food sources (Johnston et al. 2019), including stripping of bark by western gray squirrels, indicating stressful conditions in 2010. Nevertheless,

habitats of gray squirrels differed between species, despite periodic shortages in important food resources.

### Riparian Affiliations

The most important difference in habitat use between eastern and western gray squirrels was the apparent dependence of eastern gray squirrels upon riparian areas on the Base. Wetlands on the Base were surrounded by a narrow band of deciduous trees within the riparian areas that transitioned to uplands dominated by conifers. Deciduous trees in riparian areas included tree species like those in eastern North America where eastern gray squirrels are native. Although oaks occurred in uplands on the Base and were important to both species of gray squirrels, other deciduous trees were uncommon away from riparian areas.



**Figure 3.** Overlap in high-use areas by eastern and western gray squirrels, as predicted by resource utilization functions, was low and occurred only near wetlands on Joint-Base Lewis McChord, Washington, USA, 2007–2012 (Esri 2014). Predictions for McChord Field (former McChord Airforce Base) are not available.

Riparian areas also had greater abundance and diversity of shrubs, some of which likely served as important food sources for squirrels (e.g., beaked hazel; Johnston 2013).

Eastern gray squirrels may be poorly adapted to conifer-dominated forests with little diversity of deciduous trees and shrubs. Douglas-fir and ponderosa pine were the dominant conifers on much of our study area, but we rarely observed eastern gray squirrels feeding on their seeds (Johnston et al. 2019). In their native range, eastern gray squirrels often use bottomland hardwood forests and avoid uplands dominated by conifers (Fischer and Holler 1991, Riege 1991, Steele and Koprowski 2001). In undeveloped areas of California, eastern gray squirrels were restricted to riparian areas, whereas western gray squirrels were most common in

upland forests dominated by conifers (Byrne 1979). These habitat differences in California may be explained by the finding that western gray squirrels consumed more truffles but fewer tree seeds than eastern gray squirrels. In Europe, eastern gray squirrels also used deciduous forests and avoided forests dominated by Douglas-fir (Bryce et al. 2002). Gray squirrels have replaced Eurasian red squirrels in <5 years in deciduous areas, whereas these species have coexisted for >40 years in areas dominated by conifers (Bryce et al. 2002). Density (Lurz et al. 1995) and survival (Kenward et al. 1998) of eastern gray squirrels is lower in areas dominated by conifers compared to deciduous trees in Europe. The occurrence of eastern gray squirrels in upland, conifer forests in Europe might be explained by the presence

of oaks and potential differences in nutritional quality of seeds from pine versus Douglas-fir. In Washington, the diversity of trees and shrubs in riparian areas may be particularly important to eastern gray squirrels for protection against food shortages during years of tree mast failure; low diversity of mast-producing species might prevent establishment of eastern gray squirrels in uplands (Nixon and Hansen 1987). Although eastern gray squirrels are common in some urban areas in western North America, they may be largely confined to developed areas where anthropogenic food sources like ornamental hardwood trees and exotic shrubs are abundant because native forests are mostly dominated by conifers in this region.

In contrast, western gray squirrels used some riparian areas on the Base but were largely found in uplands dominated by conifers with little shrub cover, consistent with studies elsewhere in Washington (Linders 2000, Gregory et al. 2010, Stuart et al. 2018). Linders (2000) indicated that some western gray squirrels briefly moved into riparian areas during breeding season to have young in tree cavities, and we observed similar behavior on the Base. Nevertheless, it was apparent that western gray squirrels do not require riparian areas to support populations in our study area. As in California (Byrne 1979), western gray squirrels on the Base, but not eastern gray squirrels, frequently foraged on seeds of conifers; however, both species consumed truffles with similar frequency in our study area (Johnston et al. 2019). Many riparian areas on the Base had dense shrub cover, which was a top predictor for discriminating habitats of eastern and western gray squirrels in analyses of vegetation at field plots (Johnston 2013). Likewise, shrub cover has been a key discriminator of habitats used by eastern gray squirrels and fox squirrels (*Sciurus niger*) in the eastern United States (Steele and Koprowski 2001). Coexistence of these species has been attributed to adaptations of eastern gray squirrels for densely vegetated bottomlands versus adaptations of fox squirrels to use upland forests dominated by pine with little shrub cover (Smith and Follmer 1972).

### Forest Structure and Composition

Our models indicated that canopy cover was important to both gray squirrels, most likely to facilitate travel, foraging, and protection from predators. Sparse canopy cover and dense shrub cover in some thinned, upland conifer stands may inhibit travel through the canopy and force western gray squirrels to travel through dense vegetation on the ground. Squirrels may avoid such areas because of predation risk and poor foraging opportunities. Although both species frequently placed nests in large Douglas-firs (Johnston 2013), the importance of tree height to western gray squirrels, but not eastern gray squirrels, in our models may be due to structural differences in forest types used by these species. Western gray squirrels often concentrated their use within forests with large, tall conifers, whereas eastern gray squirrels used deciduous forests with trees shorter than surrounding conifers.

Eastern and western gray squirrels on the Base shared affiliations with oaks, which may have led to convergence of these squirrels in some areas. All western gray squirrels had

oaks within their home ranges, and distance to oaks was the most important variable in the RUF analysis. The general distribution of western gray squirrels is mostly tied to oaks (Dalquest 1948, Carraway and Verts 1994), although there are exceptions beyond the range of oaks (Stuart et al. 2018). In addition to riparian areas, eastern gray squirrels also may be restricted to the distribution of oaks in undeveloped areas of Washington. Although riparian areas provided the greatest diversity of food sources, acorns likely provided substantially higher calories compared to other common food sources in this region. Eastern gray squirrels do not show similar limitations in the eastern United States because of the abundance and diversity of other mast-producing deciduous trees like hickory (*Carya* spp.) and walnut (*Juglans* spp.) in uplands.

### Habitat Distribution and Overlap

Our habitat suitability maps indicated that most habitat for western gray squirrels was uncontested by eastern gray squirrels because of the apparent restriction of eastern gray squirrels to riparian areas. Western gray squirrels often used forests strongly dominated by Douglas-fir with little shrub cover, provided that oaks were available somewhere within the squirrel's home range. These land cover types were common where prairie had been recently colonized by conifers and moss had replaced grass as the dominant ground cover (Foster and Shaff 2003). Eastern gray squirrels appeared unable to establish populations in such land cover types, even in the absence of western gray squirrels. Many eastern gray squirrels occupied pure deciduous stands in riparian areas, such as those of cottonwood or oak with dense shrub cover. The use of pure deciduous stands by western gray squirrels occurred primarily during bouts of foraging for acorns in the fall. These differences suggest that interactions between eastern and western gray squirrels may be concentrated in oak stands when seasonally available mast attracts both species.

Historically, habitat for western gray squirrels in the South Puget Sound lowlands occurred patchily over much of the region but now is largely confined to the Base (Linders and Stinson 2007). Sources of habitat loss for western gray squirrels in this region include urbanization, forest succession, and forestry practices that reduce the tree canopy to unsuitable levels (Gregory et al. 2010, Johnston 2013, Stuart et al. 2018). Western gray squirrels do not inhabit urban areas in western Washington, but areas surrounding the Base have become increasingly urbanized and support source populations of eastern gray squirrels. With a small, insular population imbedded in a largely urban and suburban landscape (Vander Haegen et al. 2018), western gray squirrels on the Base may be vulnerable to competition from invading species like eastern gray squirrels and to further habitat loss caused by changing forest structure and composition.

## MANAGEMENT IMPLICATIONS

Differential habitat use between eastern and western gray squirrels may limit the potential for competitive interactions, allowing coexistence where upland and riparian areas are abundant and distinct. High-resolution measures of forest

structure from LiDAR were useful to model squirrel habitat and allow managers to pinpoint areas for protection or treatment to conserve western gray squirrels. Western gray squirrels use conifer-oak ecotones that have historically been maintained by fire, so efforts to maintain or restore habitat for this species need to address the absence of this disturbance and the continued encroachment of human development on western gray squirrel habitat. Moreover, forestry practices that reduce canopy cover to levels that prohibit arboreal travel or stimulate growth of dense shrub layers likely reduce habitat quality for western gray squirrels on the Base. A significant challenge will be designing forest treatments that improve forest health and biodiversity while retaining the open understory preferred by western gray squirrels. Managers can conserve western gray squirrels by exploiting the differences in habitat requirements with eastern gray squirrels and minimize interspecies interactions by ensuring adequate habitat for western gray squirrels away from riparian areas.

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