Note

Diets of Native and Introduced Tree Squirrels in Washington

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ABSTRACT Competition for food resources can be a primary mechanism for displacement of native species by introduced species. Investigation of dietary partitioning between potential competitors and spatiotemporal variability in food resources can reveal contested food items and intensity of competition. Introduced eastern gray squirrels (*Sciurus carolinensis*) have been implicated as competitors with western gray squirrels (*S. griseus*) and Douglas' squirrels (*Tamiasciurus douglasii*), but little is known about interactions among these species. We collected foraging observations and fecal pellets of sympatric gray and Douglas' squirrels trapped and radio-tracked in western Washington, USA, from 2007 to 2012. We compared food resources consumed across species, seasons, and years to evaluate dietary overlap and the potential for competitive interactions. All squirrel species ate hypogeous fungi throughout all seasons; spores of several genera were present in 272 of 275 fecal samples and observed in all months. *Rhizopogon*, *Geopora*, and *Melanogaster* spp. occurred in most fecal pellets for all squirrels, but the diet of the Douglas' squirrels had slightly lower richness of hypogeous fungi than gray squirrels. Although foraging observations suggest that eastern and western gray squirrels shared important dietary items such as acorns, strong differences in consumption of seeds of a common conifer may facilitate their coexistence. Our results suggest that dietary overlap among arboreal squirrels could lead to competitive interactions during periods of food scarcity, but subtle differences may be sufficient to permit long-term coexistence. Tree squirrels in Washington would likely benefit from forest management practices that promote or sustain robust crops of hypogeous fungi. © 2019 The Wildlife Society.

KEY WORDS competition, diet, Douglas' squirrel, eastern gray squirrel, fungi, *Sciurus carolinensis*, *Sciurus griseus*, *Tamiasciurus douglasii*, western gray squirrel, Washington.

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 (Doherty et al. 2016, Gao and Reitz 2017, Young et al. 2017). Competitive interactions between native and introduced species can occur when animals are territorial or share dependence on limited resources (Keddy 2001). Because competition can have strong influence on ecological communities (Chesson 2014), competition often is implicated as a threat to native species when introduced species share similar life-history characteristics. But, extinction of native species from competition by introduced species is considered uncommon and more often is attributed to mechanisms of predation and disease (Davis 2003). 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 (Tilman 2004, Chase 2011). Furthermore, 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 of introduced species so that conservation efforts to maintain biological diversity or recovering rare species are efficient and effective.

Exploitation competition for food resources is a mechanism by which introduced species can displace natives (Petren and Case 1996, Morin 2011, David et al. 2017). Dietary similarity between competing species should correlate with the intensity of competition when food resources are limited. Diet studies of potential competitors may reveal shared dependence on limited resources and other important information about interspecies interactions (e.g., when and where interactions may occur). Foraging is central to survival and reproduction and requires consideration of the availability, quality, and associated risks of food items (Stephens et al. 2007). Diets reflect these decisions and other important information about resource use needed to

evaluate competitive interactions. For example, subtle differences in the sizes of pine cones selected by eastern gray squirrels (*Sciurus carolinensis*) and fox squirrels (*S. niger*) have explained differences in their habitat use and abilities to exploit distinct land cover types (Steele and Koprowski 2001). Competition for food resources has been identified as a mechanism for displacement of Eurasian red squirrels (*S. vulgaris*) by invasive eastern gray squirrels in the United Kingdom (Wauters et al. 2002). Therefore, differences in diet and species can dictate competitive outcomes, so it is important to evaluate dietary similarity of potential competitors to determine if resources are under competition.

Eastern gray squirrels 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, Shuttleworth et al. 2016). In the western United States, eastern gray squirrels have invaded some areas that support native western gray squirrels (*Sciurus griseus*) and Douglas' squirrels (*Tamiasciurus douglasii*), where they may compete for food resources (Byrne 1979, Linders and Stinson 2007, Gonzales et al. 2008). Western gray squirrels are state-listed as a threatened species in Washington, and intensive efforts to recover a population that coexists with eastern gray squirrels in western Washington began in 2007 (Vander Haegen and Orth 2011, Vander Haegen et al. 2018). Eastern gray squirrels were introduced to this region in the early twentieth century and quickly spread throughout urban areas around Puget Sound (Linders and Stinson 2007). Colonization of undeveloped forests that support western gray squirrels may have occurred only recently (Fimbel and Freed 2008) and has raised concern that competitive interactions may be detrimental to western gray squirrels.

Dietary overlap for eastern and western gray squirrels may be high because they consume and store acorns as a primary food source over winter (Carraway and Verts 1994, Steele and Koprowski 2001); however, dietary similarity for food resources other than acorns is poorly understood because only 1 study has compared their diets in areas of sympatry (Byrne 1979). Unlike eastern gray squirrels, western gray and Douglas' squirrels consume hypogeous fungi (i.e., truffles) frequently (Byrne 1979, Carraway and Verts 1994, Koprowski 1994, Steele 1999). Squirrels consume and disperse truffles, which form mycorrhizal symbioses that enhance nutrient uptake and growth in trees and shrubs (Maser et al. 2008). The abundance of truffles can be significantly influenced by mycophagists (e.g., squirrels; North et al. 1997) and by forest management treatments such as overstory thinning (Colgan et al. 1999, Carey et al. 2002, Lehmkuhl et al. 2004), potentially disrupting these ecological interactions. Some truffle species are widespread, whereas others are associated with specific tree species or forest types (Trappe et al. 2009). Greater understanding of squirrel diets might reveal mechanisms that explain observed differences in habitat associations of gray squirrels (Johnston 2013) and provide guidance for habitat management to benefit western gray squirrels.

The objective of this study was to compare diets of sympatric eastern gray squirrels, western gray squirrels, and Douglas' squirrels to learn more about their ecology and to evaluate the potential for exploitation competition. We tested the null hypothesis of no difference in truffle consumption among squirrel species after accounting for seasonal effects. We also tested for differences between eastern and western gray squirrels in their consumption of tree seeds and described diet variation by season and year.

STUDY AREA

We studied gray and Douglas' squirrels from April 2007 to April 2012 on Joint Base Lewis-McChord (i.e., Base), a military reservation near Tacoma, Washington, USA. The Base covered 35,000 ha, most of which was set aside as managed forests, prairies, and woodlands for use as training areas for military personnel. Elevation ranged from 120 m to 160 m, and terrain was mostly flat. Average precipitation in February and August from 1981 to 2010 was 14 cm and 2.5 cm, respectively (Daly et al. 2008). Average minimum temperature in February was 0°C, and average maximum temperature in August was 26°C. Historically, much of this region was maintained as prairie and oak woodlands through burning practices of Native Americans (Norton 1979). Over the past century, fire exclusion has allowed succession to proceed and at the time of this study, most of the Base was densely forested by young or mature (20–80 years) Douglas-fir (*Pseudotsuga menziesii*). Prairie remnants, Oregon white oak (*Quercus garryana*) woodlands, and ponderosa pines (*Pinus ponderosa*) were sparsely distributed throughout the Base. Riparian areas supported Oregon white oak, Oregon ash (*Fraxinus latifolia*), bigleaf maple (*Acer macrophyllum*), black cottonwood (*Populus trichocarpa*), red alder (*Alnus rubra*), and western red cedar (*Thuja plicata*). Common shrubs included snowberry (*Symphoricarpos albus*), beaked hazelnut (*Corylus cornuta*), Indian plum (*Oemleria cerasiformis*), and ocean spray (*Holodiscus discolor*). Eastern gray squirrels were present in developed and undeveloped portions of the Base, whereas western gray squirrels were only in undeveloped forests and woodlands (Johnston 2013). Much of the Base was surrounded by urban or agricultural areas that supported eastern gray squirrels but not western gray squirrels. Eastern gray squirrels were known to occur on developed portions of the Base since at least the early 1980s, but their colonization of undeveloped forests could be more recent (Fimbel and Freed 2008). Douglas' squirrels were common throughout conifer forests. Other sciurids on the Base included northern flying squirrels (*Glaucomys sabrinus*) and Townsend's chipmunks (*Tamias townsendii*). Potential predators of tree squirrels included coyotes (*Canis latrans*), bobcats (*Lynx rufus*), cougars (*Puma concolor*), red-tailed hawks (*Buteo jamaicensis*), great horned owls (*Bubo virginianus*), and barred owls (*Strix varia*). Parturition for gray squirrels began in March, and young dispersed by September. Acorns and conifer seeds developed late summer through fall. Truffles were present year round, but biomass was generally greatest in spring and fall (Colgan et al. 1999).

METHODS

Field Methods

We trapped and radio-collared eastern and western gray squirrels at 5 study sites on the Base that were designated as units for experimental removals of eastern gray squirrels from April 2007 to April 2012 (Johnston 2013). In addition, state 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, Vander Haegen et al. 2018). In October 2010, we began marking Douglas' squirrels and radio-tracked several individuals alongside eastern gray squirrels from January 2011 to March 2012.

We trapped squirrels with box traps (models 105 and 106, Tomahawk Live Traps, Hazelhurst, WI, USA) baited with whole walnuts. We placed trap transects in squirrel 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 spaced traps 50–100 m apart and trapped for 3 to 7 days every 3 to 5 months in each study area. We restrained captured squirrels in a cloth handling cone (Koprowski 2002), which allowed us to assess squirrel condition, attach ear tags (number 1005, National Band and Tag Co., Newport, KY, USA), and for a selection of squirrels, attach radio-collars (model SC-2, Holohil Systems, Carp, Ontario, Canada) that weighed 15 g with projected battery life of 18 months. We collected fecal pellets left by squirrels in traps and stored them in vials with 100% ethanol for examination in the laboratory. We attributed pellets to specific squirrels by ensuring that traps were clean and areas around traps were free of pellets prior to trapping. We collected pellets from each squirrel no more than once per trapping session to ensure that samples were independent. All trapping, handling, and monitoring of squirrels followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) and protocols were approved by the Institutional Animal Care and Use Committee at the University of Washington (protocol number 2479-28).

We relocated squirrels equipped with radio-collars 3 times/week by homing in on their location using radio-telemetry techniques (White and Garrott 1990). We obtained no more than 1 location/day to ensure independence among locations. We tracked squirrels year-round until death or the end of study in April 2012. We recorded the location of the squirrel with a global positioning system (GPS) unit (Trimble Navigation Limited, Westminster, CO, USA) once we saw the individual or estimated location to within 10 m based on the radio-signal. We saw squirrels on 18% of relocation efforts, and we typically observed behaviors for <10 minutes. We recorded any food items consumed during bouts of foraging by observing squirrels with binoculars.

Laboratory Methods and Statistical Analyses

For each sample of fecal pellets, we macerated 1 or 2 pellets in water and added 1 drop of potassium hydroxide. We created 3 slides/sample from the solution and recorded presence of fungal spores, vegetation, and insects within 10 fields of view spaced 1 mm apart along each of 2 transects per slide at 40x magnification (Colgan et al. 1997). We combined observations across slides to record richness and composition of truffle genera for each sample. Examination of additional slides was unnecessary because richness of truffle genera often was evident within 1 or 2 slides and rarely increased with >3 slides in our evaluation of sampling effort. We identified fungal spores to genus following synoptic keys of Castellano et al. (1989). When needed, we added Melzer's reagent (iodine, potassium iodide, and chloral hydrate in aqueous solution) to slides to stain spores for identification (Castellano et al. 1989). We recorded presence of insect parts and noted plants when pollen, cell walls, or starches were present.

We tested for differences in truffle consumption among squirrels ($\alpha = 0.05$) after accounting for effects of season (fall, winter, spring, and summer defined by dates of equinox and solstice) with permutational multivariate analysis of variance (perMANOVA) from the vegan package in R version 3.1.0 (R Development Core Team 2014). 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 3 samples that had no spore detections for similar reasons. We combined observations of *Geopora*, *Barssia*, and *Balsamia* spp. into a group we called the *Geopora* complex because of their ecological similarity and difficulties in distinguishing genera based on spore characteristics (Castellano et al. 1989). Likewise, we combined observations from members of *Russulaceae* because genera cannot be differentiated based solely on spores (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 for multivariate analyses (Legendre and Legendre 2012). Following analysis of the full data set, we repeated perMANOVA to test pair-wise differences in species after accounting for seasonal effects and adjusted P-values with the Bonferroni correction for multiple comparisons ($\alpha = 0.02$). We also tested pair-wise differences in seasons after accounting for species (Bonferroni $\alpha = 0.008$). We estimated 95% confidence intervals for the mean richness of truffle genera in samples to describe interspecies differences in diet that were identified by the multivariate analysis. We plotted samples in ordination space following non-metric dimensional scaling to visualize dietary patterns (Kruskal and Wish 1978). Finally, we summarized foraging observations for gray squirrels into contingency tables and tested for differences in food items among seasons, years, and between squirrel species with chi-square tests (Ramsey and Schafer 2002), after excluding rare food items ($n < 5$).

RESULTS

From April 2007 through April 2012, we captured 145 western gray squirrels, 101 eastern gray squirrels, and 119 Douglas' squirrels on the Base; most were captured repeatedly throughout the year as part of the radio-telemetry

study. The number of Douglas' squirrels captured represented our trapping efforts for October 2010 through March 2012 when we marked individuals of this species to incorporate it into our study of gray squirrels. We analyzed 275 samples of fecal pellets collected during these capture events: 167 samples from 80 western gray squirrels, 60 samples from 34 eastern gray squirrels, and 48 samples from 48 Douglas' squirrels. There was no evidence that the imbalance of sample sizes affected results based on analysis of a randomly selected subset of 48 samples per species. Therefore, we reported results for the full data set.

Gray and Douglas' squirrels ate truffles frequently throughout the year based on our finding of fungal spores in 272 of 275 fecal samples that documented truffle consumption in all months. We found ≥14 genera of truffles and 1 genus of epigeous fungi in our samples (Table 1). Although we combined observations of *Geopora*, *Balsamia*, and *Barssia* into 1 group, all 3 genera likely were present in our samples based on spore characteristics. Spores of *Rhizopogon*, *Geopora*, and *Melanogaster* were in our samples during all seasons and occurred far more frequently than other genera (Fig. 1). Spores from *Russulaceae*, *Hymenogaster*, *Tuber*, *Elaphomyces*, and *Hydnotyra* were frequently in fecal pellets during some seasons but rarely in others. Plants, insect parts, and other food items were relatively rare in our samples and probably were underestimated because our methodology was aimed at identifying fungal spores.

We found differences in truffle consumption among tree squirrels ($F_{2, 266} = 2.25$, $P = 0.01$) after accounting for seasonal effects. Pair-wise comparisons of truffle consumption between species (Bonferroni $\alpha = 0.02$) suggested that Douglas' squirrels differed from eastern gray squirrels ($F_{1, 100} = 2.25$, $P = 0.04$) and western gray squirrels ($F_{1, 210} = 3.34$, $P = 0.01$), but diets were similar between gray squirrel species ($F_{1, 219} = 1.47$, $P =$

0.18). Consistent with perMANOVA results, ordinations of truffle genera within fecal samples showed high overlap between eastern and western gray squirrels but some separation between Douglas' and gray squirrels (Fig. 2). Although *Rhizopogon*, *Geopora*, and *Melanogaster* were common in the diets of each squirrel species, richness of truffle genera was lower in fecal samples of Douglas' squirrels ($\bar{x} = 3.04 \pm 0.14$ [SE], 95% CI = 2.75–3.33) compared to eastern ($\bar{x} = 3.32 \pm 0.16$, 95% CI = 3.01–3.63) and western ($\bar{x} = 3.54 \pm 0.09$, 95% CI = 3.36–3.73) gray squirrels. There was strong evidence of seasonal differences in truffle consumption by squirrels ($F_{3, 266} = 5.87$, $P < 0.001$), and subsequent pair-wise comparisons indicated differences among all seasons ($P < 0.008 =$ Bonferroni α), except between winter and summer ($F_{1, 105} = 2.71$, $P = 0.01$) or winter and fall ($F_{1, 100} = 3.09$, $P = 0.02$).

We used radio-telemetry to locate gray squirrels 22,663 times and observed squirrels foraging 586 times (Table 2). We saw western gray squirrels 3,268 times during 18,844 relocations and made 302 foraging observations in which we identified the food item. We saw eastern gray squirrels 419 times during 4,227 relocations, and we identified food items on 45 of these foraging observations. We were unable to identify food items on 30 and 220 foraging observations for eastern and western gray squirrels, respectively. Often, we could not identify the food item because the squirrel was foraging on the ground in dense vegetation. We located Douglas' squirrels 1,146 times with radio-telemetry and observed them foraging on 10 occasions, of which we determined they were consuming pollen or seeds of Douglas-fir (3), acorns (1), or maple samaras (1).

Frequencies of food items observed during foraging bouts differed between eastern and western gray squirrels ($\chi_6^2 = 39.7$, $P < 0.001$) and across seasons ($\chi_3^2 > 11.3$, $P \le 0.01$; Table 2). Species differences were primarily due to

Table 1. Percent occurrence of food items in fecal pellets of arboreal squirrels and tree associations of genera, Joint Base Lewis-McChord, Washington, USA, 2007–2012.

Food item[a]	Eastern gray squirrel $n = 60$	Western gray squirrel $n = 167$	Douglas' squirrel $n = 48$	Tree associations[b]
Elaphomyces	12	16	4	Douglas-fir, pine, oak
Gautieria	2	3	10	Douglas-fir, pine
Genabea	7	9	8	Douglas-fir, pine, oak
Genea	2	2	2	Douglas-fir, oak
Geopora	82	93	77	Douglas-fir, pine
Hydnotyra	15	18	19	Douglas-fir, pine
Hymenogaster	15	16	6	Douglas-fir
Hysterangium	2	4	4	Douglas-fir
Leucangium	8	6	0	Douglas-fir
Melanogaster	63	78	79	Douglas-fir, pine
Radiigera	2	1	0	Cottonwood, oak, pine
Rhizopogon	77	90	90	Douglas-fir, pine
Russulaceae	23	9	15	Douglas-fir
Tuber	13	19	6	Douglas-fir, pine, oak
Epigeous (*Boletus*)	7	2	0	
Plant	12	14	13	
Other	2	1	2	
Unknown	2	5	8	

[a] Fungal spores were identified to genera, except those of the family *Russulaceae* and *Boletus*. Spores of *Russulaceae* likely were from *Gymnomyces*, a hypogeous genus with species that resemble truffles but that cannot be distinguished from other genera in *Russulaceae* based only on spore characteristics (Trappe et al. 2009). *Geopera* may include observations of *Barssia* and *Balsamia* because of similar spore characteristics and ecology among these genera.

[b] Tree associations (Trappe et al. 2007) are limited to common tree species on the Base. Some genera are also associated with true firs (*Abies* spp.) and hemlocks (*Tsuga* spp.), in addition to Douglas-fir.
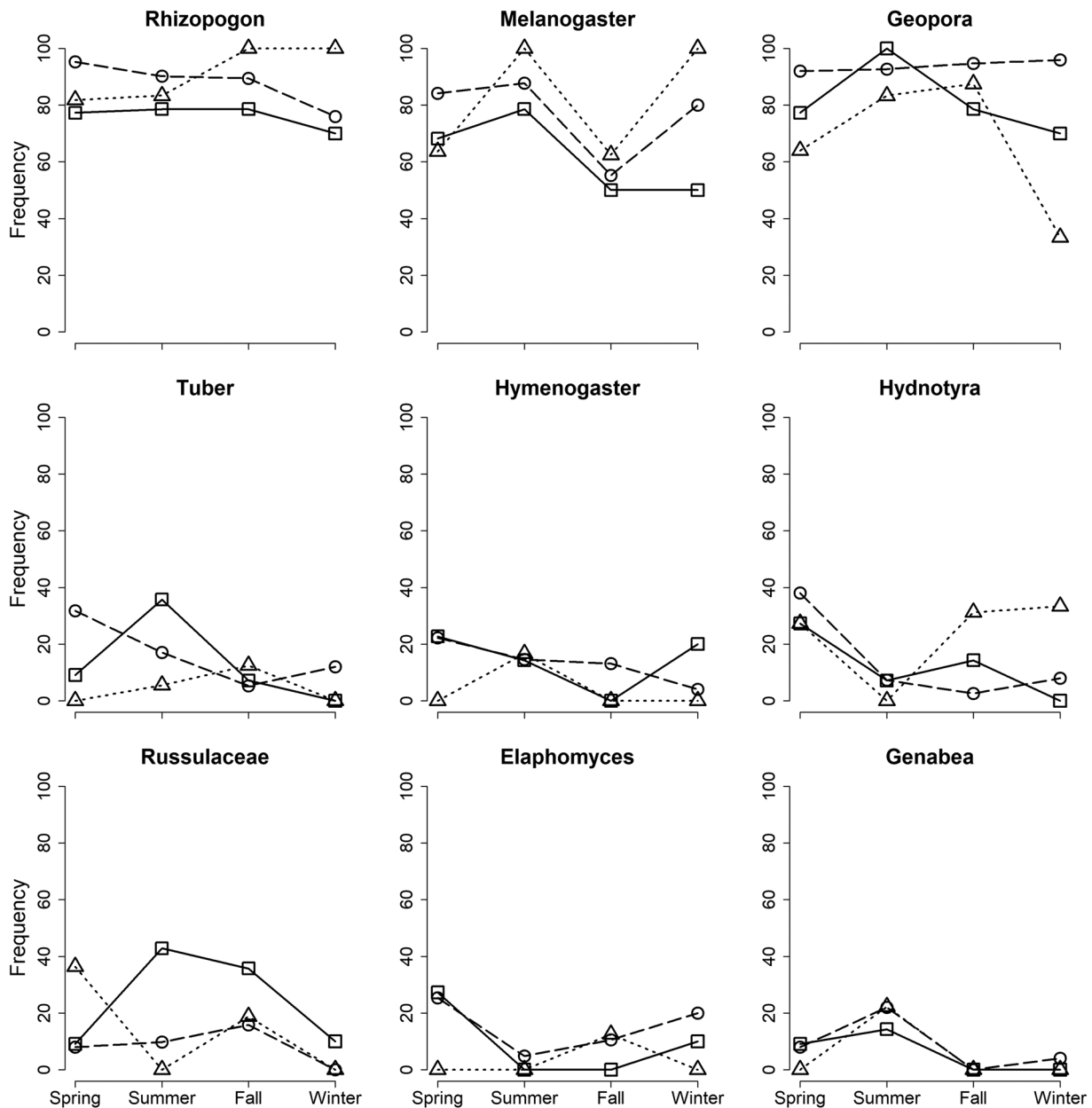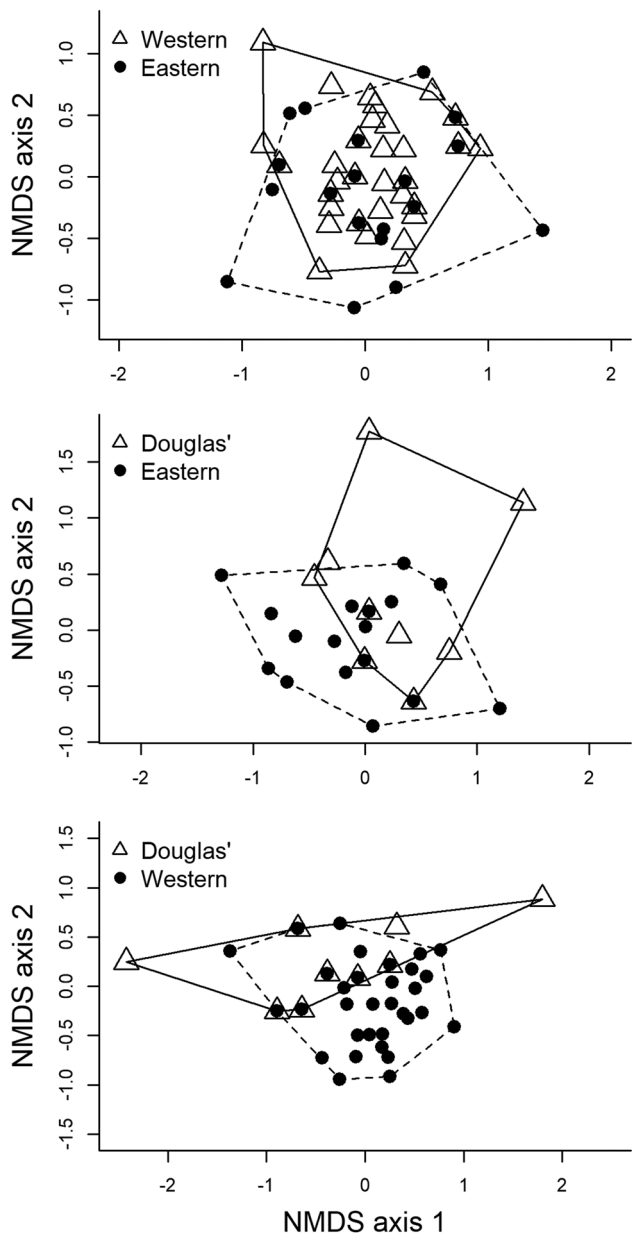
Figure 1. Frequency (i.e., percent occurrence) of common truffles by genera in fecal samples by season for western gray squirrels (*n* = 167, squares, solid line), eastern gray squirrels (*n* = 60, circles, dashed line), and Douglas' squirrels (*n* = 48, triangles, dotted line), Joint Base Lewis-McChord, Washington, USA, 2007–2012.

consumption of more maple samaras and acorns but fewer Douglas-fir seeds than expected by eastern gray squirrels. Squirrels ate hazelnuts during summer, whereas consumption of acorns and maple samaras began in late summer and continued through the fall. Aside from truffles, Douglas-fir seeds were the only food items eaten by squirrels that we observed with any regularity outside of summer and fall. Western gray squirrels foraged heavily on green cones as they began to develop in July and August each year, whereas we rarely saw eastern gray squirrels eating conifer seeds or cones at any time during the study. We observed western gray squirrels stripping bark of Douglas-fir trees during winter after a severe mast failure in 2010, presumably to consume cambium. The frequency of observations for Douglas-fir seeds, maple samaras, hazelnuts, and cambium each varied by year ($\chi^2_3 > 26.0$, $P < 0.001$), but observations of acorn consumption for gray squirrels combined did not differ by year during this study ($\chi^2_3 = 2.90$, $P = 0.41$).

DISCUSSION

The presence of truffle spores in nearly all fecal samples of gray and Douglas' squirrels indicated their importance as a food resource. We identified some differences between gray and Douglas' squirrels in truffle genera consumed, but native and introduced squirrels differed most in their consumption of Douglas-fir seeds. Year-round availability of truffles on the Base may support squirrels in seasons of low availability of tree seeds and prevent starvation during

Figure 2. Non-metric dimensional scaling (NMDS) ordinations of fungal spores found in fecal samples of Douglas' and eastern and western gray squirrels during spring, Joint Base Lewis-McChord, Washington, USA, 2007–2012. The outer extent of samples for each species is outlined in ordination space. Truffle consumption by squirrels differed significantly across seasons.

also suggests that these species may compete for limited food resources in areas of sympatry. Although we did not estimate available biomass of truffles, North et al. (1997) demonstrated that above ground mycophagists (like sciurids) can significantly reduce the standing crop of truffles. Annual and seasonal fluctuations in the availability of tree seeds occurred on the Base during this study (Washington Department of Fish and Wildlife [WDFW], unpublished data) and could have increased competition for some food resources like truffles. Acorns and Douglas-fir seeds were important food sources that varied in availability over time and were nearly absent during years of mast failure.

Truffles commonly eaten by western gray squirrels on the Base were similar to those in squirrel diets from other regions. *Rhizopogon* spores occurred in most fecal samples from the Base and were the most common spores found in feces of western gray squirrels in North Cascades (Stuart 2012), Oregon (Maser and Maser 1988, Foster 1992), and California, USA (Stienecker and Browning 1970). *Melanogaster*, *Hysterangium*, and *Gautiera* also were relatively common genera consumed by western gray squirrels in other regions (Stienecker and Browning 1970, Stuart 2012). Spores of the *Geopora* complex (*Geopora*, *Barssia*, and *Balsamia*) occurred most frequently in our samples from the Base and were common food for western gray squirrels in the North Cascades (Stuart 2012) and in Oregon (Foster 1992) and for northern flying squirrels (Lehmkuhl et al. 2004). A previous study on the Base (Colgan et al. 1997, Carey et al 2002) examined availability of truffle genera and frequency in the diet of 2 other sciurids, sampling a site 20 km from our study area in uplands dominated by Douglas-fir with little oak and no pine. Several genera, including *Rhizopogon*, *Hysteranguim*, and *Melanogaster*, were common in the soil sampling and in the diets of northern flying squirrels and Townsend's chipmunks (*Tamias townsendii*). Although *Rhizopogon* and *Melanogaster* also occurred with high frequency in our sampling of gray and Douglas' squirrels, *Geopora*, the most frequent genus occurring in our samples, was not detected at this second site.

The contrast between eastern and western gray squirrels in their consumption of Douglas-fir seeds may be important to their coexistence on the Base. We frequently observed western gray squirrels eating seeds of Douglas-firs throughout the year; foraging in conifers 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 potential 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 rarely saw eastern gray squirrels foraging in Douglas-fir trees despite high availability within their home ranges. Douglas-firs are not native to the historical range of the eastern gray squirrel, and their small seeds may have low value as a food resource compared to acorns, pine seeds, and other tree seeds commonly eaten by eastern gray squirrels in their native geographic range

times of mast failure. For example, body mass of gray squirrels did not decrease in fall 2010 despite widespread failure in development of acorns and conifer seeds (Johnston 2013). This mast failure seemingly led squirrels to spend more time foraging for maple samaras and hazelnuts, which were relatively more abundant than acorns and fir seeds in 2010. Although lower than many tree seeds (Steele and Koprowski 2001), the nutritional value of truffles can be nearly sufficient to sustain squirrel energy balance (Cork and Kenagy 1989), and truffles can help squirrels meet water requirements (Claridge et al. 1999). Consistent, high use of truffles by eastern and western gray squirrels on the Base

Table 2. Foraging observations by season for eastern and western gray squirrels, Joint Base Lewis-McChord, Washington, USA, 2007–2012.

	Eastern gray squirrel					Western gray squirrel				
	Spring[a]	Summer	Fall	Winter	Total[b]	Spring[a]	Summer	Fall	Winter	Total[b]
Douglas-fir seeds	1	4	0	0	5 (21)	46	59	38	19	162 (146)
Ponderosa pine seeds	0	0	0	0	0 (1)	0	5	1	0	6 (5)
Oregon white oak acorns	1	7	7	0	15 (8)	6	25	17	0	48 (55)
Big-leaf maple samaras	1	2	10	0	13 (5)	0	15	14	0	29 (36)
Vine maple samaras	0	3	2	0	5 (5)	0	13	5	0	18 (20)
Hazelnuts	0	5	0	0	5 (3)	0	18	0	1	19 (21)
Truffles	0	0	0	0	0	0	2	0	1	3
Hawthorn berries[c]	0	0	0	0	0	0	0	1	0	1
Blackberries[c]	0	0	0	0	0	0	0	0	1	1
Cottonwood catkins	0	0	0	0	0	2	0	0	0	2
Bark	0	0	0	0	0 (2)	4	0	0	9	13 (11)
Birdfeeder[d]	0	0	0	2	2	0	0	0	0	0

[a] Spring or late-winter foraging on oaks, maples, and blackberries was for buds and flowers.
[b] 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.
[c] Hawthorn = *Crataegus monogyna*; Blackberry = *Rubus armeniacus*.
[d] 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.

(Smith 1981, Steele and Koprowski 2001). Douglas-fir seeds 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 also an introduced species (Robinson and McTaggart-Cowan 1954, Shorten 1954, Byrne 1979). In the United Kingdom, eastern gray squirrels avoided Douglas-fir forests (Bryce et al. 2002), and conifers were largely absent from sites that had eastern gray squirrels in California (Byrne 1979).

Eastern and western gray squirrels had low spatial overlap in their areas of use on the Base and exhibited significant differences in habitat use (Johnston 2013), possibly reducing the consequences of overlap in diets. Habitat use by eastern gray squirrels strongly favored riparian areas dominated by deciduous trees and with high diversity of shrubs that included mast producing species like beaked hazelnut, rather than conifer-dominated uplands (Johnston 2013). Western gray squirrels, in contrast, used primarily uplands dominated by fir and pine. Although eastern gray squirrels had ample access to Douglas-fir trees, our foraging observations suggest they failed to use this food resource, instead focusing their efforts on hardwood trees and shrubs. Eastern gray squirrels may be unable to establish populations in uplands on the Base because of these differences in food use and availability. Eastern gray squirrels can feed heavily on pine seeds in their native range, but ponderosa pines were scarce on the Base. Douglas' squirrels had high spatial overlap with eastern gray squirrels based on our trapping records and telemetry data (Johnston 2013) but had more substantial dietary differences, particularly with their consumption of truffles and fir seeds. Although we made few foraging observations of Douglas' squirrels during radio-tracking (typically, they were high in the dense canopy of fir trees), this species forages heavily on Douglas-fir seeds (Steele 1999). We cannot attribute any differences in truffle consumption between gray and Douglas' squirrels to habitat associations because we also observed Douglas' squirrels frequently in areas used by both species of gray squirrels, and nearly all truffles were associated with Douglas-fir, which was nearly ubiquitous in areas used by squirrels.

Byrne (1979) reported introduced eastern gray squirrels depended on cultivated food resources in California and restricted diets that were composed of items that resembled food resources of deciduous forests of the eastern United States. Robinson and McTaggart-Cowan (1954) reported that eastern gray squirrels had a restricted diet comprised of samaras from big-leaf and vine maples (*Acer circinatum*) in British Columbia, Canada. Similarly, eastern gray squirrels on the Base ate primarily maple samaras and acorns, based on our foraging observations. The preponderance of forests dominated by Douglas-fir or other conifers in Washington may inhibit spread of eastern gray squirrels beyond areas with human-cultivated food resources or limit them to riparian areas. Differential habitat use between eastern and western gray squirrels on the Base did not result in differences in truffle consumption between species. Although they used riparian areas extensively, the home ranges of most eastern gray squirrels included upland areas of Douglas-fir, oak, and in some cases pine, suggesting that truffles common to these conifer-oak systems were available to both species. Extensive use of truffles by eastern gray squirrels is a finding new to this study and may be related to the relatively low availability of hardwood seeds on our study area, relative to where the species has been studied previously.

In California, Byrne (1979) also reported eastern gray squirrels in riparian areas, whereas western gray squirrels were most common in conifer-dominated uplands. However, 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 in California, whereas they accounted for a third of the stomach contents by volume for western gray squirrels (Byrne 1979). 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, USA, fungi were eaten by eastern gray squirrels primarily during early summer and ranked behind acorns, beechnuts (*Fagus* spp.), and hickory (*Carya* spp.) nuts in proportion of stomach volumes of collected squirrels (Nixon et al. 1968). Eastern gray squirrels likely prefer tree seeds over truffles but will eat truffles when hardwood tree seeds are lacking. In contrast, truffles have been a major dietary component 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, Foster 1992, Stuart 2012, this study).

MANAGEMENT IMPLICATIONS

Shared use of several food resources among arboreal squirrels demonstrated in our study raises the potential for competition over food resources during times of food shortage and may lead managers to control eastern gray squirrels to conserve native species; however, significant differences in habitat use between eastern and western gray squirrels on the Base probably minimize competitive interactions between these species. Differences in consumption of fir seeds between eastern and western gray squirrels may partially explain their differences in habitat use and could be exploited by managers to conserve western gray squirrels. The diversity of food resources and spatiotemporal variability in their availability should be considered in conservation planning for gray squirrels. Oak management has been the focus of western gray squirrel habitat management on the Base and is critically important, but habitat provision also needs to account for the resources provided by conifers, including conifer-associated truffles like *Rhizopogon*. Forest management activities can affect truffle abundance and composition in forests used by western gray squirrels, but their effects are poorly understood. Improved understanding of factors that affect the abundance and distribution of food resources important to arboreal squirrels will aid in their conservation.

ACKNOWLEDGMENTS

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Associate Editor: Amy Kuenzi.