Eastern Gray Squirrel Ecology and Interactions with Western Gray Squirrels

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Abstract

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Populations of State-threatened western gray squirrels (*Sciurus griseus*) have declined in areas invaded by introduced eastern gray squirrels (*S. carolinensis*) in the Western United States, but little is known about competitive interactions between these species. The western gray squirrel is an ecologically important member of oak woodlands, and intensive efforts to recover this species are underway in Washington. We tracked eastern and western gray squirrels with radio-telemetry for over four years to investigate resource use and interactions between species on Joint Base Lewis-McChord near Tacoma, WA. Following a pre-treatment monitoring period of 1-2 years, we experimentally removed eastern gray squirrels from two sites and monitored both species at two control sites for up to 2.5 years to measure competitive effects on western gray squirrels based on measures of spatial-partitioning, body mass, fecundity, and survival rates. We also described dietary overlap between species based on foraging observations and examination of fungal spores in fecal pellets collected from squirrels during the study. Dietary overlap for most food resources was high between eastern and western gray squirrels but they did not share space and had little overlap in their use of habitat types. Western gray squirrels were found primarily in coniferous uplands with little cover of understory vegetation, whereas eastern gray squirrels were in riparian areas with deciduous trees and dense cover of understory vegetation. Following removal treatments, few western gray squirrels used areas formerly occupied by eastern gray squirrels, and we found no increases in body mass, fecundity, or survival for western gray squirrels. Although interspecies avoidance or competitive interactions may occur in habitats suitable for both species, such habitats were rare on our study area. Coexistence of eastern and western gray squirrels appears possible where distinctly different upland and riparian habitats occur in an area.

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EASTERN GRAY SQUIRREL ECOLOGY AND INTERACTIONS WITH WESTERN GRAY SQUIRRELS

INTRODUCTION

Introduced species are among the most serious threats to biological diversity because they can negatively affect native species through mechanisms that include competition, disease, parasitism, and predation (Vitousek et al. 1996, Wilcove et al. 1998, Sax et al. 2005). Competitive interactions between native and introduced species most likely occur when animals are territorial or share dependence on limited resources (Keddy 2001). Consequently, competition from invasive species has been commonly cited as a cause for declines of native species with similar life history characteristics. However, the causes of species loss where biological invasions have occurred may be attributed to factors other than competition because subtle differences in niches can allow for coexistence of similar species (Hutchinson 1957, Hardin 1960). Invasions by introduced species often coincide with other environmental changes, such as habitat loss, that may obscure the negative effects of introduced species and complicate recovery strategies for imperiled species. It is important to understand potential threats to native species posed by introduced species so that conservation efforts aimed at maintaining biological diversity or recovering rare species are used efficiently.

Eastern gray squirrels (*Sciurus carolinensis*) are native to eastern North America but have been successfully introduced to the western United States, British Columbia, United Kingdom, Italy, South Africa, and Australia (Flyger and Gates 1982, Bryce et al. 2002) and replaced native tree squirrels in some regions (Wauters et al. 2005). Studies have suggested that eastern gray squirrels have replaced Eurasian red squirrels (*Sciurus vulgaris*) in the United Kingdom and Italy through exploitation competition, suppression of recruitment, and spread of parapox virus (Wauters et al. 2002, Tompkins et al. 2003, Gurnell et al. 2004). In the western United States, populations of western gray squirrels (*S. griseus*) have also declined in areas invaded by eastern gray squirrels, but competitive interactions between these species are poorly understood (Linders and Stinson 2007).

The western gray squirrel is native to Washington, Oregon, and California. Populations of western gray squirrels have declined throughout their range over the past century for many reasons including overhunting, habitat loss, automobile traffic, and possibly competition with introduced squirrels (Byrne 1979, Foster 1992, Weston 2005, Linders and Stinson 2007). The state of Washington listed the western gray squirrel as a threatened species in 1993 because populations had declined significantly, remaining in three disjunctive locations in the Puget Trough, North Cascades, and Klickitat County. The Puget Trough population is close to extinction and resides primarily on Joint Base Lewis-McChord (Base, hereafter), a military installation with approximately 35,000 ha of undeveloped forests, woodlands, and prairie that includes most of the remaining habitat suitable for western gray squirrels in the South Puget Sound region (Bayrakci et al. 2001, Warheit 2003, Fimbel and Freed 2008). Linders and Stinson (2007) estimated the breeding population of western gray squirrels in the Puget Trough to be 42 squirrels based on home range size, habitat availability, and squirrel detections between 1994 and 2005. In 2007, Washington Department of Fish & Wildlife began a 5-year project to augment the population of western gray squirrels on the Base with individuals from other populations in Washington and Oregon (Vander Haegen and Orth 2011). Competition from eastern gray squirrels present on the Base may jeopardize success of such a project and others to recover western gray squirrels.

Little is known about the timing and extent of invasion by eastern gray squirrels on the Base. Eastern gray squirrels were introduced to Seattle in 1925 and spread throughout urban areas around Puget Sound (Dalquest 1948). Eastern gray squirrels were present in developed areas of the Base at least as early as 1982 (Dave Clouse, pers com) and may have invaded this area much earlier. 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 with western gray squirrels in undeveloped portions of the Base. Bayrakci et al. (2001) observed eastern gray squirrels in areas occupied by western gray squirrels on the Base in 1998-1999, but only within 1 km of residential areas. Fimbel and Freed (2008) showed that eastern gray squirrels were widespread in the interior portions of the Base and suggested that the invasion of undeveloped forests was relatively recent. In 2006, The Nature Conservancy (TNC, unpublished data) removed 31 eastern gray squirrels from a 4,000 ha area on the Base to protect western gray squirrels and evaluate whether extermination of eastern gray squirrels was a viable option for conservation of western gray squirrels. Evidence of competition between these species from rigorous study or experimentation, however, has not been available to justify such management strategies.

Eastern gray squirrels are common in urban areas elsewhere in the Pacific Northwest and may interact with western gray squirrels in surrounding areas. Recently, eastern gray squirrels invaded Klickitat County, which supports the largest population of western gray squirrels in Washington. Eastern gray squirrels are known to occur along the Columbia River and its tributaries around Lyle and White Salmon, WA but the status and distribution of this population is unknown (Linders and Stinson 2007). In Oregon, eastern gray squirrels are thought to be confined to urban areas because they have been rarely observed in undeveloped habitats (Verts and Carraway 1998, Weston 2005). Eastern and western gray squirrels may co-occur in The

Dalles, Corvallis, and Eugene but the distribution of eastern gray squirrels and their effects on western gray squirrels in these locations are poorly understood.

Western gray squirrels bear ecological, social, and economic importance. Western gray squirrels are associated with oak woodlands, which is a high priority habitat type for conservation by state agencies (Larsen and Morgan 1998). Western gray squirrels help sustain oak communities by dispersing hypogeous fungi and acorns and serve as important prey items for raptors, bobcats, coyotes, and other predators (Maser et al. 1981). Western gray squirrels provide recreational opportunities for the public whether they are hunted or admired by wildlife viewers. In Washington, the western gray squirrel’s status as a threatened species has economic repercussions because it incurs restrictions on some management activities such as tree harvest. The presence of eastern gray squirrels complicates management activities and recovery efforts for western gray squirrels. Therefore, it is important to understand interactions between eastern and western gray squirrels and to determine whether control of eastern gray squirrels is needed to recover western gray squirrels.

The objective of this study was to test hypotheses that reveal the nature of competition between eastern and western gray squirrels. I monitored eastern and western gray squirrels with radio telemetry on the Base to examine resource use and interactions between species. I used an experimental removal of eastern gray squirrels to test for competitive effects of eastern gray squirrels on western gray squirrels based on measures of spatial partitioning and fitness correlates. I examined habitat use and diet of eastern and western gray squirrels to evaluate similarity in resource requirements and potential mechanisms of competition. Finally, I provided recommendations for management and recovery of western gray squirrels in the presence of eastern gray squirrels.

CHAPTER 1

Competitive Interactions of Eastern and Western Gray Squirrels

Eastern gray squirrels (*Sciurus carolinensis*) have invaded many areas throughout the Western United States including some that support western gray squirrels (*S. griseus*). Coincident losses of western gray squirrels in areas invaded by eastern gray squirrels suggest competitive interactions may threaten populations of western gray squirrels (Linders and Stinson 2007). Little is known about the nature of competition between eastern and western gray squirrels because few researchers have studied both species in sympatry (Byrne 1979, Fimbel and Freed 2008) and no study has manipulated populations to test hypotheses of competition.

Competitive interactions of eastern gray squirrels with other species have been studied for Eurasian red squirrels (*S. vulgaris*) and fox squirrels (*S. niger*) with differing conclusions. Considerable evidence has indicated that eastern gray squirrels out-compete red squirrels in Europe, though the mechanisms of competition have been elusive (Wauters et al. 2005). Eastern gray squirrels share high-use areas with red squirrels and interspecies interactions are rarely aggressive, which suggests that territorial behavior is nonexistent or ineffective between these species (Wauters and Gurnell 1999, Wauters et al. 2002). However, eastern gray squirrels may suppress recruitment and pilfer food caches of red squirrels (Wauters et al. 2002, Gurnell et al. 2004). In addition, spread of parapox virus to red squirrels by eastern gray squirrels may have contributed to their decline (Tompkins et al. 2003). In contrast, there is little evidence of competition between eastern gray squirrels and fox squirrels as differential habitat use seems to explain coexistence of these two species in most regions, and competition has not been detected where they share habitat (Brown and Batzli 1985, Steele and Koprowski 2001).

Interactions between eastern and western gray squirrels may differ from those of competitors studied elsewhere because western gray squirrels occupy a distinct geographic region and may have unique behaviors and social structures. Unlike red squirrels, western gray squirrels are larger than eastern gray squirrels and have larger home-ranges. Unlike fox squirrels, western gray squirrels have interacted with eastern gray squirrels only recently since their introduction to the Western United States during the past century.

Intraspecific partitioning of space reflects social structure of animals and varies widely among *Sciurids* from territorialism of *Tamiasciurus* to colonial behaviors of *Cynomys*. Patterns in spatial partitioning may result from behavioral interactions in which outcomes are determined by social dominance or in cases of interspecific partitioning, competitive dominance. Therefore, it is important to understand patterns of intraspecific spatial partitioning and to know whether potential competitors share space, avoid one another, or use different habitat types. Previous studies found low spatial overlap among female western gray squirrels, which suggests they may exclude others to control limited resources (Gilman 1986, Linders 2000, Gregory 2005). If interspecies overlap between eastern and western gray squirrels is similarly low, then spatial partitioning between these species may suggest avoidance behavior or differential habitat use. Exclusive control of areas important to western gray squirrels by eastern gray squirrels should suppress reproduction, survival, and immigration of western gray squirrels. Furthermore, a reduction in habitat available to western gray squirrels due to presence of eastern gray squirrels should increase intraspecific competition for western gray squirrels because of density-dependent relationships with habitat quality.

Intrinsic differences in demographic parameters such as reproductive rates between competing species can influence outcomes of competition. Eastern gray squirrels are capable of reproducing twice per year and may overwhelm western gray squirrels through higher recruitment rates (Nixon and McClain 1975, Layne 1998). Likewise, higher survival rates for eastern gray squirrels could lead to populations that exceed those of western gray squirrels. Measures of these demographic parameters may provide important insights into mechanisms of competition but have been unavailable from sympatric populations of eastern and western gray squirrels.

The ideal free distribution provides a theoretical framework for evaluating competitive effects between animals (Fretwell and Lucas 1969) by assuming that they can move freely among habitats and effectively evaluate the fitness rewards offered by each habitat. Animals achieve equilibrium when they are distributed such that no individual can achieve higher fitness by moving to another location. One implication of the ideal free distribution is that habitat quality is a function of the animal density, and it follows that removal of competitors should increase habitat quality by freeing resources for other consumers. Remaining individuals should then adjust their use of resources to maximize their fitness. Assuming squirrels follow an ideal free distribution, focused use of radio telemetry coupled with a manipulation of the abundance of competitors should facilitate hypothesis tests about competition between eastern and western gray squirrels.

The objective of this study was to test the hypothesis of competition through experimental removals of eastern gray squirrels and to compare measures of fitness correlates between eastern and western gray squirrels. We tested for a competitive release by western gray squirrels following removal of eastern gray squirrels based on metrics of spatial partitioning, body mass, survival, and reproductive rates. We examined patterns of spatial partitioning within and between species to evaluate its role in social structuring for each species and implications for interspecies interactions.

METHODS

Study area - We studied gray squirrels on Joint-Base Lewis-McChord (Base, hereafter), a military reservation near Tacoma, WA. The Base covers 35,000 ha, most of which was set aside as undeveloped forests, prairies, and woodlands for use as training areas for military personnel. Elevation ranges from 120 to 160 m, and average annual precipitation is 800-900 mm. Historically, much of this region was prairie and oak woodlands maintained 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 years) Douglas-fir (*Pseudotsuga menziesii*). Prairie remnants, oak woodlands, and Ponderosa pines (*Pinus ponderosa*) were sparsely distributed throughout the Base. Riparian areas supported Oregon white oak (*Quercus garryana*), Oregon ash (*Fraxinus latifolia*), big-leaf 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*). Eastern gray squirrels were present in developed and undeveloped portions of the Base, whereas western gray squirrels were found only in undeveloped forests. Much of the Base was surrounded by urban or agricultural areas that supported eastern gray squirrels but not western gray squirrels.

Field methods

We trapped and radio-collared eastern and western gray squirrels from July 2007 to April 2012 at four study sites on the Base that were designated as experimental units for removals of eastern gray squirrels. In addition, Washington Department of Fish and Wildlife biologists trapped and radio-collared western gray squirrels at nearby sites for a concurrent project to study and augment the population as part of a recovery strategy for this species (Vander Haegen and Orth 2011). We placed trap transects in forested habitats within each study site with the objective of saturating the site with traps to ensure that we captured most, if not all, gray squirrels in the area. We usually ran 30 to 50 traps per site depending on the extent and configuration of habitat. Traps along transects were spaced 50 to 100 m apart. Trapping sessions of 3 to 7 days occurred every 3 to 5 months at each study area. In addition, we frequently target trapped specific areas of each site between these sessions to recollar squirrels or assess squirrel condition, and these efforts occasionally captured new squirrels that had dispersed into the area. Overall, our trapping effort was intensive and sufficiently frequent throughout the duration of the study to track at least the majority of squirrels at any given site. Furthermore, our trapping records indicated high site fidelity of squirrels, and the ratio of recaptures to new captures suggested we had marked most or all squirrels at each site during the study.

We used Tomahawk live-traps baited with whole walnuts to trap squirrels. Traps were typically opened shortly after dawn and checked every 2 hours until early afternoon when traps were closed. Trap sessions were preceded by a 2-week pre-baiting period to acquaint squirrels with traps and improve capture probabilities. Traps were pre-baited by wiring the door open and baiting with walnuts 2 or 3 times per week. Upon capture, we restrained squirrels in a cloth-handling cone (Koprowski 2002) which allowed us to assess squirrel condition and attach a radio-collar. For each captured squirrel, we recorded body mass, reproductive condition, and noted any peculiar condition such as presence of alopecia or ectoparasites. Reproductive condition for females was evaluated by sign of nuzzle marks around teats, size of teats, and swelling of vulva. We palpated abdomens of females to check for imminent litters during breeding season. We noted whether males were scrotal upon capture. All adult female gray squirrels were equipped with radio-collars and ear-tags. We subsequently recaptured and weighed female squirrels every 3-4 months to monitor changes in body mass. We also applied ear-tags to all male gray squirrels and equipped a subset of males with radio-collars. We focused our resources on tracking all female gray squirrels because they are most important for driving population dynamics.

We relocated squirrels equipped with radio-collars three times per week by homing in on their location using radio-telemetry techniques. Squirrels were tracked throughout the diurnal period and were relocated once per day to ensure independence among locations. We tracked squirrels year-round until death or the end of study in April 2012. Squirrel locations were recorded with a GPS unit (Trimble Navigation Limited, Westminster, CO) once the squirrel was seen or estimated to within 10 m based on the radio-signal. Locations were differentially corrected to obtain accuracies of <5 m. At each location, we recorded squirrel behaviors, interactions, and general habitat characteristics of the area.

Following pre-treatment monitoring periods of 1-2 years, we selected two sites to remove eastern gray squirrels, and continued monitoring both species at the other two sites as controls. Post-treatment monitoring occurred for 1.5-2.5 years following the initial removal. Removal of eastern gray squirrels at the first removal site occurred in fall 2009, followed by removals at the second site beginning in fall 2010. We staggered removal treatments because of the high labor associated with radio-tracking squirrels and removal trapping. At removal sites, we laid trapping grids with 100-m spacing over the home-ranges of female eastern gray squirrels that we monitored during the pre-treatment period. We trapped removal sites for 7-day sessions every 3-

4 months during the post-treatment period, removing all eastern gray squirrels and equipping new female western gray squirrels with radio-collars. We also equipped most male western gray squirrels with radio-collars in the removal sites to monitor their use of areas formerly occupied by eastern gray squirrels. All eastern gray squirrels trapped at removal sites were euthanized within a CO_2 chamber following Institutional Animal Care and Use Protocol #2479-28.

We placed hair-snags at each trap station in the removal sites as a secondary means of monitoring squirrel activity (Fimbel and Freed 2008). Hair-snags were deployed with traps at the beginning of the pre-baiting period of each trapping session. Hair-snags were replaced at the end of the trapping session and retrieved approximately 2 weeks following trapping. Detection of eastern gray squirrel hair following trapping triggered additional trapping until intruding eastern gray squirrels were removed and additional sampling with hair-snags found no further detections.

In addition to these four study sites, we removed eastern gray squirrels from a third site (Debalon) that supported only male eastern gray squirrels. We reported results of this removal separately because unlike female eastern gray squirrels, intraspecific overlap among male squirrels was high. Although habitat use was similar between sexes for eastern gray squirrels, inclusion of data on interspecies overlap from male eastern gray squirrels at the Debalon site would confound results from other sites because the sums of overlap measures would be much higher for a western gray squirrel overlapping one area used by multiple male eastern gray squirrels than the overlap measures of a female squirrel.

We counted offspring of eastern and western gray squirrels through intensive monitoring and observation during the breeding season. Female squirrels were captured about every 3 months during the breeding season to examine reproductive condition. We identified nests used by squirrels showing signs of reproduction (nuzzle marks or pregnancy) by tracking their location before dawn. We then climbed the nest to count juveniles or placed cameras to record juveniles emerging from the nests. When juveniles were counted or observed by video cameras, we attempted multiple emergence counts and recorded the highest number of juveniles observed as the reproductive output. We estimated litter size using counts of juveniles (<5 weeks old) when nests were climbed or when cameras observed squirrels moving young to different nests. Fecundity was estimated by counts of juveniles during emergence when they began exploring the branches around the nest (approximately 5-8 weeks old). We considered emergence counts with <2 observations of the litter incomplete and omitted them from estimates of fecundity.

Statistical methods

We plotted squirrel locations onto maps with ESRI ArcGIS 10.0 and used a fixed-kernel density estimator in the Geospatial Modeling Environment 0.7.1.0 (Beyer 2012) to measure home-range size and create utilization distributions for measures of spatial overlap at 10-m resolution (Kernohan et al. 2001). We used a bi-variate plug-in estimator from the KS package in R for the smoothing parameter (Wand and Jones 1995, Wand 2006) because it should perform well based on the spatial configurations of our squirrel locations (Gitzen et al. 2006). For squirrels with >30 relocations, we measured areas of 95% home-ranges excluding repeat observations at nest locations to minimize bias in the kernel for repeated use of nest sites. We compared home-range size by species and sex with ANOVA and Tukey's HSD for multiple comparisons after log transformation (Zar 2010).

We measured the volume of intersection as an index of spatial overlap between individuals which used utilization distributions to account for squirrel activity within home-ranges (Seidel 1992). First, fixed-kernel densities were converted to volumes by dividing each cell by the sum of the cells within the squirrel’s home-range. Then, we summed the minimum volume shared by two individuals at each cell location to find the volume of intersection which was interpreted as the percent of shared space between individuals. Squirrels shared space with some individuals only part of the time in which they were monitored. Because squirrels may shift their use of space in response to vacancy of an area by a neighboring squirrel, we only used telemetry locations from periods of coincident monitoring to create utilization distributions for measures of overlap between squirrel pairs. For each squirrel, we measured its volume of intersection with all neighboring squirrels and summed those measures to find total overlap with other squirrels by sex and species. We measured total overlap because it is an index of interaction frequency among competitors, whereas other indices such as mean or maximum-individual overlap among neighbors may be inadequate to characterize such relationships. For example, important interactions between two individuals that share high-use areas may be masked using mean overlap when many competitors occupy the outlying portions of the focal squirrel’s home-range. Similarly, maximum overlap may underestimate interactions when multiple competitors have high overlap with the focal squirrel. Overlap measures were log-transformed and compared with ANOVA and Tukey’s HSD for multiple comparisons (α=0.05). Measures of overlap with male eastern gray squirrels were made at two sites (Ammo and DeBalon) where we attempted to collar all male squirrels. Similarly, overlap measures for male western gray squirrels were measured only from the Spanaway site because other sites had many male squirrels that were not monitored.

The total spatial overlap of each female western gray squirrel with eastern gray squirrels was averaged among all squirrels with overlaps >0 at each site for pre- and post-removal periods. At removal sites, the measure of post-removal overlap was between the utilization distributions of western gray squirrels measured after the removal and the utilization distributions from the eastern gray squirrels that had been removed. The pre-removal average was then subtracted from the post-removal average to calculate the change in the overlap from pre- to post-treatment monitoring periods. We log-transformed measures of change in overlap and used a *t*-test to test the null hypothesis that female western gray squirrels would not increase their use of areas occupied by eastern gray squirrels following their removal. A significantly positive value for the removal versus control sites would indicate western gray squirrels used areas formerly occupied by eastern gray squirrels more than expected following their removal. Although ANCOVA is commonly applied in analyses of data collected pre- and post-treatment where post-treatment data is modeled using the pre-treatment data as a covariate (Senn 2006), it was not applicable because most squirrels did not live during both pre- and post-treatment periods. Results of ANOVA for repeated measures were equivalent to those of the two-sided *t*-test.

We used one-sided *t*-tests to compare the change in the response variable between pre- and post-removal periods for our measures of body mass, reproduction, and survival. Body mass of each adult female western gray squirrel was averaged for pre- and post-removal periods using all measures taken within the respective monitoring periods. Measures of body mass for squirrels captured as juveniles were omitted from calculations of the average body mass until the squirrel lived beyond April 1 of the year following its birth. The average masses of these squirrels were then averaged among all females by site and monitoring period. We calculated fecundity for each squirrel and averaged them among females by site and monitoring period. As with body mass and spatial overlap, pre-treatment values were subtracted from post-treatment values, and we then used a *t*-test to compare these differences between control and removal sites.

Survival rates of female western gray squirrels were calculated by site and monitoring period with the known-fate estimator in R package Rmark (Cooch and White 2012). Models used monthly time-intervals, and squirrels were grouped into cohorts by the year tracking began. We used a biological year for this analysis that began April 1 because squirrels become capable of breeding and survival rates increase after their first year (Carraway and Verts 1994, Koprowski 1994). Juvenile squirrels tracked during their first year were censored until April 1 of the year following their birth. For each site and monitoring period, we censored observations outside of the monitoring period and used a covariate to identify squirrels at the site of interest. We added one dummy squirrel that was censored after 4 months to the data for 4 of the 8 data sets that each represented a site and monitoring period because Rmark would not estimate survival without at least one squirrel in each cohort. Point estimates for annual survival of squirrels at each site and monitoring period were recorded for subsequent analysis. Survival rates from each site during the pre-treatment period were subtracted from their post-treatment counterparts to calculate the change in survival rates for female western gray squirrels following removal of eastern gray squirrels. These changes in survival rates were compared between control and removal sites with a *t*-test that accounted for unequal variances (Zar 2010). We also estimated annual survival by species and sex using all data collected from April 2007 through March 2012. For comparisons of sex, eastern and western gray squirrels were analyzed separately, and survival estimates by sex were estimated by including a sex covariate in the model. Eastern and western gray squirrels required two and one dummy squirrels, respectively, that were censored after 4 months to ensure at least one squirrel in each cohort for their analyses. We combined sexes for species comparison because we found no differences between sexes in the previous analyses. We obtained annual survival estimates for each species by including a species covariate in the model. No dummy squirrels were required for this analysis.

We also calculated population level estimates of body mass, fecundity, and litter size for both eastern and western gray squirrels using all data collected throughout the duration of the study to compare demographic parameters by sex and species. We used ANOVA to test for effects of species, sex, season, and year on body mass of all adult squirrels captured from September 2007 through August 2011. Season was defined by categorizing 3-month intervals as fall, winter, spring, and summer where fall began September 1. For this analysis, years began in September because fall mast production should influence squirrel condition through winter and spring. We also tested for interaction between sex and season because of anticipated differences in body condition between sexes during breeding season (Koprowski 2005). We used log-linear regression for Poisson counts to compare fecundity between species and across years from 2008 through 2011 (Ramsey and Schafer 2002). Main effects and the interaction between species and year were tested based on the drop in deviance between full and reduced models for each factor. We repeated these procedures for analysis of litter size for years 2008-2010. Litter sizes from 2011 were omitted from this analysis because no eastern gray squirrels had litters that year.

RESULTS

From April 2007 through April 2012, 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 >30 locations on 54 female and 17 male western gray squirrels of which 35 females and 13 males were within the 4 sites of the removal experiment. Tracking periods for western gray squirrels included in the removal analysis ranged from 6 to 50 months, and the 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 >30 locations on 16 female and 14 male squirrels. Tracking periods for female eastern gray squirrels ranged from 5 to 49 months, and the number of relocations ranged from 55 to 322. The number of female eastern gray squirrels monitored at each site ranged from 3 to 5 and averaged 4, whereas the number of female western gray squirrels monitored at each site ranged from 6 to 10 and averaged 8.8. Study sites averaged 269 ha based on minimum convex polygons fitted around all telemetry locations of female gray squirrels within each site, and western gray squirrels occupied much larger areas than eastern gray squirrels within sites (Table 1.1).

We used radio-telemetry to home-in on squirrels 22,663 times. We observed behavior of western gray squirrels 3,268 times during 18,844 relocations and behavior of eastern gray squirrels 419 times on 4,227 relocations. During this study we observed interactions between eastern and western gray squirrels on nine occasions. On four occasions, two or more eastern gray squirrels were vocalizing at a western gray squirrel nearby. On one occasion, an eastern gray squirrel fled as a western gray squirrel approached within the same tree. Interactions in the remaining four observations were non-agonistic as eastern and western gray squirrels ignored one another as they foraged within the same tree or in close proximity (<25m).

Sizes of 95% fixed-kernel home-ranges differed significantly between eastern and western gray squirrels and between sexes within each species ($F_{3, 97}$=, $P<0.001$). Male western gray squirrels had the largest home-ranges, followed by female western gray squirrels, then male eastern gray squirrels, and finally female eastern gray squirrels (Table 1.2). All pair-wise comparisons of home-range sizes found differences ($P<0.001$) except between female western gray squirrels and male eastern gray squirrels ($P=0.955$). At 180.7 ha, home-ranges of male western gray squirrels were over 5 times larger than those of female western gray squirrels and over 23 times larger than those of female eastern gray squirrels.

Spatial overlap differed between species and between sexes within species ($F_{11, 121}$=36.8, P<0.001). The highest overlaps observed were among male western gray squirrels at 205% followed by their overlap with female western gray squirrels at 110% (Table 1.3). Overlap among female western gray squirrels was low at 41.7% but was still higher than overlap among female eastern gray squirrels at 5.7%. Western gray squirrels experienced little overlap by female eastern gray squirrels and vice versa. The highest overlap between a pair of female eastern and western gray squirrels was 26.5%, and most measures were <10%. Similarly, interspecies overlaps of male and female squirrels were low. Measurements of overlap by male squirrels with others were not available for some species by sex combinations because we attempted to monitor all males at only one or two sites for each species.

From October 2009 through 2011, we removed 28 eastern gray squirrels from the two removal sites of the experiment and five squirrels from DeBalon (Table 1.4). Following initial removal at each site, few eastern gray squirrels were captured within removal sites until fall 2011 when several eastern gray squirrels dispersed into these sites. Hair-snags detected presence of eastern gray squirrels following removal trapping on three occasions, where upon additional trapping succeeded in removing intruding squirrels.

Post-removal use of former territories of eastern gray squirrels by western gray squirrels remained low for most squirrels (Table 1.5). The change in overlap increased slightly at removal sites but decreased at control sites following removal (t_2=1.65, P=0.120). Five of six female western gray squirrels that used former territories of eastern gray squirrels likely dispersed into the study areas after the initial removals as they were not captured beforehand. The top three squirrels with the highest post-treatment overlap values (27, 47, and 59%) each concentrated their use within the former home-range of one eastern gray squirrel which suggests shared-selection of high-use areas. The squirrel with the highest overlap (59%) occupied this area for only three months before dispersing and settling elsewhere after the end of this study. The only squirrel that shared any space with eastern gray squirrels and that was present before and after removal treatments showed a slight increase from 2 to 11% in overlap after removal. Three other squirrels at removal sites that were tracked during both pre- and post-treatment periods maintained zero overlap with areas used by eastern gray squirrels after treatments. At the Debalon site, western gray squirrels decreased their use of areas occupied by male eastern gray squirrels following their removal. Three squirrels had low overlap (<5%) with eastern gray squirrels before and after removal treatment, but one squirrel had relatively high overlap, 80%, which decreased by 10% after the removal treatment. Body mass (t_2=0.23, P=0.421), fecundity (t_2=-3.6, P=0.966), and survival (t_2=2.1, P=0.139) for female western gray squirrels did not increase at removal sites from pre- to post-removal periods (Table 1.5).

Population level measures of body mass (Table 1.6) indicated western gray squirrels were 146 g (95% CI 135, 157) larger than eastern gray squirrels ($F_{1,\,470}$=789, P<0.001), and females were heavier than males for both species ($F_{1,\,470}$=10.5, P=0.001). Body mass fluctuated significantly by season ($F_{3,\,470}$=9.3, P<0.001) but not year ($F_{3,\,470}$=2.0, P=0.120), as squirrels were heaviest during winter and lightest during summer. There was no evidence of an interaction between sex and season ($F_{3,\,470}$=0.73, P=0.535) because body mass of male and female squirrels responded similarly to seasonal effects. Fecundity of eastern gray squirrels was lower than western gray squirrels (χ^2_1=10.8, P=0.001), and main effects for year was not significant (χ^2_1=2.5, P=0.117; Table 1.7). There was some evidence of an interaction between species and year (χ^2_1=3.4, P=0.064) because all eastern gray squirrels failed to reproduce in 2011, whereas fecundity of western gray squirrels was similar to previous years. Litter size did not differ between species (χ^2_1=0.23, P=0.631) or across years (χ^2_1=0.20, P=0.653), and there was no interaction between species and year for litter size (χ^2_1=1.4, P=0.237). Annual survival rates were similar between sexes for both eastern (male $\bar{x}$ = 0.593, 95% CI 0.375, 0.780; female $\bar{x}$ = 0.553, 95% CI 0.369, 0.724) and western gray squirrels (male $\bar{x}$ = 0.617, 95% CI 0.454, 0.757; female $\bar{x}$ = 0.604, 95% CI 0.503, 0.697). Annual survival was also similar between species (Table 1.7).

DISCUSSION

Low levels of spatial overlap between eastern and western gray squirrels suggest interspecies avoidance or differential habitat use occurred in areas of sympatry. Fine-scale spatial partitioning was evident where home-ranges of eastern and western gray squirrels overlapped because no squirrels shared high-use areas with those of the competing species. If female squirrels did not avoid other females of their own species or competing species, then we would expect to see overlap values similar to those of males. High intraspecific overlap among males and between males and females should be expected as males pursue females during the breeding season, but we found high overlap among males throughout the year which suggests greater tolerance of conspecifics within their core (ie. high-use) areas compared to females. Therefore, female squirrels appeared to occupy distinct territories from other females within and between species, and territory is likely the most important resource for which eastern and western gray squirrels may compete.

Western gray squirrels increased overlap with former territories of eastern gray squirrels at both removal sites while overlap decreased on controls, yet we failed to reject the hypothesis of no increase in overlap because of high variation in the responses between removal sites. Three western gray squirrels frequently used high-use areas of eastern gray squirrels after their removal at Shaver Lake, but such areas remained largely unused at Spanaway. Reasons for this variability may be related to differential habitat use between species, habitat variability between sites, low abundance of western gray squirrels, and the duration of post-treatment monitoring. Habitats used by eastern and western gray squirrels differed in forest structure and composition (see Chapter 2), so greater availability of habitats suitable for both species may have occurred at Shaver Lake. It is unlikely that eastern gray squirrels were excluding western gray squirrels from areas of substantially higher habitat quality because western gray squirrels with pre-established territories prior to removal treatments did not shift into areas used by eastern gray squirrels. Differential habitat use was the most likely reason for low interspecies overlap as we found few areas that were suitable to both species on the Base (see Chapter 2).

Although the population of western gray squirrels on the Base was believed to be critically low (Linders and Stinson 2007), we found areas vacated by western gray squirrels following mortality became occupied by other western gray squirrels within one year on several occasions. This suggests that the local population was sufficiently abundant such that dispersing squirrels likely encountered removal areas during the post-treatment monitoring period but chose to settle elsewhere. We monitored sites 1.5 to 2.5 years following removal of eastern gray squirrels that included up to 3 annual cycles of juvenile dispersal which was likely sufficient to detect moderate or strong effects of competition for territory.

Use of areas formerly occupied by eastern gray squirrels by some western gray squirrels was higher than any pre-treatment level measures which suggests that some areas occupied by eastern gray squirrels hold value for western gray squirrels. Consequently, the presence of eastern gray squirrels may prevent populations of western gray squirrels from meeting their full potential in distribution and abundance. Type II error may have occurred for tests that compared change in the response between pre- and post-treatment periods because treatments were applied to sites rather than squirrels, so sample size was four for each test despite the high numbers of squirrels tracked within each site. We surveyed a substantial proportion of the Base with hair-snags and traps to find sites with eastern and western gray squirrels within close proximity of one another but found only four sites suitable for the removal experiment. Low squirrel abundances and differential habitat use between eastern and western gray squirrels likely limited the number of areas that supported both species.

Few studies have described spatial partitioning between eastern gray squirrels and potential competitors. Interactions of eastern gray squirrels with other species have been studied most intensively for Eurasian red squirrels and fox squirrels. Most investigations of eastern gray squirrels and fox squirrels concluded coexistence was facilitated by differential habitat use (Edwards et al. 1998, Steele and Koprowski 2001). Some studies, however, found high spatial overlap between these species but failed to detect evidence of interspecific competition (Armitage and Harris 1982, Brown and Batzli 1985). Despite shared-use of space between species, Armitage and Harris (1982) indicated nearest neighbors were most likely conspecifics and fine-scale partitioning between species was evident based on activity centers. Although these studies measured spatial overlap based on results of trapping or visual encounter techniques, their results suggested higher levels of spatial overlap between species than we found for eastern and western gray squirrels with radio-telemetry. Wauters and Gurnell (1999) indicated intraspecific overlap of Eurasian red squirrels was similar to interspecific spatial overlap with eastern gray squirrels based on radio-telemetry data in Italy. They witnessed 32 interactions between species over one year or radio-tracking, whereas we observed only 9 interactions between eastern and western gray squirrels in >4.5 years of tracking. Wauters et al. (2002) reported interspecific overlap of 70% core (ie. high-use) areas of Eurasian red squirrel by eastern gray squirrels exceeded 100% for most squirrels and ranged upwards of 400% in this population. In England, interspecific overlap of Eurasian red squirrel core areas by eastern gray squirrels was higher than intraspecific overlap (Wauters et al. 2000). Therefore, spatial segregation appeared relatively strong between eastern and western gray squirrels compared to that of eastern gray squirrels with fox squirrels or Eurasian red squirrels.

Some patterns of intraspecies spatial overlap for western gray squirrels on our study area were similar to those found elsewhere in Washington. Spatial overlap among female squirrels was ≤7% in both Klickitat and the North Cascades populations (Linders 2000, Linders et al. 2004, Gregory 2005). Overlap among males was similarly low (≤17%) in these populations which was considerably lower than our overlap measures. In California, overlap among females was 13%, and male overlap was 26.9% (Gilman 1986). Notably these studies used two-dimensional measures of overlap following home-range estimation using minimum convex polygon or fixed-kernel methods which likely yield different estimates of overlap compared to the volume of intersection that accounts for squirrel activity within the home-range. Nevertheless, their results also suggest low levels of intraspecies overlap for western gray squirrels, particularly for females. Although gray squirrels are not considered territorial and we did not observe any squirrels actively defending territory, these patterns of exclusive core areas for female western gray squirrels suggest they communicate occupancy to other squirrels for purposes of exclusion, perhaps through scent marking (Koprowski 1993). Male gray squirrels are socially dominant over females and appeared to use their core areas freely (Koprowski 1994). Female gray squirrels may exclude subdominant females from their core areas to exert some control over resources. We observed some variation in overlap among females, so overlap may depend on habitat quality or relatedness among squirrels.

Patterns of intraspecies overlap for eastern gray squirrels were remarkably similar to those of western gray squirrels. Females had little overlap with other females and relatively high overlap with males. Overlap among males was highest for all possible comparisons of intraspecies overlap by sex for eastern gray squirrels. Gurnell et al. (2001) found similar patterns for eastern gray squirrels in Italy where overlap of 70% core areas between females was <1%. They also found highest overlap among males followed by male-female overlap. They described their study area as high quality habitat and found high reproductive rates for eastern gray squirrels which suggests patterns of low overlap among females is unrelated to habitat quality. There are no comparable studies of intraspecies overlap among eastern gray squirrels that used radio-telemetry techniques from within their native geographic range. Studies that used trapping and visual encounter techniques indicated high levels of intraspecies spatial overlap regardless of sex (Thompson 1978a, Don 1983). Eastern gray squirrels may achieve densities within their native range that are far greater than those observed in our study area which might suggest higher overlap among females (Fischer and Holler 1991). However, home-ranges reported from these regions are also relatively small (<1 ha), so fine-scale partitioning may not be detectable using trapping or visual encounter techniques. It is unlikely eastern gray squirrels will reach high densities on the Base as seen elsewhere due to poor habitat quality and the limited distribution of suitable habitat (see Chapter 2).

Home-ranges of male and female western gray squirrels were much larger than their eastern gray squirrel counterparts, a discrepancy that could have important implications for interspecies interactions. If habitat use was similar for these species and if females compete for space, a given area could support four times as many female eastern gray squirrels as western gray squirrels which may allow eastern gray squirrels to overwhelm western gray squirrels by force of numbers. Larger home-ranges for western gray squirrels, however, may result from differences in habitat use or diet and expose western gray squirrels to greater predation risks.

Home-ranges of western gray squirrels on the Base were smaller than those measured at the northern edge of their geographic range (Gregory 2005) but larger than those in Klickitat Country, WA (Linders et al. 2004). Home-ranges of western gray squirrels in all three Washington populations are larger than those found in Oregon and California (Cross 1969, Gilman 1986, Foster 1992), which is thought to be related to low habitat quality in Washington (Linders et al. 2004). Home-ranges of eastern gray squirrels in our study area were similar in size to those found in England (Wauters et al. 2000) but more than double the size of home-ranges measured in Italy (Gurnell et al. 2001). In the Eastern United States, home-ranges for female eastern gray squirrels are commonly <5 ha and fall below 1 ha in some areas (Flyger and Gates 1982, Don 1983). Relatively large home-ranges for eastern gray squirrels on the Base support our finding of limited habitat availability for this species (see Chapter 2).

We found no evidence for competitive effects of eastern gray squirrels on survival, reproduction, or body mass of western gray squirrels. It is not surprising that these fitness correlates were unaffected by removals of eastern gray squirrels because low levels of overlap between areas used by eastern and western gray squirrels remained unchanged following treatments. Survival and reproductive rates were similar between species which suggests that eastern gray squirrels will not outnumber western gray squirrels based solely on these demographic parameters. We did not observe any eastern gray squirrels produce more than one litter per year as reported elsewhere in the Eastern United States and England (Nixon and McClain 1975, Layne 1998, Wauters et al. 2000). It is noteworthy that most of these reports have been based on observations of placental scars which are not necessarily indicative of successful weaning of juveniles because intrauterine losses can account for >30% of implanted embryos (Swift 1977, Nixon and McClain 1975). To our knowledge, no study has confirmed successful weaning of two litters in a year by eastern gray squirrels based on counts of juveniles at nests. Wauters et al. (2000) reported 40% of the eastern gray squirrels they tracked in England had two litters in a year based on observations of lactation during captures. We observed two instances where western gray squirrels produced two litters in a year based on counts of juveniles which are the first confirmed cases for this species despite >10 years of monitoring reproductive rates in Washington. Each of these litters was small, 1 or 2 individuals, so second litters may have been possible due to relatively low energy expenditure on the first litter. Habitat availability and proximity of source populations, rather than differences in reproductive and survival rates, may best explain reasons eastern gray squirrels outnumber western gray squirrels in some areas as much of the Base was surrounded by urban areas that supported eastern gray squirrels but not western gray squirrels.

Reproductive rates and litter sizes for eastern and western gray squirrels were mostly similar to those of populations in other regions. Vander Haegen et al. (2005) reported means of 3.3 squirrels per litter and 2.5 juveniles per litter that survived >8 weeks for western gray squirrels in

Southcentral Washington which suggests slightly higher reproductive rates than those found on the Base. Average litter sizes for western gray squirrels in California ranged from 2.2 to 2.8 based on embryo counts (Ingles 1947, Fletcher 1963, Swift 1977). Litter sizes of 2-3 eastern gray squirrels are typical with little regional variation based on reports from 20 studies throughout the Eastern United States and Canada (Layne 1998). Comparable fecundity estimates for eastern gray squirrels based on emergence counts from other regions are not available (Layne 1998). Wingard (1950) reported litter sizes of 2.8 juveniles for eastern gray squirrels based on the number juveniles seen outside of nests in Pennsylvania but this value does not account for squirrels that failed to reproduce. The large discrepancy between litter size and fecundity that we found was due to the high numbers of eastern gray squirrels that failed to reproduce which might be explained by the scarcity of suitable habitat for eastern gray squirrels on the Base (see Chapter 2).

Annual survival rates of eastern and western gray squirrels were similar to those found elsewhere. Annual survival rates for male and female western gray squirrels in Southcentral Washington were 0.55 and 0.62, respectively (Vander Haegen et al. *in press*). Survival rates of adult eastern gray squirrels in the Eastern United States range from 43 to 57% (Mosby 1969, Barkalow et al. 1970, Thompson 1978b). Kenward et al. (1998) reported that annual survival rates of eastern gray squirrels in England ranged from 50% at conifer sites to 82% at deciduous sites.

Western gray squirrels were considerably larger than eastern gray squirrels which may have important implications when these species interact because large body size should be advantageous in one-on-one encounters. Western gray squirrels on the Base weighed less than those in Klicktitat County, WA (mean = 842g; Linders 2000) and in some regions of California (mean = 895g; Gilman 1986) but not others (mean = 749g; Crase 1973). Regional variation in body mass has been observed in fox squirrels and may be related to regional variation in food availability or habitat quality (Weigl et al. 1998). Fox squirrels are largest in regions with abundant pine or hardwoods and smallest in regions at moisture extremes. Likewise, western gray squirrels in Washington are largest in areas dominated by pine (Linders and Stinson 2007). Small body size, coupled with large home-ranges and declining populations, might suggest poor habitat quality for western gray squirrels on the Base.

Body mass of adult eastern gray squirrels ranges from 300 to 710 g and follows Bergmann's rule within their native geographic range (Uhlig 1955, Havera and Nixon 1978, Koprowski 1994). Eastern gray squirrels on the Base were heavier than those reported from several States where mean female weights ranged from 450 g in Florida to 560 g in Michigan (Uhlig 1955). Havera and Nixon (1978) reported weights of eastern gray squirrels from Illinois were more similar to those on the Base.

Variation in body mass across years may be associated with mast production which can be highly variable in our study area. Oregon white oak is known for periodic mast failures (Peter and Harrington 2002) and is the only oak native to Washington. However, body mass remained steady across years despite severe mast failure for oaks and conifers on our study area during fall 2010. Body mass for both species may have been maintained through consumption of truffles, an important food source for both squirrel species (see Chapter 3). The absence of interaction between season and sex in the analysis of body mass suggested that mass of males and females was affected similarly by seasons despite extraordinary movements by males as they pursued females in the breeding season. Koprowski (2005) found such an interaction for red squirrels in

Arizona and concluded males had greater weight loss during breeding season due to pursuit of females.

Manipulation of animal populations facilitates straight-forward tests of competition but is rarely attempted in ecological studies because of logistical difficulties in applying experimental treatments to open populations. Our protocol for removal trapping in this study appeared effective for excluding eastern gray squirrels from study areas for several months following trapping sessions. Fall trapping was most important for affecting removal treatments because eastern gray squirrels from surrounding areas dispersed into our removal sites during this season. Abundance of eastern gray squirrels on the Base was low compared to populations within their native range, and immigration into our study areas may have been restricted for eastern gray squirrels because of limited habitat availability on the Base (see Chapter 2). Consequently, effective removals of eastern gray squirrels in other regions with greater squirrel abundances and habitat availability may be more difficult.

Radio-telemetry provided evidence of fine-scale partitioning that may have been difficult to detect with trapping or visual encounter surveys used in previous studies. We occasionally captured individuals of both squirrel species at the same trap station but found they used different areas based on tracking their movements with telemetry. Squirrels on the Base were extremely difficult to observe because of dense vegetation and both species often became motionless high in trees when we approached. Previous studies of western gray squirrels on the Base abandoned attempts to capture squirrels due to poor capture rates, and their alternative strategies of visual encounter surveys yielded few observations (Ryan and Carey 1995, Bayrakci et al. 2001).

In conclusion, interspecies avoidance between eastern and western gray squirrels probably occurred in habitats suitable to both species. However, few areas of the Base had such habitat which minimized interactions between eastern and western gray squirrels (see Chapter 2) and likely explains why we found little response of western gray squirrels to removals of eastern gray squirrels. Where habitat is suitable for both species, residence dominance may dictate which species controls the site because squirrels seeking new territory may be more likely avoid conflict with residents of the competing species in favor of finding vacant habitat elsewhere (Steele and Koprowski 2001). Western gray squirrels likely began declining in our study area prior to invasion by eastern gray squirrels for reasons that include habitat loss, overhunting, and automobile traffic (Linders and Stinson 2007). Because the Base is surrounded by urban areas which are a stronghold for eastern gray squirrels, some habitats vacated by western gray squirrels may become occupied by dispersing eastern gray squirrels. Coexistence of these species for any given area will most likely depend on similarity in habitat use and the availability of habitat. Further study is needed to determine whether patterns of spatial partitioning between eastern and western gray squirrels found on the Base vary across regions and with competitor abundances.

Table 1.1. Area (ha) of experimental sites, area occupied by female eastern (EFA) and western (WFA) gray squirrels, squirrel abundance, and the minimum number of eastern (E) and western (W) gray squirrels known alive at each study area (R=removal, C=control) by sex (F=female, M=male) for breeding (B=February-July) and non-breeding (N=August-January) seasons.

						2008		2009				2010				2011					
						N		B		N		B		N		B		N			
	Area[1]	WFA[2]	EFA[3]	Spp	TRT	F	M	F	M	F	M	F	M	F	M	F	M	F	M	$\bar{x}$[4]	Abundance[5]
Spanaway	274	252	49	W	R	2	4	5	6	5	9	4	9	5	5	4	6	5	7	10.9	0.043
				E	R	3	0	3	3	3	3									5.0	0.102
Shaver	261	252	98	W	R					2	1	3	0	3	2	4	1	5	0	4.2	0.017
				E	R					4	10	3	6	2	5					10.0	0.102
Ammo	293	258	134	W	C	4	6	3	3	2	3	4	7	5	5	4	3	3	1	7.6	0.029
				E	C	6	6	4	8	4	7	6	9	4	2	3	1	1	1	8.9	0.066
7s	247	247	28	W	C							4	6	7	3	7	3	7	3	10.0	0.040
				E	C							3	4	2	6	0	2	1	2	5.0	0.179

[1] Area measured by minimum convex polygon around all telemetry locations for female eastern and western gray squirrels within the site.

[2] Area measured by minimum convex polygon around all telemetry locations for female western gray squirrels within the site.

[3] Area measured by minimum convex polygon around all telemetry locations for female eastern gray squirrels within the site.

[4] Mean number of squirrels (male and female combined) known alive during each season.

[5] Abundance estimated as the mean number of squirrels known alive during each season divided by the area of the minimum convex polygon of the associated species.

Table 1.2. Means and 95% confidence intervals for 95% fixed-kernel home-ranges (ha) of eastern and western gray squirrels ranked largest to smallest on Joint Base Lewis-McChord, 2007-2012.

	Sex	*n*	$\bar{x}$	LCI	UCI	Rank[1]
Western gray squirrel	M	17	180.7	120.9	270.0	1
Western gray squirrel	F	54	35.2	28.1	44.1	2
Eastern gray squirrel	M	14	30.9	19.9	48.2	2
Eastern gray squirrel	F	16	7.7	5.1	11.6	3

[1] Shared-ranks indicate no significant difference ($P>0.05$) based on Tukey's HSD.

Table 1.3. Means and 95% confidence intervals for total spatial overlap within and between eastern (E) and western (W) gray squirrels by sex (M=male, F=female) ranked from largest to smallest and the mean number of overlapping squirrels for each group (No. OL) on Joint Base Lewis-McChord, 2007-2012.

Group	Overlapping group	*n*	No. OL	$\bar{x}$	LCI	UCI	Rank	Tukey[1]
WM	WM	6	5.0	205.3	186.3	224.3	1	1
WF	WM	2	6.0	110.0	77.1	142.9	2	3
EM	EM	7	3.0	70.1	52.5	87.7	3	2-7
WF	WF	44	2.8	41.7	34.7	48.7	4	3-9
WM	WF	6	3.0	39.5	20.5	58.5	5	3-12
EF	EM	3	3.7	33.7	6.8	60.6	6	3-12
EM	EF	4	2.8	25.3	2.0	48.6	7	3-12
EM	WF	7	3.9	23.5	5.9	41.1	8	4-12
WF	EM	8	3.4	20.5	4.1	36.9	9	4-12
WF	EF	14	2.6	16.8	4.4	29.2	10	5-12
EF	WF	16	2.8	14.7	3.1	26.3	11	5-12
EF	EF	16	1.0	5.7	-5.9	17.3	12	5-12

[1] Groups with similar means for overlap based on Tukey's HSD (*P*>0.05) identified by rank.

Table 1.4. Number of eastern gray squirrels removed from selected sites during each 7-day trapping session.

		2009		2010				2011			
	No. traps	Fall	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
Spanaway	50	6	4		0[1]	0		0	1	1	0
Shaver Lake	40					8		0	0	8	0
DeBalon	12			4		0	0	0	0		1

[1] Zeros indicate no squirrels were captured during a trapping session, whereas blanks indicate no trapping was attempted.

Table 1.5. Means and 95% confidence intervals for the change (post-treatment - pre-treatment) in body mass, fecundity, survival rates, and spatial overlap with eastern gray squirrels for female western gray squirrels following removal of eastern gray squirrels on Joint Base Lewis-McChord, 2007-2012.

	Control Sites			Removal Sites		
	$\bar{x}$	LCI	UCI	$\bar{x}$	LCI	UCI
Overlap	-14.0	-102	75.6	20.1	-68.5	109
Body mass	-12.9	-173	147	-1.0	-161	159
Fecundity	$-5.75e^{-2}$	-1.38	1.26	-1.63	-2.94	-0.306
Survival rate	-0.171	-0.911	0.569	0.197	0.190	0.203

Table 1.6. Means and 95% confidence intervals for mass (g) of eastern and western gray squirrels by season and sex on Joint Base Lewis-McChord, 2007-2011.

		Fall			Winter			Spring			Summer		
	Sex	$\bar{x}$	LCI	UCI	$\bar{x}$	LCI	UCI	$\bar{x}$	LCI	UCI	$\bar{x}$	LCI	UCI
Western gray squirrel	F	780	763	797	825	807	843	788	775	801	780	767	793
Western gray squirrel	M	780	759	801	802	785	819	764	750	778	756	740	772
Eastern gray squirrel	F	641	613	669	638	609	667	636	614	658	640	618	662
Eastern gray squirrel	M	636	618	654	644	619	669	639	619	659	612	582	642

Table 1.7. Means and 95% confidence intervals for reproductive and survival rates of eastern and western gray squirrels on Joint Base Lewis-McChord, 2007-2012.

	Fecundity				Litter Size				Survival Rates			
	n	$\bar{x}$	LCI	UCI	*n*	$\bar{x}$	LCI	UCI	*n*	$\bar{x}$	LCI	UCI
Western gray squirrel	47	1.77	1.35	2.19	15	3.00	2.49	3.51	76	0.607	0.521	0.686
Eastern gray squirrel	12	0.583	0.011	1.15	7	3.43	2.53	4.33	35	0.564	0.421	0.697

CHAPTER 2

Resource Use by Eastern and Western Gray Squirrels

Animals select habitats based on many factors including their ability to meet needs for foraging, safety, shelter, and breeding. Some species utilize distinct habitat types to meet specific needs as areas that provide forage, for example, may not be similar to those that provide safety or shelter (Stephens et al. 2007). When identifying habitat requirements for a species, it is important to understand the reasons animals use areas and the ways in which habitat use varies over space and time. Separate measures of resource use by animals according to behaviors such as foraging, resting, and breeding may be needed to identify specific resources important for conservation of rare species or to discover mechanisms of competition, especially when resource partitioning occurs at fine scales and competitive interactions are obscure.

Provision of habitat is often the primary strategy for management and recovery of rare species. Consequently, it is important to identify habitat components important to rare species, particularly those manipulated by human activities such as forest structure and composition. Western gray squirrels were listed as a threatened species by the state of Washington in 1993 and habitat loss, along with competition with introduced squirrels, was cited as a primary reason for population declines (Linders and Stinson 2007). Previous studies have described habitat associations of western gray squirrels in the Cascades in some detail (Linders 2000, Gregory et al. 2010, Stuart 2012), but only broad associations have been described for this species in western Washington (Ryan and Carey 1995, Bayrakci et al. 2001, Fimbel and Freed 2008). Most remaining habitat in western Washington for western gray squirrels is in areas subject to timber harvest or expanding urban development. Detailed, multi-scale habitat assessments are needed to guide habitat management for this species.

Niche theory suggests that coexistence among similar species may be achieved through differential habitat use (Hutchinson 1957, Hardin 1960, Keddy 2001). The degree of overlap in habitat use among species should then indicate the potential of competition. Although resource partitioning within habitat types can minimize or negate competitive interactions among species, it is important to evaluate similarity in habitat use by potential competitors because at least some overlap in habitat use is usually needed for competition to influence population dynamics.

Similarity in habitat use by eastern and western gray squirrels may vary by use of areas for foraging, overnight shelter, and natal dens. Food availability largely drives habitat use by squirrels, and habitat characteristics in areas used for foraging may differ from those that provide safety or shelter (Steele and Koprowski 2001). Gray squirrels frequently use stick nests for overnight shelter but often use tree cavities as natal dens during the breeding season. This dichotomy in nest use is apparent for western gray squirrels in Washington where they may leave high-use areas to find cavity trees elsewhere for rearing young (Linders et al. 2004). Because nests and cavities may be used by squirrels for different purposes and because nests, unlike cavities, are constructed by squirrels in locations of their choice, habitat characteristics around these two shelter types may differ.

Both eastern and western gray squirrels have been associated with oak woodlands in previous studies which suggests similarity in habitat use and high potential for competition (Carraway and Verts 1994, Koprowski 1994). Anecdotal observations of eastern gray squirrels in areas formerly occupied by western gray squirrels further suggest that competitive interactions occur between these species (Linders and Stinson 2007). However, some differences in habitat use between these species are evident from previous studies and may minimize competitive interactions. Eastern gray squirrels are native to the deciduous forests of the Eastern United States where the abundance and diversity of mast producing trees is high compared to western states. Western forests are dominated by conifers, particularly Douglas-fir, a forest type avoided by eastern gray squirrels in the United Kingdom (Bryce et al. 2002). Western gray squirrels are known to use conifer forests mixed with oaks extensively and in some regions, occupy Ponderosa pine forests that lack oaks (Linders 2000, Gregory et al. 2010, Stuart 2012). In California, Byrne (1979) observed eastern gray squirrels in riparian areas, whereas western gray squirrels were common in upland forests. Unlike western gray squirrels, eastern gray squirrels are abundant in urbanized areas in western states but appear unable to expand into most undeveloped forests. Therefore, habitat use by these species may differ sufficiently to minimize competitive interactions, but it is poorly understood where they co-occur.

The objectives of this study were to identify habitat characteristics important to eastern and western gray squirrels at multiple spatial scales and then compare these characteristics between species to test the null hypothesis of no difference in habitat use. We examined use of nest sites, nest trees, and areas of high- and low-use within home-ranges of individual squirrels. We evaluated overlap in habitat use between eastern and western gray squirrels to determine whether differential habitat use may facilitate coexistence for these species.

METHODS

Study area - We studied gray squirrels on Joint-Base Lewis-McChord (Base, hereafter), a military reservation near Tacoma, WA. The Base covers 35,000 ha, most of which was set aside as undeveloped forests, prairies, and woodlands for use as training areas for military personnel and timber harvest. Elevation ranges from 120 to 160 m, and average annual precipitation is 800-

900 mm. 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 years) Douglas-fir (*Pseudotsuga menziesii*). Prairie remnants, oak woodlands, and Ponderosa pines (*Pinus ponderosa*) were sparsely distributed throughout the Base. Riparian areas supported Oregon white oak (*Quercus garryana*), Oregon ash (*Fraxinus latifolia*), big-leaf 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*). Eastern gray squirrels were present in developed and undeveloped portions of the Base, whereas western gray squirrels were found only in undeveloped forests. Much of the Base was surrounded by urban or agricultural areas that supported eastern gray squirrels but not western gray squirrels.

Field methods

We trapped and radio-collared eastern and western gray squirrels at four study sites on the Base that were designated as units for an experimental removal of eastern gray squirrels from July 2007 to April 2012 (see Chapter 1). In addition, Washington Department of Fish and Wildlife biologists trapped and radio-collared western gray squirrels at nearby sites for a concurrent project to study and augment the population as part of a recovery strategy for this species (Vander Haegen and Orth 2011). We placed trap transects in suitable habitat within each study site with the objective of saturating the site with traps to ensure that we captured most, if not all, gray squirrels in the area. We usually ran 30 to 50 traps per site depending on the extent and configuration of habitat. Traps along transects were spaced 50 to 100m apart. Trapping sessions of 3 to 7 days occurred every 3 to 5 months at each study area. In addition, we frequently trapped specific areas of each site between these sessions to recollar squirrels or assess squirrel condition, and these efforts occasionally captured new squirrels that had dispersed into the area. Overall, our trapping effort was intensive and sufficiently frequent throughout the duration of the study to track at least the majority of squirrels at any given site. Furthermore, our trapping records indicate high site fidelity of squirrels, and the ratio of recaptures to new captures suggested we had marked most or all squirrels at each site during the study.

We used Tomahawk live-traps baited with whole walnuts to trap squirrels. Traps were typically opened shortly after dawn and checked every 2 hours until early afternoon when traps were closed. Trap sessions were preceded by a 2-week pre-baiting period to acquaint squirrels with traps and improve capture probabilities. Traps were pre-baited by wiring the door open and baiting with walnuts 2 or 3 times per week. Upon capture, we restrained squirrels in a cloth-handling cone (Koprowski 2002) which allowed us to assess squirrel condition and attach a radio-collar. For each captured squirrel, we recorded body mass, reproductive condition, and noted any peculiar condition such as presence of alopecia or ectoparasites. At all sites, we equipped all female gray squirrels captured with radio-collars and ear-tags. Similarly, we applied ear-tags to all male gray squirrels but radio-collared only a subset of males. We focused our resources on tracking all female gray squirrels because they are most important for driving population dynamics.

We relocated squirrels equipped with radio-collars three times per week by homing in on their location using radio-telemetry techniques. Squirrels were tracked throughout the diurnal period and were relocated once per day to ensure independence among locations. Squirrels were tracked year-round until death or the end of study in April 2012. The location of the squirrel was recorded with a GPS unit (Trimble Navigation Limited, Westminster, CO) once the squirrel was seen or estimated to within 10m based on the radio-signal. Locations were differentially corrected to obtain accuracies of <5m. At each location, squirrel behavior and general habitat characteristics of the area were recorded. Prior to tracking each squirrel, we determined whether the squirrel was active by listening to its signal for up to 3 minutes. A squirrel was considered active when its signal fluctuated in volume due to the squirrel moving through the forest, whereas, inactive squirrels had signals with constant volume for 3 minutes. When squirrels were pinpointed to trees with nests or cavities, we recorded the tree species, diameter at breast height (dbh), and marked the tree with a numbered metal tag.

Squirrel locations were plotted on maps with ArcMap 9.3 to facilitate placement of plots for habitat surveys. We excluded repeat observations of squirrels within nests to avoid biasing measurements of use toward nest sites. We used a fixed-kernel density estimator in Hawth’s tools (Beyer 2004) to create utilization distributions at 10m resolution to identify core and low-use areas by squirrels (Kernohan et al. 2001). We used the bi-variate plug-in from the KS package in R to estimate the smoothing parameter for each squirrel in the kernel density calculation (Wand and Jones 1995, Wand 2006) because it should work well based on the spatial configuration of our squirrel locations (Gitzen et al. 2006). We converted utilization distributions to percent volume contours and defined the upper quartile of use as the core area for each squirrel, whereas low-use areas were defined by the lower quartile. We selected these values for core and low-use to maximize the difference in use between levels while providing ample space to for habitat plots. We placed 12 habitat plots split evenly between core and low-use areas for each of 30 female gray squirrels (15 squirrels per species) for a total of 360 plots. Plot locations within each level of use were chosen at random using Hawthe’s tools. We sampled habitat for squirrels for which we had recorded at least 30 locations during the breeding season (February to July) and the non-breeding season (August to January). Because we had sufficient data for more than 15 western gray squirrels to sample habitat, we randomly selected 15 squirrels with non-overlapping core areas for habitat sampling. We did not measure habitat characteristics for all squirrels because time and resources were limited.

In addition, we centered habitat plots on nests and dens for separate analyses of characteristics around each nest type. Nests (ie. dreys) were spherical masses of woven sticks, leaves, and other vegetative material placed near the bole of the tree, whereas dens were tree cavities where squirrels reared young. We randomly selected up to 4 conifer nests for each of the 30 squirrels chosen for comparisons of core and low-use areas. We did not survey nests in deciduous trees because most (>90%) were in conifers. We maintained at least 50m between any two nests sampled and made random selections of nests when they were in close proximity to one another (<50 m) to avoid double-sampling. We surveyed 53 and 52 nests and 31 and 47 dens for eastern and western gray squirrels, respectively.

We measured forest structure and composition within 10.6 m-radius plots placed in core and low-use areas and centered on nests and dens during July through September, 2009-2011. We recorded species and diameter at breast height (dbh) for all trees ≥5 cm dbh within the plot. We counted and classified decay of all coarse-woody debris ≥10 cm at maximum diameter within or penetrating the plot. To sample understory and shrubs, we followed line-transect methods using a 3 cm-diameter height pole along 3-18.4 m transects placed in the form of a triangle within the plot. We sampled vegetation at each meter along transects by placing the pole vertically and recording presence of all species of vegetation intercepted by the pole within each of seven height strata. The first six strata corresponded to half-meter increments beginning at the ground and ending at 3 m above ground. We used the seventh stratum to record shrub presence beyond the reach of the height pole (>3 m). Relative abundance of each species within each stratum was calculated as the proportion of sample points where the species was present. Then, we calculated an index of shrub cover by summing these proportions for all shrub and fern species over all height strata. We estimated canopy cover by averaging three measures from a densiometer taken facing the plot center, three paces inward from each point of the triangle. We also measured canopy connectivity by selecting the tree nearest each point of the triangle within the plot and counting the number of trees with live branches that were within 1 m of live branches of the focal tree.

At nest plots, we measured characteristics of each nest tree (all nests were in conifers) and on 8 random conifers ≥20 cm dbh that did not have visible nests and were within 25 m of the plot center (Skalski 1987). For each of these trees, we measured dbh, canopy connectivity, tree height, and height of lowest-living crown. Tree heights and heights of other attributes were measured with an electronic clinometer and range finder. We noted any sign of mistle-toe infection and estimated percent of the tree canopy that was live (Gregory et al. 2010). Relative height of each tree to those within the stand was calculated by dividing the height of each tree by the median height of the nine trees measured within each plot. We also measured the height and aspect of the nest or den for trees used by squirrels.

We acquired GIS layers from the Base that described forest structure and composition for habitat analyses. Rasters of 20-m resolution for canopy height, standard deviation of tree heights, canopy cover, and shrub cover were derived from LIDAR data collected on the Base with an Optec-Gemini Airborne Laser Mapping system in June and July 2010. This scanner recorded up to four returns per pulse with an average density of about six points per square meter. We resampled a canopy height model from 2.5 to 20-m resolution by assigning the cell value as the maximum 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 tree heights. Canopy cover and shrub cover were calculated for each 20-m cell using the number of returns within specified height strata. Canopy cover was calculated as the proportion of returns that occurred above 1 m. Shrub cover was calculated as the proportion of returns that occurred between 1 and 3 m where only returns below 3 m were considered. We found good correlation (R^2=0.67, n=211) between our index of shrub cover measured at ground plots and LIDAR estimates of cover for this height stratum (Appendix A). We obtained a highly accurate map of wetlands that was created and extensively field-validated as part of the National Wetlands Inventory under the United States Fish and Wildlife Service. We also obtained a map of oak woodlands created by the Department of Natural Resources through a compilation of source maps from the Base that were updated based on interpretation of aerial photography and field reconnaissance in 2003 (Chappell et al. 2003). We combined the oak map with one that was created through a fusion of LIDAR and high-resolution satellite imagery by researchers on the Base in 2007 (Chastain 2007). This map used LIDAR collected in 2005 on the Base where point density averaged 4.5 points per square meter. We then edited this map in ArcMap to correct errors of omission and commission that we identified through field reconnaissance.

Statistical methods

For each set of analyses, we identified important habitat characteristics for each squirrel species through comparisons of core and low-use areas or used versus available nest sites. We then compared habitat characteristics of core areas and nest sites between squirrel species. We used discriminate function analyses (DFA) to find linear functions that best distinguished (1) core from low-use plots for each species, (2) core plots between species, (3) nest sites from available sites for each species, (4) nest sites between species, (5) den sites between species, (6) characteristics of nest trees between species, and (7) characteristics of trees with dens between species (McGarigal et al. 2000). For comparisons of nest sites with available sites, we used plots from core and low-use areas that did not have any nests within 25 m of the plot center as available sites. We reported classification success rates and plotted the frequencies of canonical scores for each group to evaluate overlap in habitat use between groups. We reported structure correlations that indicated the relative contribution of each variable to distinguishing between groups in the DFA. We then tested the null hypothesis of no differences between groups using analysis of similarities (ANOSIM) with Euclidean distance as the measure of dissimilarity (Clark 1993).

Prior to each DFA, we screened correlated habitat variables and assessed assumptions of multivariate normality. Habitat variables considered in analyses of plot data were average dbh, maximum dbh, standard deviation of dbh, tree density, canopy cover, canopy connectivity, shrub abundance, number of logs, tree richness, shrub richness, tree evenness, and shrub evenness. We first examined box plots for each group and *F*-tests for the ratio of variances between groups to determine whether transformations were needed to normalize distributions or equalize variances. We used log, square root, arcsine square-root, and logit transformations where appropriate to improve distributions. Few variables departed from assumptions of normality and homoscedasticity either before or after transformations. Univariate normality and homoscedasticity may serve as precursors for but do not ensure multivariate normality. We reviewed a correlation matrix of potential habitat variables and eliminated correlated variables ($r > 0.7$) that had the lowest *t*-statistic in univariate comparisons between groups. We then tested for homogeneity of multivariate dispersions, a more direct test of the multivariate normality assumption, to determine whether DFA results should be considered valid or exploratory (McGarigal et al. 2000, Anderson 2006). For these tests, coefficients were placed in Euclidean space by principal coordinate analysis, and a permutation test compared Euclidean distances to the centroid between groups. Multivariate outliers were identified with a function from the BIOSTATS library in R using Mahalanobis distance where values exceeding three standard deviations were considered outliers. We reran DFAs after removing outliers to determine whether they strongly influenced results. Similarly, we screened outliers using Euclidean distance for ANOSIM.

We used conditional logistical regression for match-case designs to compare nest trees to available trees within each plot (Hosmer and Lemeshow 2000, Gregory et al. 2010). We tested the need for log transformations and quadratic terms through a univariate analysis on each habitat variable. We used log transformations or quadratic terms when *P*-values from Wald's tests were <0.1. We reviewed correlation matrices of potential habitat variables to identify correlated variables (r >0.7). Habitat variables considered in these analyses were dbh, tree height, canopy volume, height of lowest living crown, canopy connectivity, and relative tree height. Canopy volume was calculated by multiplying dbh by the difference between tree height and height of the lowest living crown. We did not consider presence of mistle-toe as a habitat variable because it was not evident at >99% of trees observed. Similarly, tree condition for >99% of trees was fully live and was not considered as a variable.

For each analysis, we constructed full models that included all uncorrelated habitat variables. For each correlated variable, we constructed a unique full model and proceeded with model selection which allowed us to consider all variables in the analysis. For each full model, we used backwards elimination to remove insignificant variables (*P*>0.1) and identify a good model (Ramsey and Schafer 2002). We then compared models with AIC and based inferences on models with the lowest AIC (Burnham and Anderson 2002). We reported competing models that had AIC values within 2 of the model with the lowest AIC. We also reported the number of nests and dens by tree species and compared their observed and expected frequencies of occurrence among tree species and between squirrel species with chi-square tests. Comparisons within squirrel species excluded tree species without nest observations, whereas comparisons between species included tree species that had at least one nest used by an eastern or western gray squirrel.

We evaluated resource use by squirrels within their home-ranges and mapped predicted use for the entire Base with resource utilization functions (RUF; Marzluff et al. 2004). A RUF is a form of multiple regression that relates an animal's measured use within its home-range to any predictor variable that can be mapped. A Matern model accounts for spatial autocorrelation among cell values for the regression and requires estimation of the range of spatial dependence and smoothness of the utilization distribution surface. We used the estimate of the smoothing parameter from the bi-variate plug-in 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.

Measures of use by the squirrel were derived from the utilization distribution where average height of the distribution for a cell measured the relative use by the squirrel within its home-range. We created a utilization distribution for each squirrel from its fixed-kernel density estimate at 20-m resolution with the Geospatial Modeling Environment (Beyer 2012) and ArcGIS. We then converted the utilization distribution to a percent volume polygon where contours identified 1-99 percentiles of use probabilities. Sampling grids with points spaced 20 m apart and centered on the cells of the rasters for habitat variables derived from LIDAR were laid over the use polygons for each squirrel. We measured distance to the nearest oak stand and wetland for each sampling point with spatial joins in ArcMap. Values of use and these habitat variables were extracted at each sampling point and used for RUF analysis with the ruf.fit package in R. We used ArcMap 10.0 for all GIS-related data preparation for RUFs.

We created RUFs for 40 western gray squirrels and 16 eastern gray squirrels comprising all female squirrels with >50 telemetry locations and that had home-ranges entirely within the area of mapped resources. We randomly selected five squirrels from each species to screen variables for correlation and evaluate model fit. All variables were retained for model building because none were consistently correlated ($r>0.7$). 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 far more low-use cells than high-use cells within UDs (Appendix B). 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 used all predictor variables to create RUFs for each squirrel and then created population-level RUFs for each species by averaging coefficient estimates across squirrels. We used *t*-tests of coefficients to determine which variables in the population-level RUF should be retained ($\alpha=0.1$), where the variance of coefficient values was a conservative estimate that accounted for inter-animal variability (Marzluff et al. 2004). Insignificant variables were eliminated from the model following a backwards selection procedure to create final models for each species (Ramsey and Schafer 2002).

For each squirrel species, we ranked standardized coefficients from the population RUF that had all variables present to identify which variables were most important in modeling squirrel habitat. Standardized coefficients with the largest magnitude were most important. Variables with significantly positive associations indicated squirrel use increased with values of that variable, whereas significantly negative associations indicated use decreased as variable values increased. We also reported unstandardized and standardized coefficients from the final population RUF for each squirrel species.

We evaluated model performance of final population RUFs for each species using *k*-fold cross validation (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. We applied a negative sign to coefficients of variation when the slope was negative to account for poor model fit in our calculations of the averages.

We used the final population RUF with unstandardized coefficients for each species to map their predicted probabilities of use for the entire Base. Mapped probabilities were back-transformed to the original scale and reclassified as high- or low-use, where probabilities >50% were considered high-use. Because predicted values ranged from about 0 to 12 on our maps and the midpoint (6) may not represent 50% probability of use, we devised the following method to estimate the predicted value from the population RUF associated with 50% probability of use. This estimate was then used as the dividing point for categorizing high- and low-use areas. For these estimates, we considered only squirrels for which the RUF performed well based on cross-validation (ie. significant positive slope for regression of observed and predicted values). For each squirrel, we sorted their observed values of use from lowest to highest and then averaged the values of use predicted by the RUF that were associated with observed values ranging from 45% to 55%. This range of observed values centered on 50% provided several measures of predicted use (~10) for an estimate that should have been close to 50% use. Averaged values for each squirrel were averaged across all squirrels for final estimates of 50% predicted use to categorize areas as high- or low-use on maps for each species. Finally, we calculated the percent of high-use areas for western gray squirrels overlapped by high-use areas of eastern gray squirrels.

RESULTS

From April 2007 through April 2012, 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 locations on 43 female and 15 male western gray squirrels. Tracking periods for western gray squirrels included in the RUF 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 RUF analysis ranged from 5 to 49 months, and number of relocations ranged from 55 to 322.

Core areas

Habitat in core and low-use areas were different ($P<0.05$) for both eastern and western gray squirrels based on ANOSIM (Table 2.1). Classification rates from DFA were only fair for both species indicating that core and low-use areas were not easily differentiated based on the characteristics we measured because canonical scores were frequently near zero for core and low-use areas (Figure 2.1). Variables related to tree diversity were top discriminating variables for both species as core areas had greater richness (eastern) or evenness (western). In addition, the percent of deciduous trees was higher in core areas of eastern gray squirrels (Table 2.2). Shrub cover was also among the top discriminating variables for eastern gray squirrels and was highest in core areas. Other variables that described shrub diversity, tree structure, and log abundance had lower correlations with the discriminant function. For western gray squirrels, canopy cover and canopy connectivity were highest in core areas and were among the best discriminating variables. Variables that described tree size, tree density, shrub cover, shrub diversity, and log abundance contributed little to the function but their values were highest in core areas. Multivariate dispersion of the habitat measures was higher in low-use areas for both eastern ($F_{1,178} = 4.0$, $P = 0.047$) and western gray squirrels ($F_{1,178} = 4.5$, $P = 0.036$) which suggested habitat selectivity occurred within the home-ranges of both species (McGarigal et al. 2000). These results also suggest that the assumption of multivariate normality was not met for analyses of core and low-use areas because of the high variability of habitat characteristics measured in low-use areas. The multitude of reasons areas were not used by squirrels led to high variability in low-use habitat characteristics. Some low-use areas were avoided by squirrels because canopy cover was too low, whereas other areas had high canopy cover but shrub cover was not suitable. Some low-use areas resembled high-use areas but likely were not used by squirrels for reasons other than habitat suitability. Consequently, results of these comparisons should be considered exploratory rather than as rigorous tests of hypotheses.

Differences in core areas of eastern and western gray squirrels were evident in ANOSIM and by a good classification rate from the discriminant function (Table 2.3, Figure 2.2). Shrub cover was the top discriminating variable, followed by percent of deciduous trees, shrub richness, and tree richness. All of these variables had higher values in core areas used by eastern gray squirrels. Variables that described tree and canopy structure had little discriminatory power for distinguishing eastern from western gray squirrel core areas. There was no evidence of differences in multivariate dispersion ($P>0.05$) in this or any of the following analyses except where noted.

Nest sites

Habitat characteristics of nest sites differed from available areas within home-ranges for both eastern and western gray squirrels ($P<0.05$) based on ANOSIM (Table 2.1, Figure 2.1). Classification rates from DFA were also fairly good which suggested that squirrels were selective in nest placement within their home-ranges. Canopy connectivity was the top discriminating variable for both eastern and western gray squirrels and was highest at nest sites (Table 2.4). Tree density and percent oak trees were also top discriminators for both species with highest values at nest sites. In addition, tree richness was a good discriminating variable for nests sites used by eastern gray squirrels. All other variables had relatively low structure correlations.

Nest sites differed between eastern and western gray squirrels based on a significant result of ANOSIM and a good classification rate from DFA (Table 2.2). As with comparisons of core areas, shrub cover was the top discriminating variable and was highest at nest sites of eastern gray squirrels. Other top discriminating variables were tree richness, tree evenness, and the abundance of logs. Tree richness and evenness were highest at nest sites of eastern gray squirrels, whereas logs were less abundant (Table 2.4).

Sites of dens were less distinctive between eastern and western gray squirrels than nest sites as results of ANOSIM were not significant ($P>0.05$) and the classification rate from DFA was relatively lower (Table 2.3, Figure 2.2). Percent deciduous trees was highest at sites with dens of eastern gray squirrels and was the top discriminating variable, followed by tree richness, tree evenness, canopy cover, and shrub cover. These measures were also highest at den sites of eastern gray squirrels (Table 2.4).

Nest trees

Comparisons of trees with and without nests consistently indicated that both eastern and western gray squirrels placed nests in large trees with high canopy connectivity (Table 2.5). The best model for western gray squirrels indicated odds of tree use for nest placement increased with canopy connectivity ($Z = 2.41$, $P=0.016$) and canopy volume ($Z = 1.96$, $P=0.050$), but decreased with height of lowest living crown ($Z = -2.93$, $P=0.003$). All competing models had significant results for canopy connectivity and height of lowest living crown. Although mean dbh, tree height, and relative tree height were higher for trees with nests (Table 2.6), these variables were not significant after accounting for canopy connectivity and height of lowest living crown except in the lowest ranked model where odds of use decreased with relative tree height. The best model for use of nest trees by eastern gray squirrels indicated the probability of use increased with canopy connectivity ($Z = 3.70$, $P<0.001$) and dbh ($Z = 3.44$, $P<0.001$). Canopy connectivity was significant in all competing models for nest trees of eastern gray squirrels. Canopy volume and dbh had significant positive associations with nest tree use in all models where they were considered, whereas tree height and relative tree height did not have any significant associations in any model.

The number of trees with nests for each tree species was equal for neither western gray squirrels (χ^2_4=1,673, P<0.001) nor eastern gray squirrels (χ^2_5=544, P<0.001). By far, most nests occurred in Douglas-fir trees compared to other species for both eastern (χ^2_1=71, P<0.001) and western (χ^2_1=367, P<0.001) gray squirrels (Table 2.7). There was no difference in the number of nest trees by tree species after excluding nests in Douglas-firs for eastern gray squirrels (χ^2_4=4.12, P=0.390). For western gray squirrels, nests were more frequently found in Ponderosa pine compared to oak, ash, or cottonwood (χ^2_3=12, P=0.007), but there were no differences within the latter group (χ^2_2=3.71, P=0.156). Apart from similar use of Douglas-fir, eastern gray squirrels had different use of nest tree species compared to western gray squirrels (χ^2_6=58.8, P<0.001) where higher frequencies of western red cedar, alder, and cottonwood for eastern gray squirrels contributed the most to the chi-square statistic.

There were no differences between eastern and western gray squirrels in the structure of trees with nests or dens based on ANOSIM and poor classification rates from DFA (Table 2.8, Figure 2.2). Canopy connectivity was the only discriminating variable with a high structure correlation for nest trees and was lower for trees used by western gray squirrels. Multivariate dispersions differed between species in comparisons of nest trees ($F_{1,84}$=8.1, P=0.006). For dens, tree height and relative tree height had the highest structure correlations, but classification rates near 0.50 for both dens and nests indicated high overlap in the structure of trees used by eastern and western gray squirrels (Tables 2.6, 2.9). Plots of canonical scores for nest and den trees show high overlap between species (Figure 2.2). Slight differences in characteristics of trees with dens between eastern and western gray squirrels were likely attributed to greater use of conifers with cavities by western gray squirrels because conifers were often larger and taller than deciduous trees. We also measured tree characteristics on 5 and 14 den trees that were snags for eastern and western gray squirrels, respectively, and were excluded from the above analysis because characteristics such as canopy connectivity and lowest living crown were not applicable for these trees. Most (15) of these snags were Douglas-fir and were similar in dbh to other den trees but average tree height was about a third of live trees with dens.

Frequencies of den trees by tree species were not equal for eastern (χ^2_6=44.6, P<0.001) or western (χ^2_4=47.8, P<0.001) gray squirrels and frequency distributions were different between species (χ^2_6=25.1, P<0.001; Table 2.7). Western gray squirrels had more dens in Douglas-fir trees compared to all other species, and there was little difference in the frequency of cavities in other tree species (χ^2_3=7.2, P=0.066). In contrast, most dens used by eastern gray squirrels were in ash followed by Douglas-fir and cottonwood.

Resource utilization functions

Population RUFs indicated distance to oaks was the most important predictor for use by western gray squirrels (t_{39}=-4.46, P<0.001) as use decreased with increasing distance from oaks (Tables 2.10, 2.11). Use by eastern gray squirrels was also lower away from oaks (t_{15}=-2.09, P=0.054), but distance to wetlands was the best predictor for this species. Use by eastern gray squirrels decreased with increasing distances from wetlands (t_{15}=-3.79, P=0.002), whereas western gray squirrels had no such relationship (t_{39}=-0.415, P=0.680). Canopy cover was the second most important predictor of use for both eastern (t_{15}=3.83, P=0.002) and western (t_{39}=6.31, P<0.001) gray squirrels as use increased with cover. Use increased with canopy height for eastern (t_{15}=1.83, P=0.087) and western (t_{39}=1.84, P=0.073) gray squirrels, but this variable was not included in the final population RUF for eastern gray squirrels because it was dropped during backwards selection (Table 2.12). The standard deviation of tree heights had little predictive power for use by eastern (t_{15}=-1.56, P=0.141) and western (t_{39}=-0.278, P=0.783) gray squirrels. Western gray squirrel use was negatively associated with shrub cover (t_{39}=-3.15, P=0.003), whereas associations for eastern gray squirrels were positive but not significant (t_{15}=0.372, P=0.715). Top predictor variables were also consistent in the direction of correlation with use across squirrels (Table 2.13).

Results of *k*-fold cross validation indicated RUFs performed well for eastern and western gray squirrels (Table 2.14). The averaged coefficients of variation were fairly high for both species despite a few squirrels that had negative relationships between observed and predicted values of use. Most relationships between observed and predicted probabilities of use were positive with significant relationships (P<0.05) for well over half of the squirrels for each species. Negative relationships typically occurred where squirrels did not follow the expected relationship with distance to water or oaks. Two eastern gray squirrels had core areas in low-lying areas that supported riparian vegetation but were away from standing water, so the population RUF predicted their use poorly. Such areas were rare on the Base. The third eastern gray squirrel was located alongside a wetland but had enough space between her core area and the wetland edge to form a positive relationship 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 (Figure 2.3). Predicted probabilities for eastern gray squirrels were highest in riparian areas, and areas away from wetlands were of little or no use. In contrast, use by western gray squirrels was limited by the distribution of oaks rather than wetlands. The area covered by ≥50% probability of use by western gray squirrels (4,591 ha) was much higher than that of eastern gray squirrels (300 ha). Accordingly, the proportion of high-use areas predicted for western gray squirrels overlapped by that of eastern gray squirrels was only 6.1% on the Base (Figure 2.4).

DISCUSSION

Resource use differed significantly between eastern and western gray squirrels based on our measures of forest structure and composition. Differential habitat use probably limited competitive interactions and explained our observations of low spatial overlap between these species better than interspecies avoidance (see Chapter 1). Fine-scale spatial partitioning between eastern and western gray squirrels occurred where riparian habitats characterized by dense shrub cover and deciduous trees transitioned to upland habitats dominated by conifers with little shrub cover. Interspecies avoidance may occur in such areas of transition, but habitats suitable for both species were rare on the Base according to probabilities of use for eastern and western gray squirrels predicted by resource utilization functions.

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. Riparian areas were unique from uplands because they were the only areas that supported all deciduous tree species found in this region. Wetlands on the Base were surrounded by a narrow band of deciduous trees within the riparian areas that gave way to uplands dominated by conifers. Deciduous trees found in riparian areas included oak, ash, maple, and cottonwood; trees similar to those found in the Eastern United States where eastern gray squirrels are native. Although oaks occurred in uplands on the Base and were important to eastern gray squirrels, no other species of deciduous tree was common away from riparian areas. Similarly, riparian areas had greater abundance and diversity of shrubs, some of which likely served as important food sources for squirrels (e.g. hazel). The diversity of trees and shrubs may be particularly important to eastern gray squirrels for protection against food shortages during years of mast failure. Acorn production by Oregon white oak is highly variable and mast failure occurs periodically (Peter and Harrington 2002, Devine and Harrington 2006) which may have prevented establishment of eastern gray squirrel populations in uplands where this was the only species of deciduous tree (Nixon and Hanson 1987). Byrne (1979) noted greater proportions of tree seeds in stomachs of eastern gray squirrels compared to western gray squirrels and found eastern gray squirrels only in riparian areas in California, whereas western gray squirrels were primarily found in upland habitats. In Europe, eastern gray squirrels also exploited deciduous forests but avoided forests dominated by Douglas-fir (Bryce et al. 2002). In the Eastern United States, eastern gray squirrels frequently have been associated with bottomland hardwood forests and avoided upland habitats dominated by conifers (Fischer and Holler 1991, Riege 1991, Steele and Koprowski 2001). This suggests that eastern gray squirrels are poorly adapted to conifer dominated habitats with little diversity of deciduous trees and shrubs. Although eastern gray squirrels are common in urban areas throughout the Western United States, they may be largely confined to developed areas where food is abundant from human cultivations because undeveloped forests are mostly dominated by conifers in this region.

Western gray squirrels used some riparian areas on the Base but were largely found in upland habitats dominated by conifers with little shrub cover. There has been little indication of riparian affiliation from previous habitat studies for western gray squirrels in Washington (Linders 2000, Gregory et al. 2010, Stuart 2012). Linders (2000) indicated that some western gray squirrels briefly moved into riparian areas during breeding season to have young. However, western gray squirrels have been studied far from riparian areas in dry forests of Washington (Vander Haegen et al. 2005) which supports our finding that riparian areas are not required to support populations of this species. The pattern of diminishing diversity of deciduous trees and shrubs from riparian to uplands found on the Base was also evident in dry forests that support western gray squirrels elsewhere in Washington (Linders 2000, Gregory et al. 2010, Stuart 2012). Shrub cover was low in core areas of western gray squirrels on the Base and was low throughout the study areas of all previous studies in Washington. In contrast, riparian areas on the Base were densely covered by shrubs, and shrub cover was the top variable for differentiating habitats of eastern and western gray squirrels. Similarly, shrub cover has been cited as one of the key differences in habitat use between eastern gray squirrels and fox squirrels in the Eastern United States (Steele and Koprowski 2001). Coexistence of these species has been attributed to differential habitat use where eastern gray squirrels were described as riparian affiliates, whereas fox squirrels inhabited dry upland forests dominated by pine with little shrub cover.

The ability of western gray squirrels to inhabit uplands on the Base that were characterized by low tree and shrub diversity relative to riparian areas suggests they are capable of exploiting resources different from those used by eastern gray squirrels. In California, western gray squirrels consumed more truffles than eastern gray squirrels which may have allowed them to establish populations in upland habitats (Byrne 1979). We found both species consumed truffles with similar frequency on the Base, so eastern gray squirrels may rely more on truffles in Washington where there are fewer mast producing trees. Western gray squirrels may exploit cones of Douglas-fir and Ponderosa pine more than eastern gray squirrels as we frequently observed western gray squirrels foraging on these resources but not eastern gray squirrels (see Chapter 3). Western gray squirrels were absent from urban areas but occupied a wider range of habitat types than eastern gray squirrels in undeveloped forests on the Base which might allow them to persist in some undeveloped areas despite invasions by eastern gray squirrels.

Canopy cover and connectivity

Western gray squirrels consistently used core areas with high canopy cover and connectivity as variables for these characteristics were top discriminators of core and low-use habitats. Our estimates of canopy cover in areas used by western gray squirrels were higher than those reported elsewhere in dry forests of central and southern Washington (Linders 2000, Gregory et al. 2010, Stuart 2012). Regional differences in canopy cover were likely related to differences in forest structure between our study area and others because canopy cover in Ponderosa pine forests should be lower than mesic Douglas-fir forests in western Washington.

Canopy cover and connectivity is undoubtedly important to tree squirrels for travel, foraging, and protection from predators, but they also affected shrub cover on the Base. Uplands with little or moderate canopy cover on the Base often had dense shrub cover which deterred use by western gray squirrels, whereas considerably less shrub cover occurred on sites regardless of variation in canopy cover in dry forests where others described habitat associations of western gray squirrels. Dense shrub cover on the Base may inhibit ground foraging by western gray squirrels, particularly for truffles. Dense shrub cover may also inhibit the ability of western gray squirrels to detect predators when traveling on the ground. Ground predators that ambush prey such as coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) may be more successful at capturing squirrels in areas of dense shrub cover. Low canopy connectivity may inhibit travel through the canopy and force western gray squirrels to travel through dense vegetation on the ground which further discourages their use of these habitat types.

Oaks

Eastern and western gray squirrels shared associations with high canopy cover and close proximity to oaks which may have led to their convergence in some areas. Our study corroborates others that indicate the distribution of western gray squirrels is mostly dependent on oaks (Dalquest 1948, Carraway and Verts 1994). Western gray squirrels appeared to require oaks within their home-ranges because their distribution on the Base aligned with oaks and distance to oaks was the most important variable in the RUF analysis. Although the geographic distribution of western gray squirrels follows those of oak or Ponderosa pine, we did not include a variable for Ponderosa pines in our RUF analyses because pines were rare on the Base. Populations of western gray squirrels are found in areas that lack oaks but have Ponderosa pine elsewhere within their range (Gregory et al. 2010, Stuart 2012). These dependencies highlight the importance of acorns and pine nuts as food sources to western gray squirrels (Cross 1969, Stienecker and Browning 1970, Stienecker 1977).

In addition to riparian areas, eastern gray squirrels are probably restricted to the distribution of oaks in undeveloped areas of Washington. Although riparian areas provided the greatest diversity of food sources, acorns probably provided substantially higher calories compared to other common food sources in this region such as maple samaras. Eastern gray squirrels do not show similar limitations in the Eastern United States because of the abundance and diversity of other mast-producing trees such as hickory (*Carya*) and walnut (*Juglans*) which are not limited to riparian areas.

Range of habitat types

The range of habitats used by eastern and western gray squirrels included habitats of exclusive-use by each species. On the Base, areas of exclusive-use by eastern gray squirrels included pure deciduous stands, such as those of cottonwood with extremely dense shrub cover within riparian areas. Western gray squirrels used deciduous stands where they included oaks and were adjacent to conifers during fall when acorns were available. Unlike eastern gray squirrels, we rarely observed western gray squirrels within these habitats outside of foraging bouts in the fall. Western gray squirrels appeared to have exclusive-use of areas that supported only Douglas-fir trees without any shrub cover. Such habitats were used intensively by western gray squirrels provided that oaks were available somewhere within the squirrel’s home-range. These habitats occurred on the Base where prairie had been recently colonized by firs and moss had replaced grass as the dominant ground cover. Eastern gray squirrels appeared unable to establish populations in such habitats even in the absence of western gray squirrels.

Resource partitioning

Despite shared use of oak and high canopy cover, our analysis indicated important differences in structure and composition between habitats used by eastern and western gray squirrels led to low overlap in their use of space. Discriminate functions found good separation between habitats of core areas used by eastern and western gray squirrels. Top discriminating variables between habitats of eastern and western gray squirrels reflected differences in riparian and upland habitats because shrub cover, shrub richness, and the percent of deciduous trees were higher in areas used by eastern gray squirrels compared to those of western gray squirrels. Separation of nest sites between species and the top discriminating variables were similar to those of core areas because squirrels often placed nests within core areas. Linders (2000) also found little differences in habitat characteristics between core areas and nest sites for western gray squirrels in Southern Washington. Nest sites for western gray squirrels on the Base shared similarities to those studied elsewhere in Washington because they had greater tree abundance, tree diversity, and canopy connectivity than available sites (Linders 2000, Gregory et al. 2010, Stuart 2012). Nest sites of eastern gray squirrels followed a similar pattern to western gray squirrels based on these characteristics.

We found less separation between species for habitat characteristics around den sites compared to results from core area and nest sites because some western gray squirrels moved into riparian areas to have young during breeding season. Tree cavities were most abundant in deciduous trees which were found primarily in riparian areas. Western gray squirrels rely on tree cavities for dens in Klickitat County (Linders 2000, Vander Haegen et al. 2005) and may interact with eastern gray squirrels when seeking these structures in riparian areas on the Base. We observed western gray squirrels at two locations using tree cavities as dens from the same trees used by eastern gray squirrels that had previously occupied the area. Competition for cavities may occur where they are a limited resource, but we found western gray squirrels often used cavities in upland areas as natal dens and even used stick nests as natal dens on the Base. Gregory et al. (2010) also found western gray squirrels reared young in stick nests in the North Cascades where oaks are not available for natal dens. Our comparison of den sites between species did not find a significant difference because enough western gray squirrels had used dens in riparian areas to suggest similarity in habitat characteristics of these sites between species.

Nest trees

Characteristics of nest and den trees were similar between eastern and western gray squirrels. Both species used Douglas-firs almost exclusively for nest placement as it was by far the most common conifer on the Base. Squirrels also tended to use among the largest Douglas-firs with high canopy connectivity in an area. Similarity in tree use was likely due to shared dependence on travel through canopy and the need for protection from predators. These requirements may be more likely met by large rather than small trees because greater connectivity provides more escape routes and large canopies obscure nests from avian predators. Similar patterns in use of nest trees by western gray squirrels were found in dry forests in Washington (Linders 2000, Gregory 2008, Stuart 2012). Although western gray squirrels used cavities in conifers as dens more so than eastern gray squirrels, both species used deciduous trees for dens which led to poor separation of tree characteristics selected by these squirrels in the discriminant analysis.

Habitat loss

Habitat loss may be an important factor that influences the outcome of competition between eastern and western gray squirrels because it may compromise the ability of western gray squirrels to compete with other squirrels. Eastern gray squirrels may invade and control areas suitable to both species after they have been vacated by western gray squirrels. Habitat loss for western gray squirrels in our study area appeared to limit population size; at low enough levels their persistence may be vulnerable to threats such as competition from eastern gray squirrels that are otherwise innocuous (Linders and Stinson 2007). Habitat for western gray squirrels in the South Puget Sound lowlands extended from Tacoma westward to the coast a century ago but is now largely confined to the Base. Sources of habitat loss for western gray squirrels in this region may include urbanization, fire exclusion, and forestry practices.

With few exceptions, western gray squirrels avoid urban areas throughout their range. Western gray squirrels were absent from developed areas on and around the Base. The Base has maintained most of the remaining squirrel habitat in the South Puget Sound by setting aside forests for military training; however, encroachment into squirrel habitat through land-use change has also occurred within these forests. Construction of new housing and other installations within areas used by western gray squirrels on the Base has increased human presence within these areas and may discourage use by squirrels. Several highways traverse the Base where automobile collisions contributed to squirrel mortality during our study. A new highway has been proposed for construction within areas that supported western gray squirrels which will likely reduce and fragment remaining habitat on the Base and increase squirrel mortality due to automobile traffic.

Succession has been a source of significant habitat loss for western gray squirrels on the Base in recent years (Thysell and Carey 2001). Historically, fires set by Native Americans maintained habitats for western gray squirrels on the Base and elsewhere within the squirrel’s geographic range because oaks and Ponderosa pines depend on frequent fires to eliminate shade-tolerant competitors and stimulate regeneration (Agee 1993). Fire exclusion over the past century has allowed Douglas-fir to shade out oaks and invade prairies on the Base (Foster and Shaff 2003). Consequently, succession of forests of conifer mixed with oaks to monoculture forests of Douglas-fir on the Base has decreased habitat availability for western gray squirrels. Habitats used by western gray squirrels resembled habitats shaped by frequent fires as indicated by the importance of oaks and low levels of shrub cover in our analyses. On the Base, oaks were most abundant where prairie transitioned to oak woodlands and then to conifer forests. Western gray squirrels frequently used areas where Douglas-fir mixed with oaks within this transitional habitat type which has been traditionally maintained by fire.

Timber harvest inherently alters forest structure and may affect habitat quality for western gray squirrels. Forests were actively managed throughout most of the Base where thinning was the primary method of harvest. Thinning forests may reduce canopy cover and connectivity which were the top variables for discriminating core from low-use areas for western gray squirrels. Thresholds at which reductions in canopy cover or connectivity diminish habitat quality for western gray squirrels were not examined in this study. Increased sunlight penetration from reduced canopy cover may also increase shrub cover which was the top variable for discriminated eastern from western gray squirrel habitat. Western gray squirrels used thinned forests heavily in the North Cascades (Stuart 2012), but their response to thinning may be different in more mesic forests found on the Base. Furthermore, squirrel responses to thinning or other harvest methods may depend on tree spacing and patch configuration.

Conclusions

Differential habitat use between eastern and western gray squirrels limited competitive interactions and may allow coexistence where upland and riparian habitats are abundant and distinct. Eastern gray squirrels appeared limited to riparian areas on the Base and our models predicted few areas to be suitable for both species. Further study is needed to determine whether differential habitat use between eastern and western gray squirrels occurs in other regions. Sources of habitat loss for western gray squirrels need further study to inform conservation strategies. Western gray squirrels avoid urban areas and use habitat types 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. Finally, forestry practices that reduce canopy cover and connectivity to levels that prohibit arboreal travel or stimulate growth of dense shrub layers likely reduce habitat quality for western gray squirrels on the Base. Further study is needed to evaluate impacts of timber harvests and devise treatments that maintain or improve habitat for western gray squirrels.

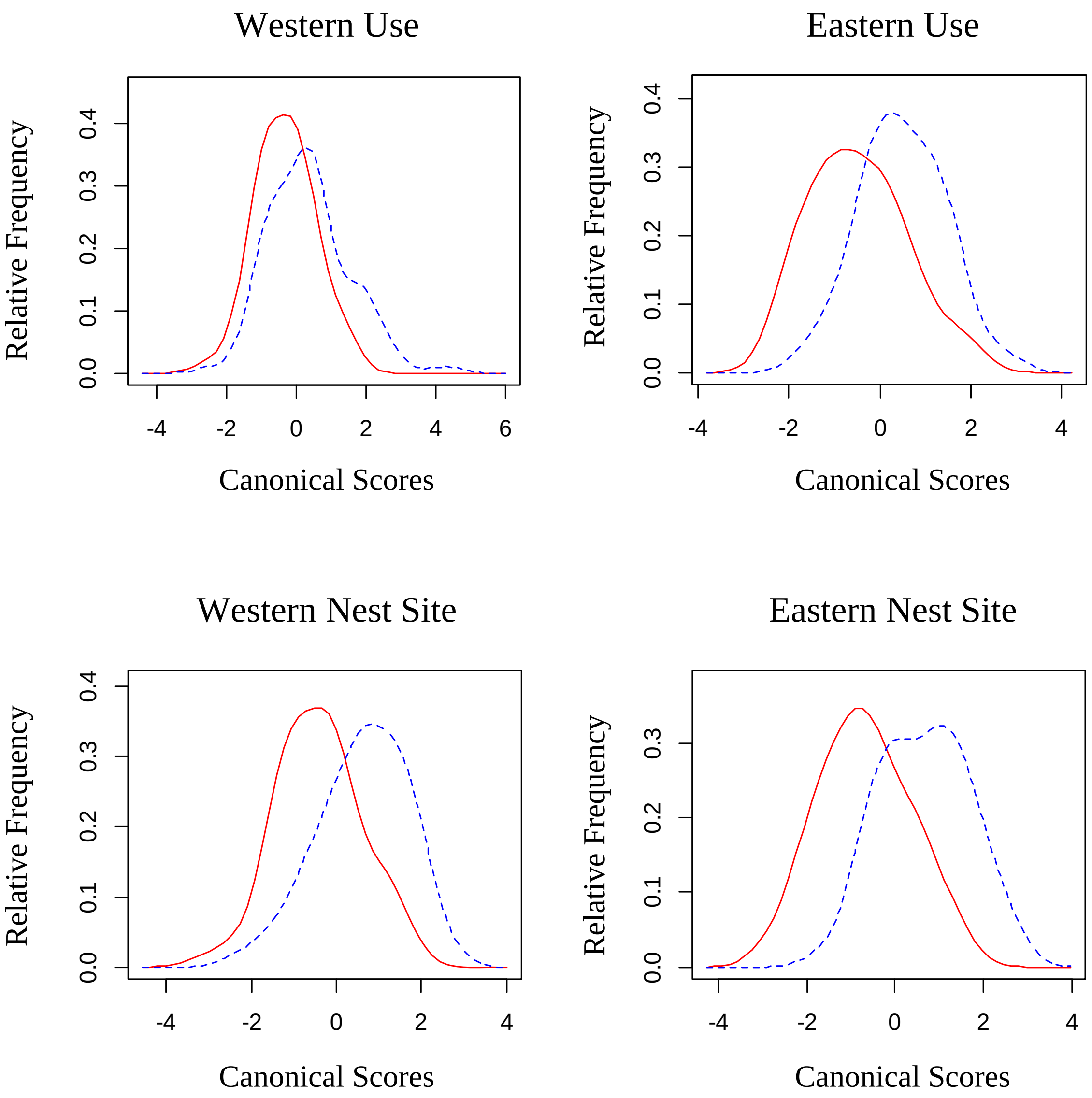

Figure 2.1. Canonical scores from discriminant functions for habitat characteristics in core (red solid line) vs low-use (blue dotted line) areas and used (blue dotted line) vs available (red solid line) nest sites for eastern and western gray squirrels.

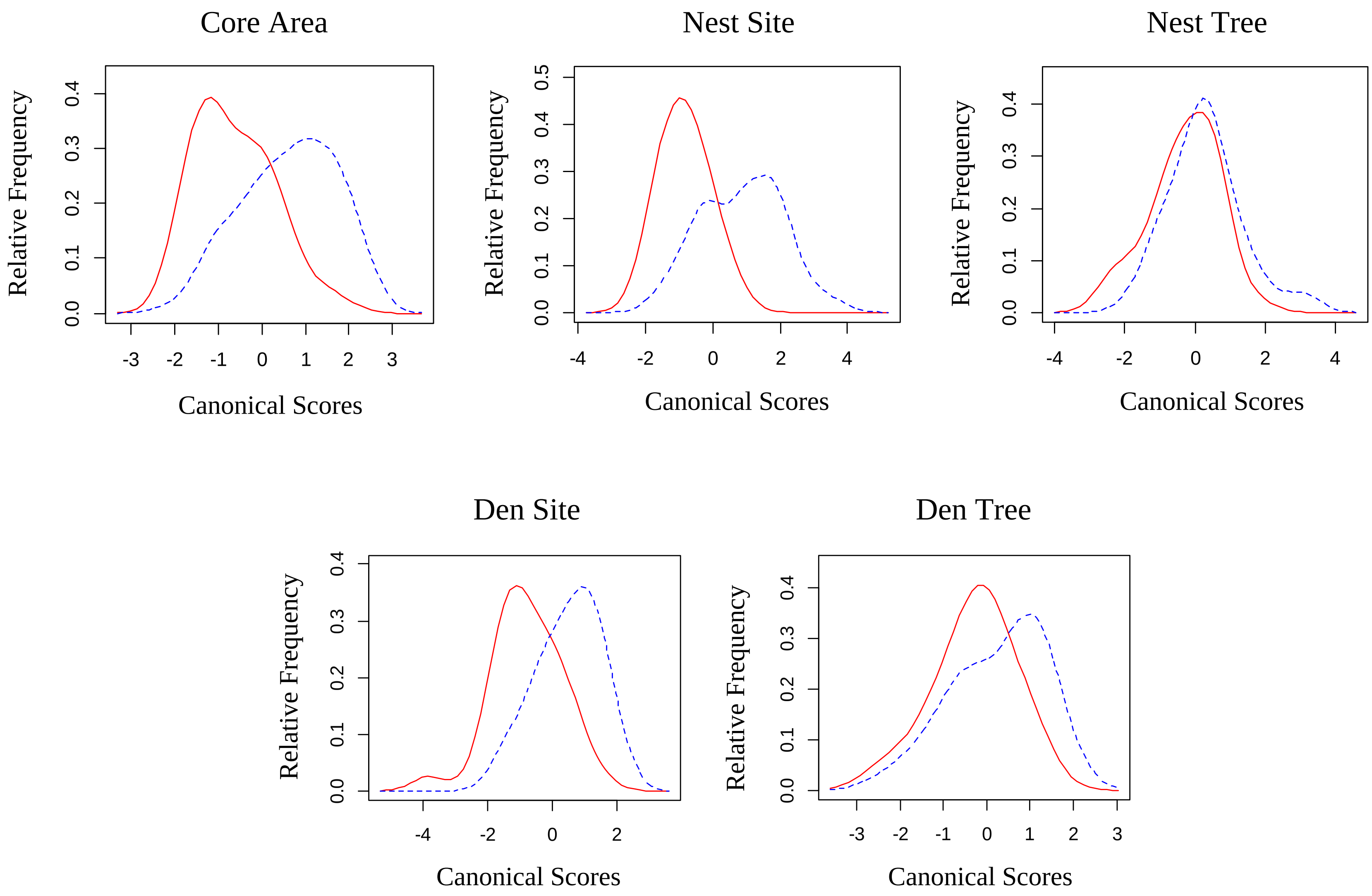

Figure 2.2. Canonical scores from discriminant functions for habitat characteristics in areas used by eastern (solid red line) and western (dotted blue line) gray squirrels.

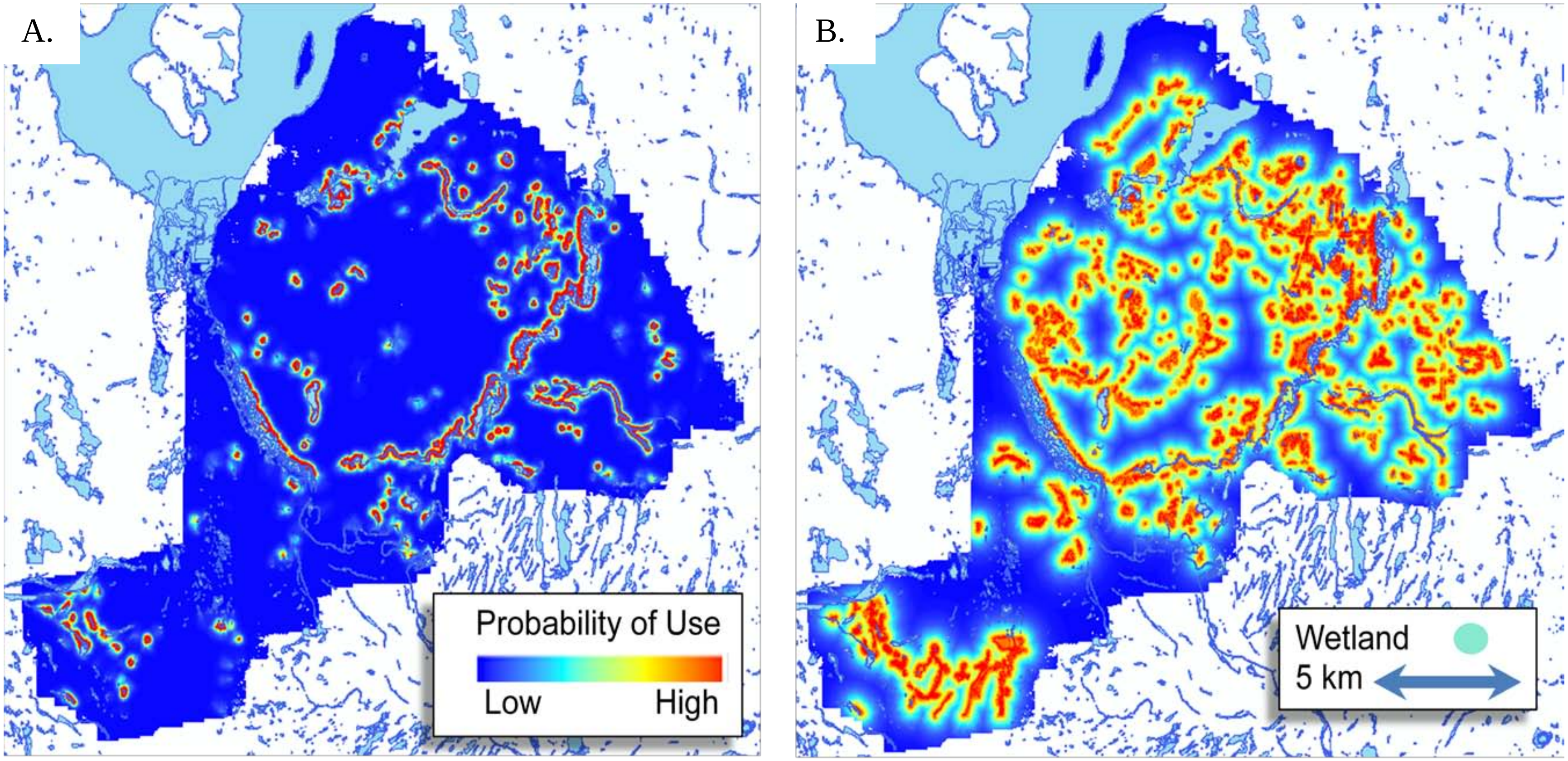

Figure 2.3. Probabilities of use by eastern (A) and western (B) gray squirrels on Joint-Base Lewis McChord predicted by population resource utilization functions.

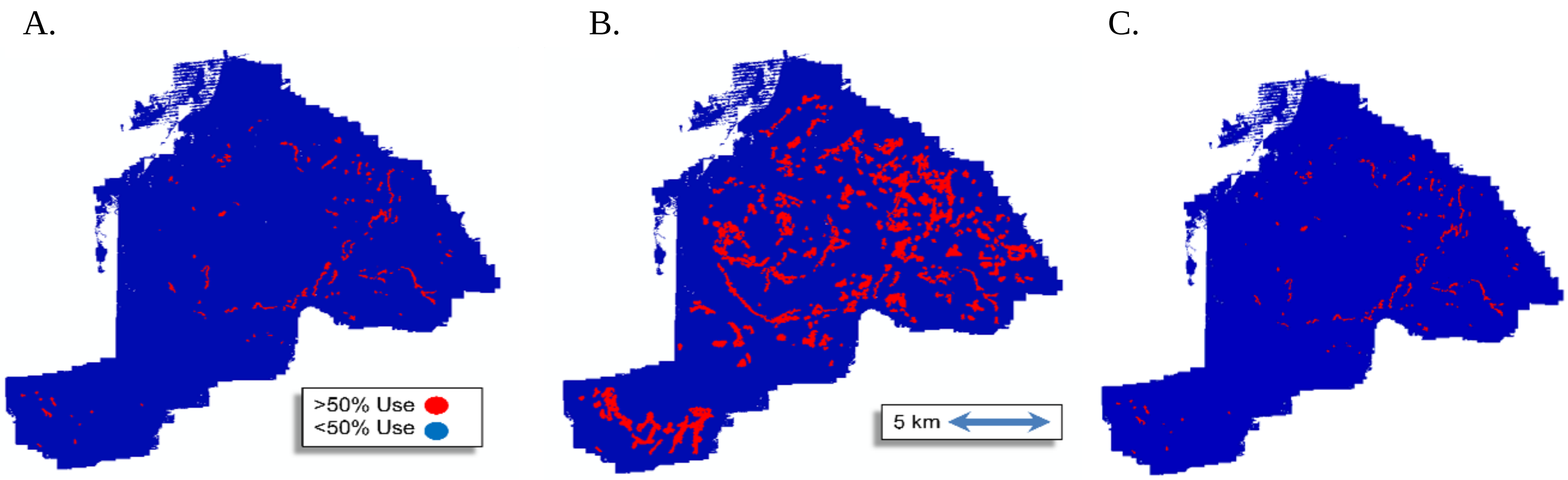

Figure 2.4. Upper 50% probabilities of use by eastern (A) and western (B) gray squirrels on Joint-Base Lewis McChord predicted by population resource utilization functions and the area of intersection between species (C).

Table 2.1. Structure correlations and classification rates from discriminant function analysis (DFA) and results of analysis of similarities (ANOSIM) for tests of no differences between groups based on habitat characteristics in core and low-use areas and used versus available nest sites for eastern and western gray squirrels on Joint Base Lewis-McChord.

	Western		Eastern	
	Core[1]	Nest[2]	Core[1]	Nest[2]
Average dbh (cm)	-0.188	-0.118	-0.067	-0.360
Maximum dbh (cm)	-0.261	0.179		
Sd dbh (cm)	-0.222		-0.187	-0.118
Tree density[3]	-0.324	0.448	0.149	0.484
% deciduous trees		0.354	-0.417	0.372
% oak trees	-0.361	0.456	-0.040	0.478
Tree richness			-0.627	0.481
Tree evenness	-0.510			0.384
Canopy cover (%)	-0.555	0.150	-0.113	-0.293
Canopy connectivity[4]	-0.465	0.581	-0.130	0.610
Shrub cover[5]	-0.122	-0.248	-0.456	0.096
Shrub richness			-0.297	0.048
Shrub evenness	-0.045	0.282	-0.370	0.172
Logs[6]	-0.370	0.326	-0.295	0.028
Classification rate	0.639	0.731	0.667	0.702
R	0.023	0.047	0.035	0.084
P	0.004	0.024	<0.001	<0.001

[1] Negative signs indicate lower values in low-use versus core areas.

[2] Negative signs indicate lower values in used versus available nest sites.

[3] Tree density = number of trees divided by the plot area (0.035ha).

[4] Canopy connectivity was the number of trees with live branches within 1m of those of the focal tree. Connectivity was recorded as the average connectivity measured on three trees.

[5] Shrub cover was measured as the sum of the relative abundances of each species measured by line transect methods.

[6] Logs = number of logs within or penetrating the plot.

Table 2.2. Means of habitat measures in core and low-use areas for eastern and western gray squirrels on Joint Base Lewis-McChord.

	Western				Eastern			
	Core	SE	Low	SE	Core	SE	Low	SE
Average dbh	31.2	1.5	31.3	2.2	31.4	1.2	32.0	1.6
Maximum dbh	75.5	2.4	70.9	3.3	76.7	2.9	73.1	3.2
Sd dbh	19.2	0.8	19.3	1.2	21.2	1.0	19.5	1.1
Tree density	511	28	449	35	474	23	514	39
% deciduous trees	28.4	3.3	23.0	3.6	57.0	3.8	43.2	4.1
% oak trees	15.8	2.5	11.3	2.3	23.0	3.0	23.1	3.4
Tree richness	2.09	0.11	1.79	0.10	2.84	0.12	2.22	0.11
Tree evenness	0.461	0.040	0.341	0.038	0.661	0.031	0.495	0.039
Canopy cover	88.9	1.0	84.6	1.5	91.8	1.2	90.6	1.2
Canopy connectivity	4.06	0.17	3.54	0.15	4.07	0.14	3.91	0.16
Shrub cover index	1.43	0.10	1.36	0.11	2.28	0.10	1.88	0.11
Shrub richness	6.46	0.30	6.48	0.39	8.42	0.27	7.72	0.29
Shrub evenness	0.705	0.021	0.673	0.029	0.744	0.014	0.694	0.018
Logs	7.22	0.69	6.03	0.63	5.54	0.58	3.89	0.39
N	90		90		90		90	

Table 2.3. Structure correlations and classification rates from DFA and results of ANOSIM for tests of no differences between eastern and western gray squirrels based on habitat characteristics at core areas, nest sites, and den sites on Joint Base Lewis-McChord.

	Core[1]	Nest	Den
Average dbh	-0.065	0.137	0.196
Maximum dbh		-0.013	
Sd dbh	-0.181		-0.182
% deciduous trees	-0.711	-0.391	-0.695
% oak trees	-0.305	-0.171	0.017
Tree density	0.144	-0.258	-0.024
Canopy cover	-0.372	-0.085	-0.500
Canopy connectivity	-0.055	-0.260	0.038
Tree richness	-0.627	-0.494	-0.595
Tree evenness	-0.298	-0.464	-0.507
Shrub cover	-0.785	-0.541	-0.449
Shrub richness	-0.638		-0.114
Shrub evenness	-0.068	0.001	0.257
Logs	0.254	0.464	-0.042
Classification rate	0.744	0.800	0.744
R	0.095	0.083	0.038
P	<0.001	<0.001	0.104

[1] Negative signs indicate lower values in core areas or nest sites of western versus eastern gray squirrels.

Table 2.4. Mean habitat measures at nest and den sites for eastern and western gray squirrels on Joint Base Lewis-McChord.

	Western				Eastern				Den			
	Nest	SE	Available	SE	Nest	SE	Available	SE	Western	SE	Eastern	SE
Average dbh	30.1	1.8	31.6	1.6	29.1	1.5	32.7	2.1	41.7	2.6	37.0	2.5
Maximum dbh	78.0	3.8	74.2	3.0	79.0	3.4	78.3	4.1	130	4	85.0	4.7
Sd dbh	19.7	1.1	20.7	1.1	19.6	1.1	21.2	1.5	35.1	1.4	24.8	1.7
Tree density	574	44	453	30	659	43	510	43	326	37	448	46
% deciduous trees	31.2	4.3	22.2	3.4	49.1	4.0	33.8	4.9	42.8	5.6	66.2	7.1
% oak trees	20.9	3.9	11.4	2.4	26.9	3.6	15.9	3.6	42.8	3.2	11.9	3.4
Tree richness	2.19	0.15	1.89	0.10	2.82	0.12	2.29	0.16	2.00	0.15	2.71	0.22
Tree evenness	0.492	0.050	0.390	0.041	0.726	0.030	0.502	0.050	0.648	0.052	0.643	0.058
Canopy cover	88.9	1.3	88.0	1.1	90.5	1.0	92.6	0.9	92.0	1.1	93.7	1.4
Canopy connectivity	4.49	0.17	3.71	0.17	4.94	0.18	3.92	0.21	4.17	0.19	3.92	0.27
Shrub cover index	1.28	0.13	1.50	0.11	2.02	0.13	1.89	0.13	1.83	0.12	2.02	0.15
Shrub richness	6.60	0.38	6.84	0.39	8.09	0.33	8.04	0.35	9.00	0.39	7.11	0.45
Shrub evenness	0.754	0.026	0.694	0.028	0.744	0.015	0.724	0.021	0.716	0.030	0.657	0.029
Logs	7.40	0.94	6.01	0.57	4.07	0.45	4.06	0.53	5.50	0.80	7.25	1.04
n	52		78		53		51		47		31	

Table 2.5. Coefficients of conditional logistic regression models that compared characteristics of trees with nests used by eastern and western gray squirrels to available trees.

Rank	Ht[1]	SE	Dbh[1]	SE	Cc[2]	SE	Llc[3]	SE	Cvol[3]	SE	Rh[1]	SE	AIC	ΔAIC
Western Models														
1					0.23	9.6e^{-2}	-0.11	3.9e^{-2}	2.9e^{-4}	1.5e^{-4}			197.5	0
2			0.67	0.41	0.24	9.6e^{-2}	-0.13	3.9e^{-2}					198.3	0.8
3					0.23	9.6e^{-2}	-8.7e^{-2}	4.8e^{-2}	5.0e^{-4}	2.7e^{-4}	-2.1	2.3	198.6	1.1
4					0.28	9.3e^{-2}	-0.12	3.8e^{-2}					199.1	1.6
5	2.2e^{-2}	1.9e^{-2}			0.26	9.5e^{-2}	-0.13	4.1e^{-2}					199.8	2.3
6			0.78	0.59	0.25	9.6e^{-2}	-0.12	4.2e^{-2}			-0.49	1.8	200.3	2.8
Eastern Models														
1			2.7e^{-2}	7.9e^{-3}	1.7	0.46							183.9	0
2			3.1e^{-2}	1.1e^{-2}	1.7	0.46					-0.50	0.87	185.6	1.7
3					1.9	0.46			5.6e^{-4}	2.0e^{-4}			188.3	4.4
4					1.9	0.46			6.5e^{-4}	2.9e^{-4}	-0.39	0.93	190.1	6.2
5					2.0	0.45					1.1	0.59	193.3	9.4
6	-2.2	2.7			2.1	0.47					3.0	2.4	194.7	10.8
7					2.2	0.45							194.9	11

[1] Tree height (Ht) was log transformed for analysis of trees used by eastern gray squirrels, whereas Dbh and relative tree height (Rh) were log transformed for western gray squirrels.

[2] Canopy connectivity (Cc) was square root transformed for analysis of trees used by eastern gray squirrels.

[3] Lowest living crown = Llc; canopy volume = Cvol.

Table 2.6. Mean habitat measures of nest trees for eastern and western gray squirrels on Joint Base Lewis-McChord.

	Western				Eastern			
	Nest	SE	Available	SE	Nest	SE	Available	SE
Tree height (m)	32.3	1.9	31.1	0.5	31.8	1.4	28.8	0.5
Nest height (m)	14.9	1.1			14.4	0.7		
Relative tree height[1]	1.05	0.09	0.992	0.013	1.11	0.04	0.994	0.013
Relative nest height (m)	0.482	0.025			0.475	0.022		
Lowest living crown (m)	10.7	0.8	12.7	0.4	10.1	0.6	9.81	0.26
Canopy volume[2]	1560	209	1073	50	1633	169	1099	46
Dbh (cm)	61.7	4.9	50.7	1.3	66.4	4.2	50.4	1.3
Canopy connectivity[3]	5.27	0.36	4.83	0.10	6.46	0.48	4.86	0.10
n	48		383		48		401	

[1] Relative tree height = tree height divided by the median tree height for the plot.

[2] Canopy volume = (tree height – lowest living crown) * dbh.

[3] Canopy connectivity was the number of trees with live branches within 1m of those of the nest or den tree.

Table 2.7. Frequency of tree species with nests and dens for eastern and western gray squirrels on Joint Base Lewis-McChord.

	Western		Eastern	
	Nest	Den	Nest	Den
Douglas-fir	472	28	146	15
Ponderosa pine	18	0	0	0
Western red cedar	0	0	8	2
Oak	10	8	10	6
Ash	8	8	4	22
Maple	0	2	0	1
Cottonwood	3	2	7	14
Alder	0	0	4	5
Other	0	0	5	2

Table 2.8. Structure correlations from DFA and results of ANOSIM for tests of no differences between eastern and western grey squirrels based on characteristics of nest trees on Joint Base Lewis-McChord.

	Nest[1]	Den
Nest height	0.181	-0.307
Tree height		0.590
Relative nest height	0.166	-0.771
Height of lowest living crown	0.200	0.493
Canopy connectivity	-0.877	0.407
Dbh	-0.254	
Classification rate	0.604	0.554
R	0.017	0.020
P	0.128	0.195

[1] Negative signs indicate lower values for nest trees of western versus eastern gray squirrels.

Table 2.9. Mean habitat measures of den trees for eastern and western gray squirrels on Joint Base Lewis-McChord.

	Western		Eastern	
	$\bar{x}$	SE	$\bar{x}$	SE
Tree height (m)	30.3	2.1	26.8	2.4
Nest height (m)	8.90	0.79	9.64	0.95
Relative nest height (m)	0.320	0.034	0.399	0.038
Lowest living crown (m)	10.8	1.0	8.74	0.89
Canopy volume[1]	1483	213	1253	255
Dbh (cm)	67.2	5.2	61.0	4.7
Canopy connectivity[2]	4.83	0.50	4.08	0.32
N	30		26	

[1] Canopy volume = (tree height – lowest living crown) * dbh.

[2] Canopy connectivity was the number of trees with live branches within 1m of those of the den tree.

Table 2.10. Means and 95% confidence intervals for unstandardized coefficients of resource utilization functions (RUFs) from individual eastern and western gray squirrels.

	Eastern Gray Squirrel			Western Gray Squirrel		
	$\bar{x}$	LCI	UCI	$\bar{x}$	LCI	UCI
Canopy cover	0.48	0.21	0.75	0.19	0.13	0.25
Canopy height	$6.0e^{-3}$	$-9.9e^{-4}$	$1.3e^{-2}$	$2.2e^{-3}$	$-2.1e^{-4}$	$4.6e^{-3}$
SD canopy height	$-8.3e^{-3}$	$-2.0e^{-2}$	$3.1e^{-3}$	$-4.1e^{-4}$	$-3.4e^{-3}$	$2.6e^{-3}$
Shrub cover	$3.8e^{-2}$	-0.18	0.25	-0.15	-0.25	$-5.5e^{-2}$
Distance to oak	$-6.1e^{-3}$	$-1.2e^{-2}$	$1.8e^{-4}$	$-2.8e^{-3}$	$-4.1e^{-3}$	$-1.5e^{-3}$
Distance to wetland	$-8.4e^{-3}$	$-1.3e^{-2}$	$-4.0e^{-3}$	$-2.2e^{-4}$	$-1.3e^{-3}$	$8.5e^{-4}$

Table 2.11. Means and 95% confidence intervals for standardized coefficients of resource utilization functions (RUFs) from individual eastern and western gray squirrels ranked (R) from most to least important.

	Eastern Gray Squirrel				Western Gray Squirrel			
	$\bar{x}$	LCI	UCI	R	$\bar{x}$	LCI	UCI	R
Canopy cover	0.12	$4.1e^{-2}$	0.20	2	$4.7e^{-2}$	$3.2e^{-2}$	$6.3e^{-2}$	2
Canopy height	$7.1e^{-2}$	$-4.7e^{-3}$	0.15	4	$3.2e^{-2}$	$3.5e^{-3}$	$6.1e^{-2}$	3
SD canopy height	$-2.6e^{-2}$	$-5.7e^{-2}$	$4.8e^{-3}$	5	$-2.6e^{-3}$	$-1.3e^{-2}$	$7.7e^{-3}$	6
Shrub cover	$-2.5e^{-3}$	$-3.4e^{-2}$	$2.9e^{-2}$	6	$-1.4e^{-2}$	$-2.7e^{-2}$	$-1.0e^{-3}$	4
Distance to oak	$-8.8e^{-2}$	-0.25	$7.5e^{-2}$	3	-0.21	-0.32	-0.10	1
Distance to wetland	-0.30	-0.48	-0.12	1	$-1.0e^{-2}$	-0.15	0.13	5

Table 2.12. Means and 95% confidences intervals for coefficients of variables included in final RUFs for eastern and western gray squirrels on Joint Base Lewis-McChord.

	Eastern Gray Squirrel						Western Gray Squirrel					
	Unstandardized			Standardized			Unstandardized			Standardized		
	$\bar{x}$	LCI	UCI	$\bar{x}$	LCI	UCI	$\bar{x}$	LCI	UCI	$\bar{x}$	LCI	UCI
Canopy cover	0.60	0.31	0.89	0.15	0.31	0.89	0.20	0.13	0.26	$5.2e^{-2}$	$3.4e^{-2}$	$7.1e^{-2}$
Canopy height							$1.7e^{-3}$	$7.5e^{-5}$	$3.4e^{-3}$	$2.2e^{-2}$	$2.1e^{-3}$	$4.2e^{-2}$
Shrub cover							-0.15	-0.30	$-1.2e^{-2}$	$-1.0e^{-2}$	$-2.6e^{-2}$	$5.9e^{-3}$
Distance to oak	$-6.6e^{-3}$	$-1.3e^{-2}$	$1.6e^{-4}$	$-9.1e^{-2}$	-0.25	$6.7e^{-2}$	$-2.7e^{-3}$	$-4.2e^{-3}$	$-1.2e^{-3}$	-0.197	-0.195	-0.198
Distance to water	$-8.6e^{-3}$	$-1.3e^{-2}$	$-4.0e^{-3}$	-0.30	-0.48	-0.13						

Table 2.13. Number of RUFs with significant (α=0.05) unstandardized coefficients for each variable from the full model for individual eastern and western gray squirrels.

	Eastern Gray Squirrel				Western Gray Squirrel			
	POS	NEG	POS(sig)	NEG(sig)	POS	NEG	POS(sig)	NEG(sig)
Canopy cover	15	1	3	0	33	7	17	0
Canopy height	9	7	3	0	29	11	8	4
SD canopy height	6	10	0	0	18	22	3	2
Shrub cover	7	9	1	0	13	27	1	9
Distance to oak	4	12	1	5	8	32	6	25
Distance to wetland	2	14	1	8	14	26	14	20

Table 2.14. Cross-validation results for resource utilization functions for eastern (n=16) and western (n=40) gray squirrels. Coefficients of determination (R^2) and t-statistics were averaged over all squirrels, whereas the number of positive (POS) and negative (NEG) and the number of significant (sig; α=0.05) slopes were tallied (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	0.64	4.6	13	3	13	0	4.3	-
Western	0.42	3.7	31	9	24	5	3.4	4.8

CHAPTER 3

Dietary Partitioning by Eastern and Western Gray Squirrels

The degree of dietary similarity between competing species should correlate with the intensity of competition when food resources are limited (Keddy 2001). Diet studies of potential competitors may reveal not only shared dependence on limited resources, but also other important information about interspecies interactions. Foraging is an important activity for tree squirrels that accounts for much of their daily activities and confers fitness rewards. Foraging decisions may consider availability and quality of food items as well as other factors such as the trade-offs of food and safety (Stephens et al. 2007). Diets can reflect these decisions and other important information about resource use. For example, subtle differences in the sizes of pine cones selected by eastern gray squirrels (*Sciurus carolinensis*) and fox squirrels (*S. niger*) has explained differences in their habitat use and abilities to exploit unique habitat types (Steele and Koprowski 2001). Differential use of food resources can facilitate coexistence of similar species that share habitat. Alternatively, shared use of food resources can lead to the competitive interactions and loss of the competitively inferior species. Competition for food resources, for example, has been identified as a mechanism of competition between invasive eastern gray squirrels and Eurasian red squirrels (*S. vulgaris*) in the United Kingdom (Wauters et al. 2002). Therefore, it is important to evaluate dietary similarity of potential competitors to determine if resources are under competition.

Eastern gray squirrels have invaded some areas that support western gray squirrels in the Western United States where they may compete for food resources. Dietary overlap for these species may be high because they are known to consume and store acorns as a primary food source over winter. Dietary similarity between eastern and western gray squirrels for items other than acorns is poorly understood because only one study has compared diets in areas of sympatry. Byrne (1979) indicated that truffles were a major dietary component for western gray squirrels in California, whereas eastern gray squirrels concentrated on tree seeds. Others have reported similar dependency on truffles by western gray squirrels (Stienecker and Browning 1970, Stienecker 1977, Stuart 2012), but the importance of truffles to eastern gray squirrels has been less clear. Fungi appear only seasonally in diets of eastern gray squirrels in the Eastern United States when tree seeds are not available (Korschgen 1981, Koprowski 1994). Food availability in forests of Western Washington likely differs from those of previous studies. Absences of preferred food items in this region may force gray squirrels to forage on alternative resources which could result in different competitive dynamics.

The objectives of this study were to describe diets of eastern and western gray squirrels and their seasonal variation based on fecal samples and foraging observations. We tested the null hypothesis of no difference in truffle consumption between species after accounting for effects of season. We also tested for differences in consumption of tree seeds and described diet variation by season and year.

METHODS

Study area - We studied gray squirrels on Joint-Base Lewis-McChord (Base, hereafter), a military reservation near Tacoma, WA. The Base covers 35,000 ha, most of which was set aside as undeveloped forests, prairies, and woodlands for use as training areas for military personnel and timber harvest. Elevation ranges from 120 to 160 m, and average annual precipitation is 800-900 mm. 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 years) Douglas-fir (*Pseudotsuga menziesii*). Prairie remnants, oak woodlands, and Ponderosa pines (*Pinus ponderosa*) were sparsely distributed throughout the Base. Riparian areas supported Oregon white oak (*Quercus garryana*), Oregon ash (*Fraxinus latifolia*), big-leaf 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*). Eastern gray squirrels were present in developed and undeveloped portions of the Base, whereas western gray squirrels were found only in undeveloped forests. Much of the Base was surrounded by urban or agricultural areas that supported eastern gray squirrels but not western gray squirrels.

Field methods

We trapped and radio-collared eastern and western gray squirrels at four study sites on the Base that were designated as units for an experimental removal of eastern gray squirrels from July 2007 to April 2012 (see Chapter 1). In addition, Washington Department of Fish and Wildlife biologists trapped and radio-collared western gray squirrels at nearby sites for a concurrent project to study and augment the population as part of a recovery strategy for this species (Vander Haegen and Orth 2011). We placed trap transects in suitable habitat within each study site with the objective of saturating the site with traps to ensure that we captured most, if not all, gray squirrels in the area. We usually ran 30 to 50 traps per site depending on the extent and configuration of habitat. Traps along transects were spaced 50 to 100 m apart. Trapping sessions of 3 to 7 days occurred every 3 to 5 months at each study area. In addition, we frequently trapped specific areas of each site between these sessions to recollar squirrels or assess squirrel condition, and these efforts occasionally captured new squirrels that had dispersed into the area.

We trapped squirrels with Tomahawk live-traps baited with whole walnuts. Traps were typically opened shortly after dawn and checked every 2 hours until early afternoon when traps were closed. Trap sessions were preceded by a 2-week pre-baiting period to acquaint squirrels with traps and improve capture probabilities. Traps were pre-baited by wiring the door open and baiting with walnuts 2 or 3 times per week. Upon capture, we restrained squirrels in a cloth-handling cone (Koprowski 2002) which allowed us to assess squirrel condition and attach a radio-collar. We collected fecal pellets left by squirrels in traps and stored them in vials with 100% ethanol for examination in the laboratory. Pellets were collected only when none were present in or beneath traps prior to trapping to ensure they came from the captured squirrel. We collected pellets from each squirrel no more than once per trapping session to ensure that samples were independent.

We relocated squirrels equipped with radio-collars three times per week by homing in on their location using radio-telemetry techniques. Squirrels were tracked throughout the diurnal period and were relocated once per day to ensure independence among locations. We tracked squirrels year-round until death or the end of study in April 2012. The location of the squirrel was recorded with a GPS unit (Trimble Navigation Limited, Westminster, CO) once it was seen or estimated to within 10m based on the radio-signal. We observed squirrel behaviors and recorded food items consumed during bouts of foraging.

Laboratory methods

For each sample of fecal pellets, we macerated 1 or 2 pellets in water and added one drop of potassium hydroxide (KOH). We then placed one or two drops of the solution on a slide for examination. We created three slides per sample and examined 10 fields of view spaced 1 mm apart along each of two transects per slide at 40x magnification to record presence of fungal spores and other food items. We identified fungal spores to genus following synoptic keys of Castellano et al. (1989). Melzer's reagent (iodine, potassium iodide, and chloral hydrate in aqueous solution) was added to slides when needed to stain spores and aid with identification. We also recorded presence of insect parts and noted plants when pollen, cell walls, or starches were present.

Statistical methods

We tested for differences in truffle consumption between eastern and western gray squirrels after accounting for effects of season with nonparametric multivariate analysis of variance (perMANOVA) using the vegan package in R. Before analysis, we screened the data and excluded spore genera present in <5% of the observations to avoid undue influence of rare genera. We also excluded three samples that had no spore detections for similar reasons. Observations of *Geopera*, *Barssia*, and *Balsamia* were combined into a group we called the *Geopera* complex because of difficulties in distinguishing genera based on spore characteristics. Castellano et al. (1989) suggest there is usually little reason to differentiate these genera because they are ecologically similar. Likewise, we combined observations from members of *Russulaceae* because genera cannot be differentiated based on spores alone (Castellano et al. 1989). We converted the matrix of presence and absences of spore genera in the samples from each squirrel to a similarity matrix based on Jaccard's index. Multivariate outliers were identified with a function from the BIOSTATS library in R where values exceeding three standard deviations were considered outliers. No outliers were identified, so analysis proceeded on the entire data set. Pairwise comparisons for unbalanced data following perMANOVA are not available in the vegan package, so we reconfigured the data and repeated perMANOVA to further investigate seasonal effects. In addition, we tested for homogeneity of variances by season and species and conducted pairwise comparisons for seasonal effects (Anderson 2006). For these tests, Jaccard coefficients were placed in Euclidean space by principal coordinate analysis, and a permutation test compared Euclidean distances to the centroid among groups. We plotted samples in ordination space following nonmetric dimensional scaling (NMDS) to visualize dietary patterns. Finally, we summarized foraging observations into contingency tables and tested for differences among seasons, years, and between squirrel species with chi-square tests. We excluded foraging observations on food items that were rare (n<5) for both squirrel species for these tests. Foraging observations from eastern and western gray squirrels were combined in contingency tables for tests of season and year effects.

RESULTS

From April 2007 through April 2012, we captured 101 eastern gray squirrels and 145 western gray squirrels on the Base, most of which were captured repeatedly throughout the year as part of the radio telemetry study. We examined 227 samples of fecal pellets collected during these capture events. We collected 60 samples from 34 eastern gray squirrels and 167 samples from 80 western gray squirrels.

We found no difference in truffle consumption between eastern and western gray squirrels after accounting for seasonal effects ($F_{1,\,219}$=1.1, P=0.331). There was strong evidence of seasonal differences in truffle consumption by squirrels ($F_{3,\,219}$=5.3, P<0.001), and subsequent pairwise comparisons indicated differences among all seasons (P<0.05) except between winter and spring ($F_{1,\,109}$=2.1, P=0.064). Multivariate dispersions differed among seasons ($F_{3,\,220}$=2.8, P=0.039), and pairwise comparisons indicated differences between spring and summer

(*P*=0.024) and strong differences between spring and winter (*P*=0.006). Ordinations of fecal samples showed high overlap between eastern and western gray squirrels (Figure 3.1), but some separation across seasons (Figure 3.2). A stress value of 0.187 from NMDS indicated ordinations provided a fair representation of dietary relationships.

Fungal spores were present in all but three samples which indicated both eastern and western gray squirrels consumed truffles frequently throughout the year. We found at least 14 genera of truffles and one genus of epigeous fungi in our samples (Table 3.1). Although we combined observations of *Geopera*, *Balsamia*, and *Barssia* into one group, we were fairly confident that all three genera were present in our samples based on spore characteristics. Most spores of *Russulaceae* appeared similar to those of *Gymnomyces*, a hypogeous fungus that resembles a truffle (Trappe et al. 2009). Spores of *Rhizopogon, Geopera*, and *Melanogaster* were in our samples during all seasons and were found far more frequently than spores of all other genera. Members of *Russulaceae* and some genera such as *Hymenogaster*, *Tuber*, *Elaphomyces*, and *Hydnotyra* were found fairly frequently in some seasons but were rare in others. Plants, insect parts, and other food items were relatively rare in our samples and probably were underestimated because our methodology was aimed toward identifying fungal spores.

We used radio-telemetry to home-in on squirrels 22,663 times and observed squirrels foraging 586 times. We saw western gray squirrels 3,268 times during 18,844 relocations and made 293 foraging observations in which the food item was identified. We saw eastern gray squirrels 419 times during 4,227 relocations and identified food items on 45 foraging observations. We were unable to identify food items on 30 and 220 foraging observations for eastern and western gray squirrels, respectively. In most of these cases, we could not identify the food item because the squirrel was foraging on the ground or in dense vegetation. Frequencies of food items consumed by eastern and western gray squirrels based on foraging observations were different (χ^2_6=48, P<0.001). The large chi-square statistic was primarily due to consumption of more maple samaras and fewer Douglas-fir cones than expected by eastern gray squirrels. Observed values were close to expected values for each food item for western gray squirrels. The frequency of foraging observations on each food item varied by season and year (χ^2_3>7.9, P<0.05; Tables 3.2, 3.3). Consumption of Douglas-fir cones and hazelnuts was most frequent in summer, whereas acorns and maple samaras were consumed during fall. Aside from truffles, Douglas-fir cones were the only food items eaten by squirrels that we observed with any regularity outside of summer and fall. We saw western gray squirrels stripping bark of Douglas-fir trees during one spring following a severe mast failure in 2010. Frequency of foraging on Douglas-fir cones, maple samaras, and hazelnuts varied by year (χ^2_3>7.9, P<0.05), but observations of acorn consumption were steady during this study (χ^2_3>2.9, P=0.407).

DISCUSSION

Dietary overlap between eastern and western gray squirrels was high on the Base, which suggests these squirrels may compete for limited food resources in areas of sympatry. Annual and seasonal fluctuations in food availability occurred on the Base during this study and could have increased competition for some food resources periodically. Acorns and Douglas-fir cones were important food sources that vary in availability over time and can be nearly absent during years of mast failure. Despite limited availability of these and other food resources during a severe mast failure by Oregon white oak, Douglas-fir, and Ponderosa pine that occurred in 2010, we did not find any increases in body mass of western gray squirrels after removal of eastern gray squirrels (see Chapter 1). Instead, we found low spatial overlap and significant differences in habitat use (see Chapter 2) which may have minimized the potential consequences of high dietary overlap.

The difference between eastern and western gray squirrels in their consumption of Douglas-fir cones may be the key to their coexistence. We frequently observed western gray squirrels eating cones of Douglas-firs throughout the year, and cone foraging was most intensive in August when green cones were developing on trees. Green cones may be especially important to western gray squirrels because their development in late summer follows a period of food shortage and precedes acorn maturation. We often saw several western gray squirrels foraging in the same tree on green cones for extended periods of time, but we saw no such behavior by eastern gray squirrels. Rather, we rarely saw eastern gray squirrels foraging in Douglas-fir trees despite high availability within their home-ranges. Douglas-firs are not found in the Eastern United States, and their cones likely have low value as a food resource compared to acorns, walnuts, beech, and other tree seeds commonly eaten by eastern gray squirrels within their native geographic range. Douglas-fir cones have not been reported as a food source where eastern gray squirrels were introduced in California, British Columbia, and the United Kingdom where Douglas-fir is an introduced species (Robinson and Cowan 1954, Shorten 1954, Byrne 1979). In the United Kingdom, eastern gray squirrels avoided Douglas-fir forests (Bryce et al. 2002), and conifers were absent from sites that had eastern gray squirrels in California (Byrne 1979). Habitat use by eastern gray squirrels on the Base strongly favored riparian areas dominated by deciduous trees and high diversity of shrubs that included mast producing species like hazel rather than conifer dominated uplands (see Chapter 2). Eastern gray squirrels may be unable to establish populations in upland habitats on the Base because of these differences in food availability. Byrne (1979) found eastern gray squirrels depended on cultivated food resources in

California and reported restricted diets composed of items that resembled food resources of deciduous forests of the Eastern United States. Robinson and Cowan (1954) reported that eastern gray squirrels had a restricted diet comprised of samaras from big-leaf and vine maples in British Columbia. Similarly, eastern gray squirrels ate maple samaras, acorns, and hazelnuts based on most of our foraging observations. The preponderance of forests dominated by Douglas-fir or other conifers of low value to eastern gray squirrels may inhibit spread of this species beyond areas with human cultivated food resources in Washington. Eastern gray squirrels probably invaded undeveloped forests on the Base because it is surrounded by urban areas and is one of few places in Western Washington that has oaks and other deciduous trees.

Differential habitat use between eastern and western gray squirrels did not result in differences in truffle consumption between species. In California, Byrne (1979) found similar patterns of differential habitat use and indicated the most important difference between diets of eastern and western gray squirrels was in truffle consumption because both species shared use of cultivated tree seeds. Truffles were nearly absent from diets of eastern gray squirrels, whereas they accounted for one third of the stomach contents by volume for western gray squirrels. Byrne (1979) suggested that eastern gray squirrels did not eat truffles at her study sites because they may have been absent due to environmental factors. Our results indicated that eastern gray squirrels frequently foraged on truffles on the Base which may have been due to their high availability and the lack of alternatives. Diet studies for eastern gray squirrels in the Eastern United States have reported high abundance and diversity of tree seeds but noted relatively fewer occurrences of fungi in the diet (Korschgen 1981, Koprowski 1994). In Ohio, fungi was eaten by eastern gray squirrels primarily during early summer and accounted for a fair proportion of stomach volumes ranking behind acorns, beechnuts, and hickory nuts (Nixon et al. 1968).

Eastern gray squirrels likely prefer tree seeds over truffles but will eat truffles in habitats depauperate of tree seeds like those of the Base. In contrast, truffles have been major dietary components for western gray squirrels in all regions regardless of season or the availability of mast producing trees (Stienecker and Browning 1970, Stienecker 1977, Byrne 1979, Stuart 2012).

The presence of truffle spores in nearly all fecal samples of eastern and western gray squirrels indicated their importance as a food resource. Year-round availability of truffles on the Base may support squirrels in seasons of low availability of tree seeds and prevent starvation during times of mast failure. For example, body mass of squirrels did not decrease in fall 2010 despite widespread failure in development of acorns and conifer cones (see Chapter 1). This mast failure compelled squirrels to spend more time foraging for maple samaras and hazelnuts, which were relatively more abundant than acorns and fir cones in 2010. Maple samaras are small compared to tree seeds eaten by eastern gray squirrels elsewhere and have been reported as food items of relatively low use in the Eastern United States. Samaras may hold greater value to squirrels on the Base because of low diversity of mast producing trees.

Truffles commonly eaten by western gray squirrels on the Base were similar to those in squirrel diets from other regions. *Rhizopogon* spores were in most of our fecal samples and were the most common spores found in western gray squirrels in North Cascades and California (Stienecker and Browning 1970, Stuart 2012). Likewise, *Melanogaster*, *Hysterangium*, and *Gautiera* were also common food resources in these regions. Spores of the *Geopera* complex (*Geopera*, *Barssia,* and *Balsamia*) occurred most frequently in our samples from the Base and were also common in North Cascades (Stuart 2012). Notably, these genera were absent in fecal samples from northern flying squirrels (*Glaucomys sabrinus*) and Townsend's chipmunks

(*Tamias townsendii*) that were collected on the Base (Colgan et al. 1997, Carey et al. 2002). This suggests differential use of truffles between gray squirrels and other *Sciurids*.

The frequency of occurrence of truffle genera in squirrel diets generally followed their relative abundances reported by Colgan et al. (1999), which suggests that squirrels were opportunistic in their use of truffles. However, gray squirrels may have strongly selected truffles of the *Geopera* complex because they were the only genera in our samples that were not detected in previous surveys of Colgan et al. (1999). Squirrels and humans likely differ in their abilities to find truffles as noted in previous studies (Carey et al. 2002, Stuart 2012). We found spores of *Rhizopogon*, *Melanogaster*, and the *Geopera* complex fecal samples collected during winter with high frequencies similar to other seasons, whereas truffle surveys by Colgan et al. (1999) reported only *Rhizopogon*, *Tuber,* and *Endogone* as common on the Base during winter.

Most food resources for squirrels varied by season based on fecal samples and foraging observations. Low truffle diversity in fecal samples during winter reflected the limited availability of fruiting bodies for most genera on the Base during this season (Colgan et al. 1999). Truffle diversity in fecal samples was highest during spring which corresponded to the flush of fruiting bodies for most genera and a season when caches of tree seeds have been exhausted and no other foods are available. We saw obvious annual fluctuations in acorn and fir cone abundance. However, high numbers of foraging observations on acorns and fir cones obscured a severe mast failure in 2010. Low foraging efficiency may have led to high numbers of foraging observations because squirrels spent more time finding food and were more conspicuous while foraging.

In conclusion, shared use of several food resources between eastern and western gray squirrels raises the potential for competition over food resources. However, significant differences in habitat use between these species on the Base probably minimize competitive interactions. Differences in cone consumption between eastern and western gray squirrels may explain their differences in habitat use and has important implications for competitive interactions that should be examined in other regions of sympatry. Although truffle consumption has been reported infrequently for eastern gray squirrels in other regions, they often ate truffles during all seasons on the Base which suggests this food source was important in Washington where availability of seeds from deciduous trees is low. The diversity of food resources and temporal variability in their availability need consideration in conservation planning for gray squirrels. Oak management has been the focus of western gray squirrel conservation and is critically important, but habitat provision also needs to account for the resources provided by conifers. *Rhizopogon*, for example, was an important food item for western gray squirrels throughout the year and is associated with conifer forests (Trappe et al. 1999). Forest management activities can affect truffle abundance and composition in forests used by western gray squirrels but their effects are poorly understood (Colgan et al. 1999).

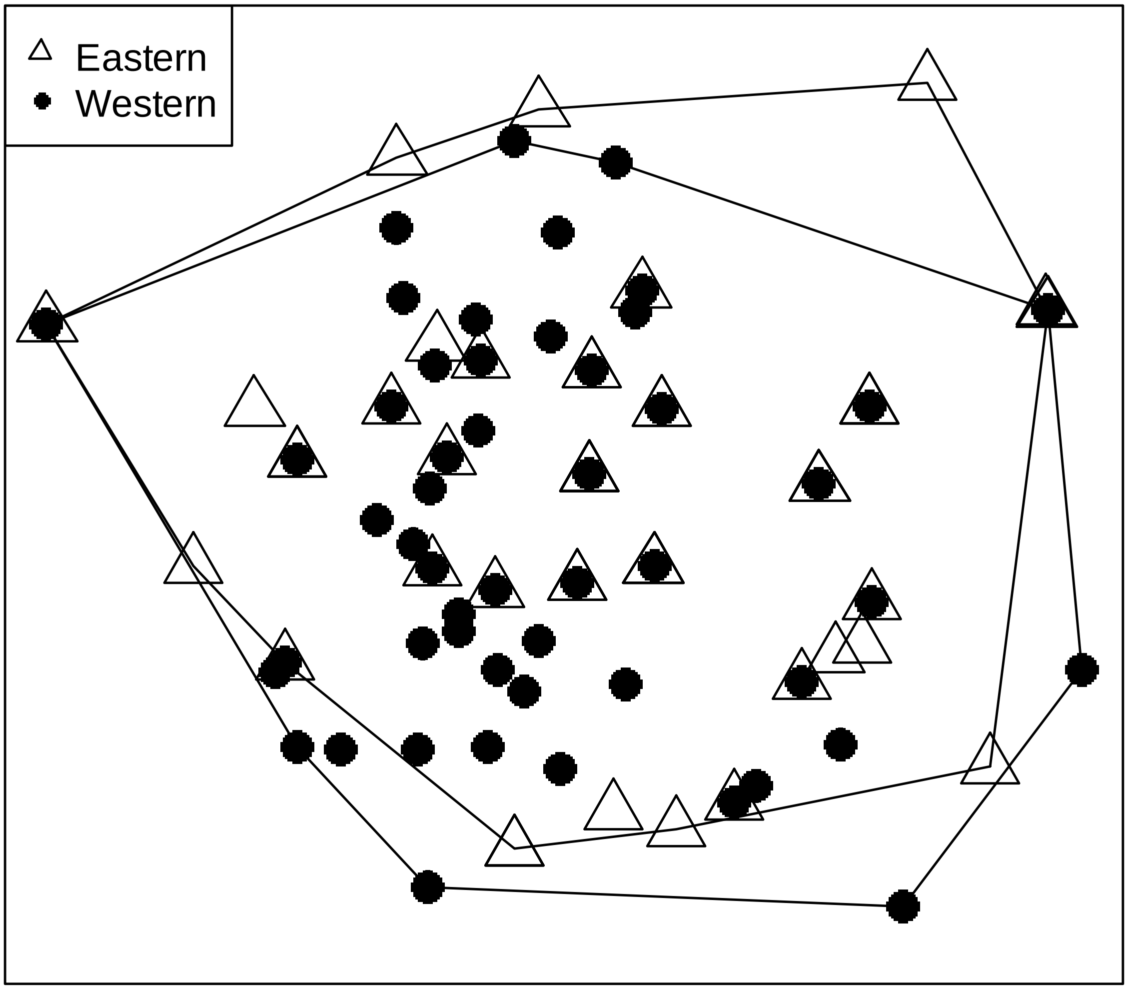

Figure 3.1. Two-dimensional NMDS ordination of fungal spores found in fecal samples from eastern and western gray squirrels on Joint Base Lewis-McChord. The outer extent of samples for each species is outlined in ordination space.

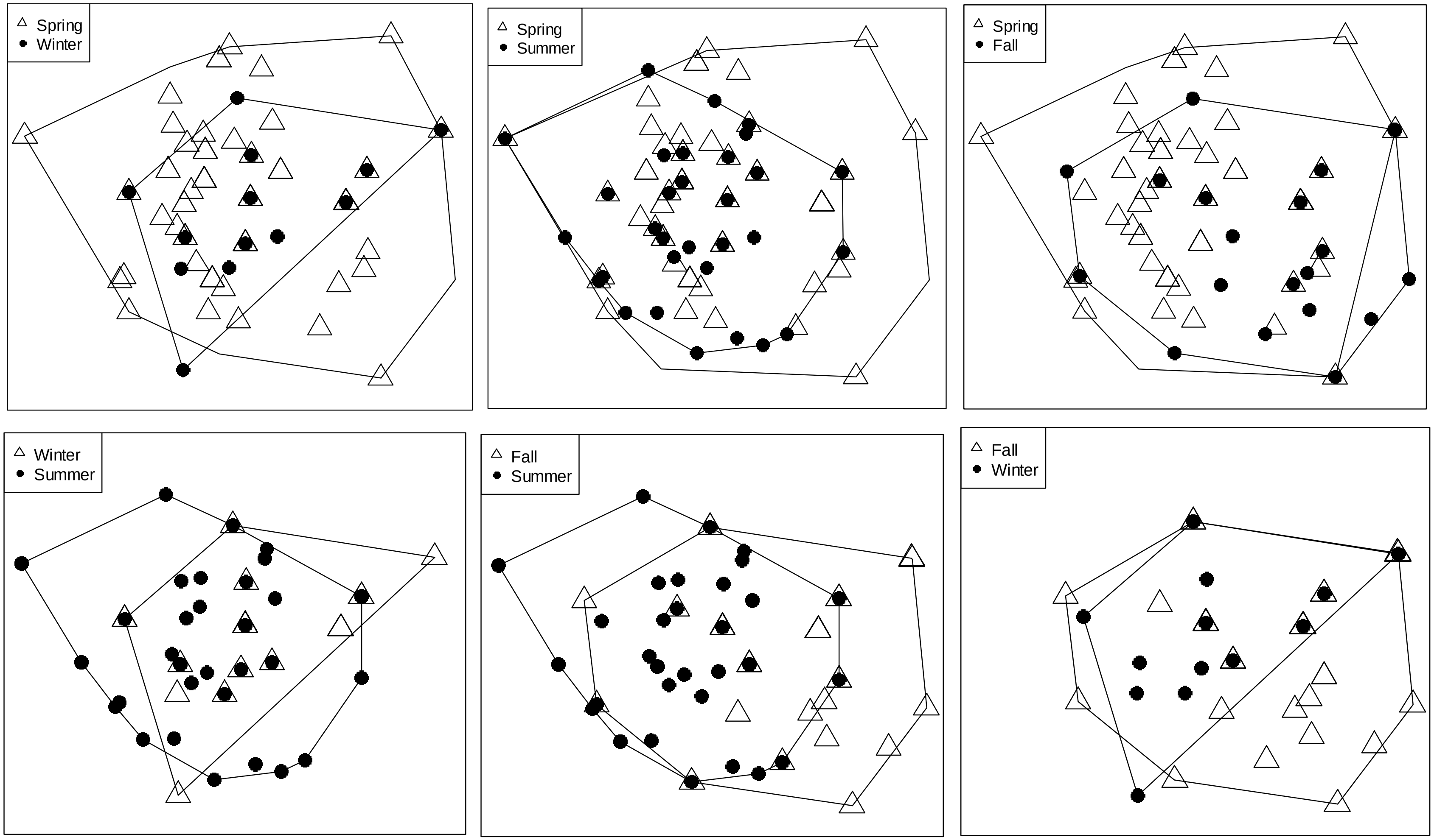

Figure 3.2. Two-dimensional NMDS ordination of fungal spores found in fecal samples from eastern and western gray squirrels by season on Joint Base Lewis-McChord. The outer extent of samples for each season is outlined in ordination space.

Table 3.1. Richness (S) and percent frequency of occurrence of fungal spores and other food items in fecal pellets of eastern and western gray squirrels on Joint Base Lewis-McChord by season.

	Eastern Gray Squirrels				Western Gray Squirrels			
	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
Rhizopogon	77	73	80	75	90	92	86	87
Gautieria	0	7	0	0	5	2	0	0
Geopera	86	87	87	50	95	89	97	96
Melanogaster	55	93	40	75	79	92	55	70
Genabea	5	20	0	0	6	19	0	4
Genea	0	7	0	0	2	4	3	0
Hymenogaster	32	7	7	0	18	17	7	17
Hysterangium	5	0	0	0	8	0	3	0
Hydnotyra	23	13	13	0	31	15	3	9
Tuber	5	33	13	0	26	21	3	17
Elaphomyces	23	7	0	13	31	4	14	9
Leucangium	14	13	0	0	15	0	0	4
Radiigera	5	0	0	0	5	4	0	0
Russulaceae	9	33	40	13	0	11	21	0
Boletus	0	20	0	0	5	0	3	0
Plant	14	0	27	0	11	2	31	26
Other	0	0	7	0	3	0	0	0
Unknown	5	0	0	0	10	2	0	4
N	22	15	15	8	62	53	29	23
S	12	13	7	5	14	12	11	9

Table 3.2. Foraging observations for eastern and western gray squirrels on Joint Base Lewis-McChord by season.

	Eastern Gray Squirrel					Western Gray Squirrel				
	Spring[1]	Summer	Fall	Winter	Total[2]	Spring[1]	Summer	Fall	Winter	Total[2]
Douglas-fir cones	1	2	2	0	5(21)	42	60	43	17	162(145)
Ponderosa pine cones	0	0	0	0	0(1)	0	4	2	0	6(5)
Acorns	1	1	13	0	15(8)	5	17	27	0	49(56)
Maple	1	1	11	0	13(4)	0	3	15	1	19(28)
Vine maple	0	3	2	0	5(3)	0	7	11	0	18(20)
Hazel	0	5	0	0	5(3)	0	18	0	1	19(21)
Truffles	0	0	0	0	0	1	2	0	0	3
Hawthorn berries[3]	0	0	0	0	0	0	0	1	0	1
Blackberries[3]	0	0	0	0	0	1	0	0	0	1
Cottonwood catkins	0	0	0	0	0	2	0	0	0	2
Bark	0	0	0	0	0(2)	9	0	0	4	13(11)
Birdfeeder[4]	0	0	0	2	2	0	0	0	0	0

[1] Spring foraging on oaks, maples, and blackberries was for buds and flowers.

[2] Expected values (rounded to the nearest integer) used in the chi-square test to compare frequency of food items between eastern and western gray squirrels appear parenthetically.

[3] Hawthorn = *Crataegus monogyna*; Blackberry = *Rubus armeniacus*

[4] An eastern gray squirrel moved 2 km to the edge of a residential area following a mast failure and was seen foraging at a birdfeeder in a backyard.

Table 3.3. Foraging observations of eastern and western gray squirrels on Joint Base Lewis-McChord by year.

	Eastern Gray Squirrel				Western Gray Squirrel			
	2008	2009	2010	2011	2008	2009	2010	2011
Fir cones	2	2	1	0	8	50	76	21
Pine cones	0	0	0	0	1	4	1	0
Acorns	3	5	3	4	13	5	16	13
Maple	0	2	11	0	0	0	28	1
Vine maple	0	0	5	0	0	0	18	0
Hazel	0	2	3	0	0	0	13	5
Truffle	0	0	0	0	0	0	2	1
Hawthorne berries	0	0	0	0	0	0	1	0
Blackberries	0	0	0	0	0	0	0	0
Cottonwood catkins	0	0	0	0	0	0	0	2
Bark	0	0	0	0	0	0	0	12
Birdfeeder	0	0	0	2	0	0	0	0

SUMMARY AND RECOMMENDATIONS

Competition between eastern and western gray squirrels on Joint-Base Lewis McChord (Base, hereafter) was minimized by differential habitat use. Eastern gray squirrels appeared limited to riparian areas where oaks mixed with other deciduous trees and dense cover by shrubs, whereas most western gray squirrels used upland habitats of conifers mixed with oaks and little shrub cover. Fine-scale spatial partitioning between eastern and western gray squirrels in habitats suitable to both species suggested interspecies avoidance occurred, but such habitats accounted for a small fraction of areas suitable for western gray squirrels on the Base. Similar use for many food resources between eastern and western gray squirrels raised potential for competitive interactions but may be mitigated by differential habitat use. Unlike eastern gray squirrels, western gray squirrels frequently ate Douglas-fir cones which further reduced competition and may explain their ability to establish populations in conifer dominated uplands with relatively low diversity of food resources. In undeveloped forests on the Base, eastern gray squirrels were likely limited to riparian areas because of their reliance on deciduous tree seeds and the diversity of food resources within those habitats.

1. Differences in habitat use between eastern and western gray squirrels may be exploited through management to favor western gray squirrels on the Base. Provision of habitat suitable to western gray squirrels away from riparian areas will likely ensure availability of uncontested habitat. Although both species shared correlations with canopy cover and proximity to oaks, shrub cover was the most important variable for discriminating habitats of eastern and western gray squirrels and may be reduced through management

practices such as prescribed burning and removal of Scot's broom. Planting oaks along edges of upland conifer-dominated forests will likely enhance these habitats for western gray squirrels but not eastern gray squirrels. It is not desirable or practical to eliminate or modify habitat for eastern gray squirrels on the Base because riparian areas are important to many wildlife species.

2. Management actions to control eastern gray squirrels may be warranted where populations of western gray squirrels are critically low or where most available habitat is around riparian areas. The population of western gray squirrels on the Base was low at the time of this study but may rebound given recent habitat enhancements and population augmentation. Continued monitoring is needed to determine whether the population of western gray squirrels is increasing, decreasing, or stabilizing. Few areas are likely to support both eastern and western gray squirrels on the Base, so control of eastern gray squirrels could be considered if western gray squirrels decline further. Areas predicted to support both species on the Base are shown in Figure 2.4 and should receive high priority in strategies to control eastern gray squirrels if needed. Trapping results from the removal experiment suggested fall trapping was most effective for removing eastern gray squirrels and 1-year intervals between extermination treatments will likely restrain invasions by eastern gray squirrels on the Base. It is unlikely that immigration of eastern gray squirrels onto the Base from surrounding urban and agricultural areas can be stopped, so it is important to focus conservation efforts on provision of habitats suitable for western gray squirrels rather than control of eastern gray squirrels. Further, large areas of the Base are uplands suitable for habitat modification; a strategy that would likely provide greater

returns on investment for recovery of western gray squirrels than control of eastern gray squirrels.

3. The clear restriction of eastern gray squirrels to riparian areas on the Base should be viewed as a hypothesis that needs further testing. If, in the future, eastern gray squirrels are found to be establishing populations in conifer-dominated uplands similar to western gray squirrels, then conclusions of this study need to be reconsidered. After nearly 5 years of continuous radio tracking and trapping on the Base, we did not find eastern gray squirrels away from riparian habitats even where western gray squirrels were absent. We believe there are sound biological explanations for the restrictions of eastern gray squirrels to riparian areas but acknowledge the possibility that eastern gray squirrels may establish populations in conifer-dominated uplands under circumstances unseen in our study area. Therefore, it is important to continue monitoring such areas for squirrel activity and investigate any potential populations that might be established in undeveloped upland habitats on the Base or in other regions where eastern and western gray squirrels are sympatric. Habitat use between eastern and western gray squirrels may be more similar in other regions, so further study is needed to describe distribution, habitat associations, and interactions in other areas invaded by eastern gray squirrels such as Southcentral Washington (Klickitat and Skamania Counties).

4. Large home-ranges and patterns of intraspecific spatial partitioning for western gray squirrels suggest the need for maintaining large areas of habitat and minimizing habitat fragmentation. Each of our study areas typically supported about 4 female western gray

squirrels within approximately 270 ha of which about 67 ha had high probabilities of use predicted by the RUF model. Based on these numbers, the Base could support roughly 274 female western gray squirrels (4*4,591/67=274) or a total population of 548 assuming equal sex ratios and that areas of predicted high-use (4,591 ha) are not unsuitable for reasons undetected by the model (e.g. habitat fragmentation). Our trapping and hair-snag surveys suggested the resident population is largely concentrated on the east side of the Base (training areas 7, 8, 10, 11, 12, 13 and the ammo storage area). If all areas of predicted high-use were occupied, the Base might support a viable population of western gray squirrels by itself. Further research, however, is needed to determine the reasons why many habitats were unoccupied by squirrels. Regional recovery efforts should consider populating habitats beyond the Base to maintain a population of western gray squirrels that would be more likely to withstand stochastic events such as disease outbreaks or wildfire.

5. Fire exclusion and urban development likely contribute to habitat loss for western gray squirrels on the Base but focused study is needed to evaluate negative impacts and identify solutions. Habitat use by western gray squirrels favored forests of conifers mixed with oaks, a forest type traditionally maintained by frequent fires set by Native Americans in the South Puget Sound area. Fire exclusion has allowed Douglas-fir to invade prairies and overtop oaks and Ponderosa pines which has converted forests of conifers mixed with oaks to monoculture forests of Douglas-firs that have low value for western gray squirrels when not in close proximity to oaks. Western gray squirrels avoid urban areas in Washington, and further construction in areas that support western gray

squirrels may also deter their use of those areas. A major highway proposed for construction on the Base may exacerbate fragmentation of squirrel habitat and increase squirrel mortality through collisions with automobiles.

6. Timber harvest inherently changes forest structure and potentially changes composition which affects habitat quality for western gray squirrels. Most importantly, timber harvest reduces canopy cover and canopy connectivity which were the best variables for distinguishing core from low-use areas. Reductions in canopy cover also can stimulate development of the shrub layer which was negatively correlated with use by western gray squirrels. Western gray squirrels used thinned forests in the North Cascades (Stuart 2012), but squirrel responses to thinning may differ in mesic forests of Western Washington. Response of western gray squirrels to timber harvest likely varies with tree spacing, and the effects of different prescriptions should be evaluated. Timber harvests may be used to enhance squirrel habitat on the Base, but further research is needed to identify appropriate treatments. For example, gap creation and subsequent planting of oaks within large blocks of monoculture Douglas-fir could increase habitat suitable to western gray squirrels on the Base. Prescriptions of uniformly thinned stands that eliminate or reduce canopy connectivity to low levels should be avoided when conservation of western gray squirrels is a priority. Snags and large trees with canopies well-connected to surrounding trees should be retained for den and nest sites for western gray squirrels. Variable density thinning could maintain or enhance squirrel habitat provided that patches with high canopy cover and connectivity are retained. Our measures of canopy cover and connectivity in core areas and at nest sites can be used to

inform guidelines for tree spacing in thinning treatments to meet needs of western gray squirrels in the South Puget Sound.

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APPENDIX A. Estimation of shrub cover with LIDAR.

Many researchers have demonstrated that LIDAR accurately models upper canopy structure and other common inventory metrics such as basal area (Van Leeuwen and Nieuwenhuis 2010), but little is known about its ability to model understory and shrub structure. Model accuracy for low vegetation such as shrub cover is less certain because fewer LIDAR data points are recorded beneath the canopy and shrubs are located close to the ground which incurs error in differentiating between ground and vegetation points. Previous studies have indicated a wide range of correspondence between LIDAR and field measures of understory and shrub structure (Andersen et al. 2003, Goodwin 2006, Su and Bork 2007, Hill and Broughton 2009, Martinuzzi 2009, Hilker et al. 2010, Miura and Jones 2010). However, many studies found high correlations suggesting good potential for LIDAR to model low vegetation. The ability of LIDAR to describe shrub cover depends on the LIDAR point density and the amount of canopy cover. Because shrub cover was the top variable for discriminating eastern and western gray squirrel core areas based on habitat characteristics measured on the ground, I evaluated the ability of LIDAR to describe shrub cover on the Base to justify its use as a predictor in resource utilization functions.

Methods

I compared ground and LIDAR measurements of shrub cover using two sets of LIDAR data collected on the Base in 2010. The leaf-on data set was collected in June and July 2010 as described in Chapter 2. The leaf-off data set was collected in late-winter 2010 and had similar specifications in scanning equipment, scan angle, and point density. Estimates of shrub cover by LIDAR were calculated as the proportion of returns within the height stratum of interest over the total number of returns that occurred below the upper boundary of this stratum. Most LIDAR data preparation and manipulation were performed in FUSION (McGaughey 2007) by David Stephens, a LIDAR specialist at Joint-Base Lewis McChord. LIDAR data were extracted from 10.6-m radius circles centered on similarly sized habitat plots for nests, dens, core, and low-use areas where vegetation was measured following line-transect methods on the ground and indices of shrub cover were calculated as described in Chapter 2. For these analyses, calculations of the shrub cover index included relative abundances of trees and other non-shrub objects such as coarse woody debris that were intercepted by the height pole because these objects would have returned signals when intercepted by LIDAR pulses. I geo-referenced 211 plot centers with Javad Maxor survey-grade GPS units and post-processed plot locations using Continuously Operated Reference Stations (CORS) data with Pinnacle software. Locations of plot centers measured by GPS had sub-meter accuracy following processing which aligned field measures of shrub cover with those of LIDAR.

I fit several regressions to compare LIDAR estimates of shrub cover to indices of shrub cover at habitat plots. Candidate models of shrub cover were compared based on coefficients of determination. I created models for height strata of 1-3 m, 0.5-3 m, and 0.1-3 m using the leaf-on data to determine whether LIDAR could describe shrub cover that occurred close to the ground. For each of these models, I calculated separate indices of shrub cover from LIDAR and habitat plots that corresponded to the stratum of interest. I repeated these analyses after adding a covariate for canopy cover to determine whether estimates of shrub cover could be improved by accounting for canopy cover. This variable was calculated as the proportion of all LIDAR returns that occurred above 3 m. I also compared LIDAR with ground estimates of shrub cover at the 1-3m stratum using the leaf-off data to determine whether there were differences between the LIDAR data sets in their ability to describe shrub cover. Finally, I compared ground and LIDAR estimates of deciduous cover at the 1-3 m stratum. I calculated deciduous cover by subtracting the leaf-off from the leaf-on estimate of shrub cover. For this comparison, I calculated the shrub cover index using only relative abundances for deciduous shrubs from the ground data.

Results

Correlations between LIDAR and ground estimates of shrub cover varied by height strata, models, and LIDAR data sets (Table A.1). Coefficients of determination were highest for the 1-3 m strata that used leaf-on data (Figure A.1). Relationships were similarly strong for the 0.5-3 m strata but rapidly weakened when cover estimates included shrubs below 0.5 m. Correlations from leaf-off data were significant but coefficients of determination were considerably lower than those of the leaf-on data. Isolation of deciduous shrubs by subtracting leaf-off from leaf-on data did not improve correlations. Canopy cover was consistently high and averaged 83.8 (95% CI = 82.0, 84.0) based on the proportion of all returns that occurred above 3 m. Covariates for canopy cover did not help explain variation in shrub cover.

Discussion

Despite dense canopy cover at my plots, LIDAR described shrub cover fairly well based on comparisons with ground measures. Correlation between ground and LIDAR estimates of shrub cover was much higher than previously found on the Base (Andersen et al. 2003) and was on par with other more recent comparisons in forested systems elsewhere (Goodwin 2006, Su and Bork 2007, Hill and Broughton 2009, Martinuzzi 2009, Hilker et al. 2010, Miura and Jones 2010). Cover estimates were not reliable for strata below 0.5 m, and leaf-on data was best for describing shrub cover. In addition to good correlation, maps of shrub cover for my study areas represented the variation in shrub cover well based on field observations. These results suggest that the model for 1-3 m that used leaf-on data and a single predictor was good for describing shrub cover. The ability of LIDAR to describe shrub cover depends on many factors associated with forest structure and specifications of LIDAR data acquisition. Data collected during this study could be explored further to improve models of shrub cover and understanding of circumstances that yield good models.

Table A.1. Comparisons of LIDAR and ground estimates of shrub cover at various height strata on Joint-Base Lewis McChord.

LIDAR	Strata	Covariates	R^2	*F*	*P-value*
Leaf-on	1.0-3.0	none	0.67	419	<<0.001
Leaf-on	0.5-3.0	none	0.63	362	<<0.001
Leaf-on	0.1-3.0	none	0.34	106	<<0.001
Leaf-on	1.0-3.0	canopy cover	0.69	227	<<0.001
Leaf-on	0.5-3.0	canopy cover	0.69	234	<<0.001
Leaf-on	0.1-3.0	canopy cover	0.48	95	<<0.001
Leaf-off	1.0-3.0	none	0.23	64	<<0.001
Leaf-off	0.5-3.0	none	0.35	112	<<0.001
On – off[1]	1.0-3.0	none	0.62	344	<<0.001
On – off	0.5-3.0	none	0.30	91	<<0.001
On – off	1.0-3.0	canopy cover	0.63	180	<<0.001

[1] Estimates of shrub cover by leaf-off data were subtracted from those of leaf-on data.

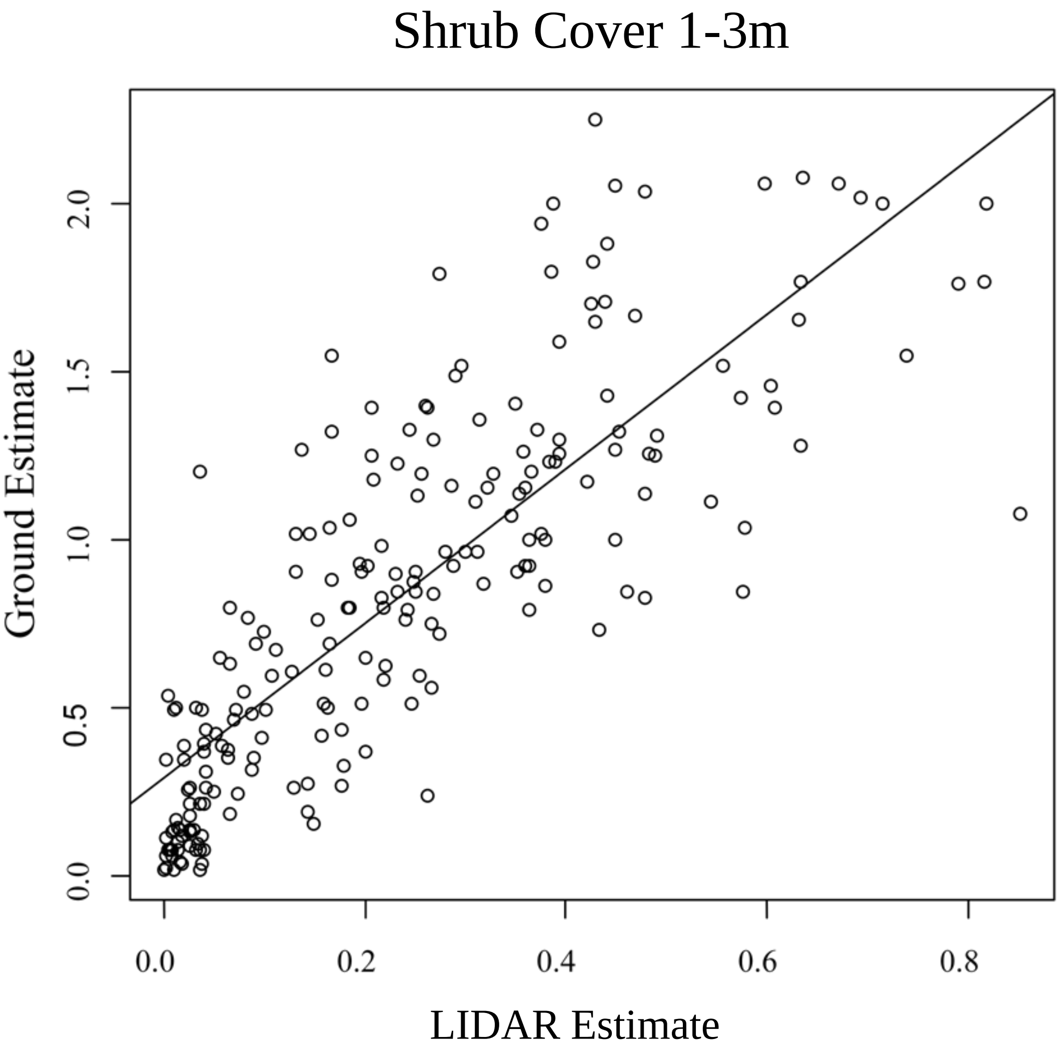


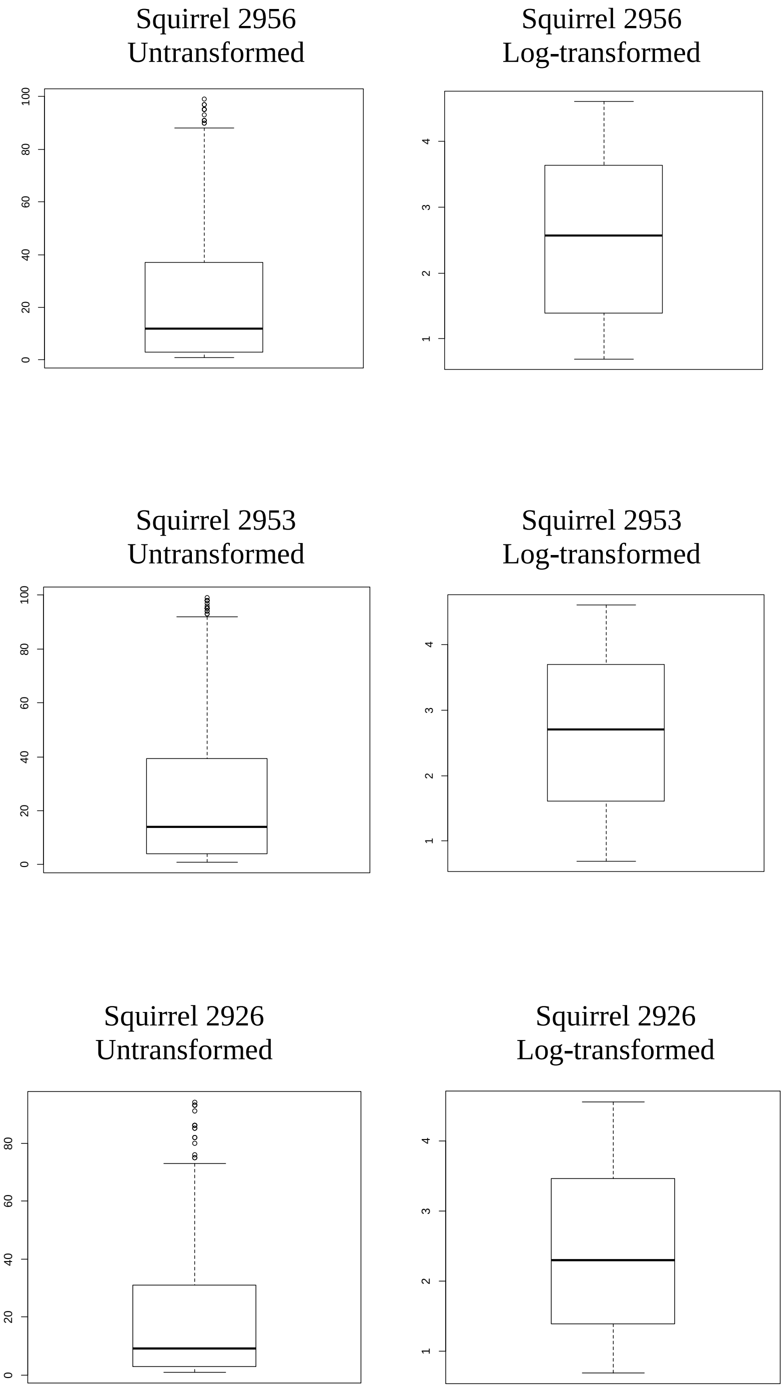
Figure A.1. Regression of leaf-on LIDAR and ground estimates of shrub cover for the 1-3 m height stratum.

APPENDIX B. Log transformation of the response variable in resource utilization functions.

Among other assumptions of multiple regression, resource utilization functions (RUF) assume homoscedasticity (Marzluff et al. 2004). I examined residual plots from individual RUFs for several squirrels and found that RUFs consistently failed to meet this assumption because the response variable was always right-skewed. The right-skew for untransformed responses was consistent for all 56 squirrels and was normalized by log transformation. Figure B.1 shows boxplots of the response variable before and after log transformation for three squirrels. I tried arcsine, reciprocal, and logit transformations, but log transformation worked best. The consistency of the right-skew was due to the fact that utilization distributions had far fewer high-use cells than low-use cells, a pattern that should be expected from response variables derived from utilization distributions of animal-use.

No command was available to view residual plots in R package ruf.fit, so I constructed residual plots manually. First, I calculated predicted values from each squirrel's RUF and then, used simple linear regression to regress the predicted values on the observed values for each squirrel. The residual plots from these regressions also represented those of the RUFs which accounted for spatial autocorrelation through the Matern model in ruf.fit. All of my residual plots for RUFs without transformation had tight fit at the left side of the plot and increasingly larger residuals at the right side (Figure B.2); a pattern typical for right-skewed responses (Ramsey and Schafer 2002). Log transformation normalized the distribution of response and most importantly, transformation consistently improved the distribution of residuals for meeting the assumption of homoscedasticity. Some plots were improved better than others, but the transformation led to an improvement in each case.

The consequences of heteroscedasticity in multiple regression models such as RUFs include underestimates of error which lead to greater occurrences of type I error for tests of coefficients (Ramsey and Schafer 2002). I found significant *P*-values ($P<0.05$) for most variables on individual RUFs when analyzing untransformed data, and others have reported high numbers of significant *P*-values for individual RUFs in previous studies where responses were not transformed (Marzluff et al. 2004, Long et al. 2009, Withey et al. 2009, Kertson et al. 2011). No previous RUF study has transformed response variables or indicated that residual plots were examined to evaluate model assumptions (Jachowski 2007, Skarin et al. 2008, Rittenhouse et al. 2008). Significance tests and associated *P*-values are not reliable if assumptions are not met and errors are underestimated. This probably explains why I found disconnect between AIC and *P*-values when analyzing untransformed data but not after log transformation. On untransformed data for example, AIC would sometimes decrease after dropping several (e.g. 3) highly significant variables ($P<0.001$). Significance tests were unreliable in these cases because the model failed to meet the assumption of homoscedasticity, so AIC probably did not increase as expected after several significant variables were dropped because those variables actually explained little variation in probabilities of use by squirrels.



Squirrel 2956
Untransformed

Squirrel 2956
Log-transformed

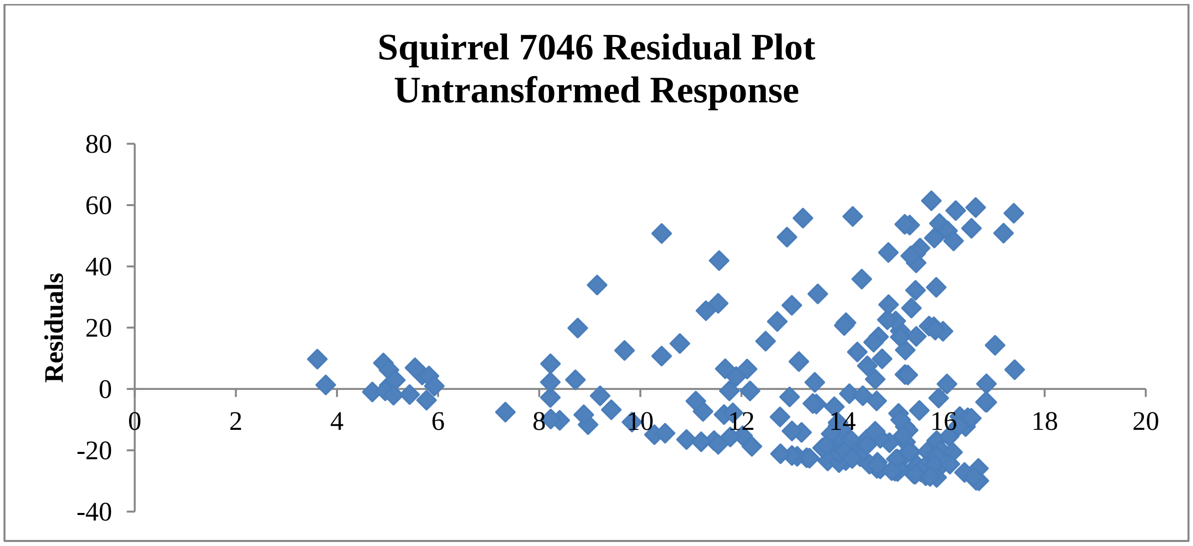
Squirrel 2953
Untransformed

Squirrel 2953
Log-transformed

Squirrel 2926
Untransformed

Squirrel 2926
Log-transformed

Figure B.1. Boxplots of squirrel-use (left) and the log of use (right) for three squirrels.



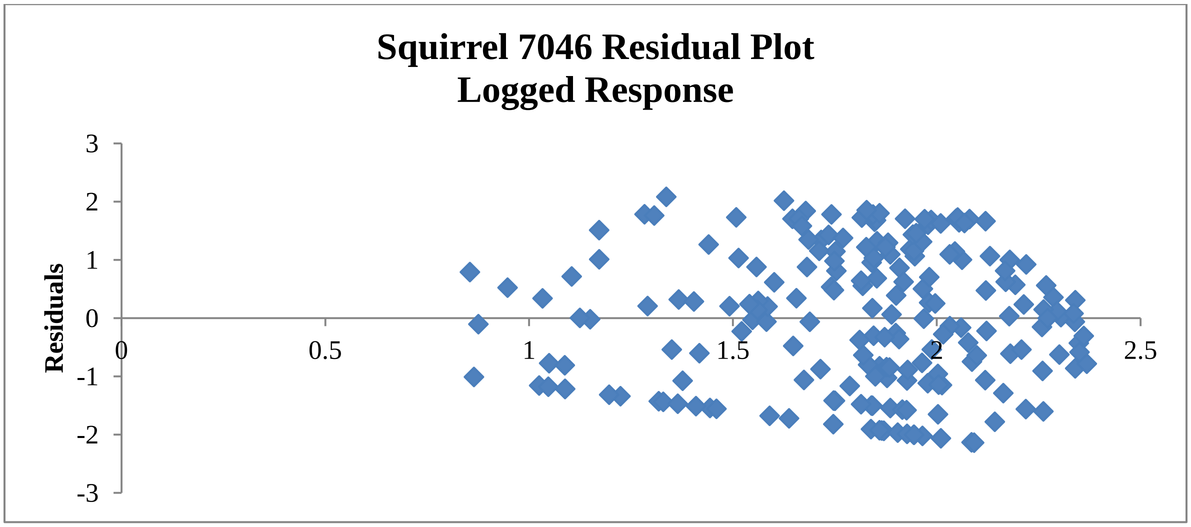
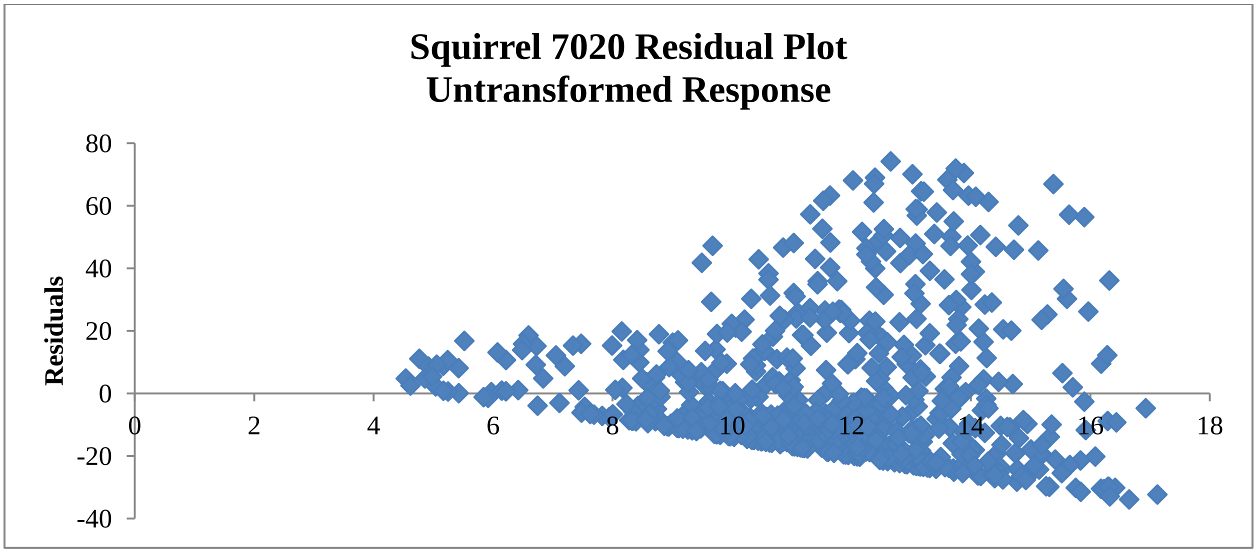
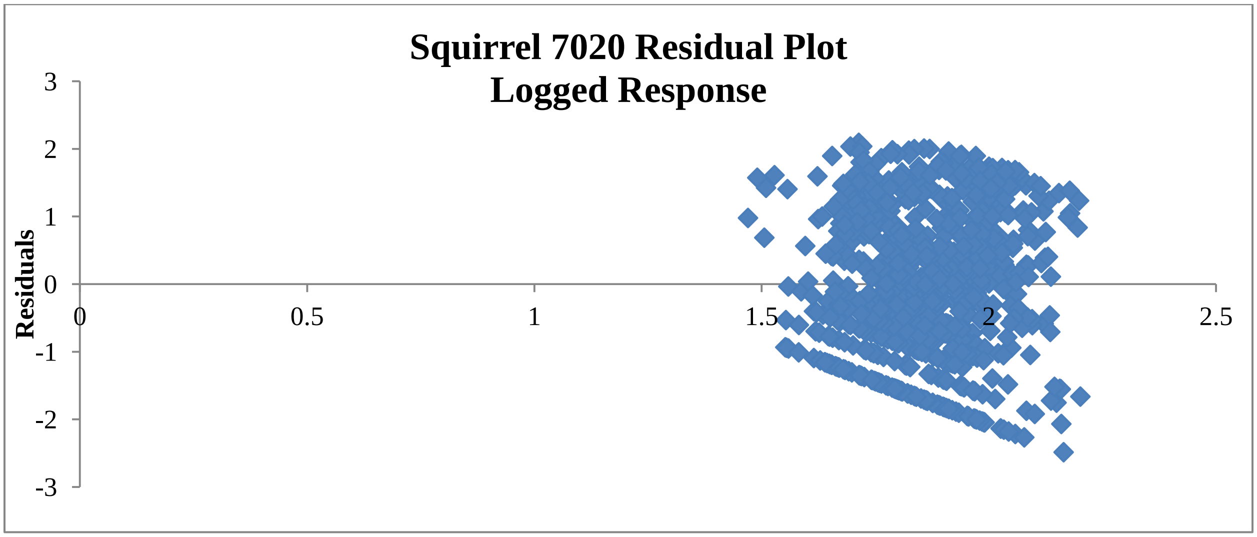


Figure B.2. Residual plots from resource utilization functions for 14 squirrels before and after log transformation of the response variable. Predictor variables were canopy cover, canopy height, standard deviation of canopy height, distance to oaks, and distance to wetlands. Figure B.2 continued on the next 13 pages.





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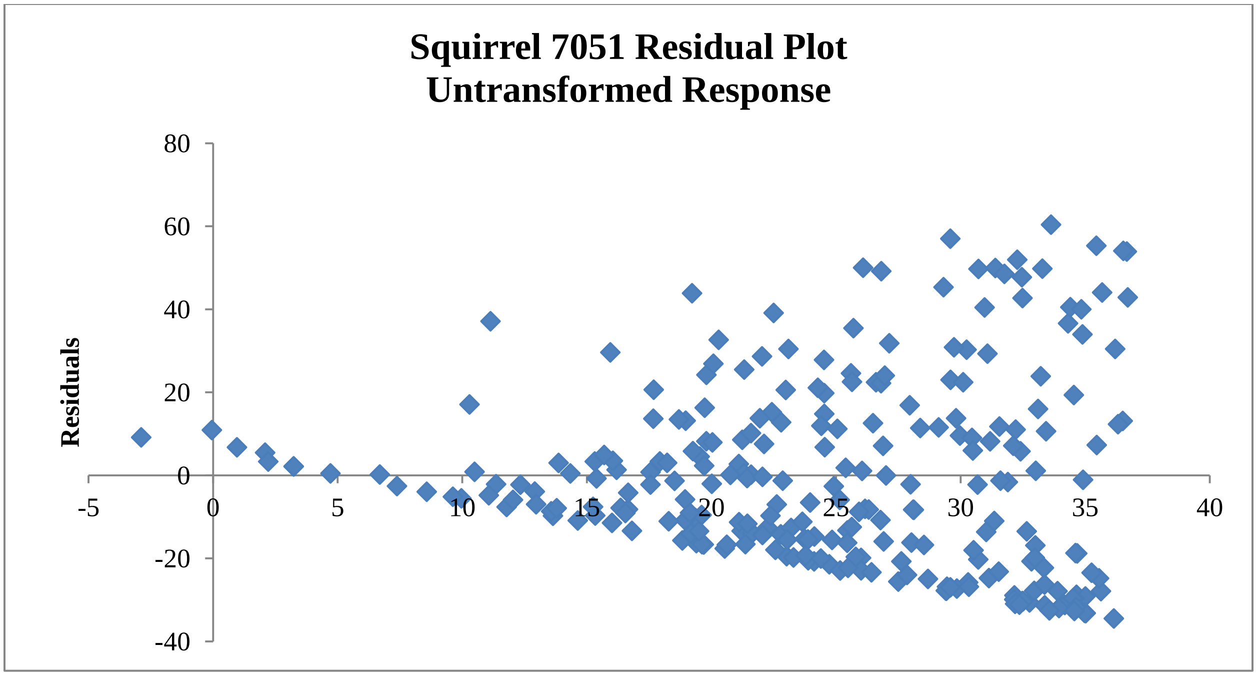

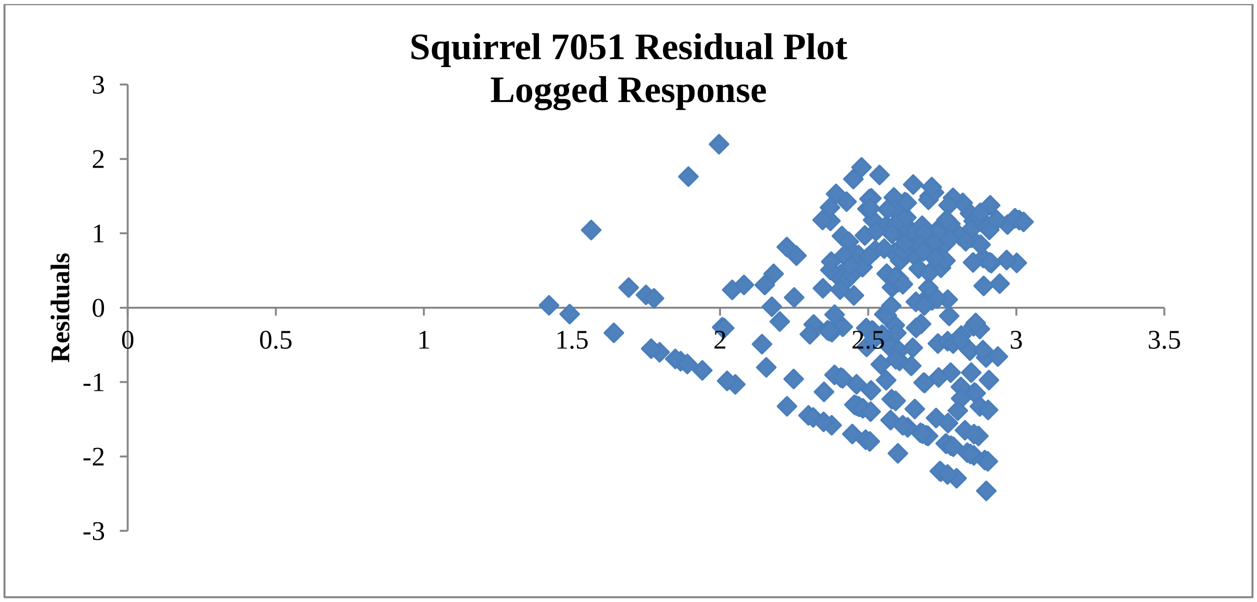

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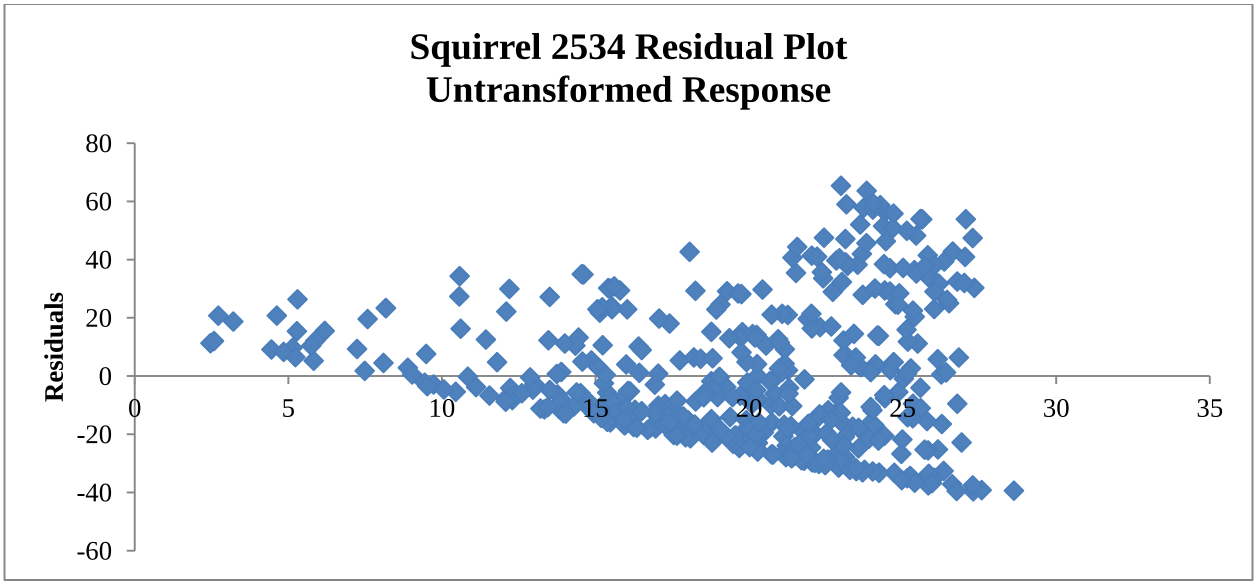

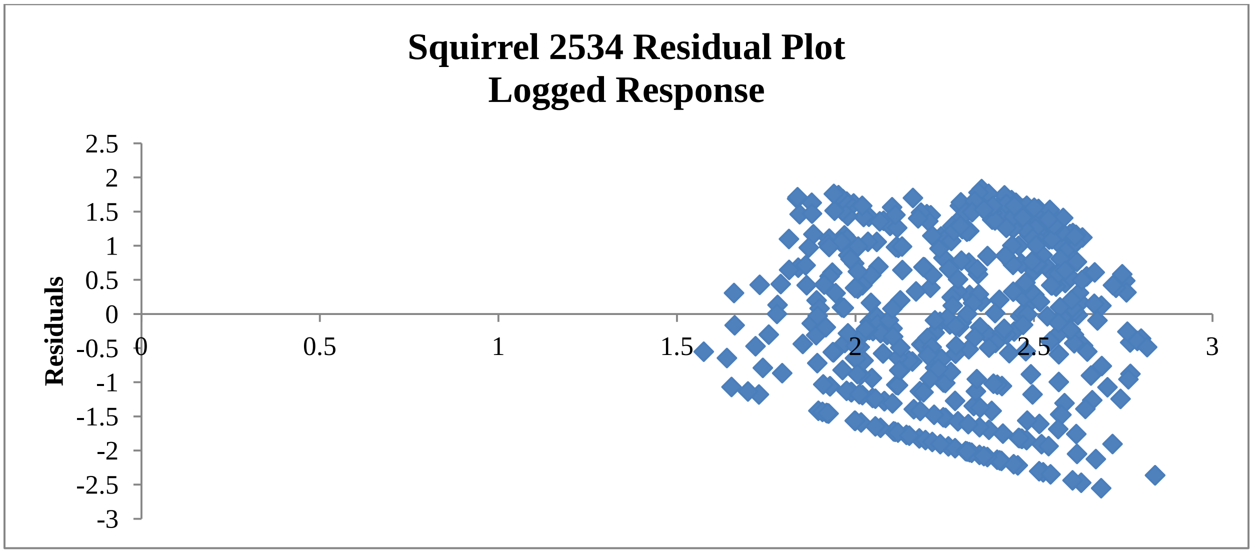

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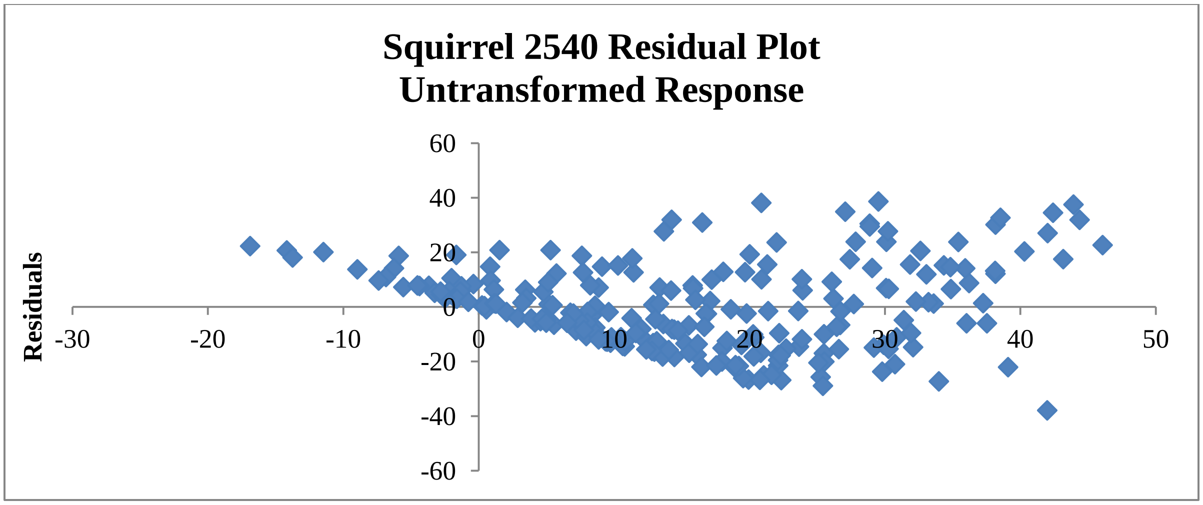

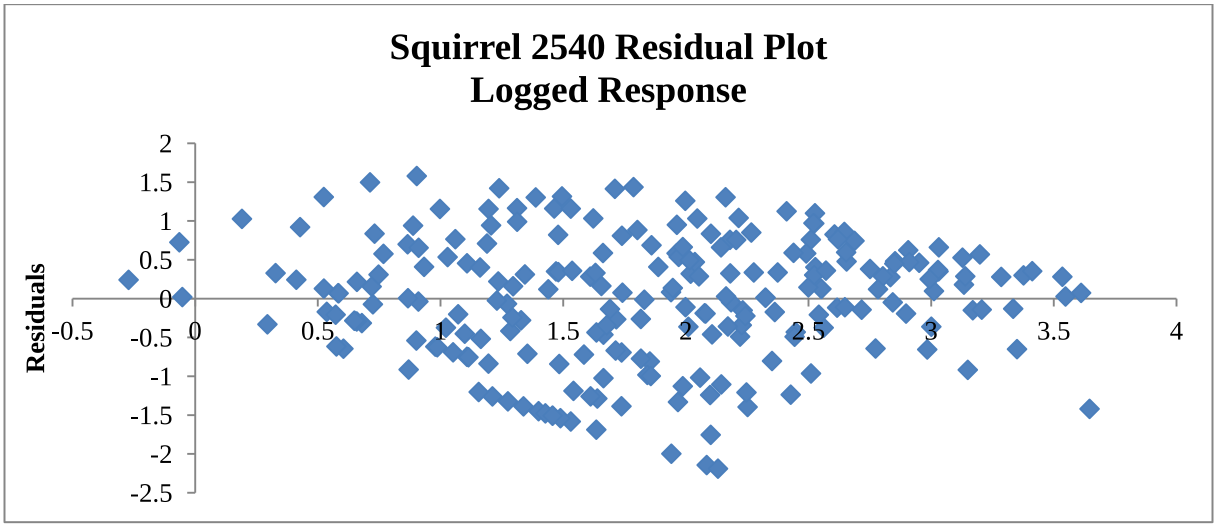

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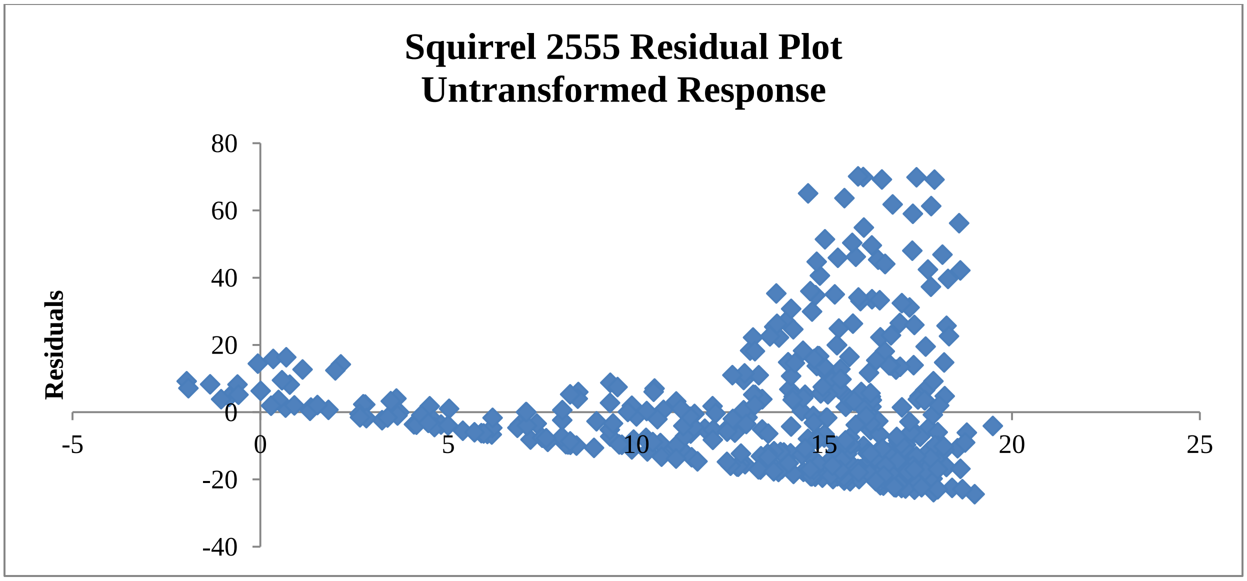

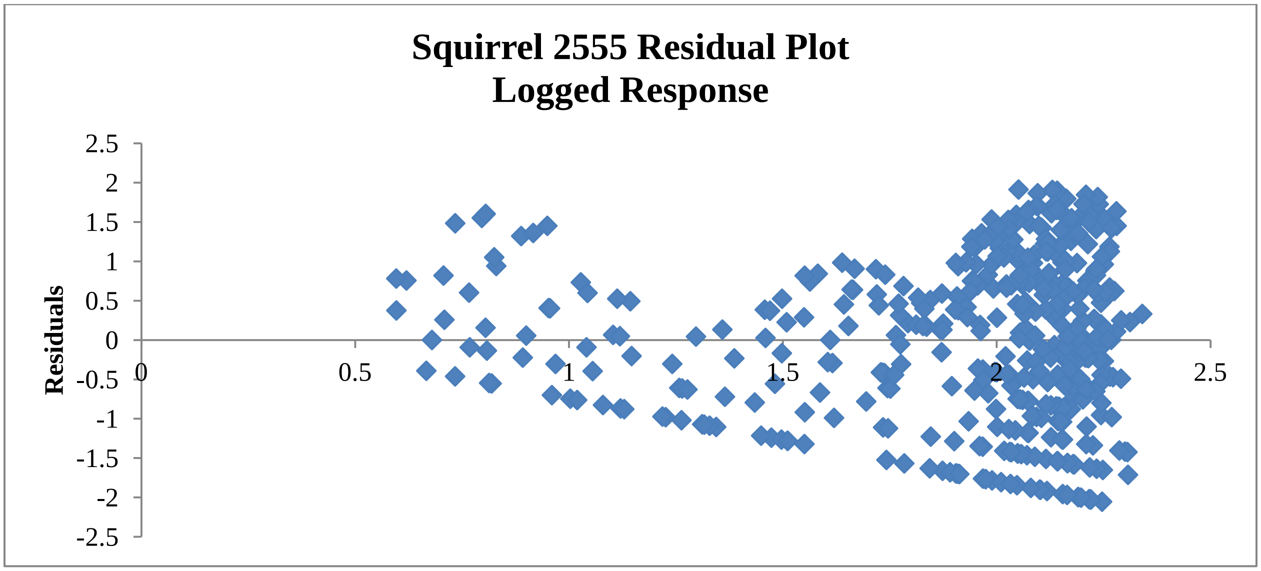

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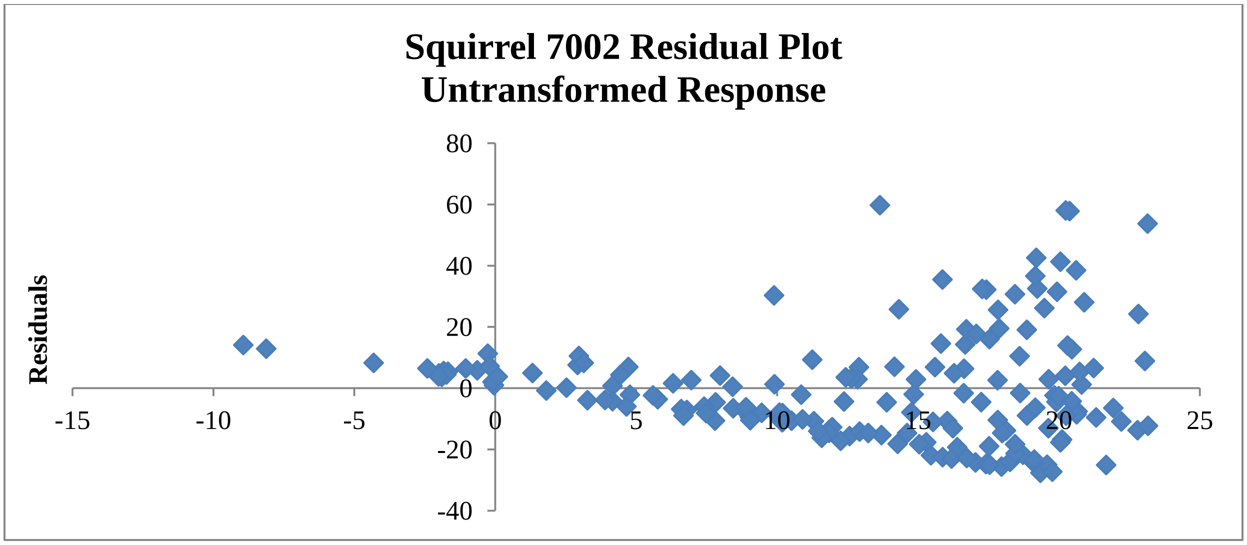

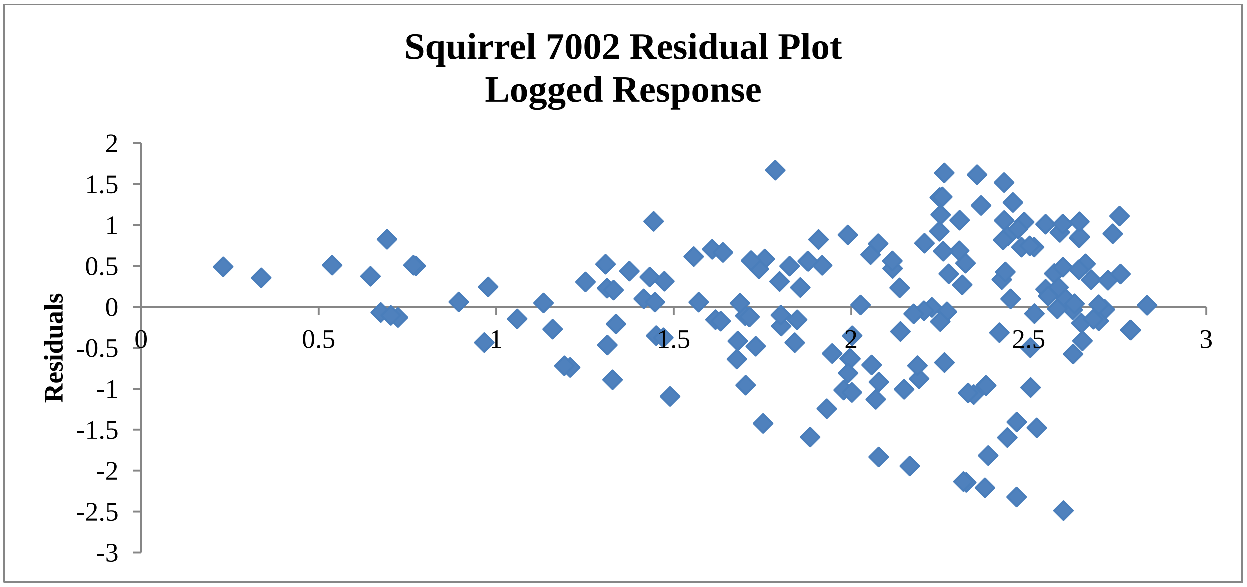

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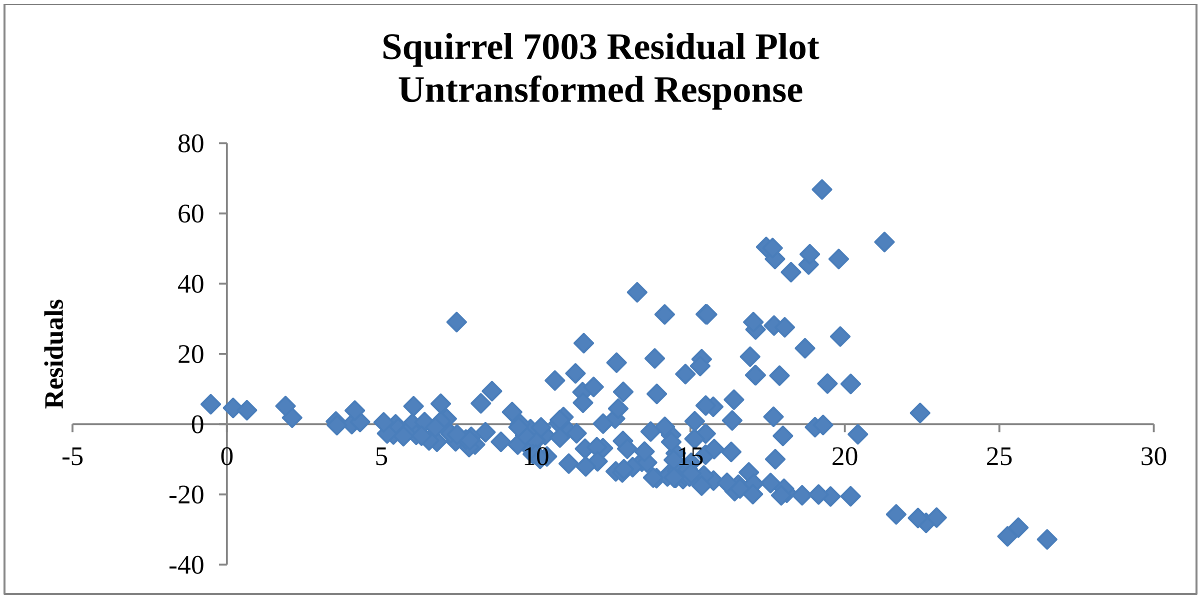

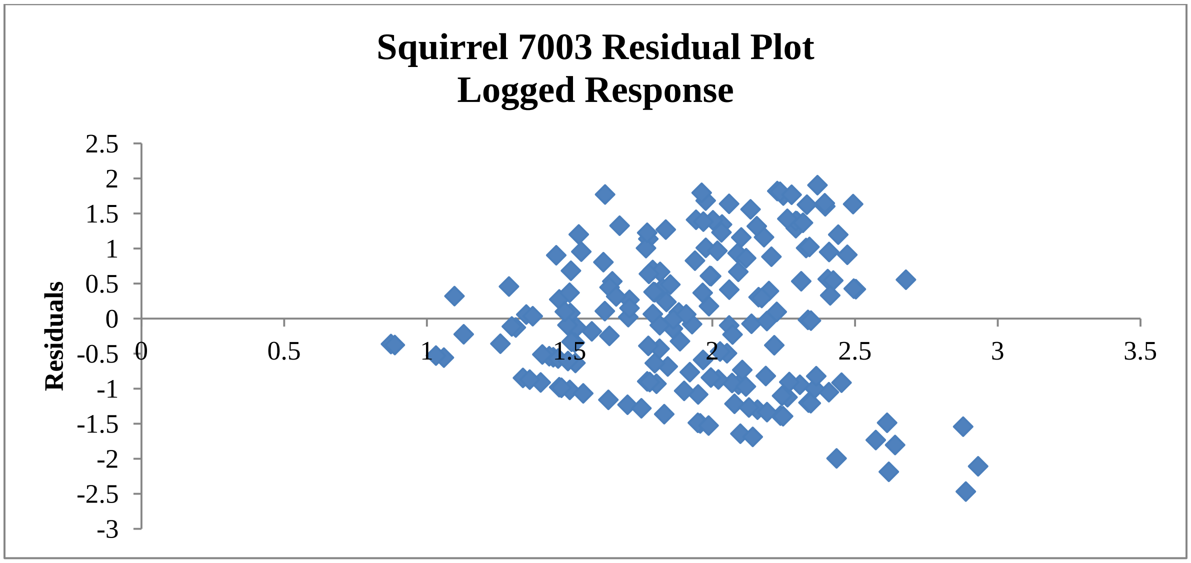

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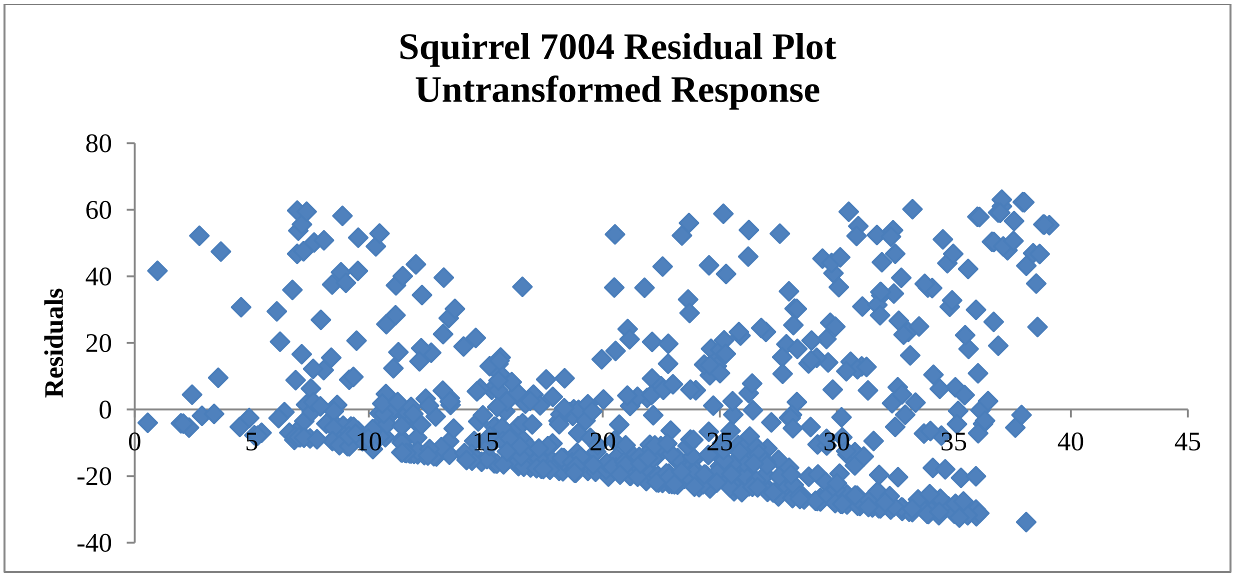

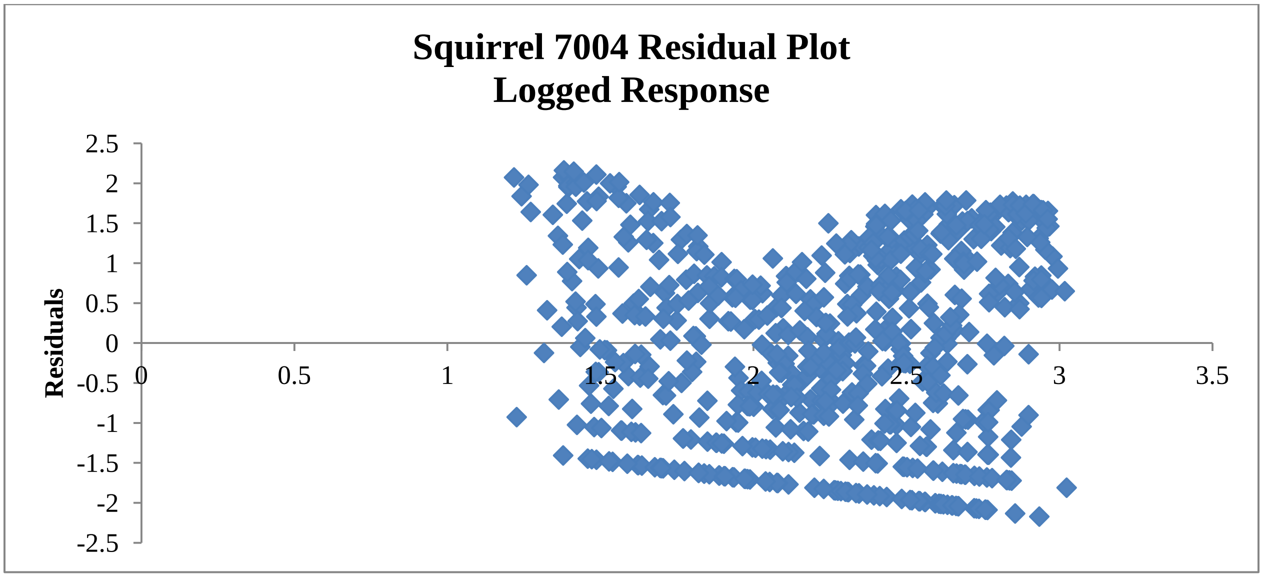

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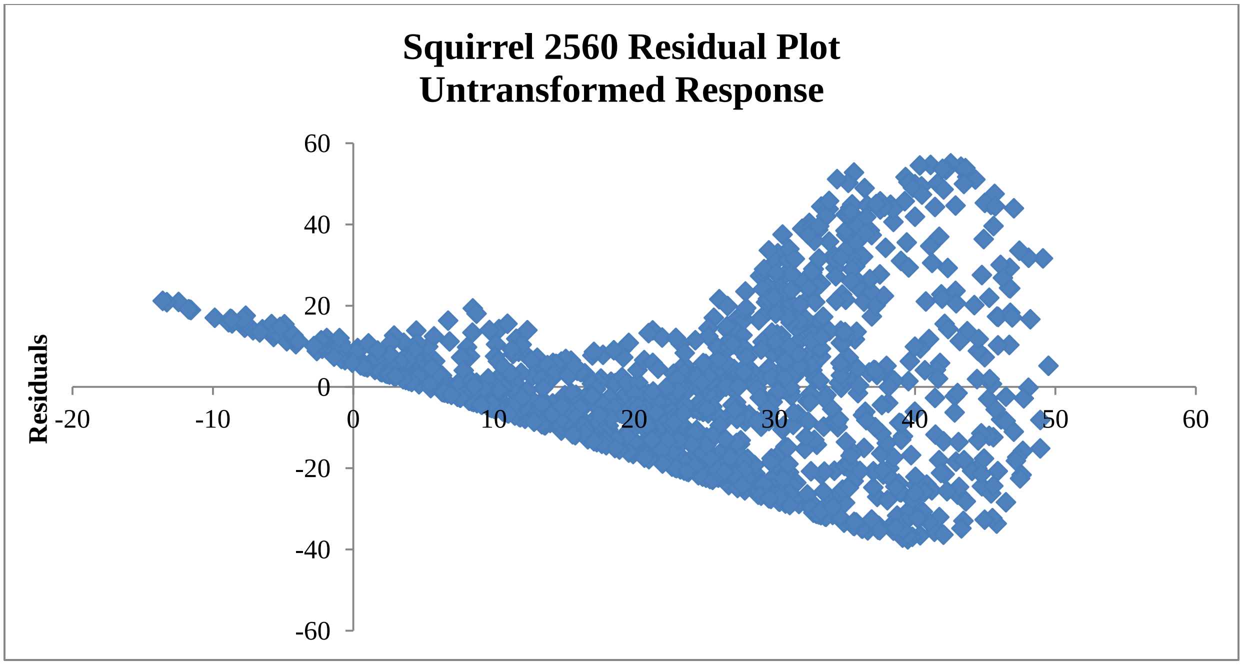

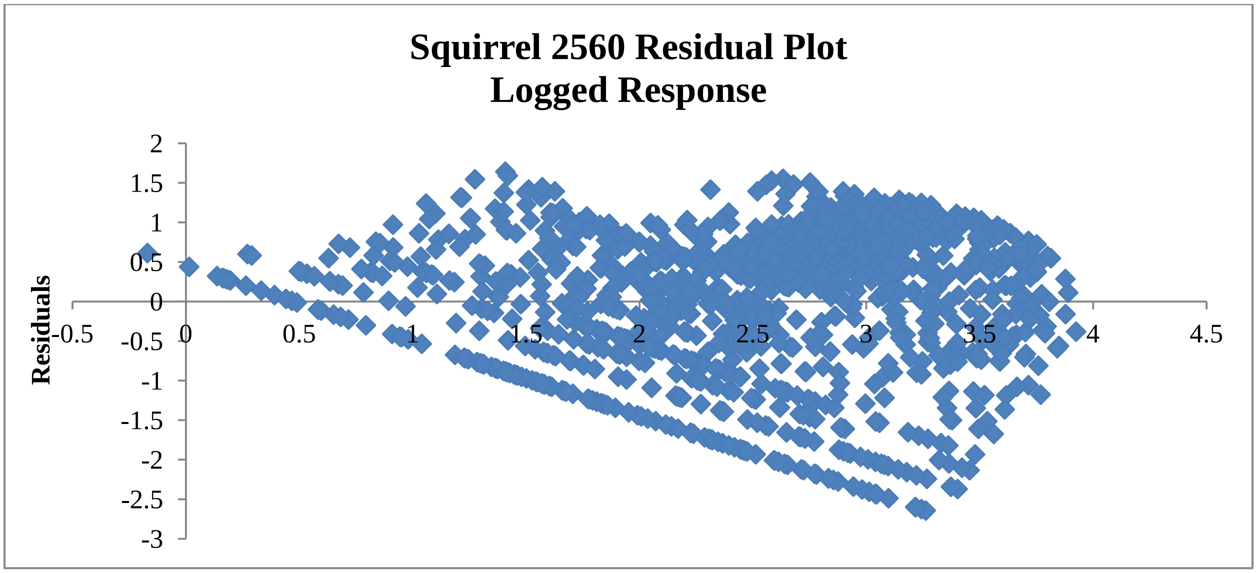

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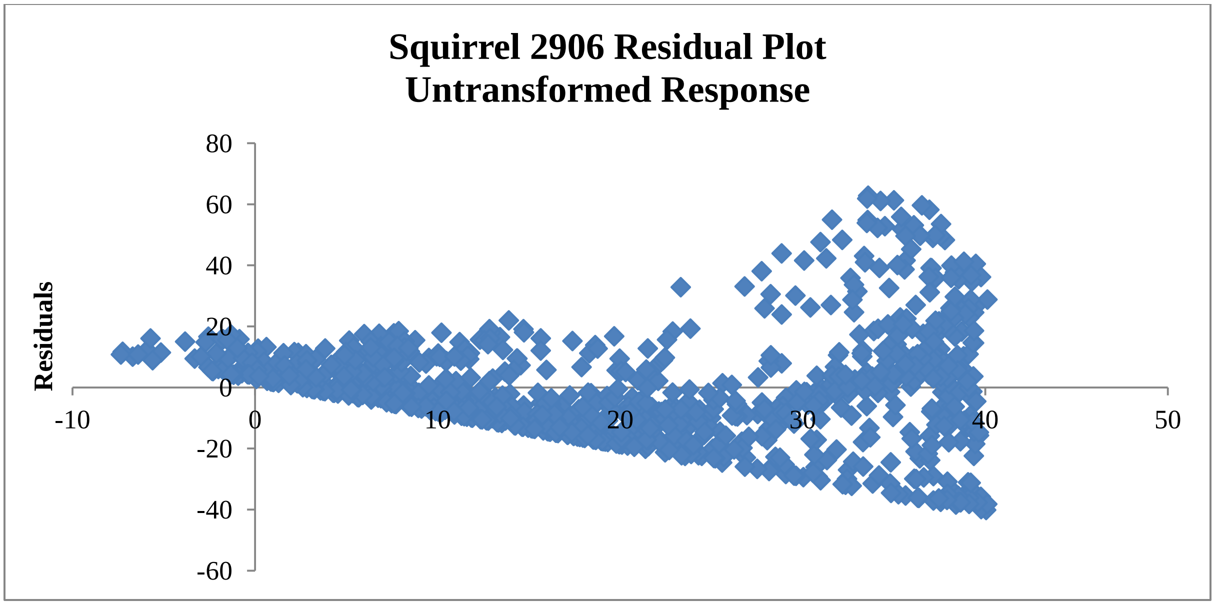

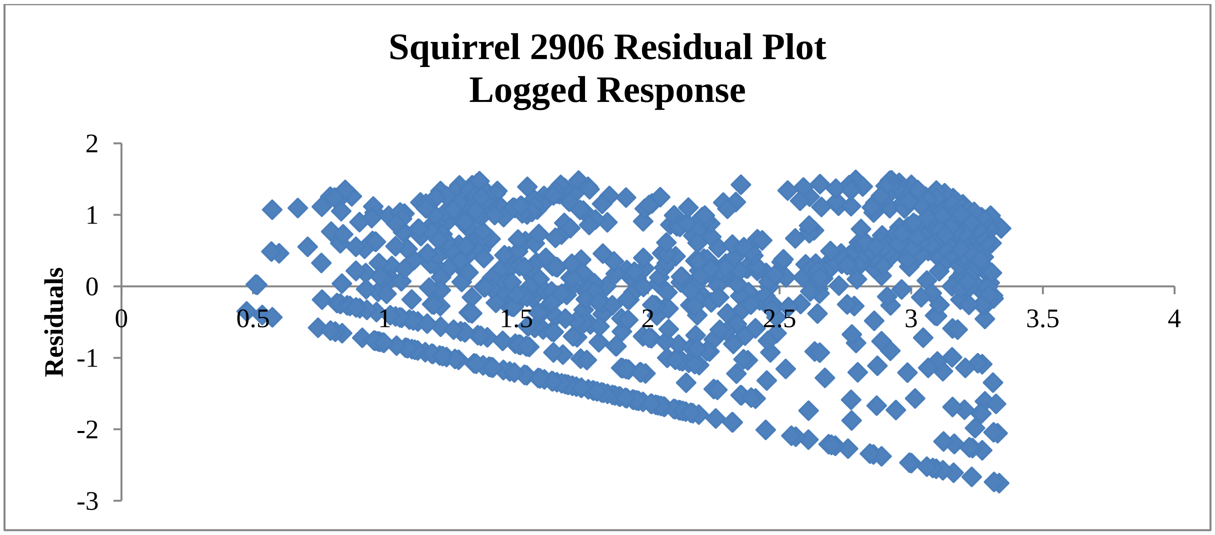

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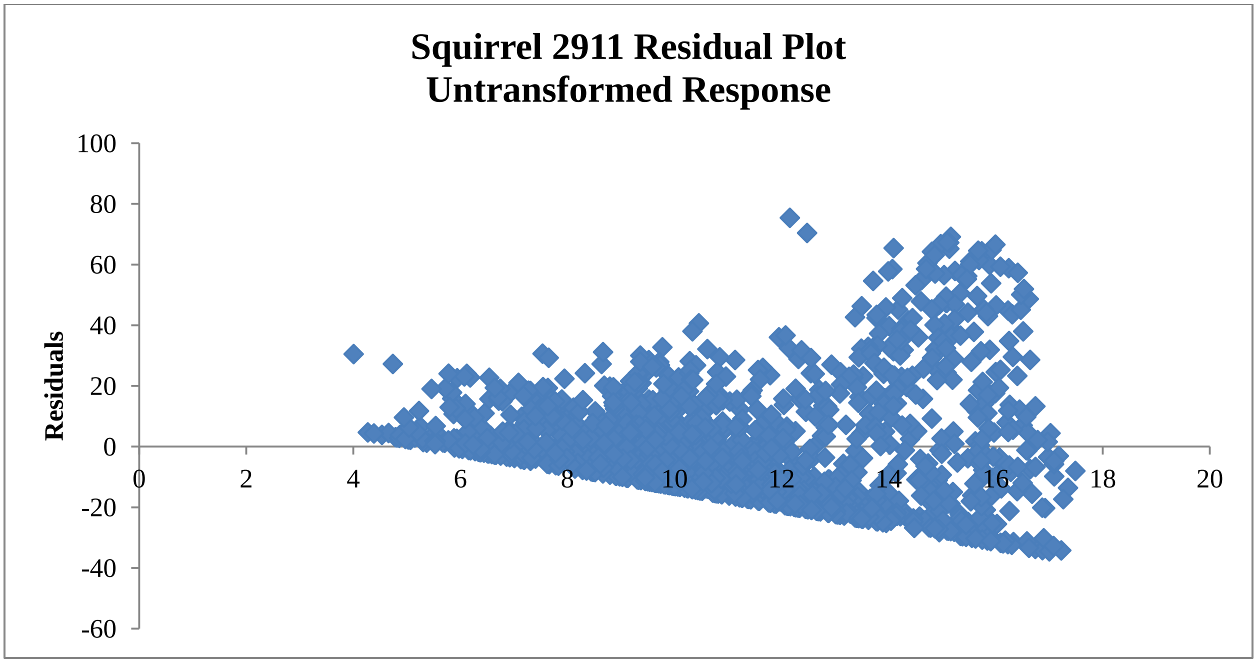

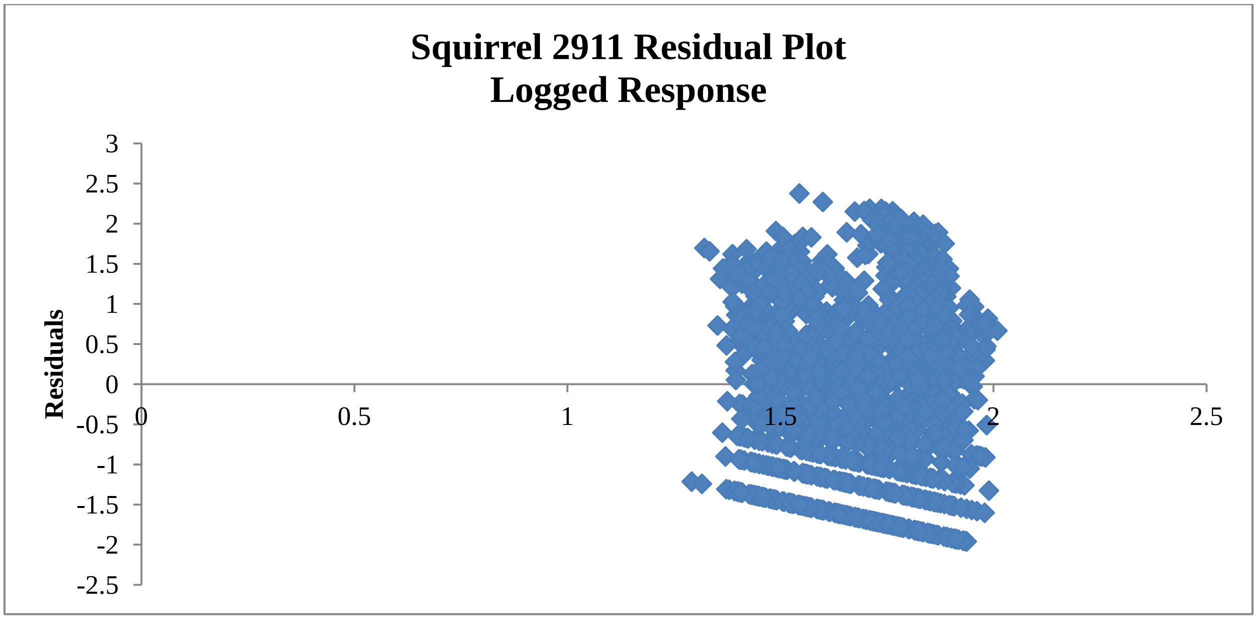

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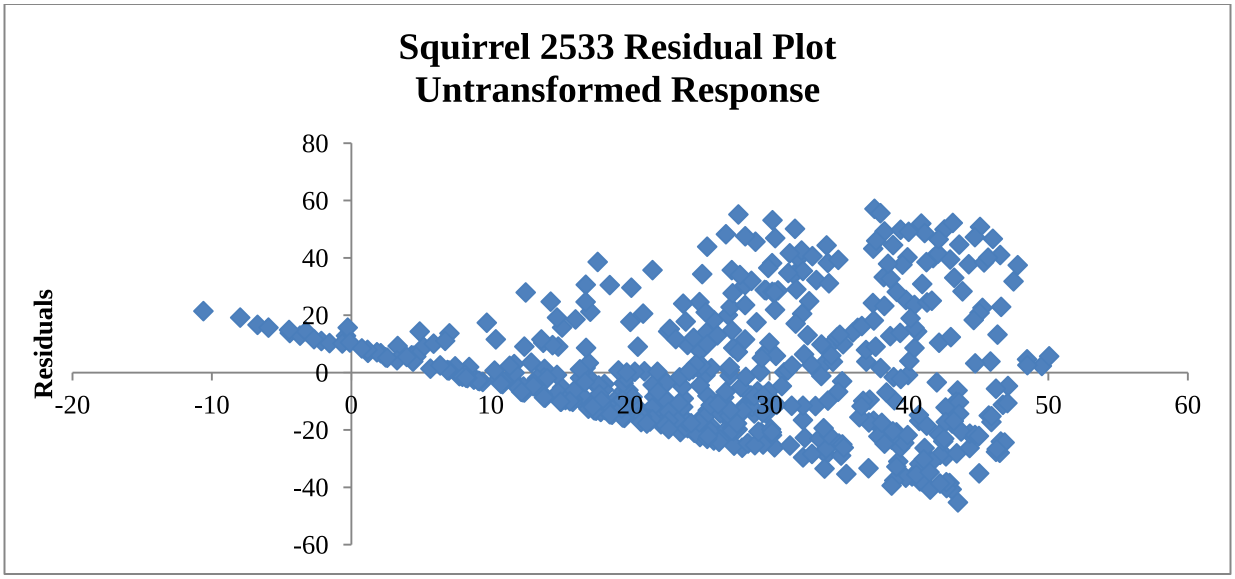

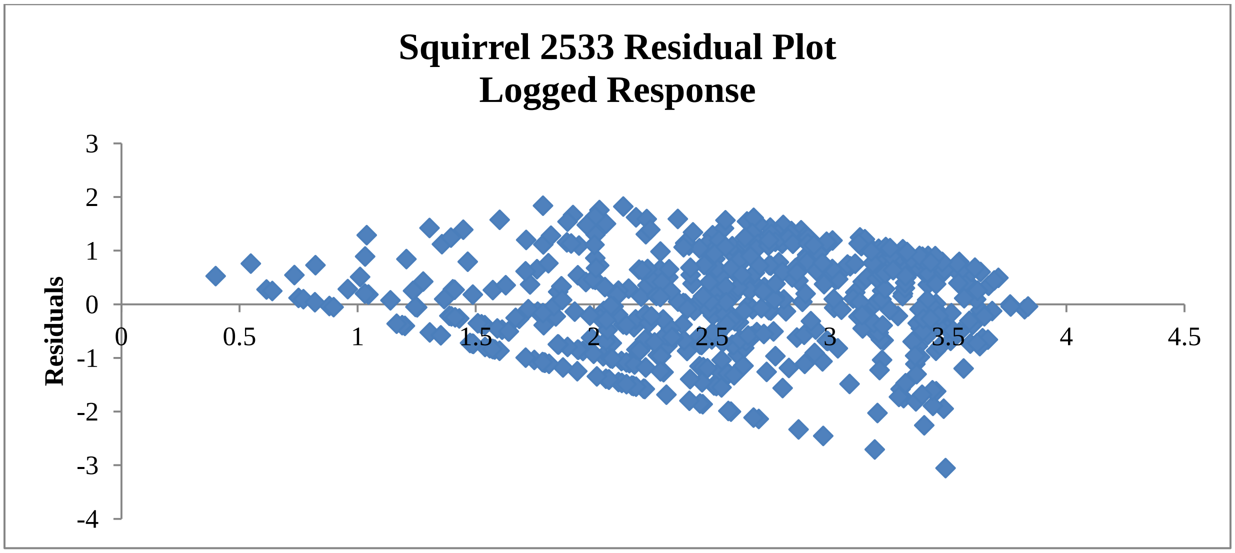

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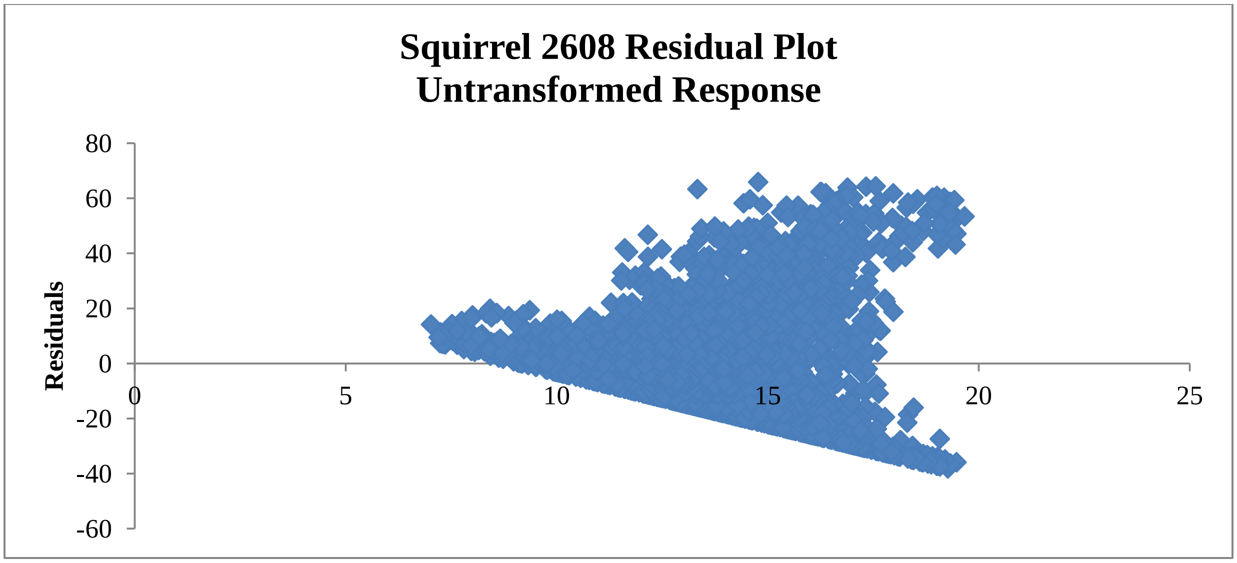

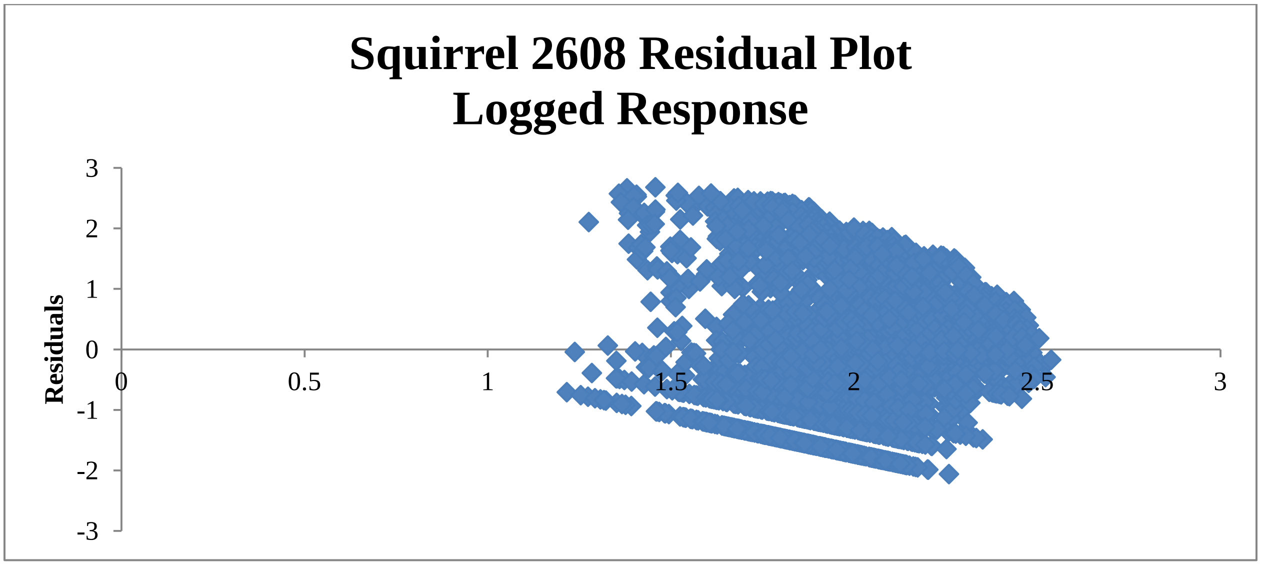

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