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Small Mammals in Oak Woodlands in the Puget Trough, Washington

Abstract

We surveyed the 22 largest sites dominated by Oregon white oaks on the Fort Lewis Military Reservation, Washington, to determine small-mammal community structure and population abundances. Study areas were in the Puget Trough physiographic province and western hemlock vegetation zone. Most oak communities were ecotonal between prairie and Douglas-fir forest. Small mammals were sampled at each site using paired lines of live traps for four nights, July and August 1999. In order of decreasing abundance, the deer mouse, vagrant shrew, Trowbridge's shrew, and creeping vole were the most abundant and widespread species. The dusky shrew and the southern red-backed vole were infrequently captured in oak ecotones but were abundant in nearby second-growth Douglas-fir forest. The relative influences of prairie versus Douglas-fir forest on oak ecotones determined understory plant composition and occurrences of small mammal species. The combination of abundant vagrant shrews and few dusky shrews in oak ecotones suggest that soil food webs and organic matter accumulation differed between oak ecotones and Douglas-fir forest.

Introduction

One of the greatest concentrations of Oregon white oak (*Quercus garryana*) within western Washington is found on the 34,400-ha Fort Lewis Military Reservation near Tacoma. There, oaks are usually ecotonal between prairie and Douglas-fir (*Pseudotsuga menziesii*) forest or between prairies and wetlands (Stein 1990; Ryan and Carey 1995*a*,*b*; Thysell and Carey 2001). The ability of Oregon white oak to colonize both dry and seasonally wet sites results in a variety of oak communities. Where oaks border wet sites, they occur with Oregon ash (*Fraxinus latifolia*), bigleaf maple (*Acer macrophyllum*), and Douglas-fir. Where oaks are ecotonal with coniferous forest, quick-growing Douglas-fir develop under oaks and eventually exclude them (Stein 1990). Oak stands that extend into prairie develop a savanna-like structure and have few competing tree species.

Historical evidence suggests indigenous people maintained Puget Trough prairies and oak woodlands by burning (Norton 1979, Kruckeberg 1991, Agee 1996). Burning ceased with settlement of the Puget Trough by immigrants from the eastern United States. Since then, urbanization, agriculture, and natural succession have destroyed many oak woodlands, Douglas-fir forests have replaced oaks in ecotones, and the extent of oaks has been much reduced (Leighton 1918, Franklin and Dyrness 1988, Kruckeberg 1991, Agee 1996). Today, even where conifer encroachment has not significantly reduced the extent of oak ecotones, weedy exotics, especially Scot's broom (*Cytisus scoparius*) and sod-forming perennial grasses (e.g., *Agrostis capillaris*), are a widespread problem (Toney et al. 1998, Ussery and Krannitz 1998).

Ongoing urbanization, fire exclusion, and invasion by exotic species threaten the remaining oak and prairie biotic communities in western Washington (Ryan and Carey 1995b, Thomas and Carey 1996). The expectation of additional loss of the oak-prairie-wetland mosaic (Thysell and Carey 2001) suggests at least two mammals are at risk: the western gray squirrel (Sciurus *griseus*) listed by the State of Washington as Threatened and a Federal Species of Concern (Ryan and Carey 1995*a*, Bayrakri et al. 2001) and the western pocket gopher (*Thomomys mazama*), a Federal Species of Concern (Ryan and Carey 1995*b*, Steinberg 1999). Concern about loss of biodiversity in the Puget Trough has prompted scientists and land managers to seek more information on all flora and fauna found in oak ecotones (Ryan and Carey 1995*b*). To date, there is little information on the distribution and abundance of cryptozoic small mammals (mice, voles, shrews) in oak-dominated communities in the Pacific Northwest.

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The roles small mammals play in oak ecosystems include dissemination of spores of ectomycorrhizal fungi to the roots of oaks; consumption of invertebrates, seeds, and vegetation; girdling and consumption of the cambium layer of young oaks and encroaching conifers (Kruckeberg 1991); chewing on twigs and branches containing galls (Stein 1990); removal, consumption, and burying acorns (Ashby 1967, Wolff 1996) and other seeds (McPherson 1997); and aerating and enriching the soil seed-bed by burrowing and defecating in the leaf litter below oaks (Stein 1990:654). Within the broader landscape, small mammals resident in oak ecotones also serve as prey for raptors, reptiles, and carnivores.

Here we report the results of a survey of small mammal communities in oak ecotones on Fort Lewis. Our objectives were: (1) determine mammal species abundances and community structure in oak-dominated biotic communities; (2) relate mammal abundances to the relative abundances of oak and Douglas-fir in the overstory, and to the cover of understory shrubs, grasses, and Scot's broom in the understory; (3) compare mammal abundances among oak ecotones with different landscape contexts (i.e., prairie, wetland, coniferous forest); and (4) compare mammal communities in oak ecotones to those in second-growth Douglas-fir forests.

Methods

Study Area

Fort Lewis lies south of Tacoma, Washington in the Puget Trough physiographic province and the western hemlock vegetation zone (Franklin and Dyrness 1988). Topographic relief is gentle and elevation is generally below 160 m (Pringle 1990). Proximity of the Pacific Ocean and Puget Sound creates a maritime climate with mild average annual temperatures (12°C). Seasons are distinct with most precipitation falling as rain between October and May and summers are mild and relatively dry (Pringle 1990). Soils are derived from glacial till and glacial outwash (Pringle 1990). Second-growth Douglas-fir forest is the most widespread community type and provides the context in which more restricted communities, such as prairie, riparian, wetland, and oak types exist (Franklin and Dyrness 1988).

Study Design and Habitat Analysis

We selected 22 sites from 573 sites occupied by Oregon white oaks on Fort Lewis (see Ryan and Carey 1995*b* or Bayrakçi et al. 2001 for maps). Selected sites were either the largest areas occupied more or less continuously by oaks (8-44 ha) or were ≥4.8 ha with a sufficient density of oaks to have been inhabited by the oak-dependent western gray squirrel in the recent past (Ryan and Carey 1995*b*). Because most oak-dominated sites were ecotonal, we determined the landscape context of each site with Fort Lewis Geographic Information System maps and databases and confirmed these by site visits. During the visits we assigned each site to one of four types: (1) oak-savanna, dominated by oak canopies with grassy understories; (2) oak-shrub, dominated by oak canopies with understories of various shrubs, commonly snowberry (*Symphoricarpos albus*); (3) oak-conifer, significant representation of oak and Douglas-fir in the canopy with understories of forest shrubs (e.g., salal, *Gaultheria shallon*); and (4) mixed deciduous, oak canopy with additional deciduous species, typically Oregon ash or bigleaf maple.

At each site we placed two transects 40 m apart, parallel to the long axis of the oak-dominated biotic community; we adjusted transect orientation to fit within the area generally occupied by oaks. Each transect had 15 stations spaced at 20-m intervals and were used both as small mammal trap-lines and as plot centers for habitat assessment. On 10-m-radius plots centered at every third station, we estimated the percent covers of oak and Douglas-fir in the overstory and grass, shrubs, and Scot's broom cover in the understory to the nearest 1%. We sampled 10 plots per site, for a total of 220 plots.

Mammal Sampling

We placed two Sherman live traps, one large (7.6 cm x 8.9 cm x 22.9 cm) and one small (5.1 cm x 6.4 cm x 16.5 cm), at each station along the transects, for a total of 60 traps/site (use of trade and firm names is for information only and does not imply endorsement by the U.S. Department of Agriculture). The use of two traps at a station decreases trap interference among species and increases trap availability in the event of trap disturbance (Calhoun and Casby 1958). We used peanut butter, whole oats, and molasses as bait to improve trap efficiency (Stickel 1948*a*) and added carrots for moisture to increase animal survival. Bait was not expected to alter unduly the normal patterns of movement by the small mammals (Stickel 1948*a*). Polyester batting was placed in each trap for bedding material. Sites were continuously trapped for four consecutive days during July and August 1999 (240 trap nights/site); traps were checked for animals each morning. Short duration trapping sessions reduced the likelihood of immigration from populations outside the study area (Myllymaki et al. 1971). Our procedure was based on the design of the North American Small Mammal Census, but with a 25% increase in sampling effort (Calhoun and Casby 1958). We recorded species, sex, age, weight, and reproductive status for each animal and noted all sprung traps. Prior to release, rodents were marked with a uniquely numbered Monel eartag (National Band and Tag Company); virtually all insectivores died during live trapping and were returned to our laboratory for post-mortem examination.

Statistical Analyses

We report total captures (includes recaptures) and the total number of individuals captured for each small mammal species. We used numbers of individuals captured per unit effort (ICPUE) as estimates of species abundances; effort was corrected for closed traps (Nelson and Clarke 1973) and standardized as 100 trap nights. We explored relationships between habitat elements and abundances of mammal species with Spearman's rank correlations. Kruskal-Wallis H tests were used to compare mammal abundance among four oak community types and among three landscape contexts (prairie, forest, or prairie + forest; for all comparisons, N=22). Kruskal-Wallis H tests were used to compare vegetative covers among oak community types and Mann-Whitney U tests were used to determine which types differed from one another. We prepared a cover type map of each site and plotted mammal captures at stations as an aid to interpreting results. Direct comparison of small mammal abundances between oak and Douglas-fir communities was not possible because (1) the communities were sampled in different years and there is substantial annual variation in population densities of small mammals, (2) probabilities of capture may vary between different environments and within and among years, and (3) our sampling differed in intensity and total effort (Hansson 1975). But Carey and Johnson (1995) demonstrated how small mammal community structure, defined as octave-scale relative abundances based on ICPUE, was a measure of biotic integrity that is robust in space and time in conifer forests across the Pacific Northwest; their results were supported by subsequent studies in conifer forests (e.g., Wilson and Carey 2000, Carey and Harrington 2001, Carey and Wilson 2001). Thus, we compared the structure of small-mammal communities found in oak communities to those found in thinned and unthinned 60-70-year - old second-growth Douglas-fir forests on Fort Lewis by Wilson and Carey (2000). We calculated the relative abundance of each species as its ICPUE as a percentage of the total ICPUE for the community. We then ranked relative abundances (1-6) on a log scale (2, 4, 8, 16, 32, 64; Preston 1981, Carey and Johnson 1995) to indicate the relative importance of each species within the oak and Douglas-fir forest communities. However, we have only one year of data from oak communities and we have not demonstrated that oak-mammal communities are as stable in structure as conifer-mammal communities.

Results

We caught 445 individual mammals of 12 species (Table 1). The deer mouse (*Peromyscus maniculatus*) and vagrant shrew (*Sorex vagrans*) were the most abundant and widespread mammals in oak communities; each was caught on 96% of the sites. Trowbridge's shrew (*Sorex trowbridgii*) and the creeping vole (*Microtus oregoni*) were captured on 77% and 68% of sites, respectively. Other species were relatively low in abundance and frequency of occurrence.

Oaks composed a greater portion of canopy cover in ecotones than did Douglas-fir (Table 2). The upper limit of oak and Douglas-fir cover was similar (ca. 35%), although one site lacked Douglas-fir. Almost one-half (45%) the sites were in the oak-conifer community type. Douglas-fir cover was negatively correlated with cover of oak (r = -0.51, P = 0.02). Among oak community types there were significant differences in Douglas-fir, grass, shrub, and Scot's broom cover (Table 2). Douglas-fir cover was negatively correlated with grass (r = -0.49, P = 0.02) and grass cover was negatively correlated with shrubs (r = -0.79, P < 0.01).

TABLE 1. Small mammal species, total captures, number of individuals captured, individuals caught per 100 trap nights (ICPUE), and number of Oregon white oak sites in which they were captured (N = 22), in the Puget Trough, Washington, summer 1999.

Species	Total captures	Individuals	ICPUE	SITES
Deer mouse	276	153	3.12	21
Vagrant shrew	138	136	2.78	21
Trowbridge's shrew	78	78	1.59	17
Creeping vole	54	46	0.94	15
Dusky shrew	11	11	0.23	8
Pacific jumping mouse	6	5	0.10	3
Shrew mole	5	5	0.10	5
Ermine	6	5	0.10	3
Northern flying squirrel	2	2	0.04	2
Townsend's chipmunk	2	2	0.04	2
Southern red-backed vole	1	1	0.02	1
House mouse	2	1	0.02	1
Total	581	445	9.08	

TABLE 2. Means (SE) and mean ranks of percent covers for Oregon white oak (*Quercus garryana*), Douglas-fir (*Pseudotsuga menziesii*), Scots' broom (*Cytisus scoparius*), grass, and native shrubs in 22 oak-dominated biotic communities of 4 types: 3 oak-shrub, 5 mixed deciduous (Mixed), 10 oak-conifer, and 4 oak savanna (Savanna) in the Puget Trough, Washington, summer 1999, and significance of differences among types (Kruskal-Wallis P); in rows, mean ranks with matching superscripts are not statistically significantly different.

Habitat element	Oak-shrub n = 3	Mixed n = 5	Oak-conifer n = 10	Savanna n = 4	All types n = 22	P
White oak						
$\bar{x}$ (SE)	23 (2.8)	20 (3.8)	17 (1.9)	24 (3.5)	20 (1.5)	
mean rank	124^{ab}	109^{ab}	100^{a}	129^{b}		0.051
Douglas-fir						
$\bar{x}$ (SE)	7 (3.3)	13 (2.3)	15 (2.5)	5 (2.5)	12 (1.6)	
mean rank	83^{a}	123^{b}	126^{b}	76^{a}		<0.001
Grass						
$\bar{x}$ (SE)	23 (5.1)	13 (5.4)	18 (4.2)	45 (4.1)	22 (3.4)	
mean rank	111^{a}	79^{b}	102^{a}	170^{c}		<0.001
Shrub						
$\bar{x}$ (SE)	38 (6.5)	38 (3.2)	31 (4.3)	31 (3.4)	31 (2.7)	
mean rank	130^{ab}	134^{a}	110^{b}	70^{c}		<0.001
Scot's broom						
$\bar{x}$ (SE)	8 (2.0)	5 (2.3)	9 (3.9)	9 (3.9)	8 (1.0)	
mean rank	118^{ab}	80^{c}	125^{b}	109^{a}		<0.001

Abundances of small mammal species did not differ significantly among oak types (Table 3) or landscape contexts (all $P \geq 0.08$). Trowbridge's shrew was negatively correlated with grass cover (r = -0.46, P = 0.03). Deer mice were negatively correlated with cover of Scot's broom (r = -0.51, P = 0.01), which was present in all but one site. Maps of captures and cover types suggested that local cover types influenced species abundance at individual trap stations; e.g., in one oak community we trapped 24 deer mice, whereas we caught 513 deer mice in other communities. Understory vegetation at this site was lush, containing several life forms from procumbent vines to tall shrubs. The creeping vole was also numerous at this site (n =10) but was trapped primarily at stations with high cover of grass. Only one other oak community had many creeping voles. There,

TABLE 3. Small mammal abundance (individuals caught/100 trap nights; ICPUE) in Oregon white oak (*Quercus garryana*) communities, Puget Trough, Washington, summer 1999, and Kruskal-Wallis test *P* values for statistically insignificant differences among oak community types.

	Oak community type				
	Shrub	Mixed	Conifer	Savanna	
Species	*n*=3	*n*=5	*n*=10	*n*=4	*P*
Deer mouse	5.7	3.8	2.5	2.4	0.56
Vagrant shrew	1.6	3.8	2.5	3.1	0.43
Trowbridge's shrew	0.6	2.7	1.8	0.5	0.06
Creeping vole	2.9	1.1	0.7	0.2	0.08
Dusky vole	0.4	0.5	0.8	---	0.08
Pacific jumping mouse	---	trace	---	trace	---
Shrew mole	trace	trace	trace	trace	
Southern red-backed vole	---	---	trace	---	

one trap line ran along a prairie edge and the other along a shrubby wetland. Creeping voles were captured only along the grassy prairie edge.

Discussion

Douglas-fir encroachment into oak communities contributes to the net loss of increasingly rare oak communities in the Puget Trough (Ryan and Carey 1995b, Thysell and Carey 2001). Negative correlations between Douglas-fir and oak and between Douglas-fir and grass on our sites indicate successional tensions among Douglas-fir forests, oak communities, and prairies. Canopy composition and structure in oak ecotones are governed by adjacent communities (landscape context) and by internal competition. Canopies, in turn, influence understory processes as indicated by the strong negative correlation between grasses and shrubs in oak ecotones. in oak ecotones. Small mammal community structure is influenced by understory processes but more local conditions also determine numbers of individuals caught (see also Southern 1965).

Mammal Community Structure

Small mammal species richness in oak communities was similar to richness in second-growth Douglas-fir forests in the Puget Trough (Wilson and Carey 2000). Second-growth Douglas-fir communities, however, include Keen's mouse (*Peromyscus keeni*) in low numbers (<1% of total individuals in the communities, on average) and we did not find Keen's mouse in the oak communities. The distribution of abundance among species was more even in thinned Douglas-fir forest than in oak communities (Table 4; Wilson and Carey 2000). For example, only three species each

TABLE 4. Ranked relative abundance of small mammals frequently captured in Oregon white oak (*Quercus garryana*) biotic communities in 1999 and in thinned and unthinned Douglas-fir (*Pseudotsuga menziesii*) communities in 1992-1994 (from Wilson and Carey 2000) in the Puget Trough, Washington. Ranks are based on octave scale percentages of total individuals captured: 6 (>48%), 5 (24-48%), 4 (12-24%), 3 (6-12%), 2 (3-6%), and 1 (<3% of captures).

	Community types[a]		
	Oregon white oak	Thinned Douglas-fir	Unthinned Douglas-fir
Small mammal species	*n* = 22	*n* = 4	*n* = 4
Deer mouse	5	4	3
Vagrant shrew	4	1	2
Trowbridge's shrew	4	5	5
Creeping vole	3	4	2
Dusky vole	1	4	4
Southern red-backed vole	1	4	4
Shrew mole	1	3	3

[a]Differences in rank are considered ecologically significant (Carey and Harrington 2001).

accounted for > 12% and 3 species each accounted for <3% of the individual mammals captured in oak communities (Table 4), whereas in thinned Douglas-fir, four species accounted for >12% of captures and in unthinned Douglas-fir no species accounted for <3% of captures. Thus, mammal community structure differed markedly between oak and Douglas-fir communities (Table 4). The deer mouse decreased in ranked relative abundance from oak ecotones, to thinned Douglas-fir forest, to unthinned Douglas-fir forest (Table 4). The vagrant shrew, important in oak ecotones, ranked last in Douglas-fir forests (Table 4). Trowbridge's shrew, the dominant species in each Douglas-fir forest community, remained relatively important in oak ecotones but the dusky shrew (*Sorex monticolus*) and southern red-backed vole (*Clethrionomys gapperi*), important in Douglas-fir forest communities, were rarely captured in oak ecotones (Tables 1 and 4). The dusky shrew, common in western Washington conifer forests (Carey and Johnson 1995, Lee 1995, Wilson and Carey 2000, Carey and Wilson 2001, Carey and Harrington 2001), was not captured in oak savanna and was in low abundance in other oak types (Table 3). Differences in soil organic-layer accumulations have been shown to influence the local distribution and interspersion of dusky and vagrant shrews (Hawes 1977). We found that dusky shrews avoided oak habitat, especially sites with grassy understories, and that the vagrant shrew was markedly more important in oak communities than in Douglas-fir forest (Tables 3 and 4). The prominence of the vagrant shrew in oak communities is consistent with its ecological distribution in other regions (Verts and Carraway 1998). Although found in Douglas-fir forest (West 1991, Carey and Johnson 1995), the vagrant shrew is more strongly associated with meadow, deciduous, and riparian vegetation (Newman 1976, Hawes 1977, Terry 1981). The southern red-backed vole achieved high ranks in Douglas-fir communities and the Oregon creeping vole achieved high ranks in oak communities (Table 4).

Species Local Abundances

Because oak ecotones are squeezed between two difering habitats, local vegetation gradients can be particularly sharp (Thysell and Carey 2001). Local conditions appeared to influence which mammals were taken at a trap station. Creeping voles were associated locally with grassy areas adjacent to heavy shrub cover. Some sites with grassy understories, however, had few creeping voles, including two sites that had been burned. Burning may reduce vole populations in the short term (Gashwiler 1970, Fala 1975). Grasses, although edible (Carraway and Verts 1998), may not pro-vide complete nourishment or sufficient cover for creeping voles, especially during the early part of the growing season (Peles and Barrett 1996). Gashwiler (1970) and Carey and Johnson (1995) found creeping voles limited by herbaceous vegetation. Wilson and Carey (2000) found numerous creeping voles where understory herbs and shrubs were abundant in thinned Douglas-fir stands, and low abundances of creeping voles in unthinned forest with mossy forest floors. Carraway and Verts (1985) suggested that young conifer forests with ground cover consisting of short grasses may be the most attractive habitats for creeping voles.

Oak savannas had low numbers of small mammals whereas, high shrub cover in mixed deciduous, oak-shrub, and thinned Douglas-fir forest communities was associated with greater numbers of small mammals, particularly deer mice and creeping voles (Tables 2-4). Deer mice, which increase with increasing production of acorns (Wolff 1996) and conifer seed (Gashwiler 1979, Halvorson 1982) were the most abundant small mammals in oak ecotones and were markedly abundant at sites with rank understory vegetation, possibly as a response to fruit and seed abundance (Tables 2 and 3; Van Home 1982). Mice may even have been underestimated at these sites because home range size can be smaller in habitats with more food, making individuals less prone to capture (Stickel 1948b). Dense vegetative cover that pro-vides protection from harsh weather and predation also may have contributed to the high density of mice. In this regard, of special note is the negative correlation we observed between Scot's broom and the deer mouse, which may signal a general decline in habitat quality for seed- and fruit-depen-dent species in oak and prairie areas invaded by Scot's broom. The effects of Scot's broom on native prairie plants has been severe (Ussery and Krannitz 1998) but its effect on prairie and oak-associated wildlife is little known.

Implications and Limitations

Without management intervention, Douglas-fir forests are poised to overwhelm a significant portion of the oak areas remaining in western Washington. Continuing encroachment of Scot's broom and non-native grasses are serious factors affecting native prairie plants (Thomas and Carey 1996, Thysell and Carey 2001) with possible implications for the small mammals. Slowing Douglas-fir regeneration, cutting Scot's broom (Ussery and Krannitz 1998), and burning prairie (Agee 1996, Leach and Givnish 1999, Tveten and Fonda 1999) in the appropriate season, may be acceptable methods for prairie and oak-site maintenance and restoration (Ryan and Carey 1995*a*, Thysell and Carey 2001). Burning could have a short-term negative effect on creeping voles (Fala 1975) and could promote Scot's broom and exotic sod-forming grasses over native grasses like Idaho fescue (*Festuca idahoensis*) if improperly or inconsistently applied (Agee 1996, Tveten and Fonda 1999). Although the small mammals that inhabit oak ecotones are common species, the dominant position of the vagrant shrew Indicated that ground level processes in oak ecotones were distinct from those in adjacent Douglas-fir forest. Loss of oaks could also mean the loss of soil food webs and invertebrate communities that support vagrant shrews (Hawes 1977). The negative relation-ship between Scot's broom and the deer mouse may indicate that broom areas have diminished value as wildlife habitat. The impact of Scot's broom on oak-ecotone fauna requires additional study.

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