

Small Mammal Communities and Habitat Selection in Northern Rocky Mountain Bunchgrass: Implications for Exotic Plant Invasions

Abstract

Agriculture and development have dramatically reduced the range of native bunchgrass habitats in the Northern Rocky Mountains, and the invasion of exotic plants threatens to greatly alter the remaining pristine prairie. Small mammals play many important roles in ecosystem functions, but little is known about small mammal community composition and structure in native bunchgrass habitats of the Northern Rocky Mountains. We live trapped small mammals along transects to study community composition, relative abundance, and habitat relationships in three native bunchgrass sites of west-central Montana. Small mammal community composition and relative abundance were consistent among sites, with deer mice (*Peromyscus maniculatus*) dominating, followed by montane voles (*Microtus montanus*), which were uncommon, and montane shrews (*Sorex monticolus*), which were rare. Deer mice and montane voles exhibited complementary habitat separation. Deer mice tended to select open microsites and avoid sites with high percentages of vegetative cover. Male and female deer mice demonstrated strong habitat separation at two sites, but the habitat variables partitioned between sexes differed by site. Montane voles avoided open sites and selected for concave microsites where the vegetative cover was relatively dense. This information provides an important baseline for understanding pre-settlement small mammal communities in the rapidly dwindling, native bunchgrass habitats of the Northern Rocky Mountains.

Introduction

Palouse prairie and sagebrush-steppe habitats of the Northwest have been dramatically altered by grazing, agriculture, and development (Tisdale 1961, Mueggler and Stewart 1980, West 1996, see Flather et al. 1999 for review), and most ecologically intact remnants persist as islands critically threatened by the invasion of exotic plants (Daubenmire 1942, Tyser and Key 1988, Lacey 1989, DeLoach 1991, Tyser 1992, Tyser and Worley 1992, Sheley et al. 1998). Valley bunchgrass habitats, occurring at or below lower timberline in the Northern Rocky Mountains, superficially resemble the Palouse prairie grasslands of the Columbia River Basin, but are unique plant communities differing in species composition and in the historical dominance of rough fescue (*Festuca scabrella*) (Lynche 1955, Stickney 1961, Mueggler and Stewart 1980). Additionally, valley bunchgrass habitats were historically much less extensive than Palouse prairie, and currently only 10 to 20% of these habitats remain in western Montana (Flather et al. 1999).

Small mammals play important roles in ecosystem functions (see Pearson 1999a) and may figure prominently in the ecology of exotic plant invasions within xeric grasslands of the West. For instance, small mammals create disturbed sites

where exotics can establish (Mielke 1977), disperse seeds of exotic plants (McMurray et al. 1997, Pearson and Ortega in press), consume native and non-native plants and their seeds (Pyke 1986), and depredate biological control agents released to control exotic plants (Pearson 1999b, Pearson et al. 2000). Reciprocally, exotic plant invasion of native grasslands can alter biomass and species composition of small mammal communities (Larrison and Johnson 1973), thereby modifying ecological roles that small mammals play in grassland systems. Although little work has been done to examine effects of exotic plants on small mammal communities (Larrison and Johnson 1973, Ellis et al. 1997, Pearson et al. 2000), current research suggests that exotic plant invasions can alter small mammal ecology in complex ways.

Interpreting the degree to which the effects of exotic plant invasions impact grassland ecosystems is contingent upon understanding conditions prior to invasion. However, a dearth of community-level studies of small mammals within valley bunchgrass habitats renders the composition and structure of these communities uncertain. For instance, although some studies suggest that *Microtus* are prominent species within many grassland habitats in western Montana (Koplin and Hoffmann 1968, Stoecker 1972, Hodgson 1972,

Douglas 1976), the relative importance of *Microtus* in native bunchgrass habitats remains unclear.

In this paper, we present data on species composition, relative abundance, and habitat use of small mammals in three pristine valley bunchgrass habitats of west-central Montana to establish baseline information on small mammal communities within these ecosystems.

Methods

Study Sites

We sampled small mammal communities at three locations in valley bunchgrass habitats of west-central Montana: Bandy Ranch, Sieben Ranch, and Wildhorse Island. All sites fall into the rough fescue/Idaho fescue (*Festuca idahoensis*) habitat types (Mueggler and Stewart 1980), but dominant grasses varied at microsites among rough fescue, Idaho fescue, and bluebunch wheatgrass (*Agropyron spicatum*) as a function of moisture and aspect. All study areas were ≥ 5 ha. The Bandy Ranch site is located about 8 km northwest of Ovando, MT at 1370 m elevation. Uplands at the Bandy Ranch are dominated by bunchgrass and big sage (*Artemisia tridentata*) habitats and interspersed by glacial potholes and their associated wetland vegetation. Trapping at this site was restricted to upland bunchgrass habitats, which included some sage and some concave microsites with mesic vegetation. Sieben Ranch is about 8 km east of Lincoln, MT at 1400 m elevation. Sieben Ranch is dominated by bunchgrasses, but also contains patches of big sage. Wildhorse Island is the largest island in Flathead Lake, Lake County, MT, covering nearly 10 km² and as such appears to function essentially as a mainland for small mammal communities. Previous trapping studies on islands in Flathead Lake suggest that many grassland small mammals have become established on the various islands (Plopper 1968) and are likely all present on the substantially larger Wildhorse Island. The trapping area on Wildhorse Island ranged from 900 to 1030 m in elevation.

Field Methods

We trapped small mammals in August 1998 using 25 Sherman live traps placed at 10-m intervals along eight transects per site. Transects were used because they generate more captures and more species than grids of equal size, thereby more

effectively sampling the small mammal community (Pearson and Ruggiero in review). Transects were spaced ≥ 100 m apart to ensure independence. The effective trapping area was therefore equal at all sites. Traps were baited with peanut butter and whole oats and checked from 0700 to 1100 hrs for four days. Small mammals were tagged with #1005-1 monel ear tags (National Band and Tag Company, Newport, Kentucky 41072-0430), and species, age, weight, sex, and reproductive condition were determined before release at the trap station. Live *Microtus montanus* and *Microtus pennsylvanicus* are not easily differentiated (Hoffmann and Pattee 1968). Therefore, since all mortalities (20% of the total capture) were identified as montane voles (*Microtus montanus*), and the habitats were generally too dry for *M. pennsylvanicus* (Koplin and Hoffmann 1968, Hodgeson 1972), we assigned all *Microtus* captures to *M. montanus*.

Small mammal habitat was assessed by visually estimating percent cover for several vegetation categories within a 5-m radius of each trap station. We estimated (1) total bunchgrasses - primarily bluebunch wheatgrass, Idaho fescue, and rough fescue, but also June grass (*Koeleria cristata*), needle and thread grass (*Stipa comata*), and other less abundant native bunch grasses; (2) total non-bunchgrasses - mostly *Poa* species; (3) shrubs - mostly big sage and rabbit brush (*Chrysothamnus* spp.); (4) native forbs - primarily arrowleaf balsamroot (*Balsamorhiza sagittata*) and lupine (*Lupinus* spp.); and (5) exotic plants - spotted knapweed, leafy spurge (*Euphorbia esula*), Eurasian toadflax species (*Linaria dalmatica* and *L. vulgaris*), and cheatgrass (*Bromus tectorum*). Additionally, physiographic and abiotic features measured included topography of the microsite (i.e., concave = 1 or not = 0; as an indicator for low, moist sites), percent cover of bare ground, and percent cover of rocks = 10 cm dia. Cover estimates were made by the same two observers at all sites.

Analytical Methods

We present frequency distributions of the number of individuals captured by species for each site. We used logistic regression to determine which habitat variables best differentiated trap stations that captured small mammals from those that did not. Traps having multiple captures were included

only once in the analysis for each species. By employing the generalized estimating equations capability in SAS GENMOD, we developed unstructured correlation models that relax the standard assumption of independence among observations within transects (SAS Institute 1990). Counting trap stations only once and controlling for spatial correlations in the data reduce the pseudoreplication that can occur in data sets due to repeated captures of a subset of individuals within a population since individuals are most often recaptured in the same or adjacent traps. Equations produced by logistic regression serve as resource selection functions and the coefficients serve as selection coefficients ($\hat{\beta}$) whose values indicate the relative importance of the predictor variables in the equation (Manly et al. 1993). Positive coefficients indicate selection for the resource and negative coefficients indicate avoidance when coefficients differ significantly from zero (Manly et al. 1993). We chose likelihood ratio tests over Wald tests to determine the significance of selection coefficients because of their greater reliability (Hauck and Donner 1977).

We used a model selection procedure (Manly et al. 1993, Arthur et al. 1996, Ruggiero et al. 1998) to determine whether habitat selection for each species differed among sites, thereby indicating whether site data should be pooled or analyzed separately. This process involves generating a null or no-selection model wherein the constant is estimated and all other coefficients are set to zero. The deviance value ($-2\log_e[\text{likelihood}]$) from the null model is then compared to the deviance value from a pooled selection model wherein coefficients are estimated using pooled data from all sites. A significant improvement in the pooled selection model over the null model indicates that habitat selection has occurred, and model selection proceeds by estimating a selection function for each site independently. If the summed deviance values from the site-specific selection models is significantly smaller than the deviance from the pooled selection model, this indicates that habitat selection differs among sites, and site-specific selection functions should be used to examine habitat selection. Because habitat segregation between sexes has been reported for deer mice inhabiting xeric grasslands and savannas (Bowers and Smith 1979, Morris 1984), we extended the model selection procedure using multinomial logistic regression with SAS CATMOD to test

whether categorizing capture sites by sex (i.e., only males captured, only females captured, males and females captured) resulted in better habitat use models than those disregarding sex. This analysis effectively examines the degree to which habitat use by males and females directly overlaps (100% overlap results in no habitat separation), testing for differences in habitat variables among the three potentially distinct groups of capture sites. Because CATMOD does not generate likelihood ratio tests for coefficients, we present Wald tests for this analysis. Correlation was not built into the multinomial models for habitat selection by sex because CATMOD does not offer this option for multinomial regression models.

Results

Bunchgrass dominated the herbaceous cover at all study sites ranging from approximately 40% cover on Wildhorse Island to 65% on Bandy Ranch (Figure 1). Sieben Ranch had the lowest cover of native forbs, nonbunchgrasses, and shrubs and the highest cover estimates for bare ground. Wildhorse Island had the highest densities of nonbunchgrasses and native forbs. Exotic plants were generally rare to absent on all sites. Spotted knapweed, toadflax, and leafy spurge cover estimates averaged <1% for all sites. Cheatgrass was the most abundant and widespread exotic with average estimates <1% on Sieben Ranch, 1% on Bandy Ranch, and 4% on Wildhorse Island. The proportion of concave microsites was approximately 40% on both Bandy Ranch and Wildhorse Island and 20% on Sieben Ranch, which also exhibited less large-scale topographic relief.

Two thousand four hundred trap nights produced 410 captures of 273 individual small mammals representing three species. Species rank-abundance was consistent among locations with deer mice dominant, followed by montane voles, which were relatively uncommon, and montane shrews, which were rare (Figure 2). It should also be noted that northern pocket gophers (*Thomomys talpoides*), as indicated by the presence of winter cores and fresh mounds, and yellow-pine chipmunks (*Tamias amoenus*), as indicated by visual observations of the animals in shrub patches, were present on the sites. However, we did not directly sample and therefore quantify the abundance of either of these species.

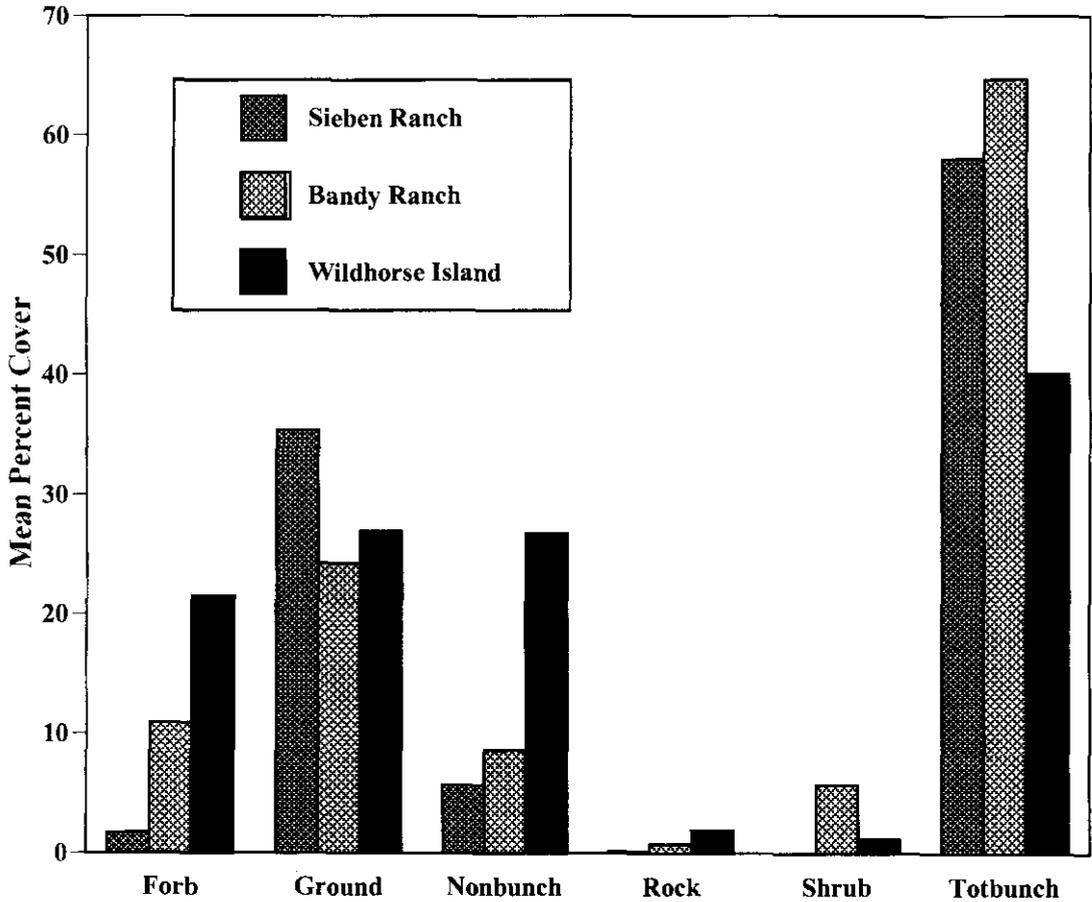


Figure 1. Mean percent cover estimates for vegetation, rocks, and bare ground within a 5-m radius of each trap station.

The pooled selection model for deer mice provided a significant improvement over the no-selection model ($\chi^2 = 100.03$, $df = 7$, $P < 0.001$), indicating deer mice exhibited habitat selection (Table 1). Furthermore, aggregation of the site-specific selection models resulted in a model that was significantly improved over the pooled selection model ($\chi^2 = 92.89$, $df = 15$, $P < 0.001$), indicating that deer mouse habitat selection differed among sites. Site-specific selection models were significant for each site ($P < 0.05$). At Sieben Ranch deer mice avoided areas with higher forb ($\chi^2 = 8.23$, $df = 1$, $P = 0.004$) and bunchgrass cover ($\chi^2 = 13.54$, $df = 1$, $P < 0.001$) and exhibited marginally significant selection for rocky areas ($\chi^2 = 3.57$, $df = 1$, $P = 0.059$). A selection coefficient for shrubs at Sieben Ranch could not be

estimated because values were zero for one category. At the Bandy Ranch deer mice avoided areas with higher cover of bunchgrass ($\chi^2 = 5.57$, $df = 1$, $P = 0.018$) and nonbunchgrass ($\chi^2 = 13.99$, $df = 1$, $P < 0.001$) and selected areas with more bare ground ($\chi^2 = 8.35$, $df = 1$, $P = 0.004$). On Wildhorse Island deer mice responded to all variables measured except topography. Mice on Wildhorse avoided most vegetative cover such as native forbs ($\chi^2 = 9.30$, $df = 1$, $P = 0.002$), nonbunchgrass ($\chi^2 = 5.62$, $df = 1$, $P = 0.018$), and shrubs ($\chi^2 = 4.75$, $df = 1$, $P = 0.029$) in favor of areas with higher percent cover of bare ground ($\chi^2 = 26.21$, $df = 1$, $P < 0.001$) and rock ($\chi^2 = 14.90$, $df = 1$, $P < 0.001$). However, deer mice on Wildhorse selected for bunchgrass cover ($\chi^2 = 6.92$, $df = 1$, $P = 0.009$), whereas they avoided it at other sites.

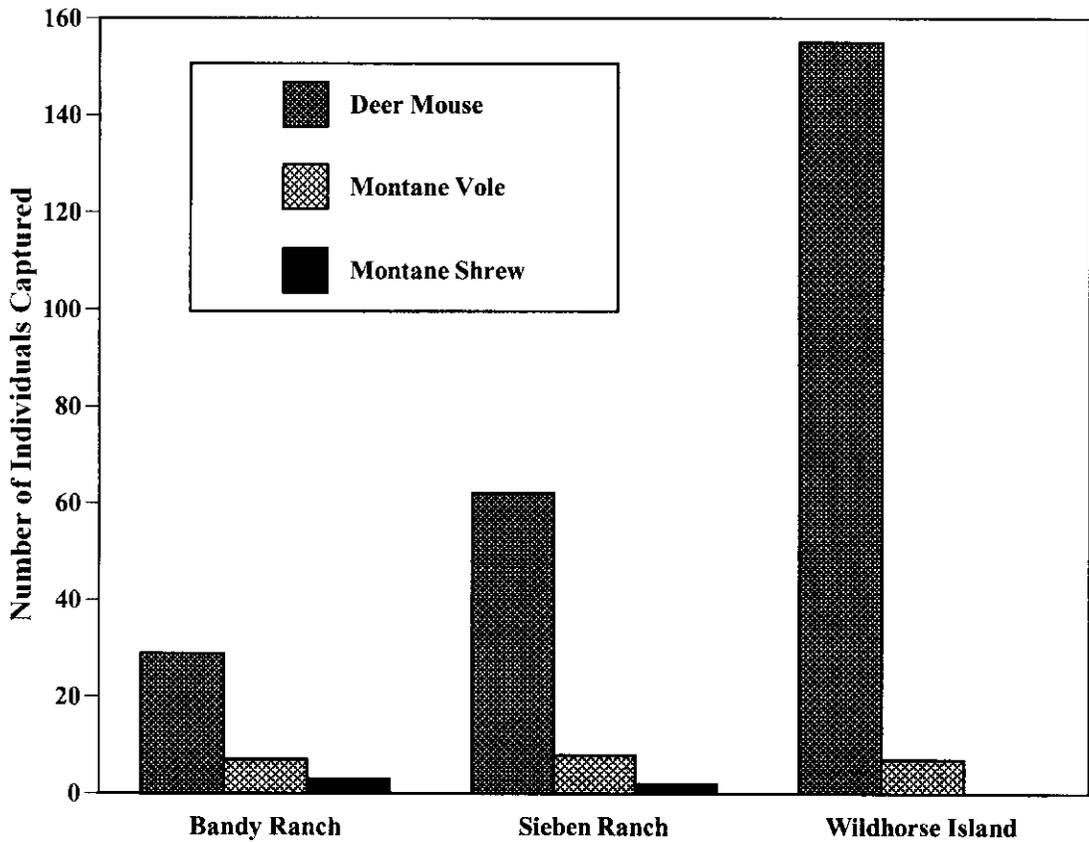


Figure 2. Species composition and relative abundance of small mammals captured in three locations within valley bunchgrass habitats of west-central Montana.

TABLE 1. Selection coefficients for deer mice in pristine valley bunchgrass habitats of west-central Montana based on logistic regression analysis. Parentheses indicate the number of stations capturing mice. A selection coefficient was not calculated for shrubs at Sieben Ranch due to singularity of the variable.

Selection coefficients										
Model	Forb	Ground	Nonbunch	Rock	Shrub	Bunch	Topo	Deviance	df	P
Null	0.00	0.00	0.00	0.00	0.00	0.00	0.00	762.42	599	
Pooled (199)*	0.014*	0.028**	0.003	0.056**	-0.015*	-0.004	0.054	662.40	592	
Sieben (48)*	-0.434**	-0.003	-0.010	0.145		-0.045**	-0.112	203.58	193	
Bandy (25)*	0.016	0.041**	-0.013**	0.019	0.015	-0.025*	0.259	131.08	192	
Wildhorse (126)**	-0.019**	0.036**	-0.013*	0.117**	-0.146*	0.010**	0.174	234.85	192	
Site deviance totals								569.51	577	
Null vs. pooled (selection)								100.03	7	<0.001
Pooled (selection) Vs site (selection)								92.89	15	<0.001

* indicates significant difference at $\alpha = 0.05$

** indicates significant difference at $\alpha = 0.01$

Sex-based habitat selection models for deer mice were significant for Sieben Ranch ($\chi^2 = 17.33$, $df = 6$, $P = 0.008$) and Wildhorse Island ($\chi^2 = 24.09$, $df = 7$, $P < 0.001$) and marginally signifi-

cant for Bandy Ranch ($\chi^2 = 13.12$, $df = 7$, $P = 0.069$). Females at Sieben Ranch used sites with more bare ground ($\chi^2 = 4.85$, $df = 1$, $P = 0.027$) and more total bunchgrass cover ($\chi^2 = 7.75$, $df =$

1, $P = 0.005$) than males. At Wildhorse Island, females used sites that were less concave ($\chi^2 = 6.17$, $df = 1$, $P = 0.013$) and had less shrub cover than males ($\chi^2 = 8.53$, $df = 1$, $P = 0.004$), and females selected microsites with lower shrub cover ($\chi^2 = 4.15$, $df = 1$, $P = 0.042$) than stations where both males and females were captured. At Bandy Ranch, habitat partitioning between sexes was not significant for any individual comparisons ($P > 0.140$). Chi-square goodness of fit tests assuming equal sex ratios indicated that sex ratios for Wildhorse Island were male biased (1.40 males to females; $\chi^2 = 6.61$, $df = 1$, $P = 0.010$), but the sex ratio for Bandy Ranch was not biased (1.59 males to females; $\chi^2 = 2.27$, $df = 1$, $P = 0.132$), nor was the sex ratio for Sieben Ranch (0.88 males to females; $\chi^2 = 0.38$, $df = 1$, $P = 0.540$).

The pooled selection model for montane voles provided a significant improvement over the no-selection model ($\chi^2 = 18.00$, $df = 7$, $P = 0.012$). However, the site-specific model provided little improvement over the pooled model ($\chi^2 = 22.94$, $df = 16$, $P = 0.115$), indicating either that habitat selection by montane voles did not differ among sites, or that we lacked sufficient power to detect such differences due to low captures of this species. Overall, montane voles selected concave microsites ($\chi^2 = 6.30$, $df = 1$, $P = 0.012$) and avoided areas with high percentages of bare ground ($\chi^2 = 7.18$, $df = 1$, $P = 0.007$), but did not exhibit selection with regard to other variables measured.

Discussion

Community Composition

The small mammal community we identified for valley bunchgrass habitats in west-central Montana was remarkably consistent with regard to species composition and relative abundance among the three distinct locations trapped. Deer mice dominated each native bunchgrass site. Montane voles were consistently captured, but relatively uncommon. Montane shrews were rare at two locations, and none were captured on Wildhorse Island. Valley bunchgrass habitats of west-central Montana appear to contain fewer species than small mammal communities described for neighboring grasslands and shrub-steppe of eastern Washington, eastern Oregon, southern Idaho, and the western Great Plains of eastern Montana (Larrison and Johnson 1973, Rogers and Hedlund 1980, Gano and Rickard 1982, Grant et al. 1982,

MacCracken et al. 1985, Groves and Steenhof 1988, Koehler and Anderson 1991, Elliot et al. 1997). Although some species that could occur in these habitats as uncommon or rare community members such as meadow voles (*M. pennsylvanicus*), jumping mice (*Zapus princeps*), vagrant shrews (*S. vagrans*), and cinereus shrews (*S. cinereus*) may have gone uncaptured, most species described for adjacent grasslands such as the prairie vole (*M. ochrogaster*), sagebrush vole (*Lemiscus curtatus*), grasshopper mouse (*Onocomys leucogaster*), plains pocket mouse (*Perognathus parvus*), olive-backed pocket mouse (*P. fasciatus*), western harvest mouse (*Reithrodontomys megalotis*), and kangaroo rat (*Dipodomys ordii*), do not occur within western Montana or are extremely rare (only a few records) (Hoffmann and Pattie 1968). One possible explanation for the lower species richness of valley bunchgrass habitats is that the presence of valley glaciers and historic Lake Missoula (Alt and Hyndman 1986) extirpated more specialized grassland species from the region. Forested mountain ranges surrounding these grasslands may further serve to prevent recolonization.

Conclusions regarding species composition and relative abundance based on a single year's data require some consideration of annual variability given the multiannual fluctuations exhibited by many small mammal species (Krebs 1996). Examination of the literature strongly suggests that deer mouse domination of xeric grasslands is the norm within much of the Northwest (Grant et al. 1982, MacCracken et al. 1985, Pyke 1986, Groves and Steenhof 1988, Elliot et al. 1997). However, deer mice can periodically decline to become less abundant than montane voles, especially if vole populations increase concurrently with the decline. Montane voles became essentially codominant with deer mice in the second year of Pyke's (1986) study in Washington, and montane voles clearly outnumbered other small mammals at Grant et al.'s (1982) ungrazed site in the Bridger Mountains of Montana. Although shrews fluctuate and can be common in moist habitats (Spencer and Pettus 1966), shrews are not reported as common within dry habitats of the Northwest (Negus and Findley 1959, Rickard 1960, Clark 1973, Pearson 1999a). Our results considered in the context of small mammal studies within other grasslands of the Northwest suggest that deer mice generally dominate valley bunchgrass habitats, with voles

being uncommon and shrews rare. However, montane voles may periodically dominate these communities during population highs. Montane voles may also play a more prominent role in higher elevation, more mesic bunchgrass habitats (e.g., Grant et al. 1982).

Habitat Selection

Deer mice are habitat generalists at the macro-habitat scale, as indicated by their viability within a wide range of habitats (Handley 1999). However, their ability to efficiently exploit a wide range of resources can render them quite specialized in their selection of microsites within habitats that differ in resource availability (e.g., Pearson 1994). In native valley bunchgrass habitats of west-central Montana, we found that deer mouse selection of microhabitats varied by site. This differential selection for resources such as bunchgrass (selected for at Wildhorse Island, but avoided at Bandy and Sieben Ranches) probably reflects 1) the fact that the distribution of these resources varies by site and 2) the fact that deer mice are responding to a complex of resources, many of which were not measured. For example, as bunchgrass distributions change so may the abundance and therefore relative value of associated resources such as seeds and insects that deer mice are foraging on. However, at all sites, deer mice tended to avoid heavy vegetative cover in favor of more open and in some cases, rockier habitats. Elliott et al. (1997) similarly reported that deer mice selected microhabitats with more bare ground and less grass cover in southeastern Wyoming grasslands. That deer mice increase in response to grazing (Larrison and Johnson 1973, Grant et al. 1982, Rosenstock 1996) may also be evidence of selection for more open vegetation, as grazing decreases the total vegetative biomass on a site (Grant et al. 1982).

Deer mouse selection for bare ground in bunchgrass habitats, which are inherently low in vegetative cover, may result from predator influences on deer mice or deer mice responding to their own prey-base. For example, use of open habitat could indicate that predation risk from weasels, which favor heavy ground cover, exceeds that from raptors, which prefer to hunt where ground cover is minimal (e.g., Korpimäki et al. 1996). Alternatively, deer mice, which are primarily insectivorous in western grasslands (Sieg et al. 1986, Pearson

et al. 2000), may be more effective at preying on particular insects in open habitats, or their preferred prey may attain higher densities within such habitats. Deer mice also tended to select rockier areas, though this relationship was only marginally significant at Sieben Ranch where rocks were relatively rare. Rocks may provide escape cover that the predominantly herbaceous vegetation does not. However, most rocks were relatively scattered, partially buried, and small (approximately 1 to 3 dm). Possibly, rocks provide cover for secure burrow sites as deer mouse burrow entrances were sometimes observed in association with rocks.

We observed habitat partitioning between male and female deer mice at Sieben Ranch and Wildhorse Island. Variables separating male and female deer mice differed by site, with females at Sieben Ranch using microsites having more bare ground and more bunchgrass cover than males, and females at Wildhorse Island using microsites with less shrub cover than males. Females at Wildhorse Island also used concave sites less often than males. Since deer mice, as a species, avoided bunchgrass at Sieben Ranch and shrubs at Wildhorse Island, the sexual separation on these variable axes would appear to result from a further partitioning of these resources between the sexes. At Wildhorse Island, the species-level response to topography may have been masked by habitat partitioning between the sexes, as males exhibited no avoidance of concave sites, whereas topography values at female trap stations and stations where both males and females were captured indicated relatively strong avoidance. At Sieben Ranch, a similar phenomenon was observed: males exhibited no selection for bare ground while females differed significantly from the males in their selection for bare ground. In general, females appeared to be more selective of microhabitats than were males. At Wildhorse Island the skewed sex ratio could have facilitated this differential habitat selection between sexes by allowing the proportionally fewer females to be more selective of microhabitat space. However, one might expect that the more abundant males would overwhelm such an effect by encompassing all female microsites as well as additional habitats. Moreover, sex ratios did not differ from random elsewhere, and so could not be invoked to explain differential habitat selection at Sieben Ranch.

Determining which sex triumphs when a resource is partitioned within a species is contingent upon correctly assessing the resource gradient. Bowers and Smith (1979) produced a defensible argument for female deer mice out-competing males by showing that females dominated microsites having higher measured soil moisture in habitats where water was clearly limited. Seagle (1985) and Belk et al. (1988) contend that structural features such as logs and woody vegetation are the preferred resources in some habitats and have shown that females are more closely associated with these resources than are males. They therefore argue that females effectively dominate the preferred resources in these systems. This argument is reasonable, but untested. Woody structure provides one important vector along a complex of resource gradients, but unless it is the limiting resource, and the added benefits of cover do not compromise other resource needs (i.e., the collective resource gradient is linear and correlated with structure), it is unclear whether the tradeoffs in other resource vectors associated with increasing cover will lead to increased fitness. Similarly, without a defensible measure of resource quality, we do not attempt to assess which sex dominated the preferred resources within the bunchgrass community that we studied. However, based on our results, we conclude that 1) resources were sufficiently limited to warrant intraspecific partitioning within the bunchgrass community (e.g., Bowers and Smith 1979), 2) resources were sufficiently variable to allow for their partitioning among conspecifics (see Seagle 1985), and 3) intraspecific resource selection pressures differed among sites.

Few studies have examined microhabitat selection of montane voles in the Northern Rocky Mountains. In our valley bunchgrass habitats, montane voles strongly avoided trap stations in open areas with more bare ground and selected concave microsites where total herbaceous cover was high. The higher herbaceous cover at concave microsites appeared to result from higher soil moisture. Hodgson (1972) found that montane voles were negatively correlated with shrubs, with the exception of big sage, and positively correlated with soil moisture and higher graminoid cover in southwestern Montana. Similarly, Belk et al. (1988) observed that montane voles selected habitats with higher herbaceous cover and lower shrub cover within a mixture of habitats in Utah;

and Randall and Johnson (1979) showed that montane voles favored bunchgrass habitat over shrubby habitats in Washington, but overflowed into shrubby habitats when populations increased. Collectively, these studies indicate that montane voles avoid open habitats in favor of microsites with higher vegetative cover and higher soil moisture. Montane voles may also avoid shrubs, with the possible exception of big sage, but since we attempted to exclude sage from our sampling and other shrubs were rare on the study sites, we could not effectively assess these relationships.

Deer mice and montane voles appear to occupy complementary niches in valley bunchgrass habitats of west-central Montana. Whereas deer mice generally selected for dryer, more open habitats with relatively little vegetative cover, montane voles avoided open areas in favor of moister concave microsites with higher herbaceous cover. Such complementary habitat selection could be construed as habitat partitioning resulting from interspecific competition, as has been argued for deer mice and other *Microtus* species in grasslands of British Columbia (Redfield et al. 1977) and Colorado (Abramsky et al. 1979). However, resource competition for food seems unlikely as deer mice are primarily insectivorous and granivorous in this region (Sieg et al. 1986, Pearson et al. 2000), and montane voles are herbivorous (Zimmerman 1965, Lindroth and Batzli 1984). Interference competition is similarly reduced by disparate activity patterns that help separate nocturnal deer mice (Falls 1968) from the largely diurnal montane voles (Drabek 1994). Furthermore, although voles avoid open habitats where deer mice abound, deer mice are smaller than *Microtus* (by 30% on average in this study) and thus unlikely to exclude voles through interference competition. Although deer mice avoid the heavier herbaceous cover, they are neither excluded from it nor from the concave microsites where voles abound. Complementary habitat selection between deer mice and montane voles in valley bunchgrass habitats may arise from noncompetitive coexistence as has been shown for deer mice and southern red-backed voles (*Clethrionomys gapperi*) in Virginia (Wolff and Dueser 1986). Determining the causal mechanism for habitat separation between deer mice and montane voles within valley bunchgrass habitats would require reciprocal removal studies.

Conclusions

Exotic plants have transformed vast regions of western grasslands and will continue to impact the remainder of these systems with potentially complex ecological consequences. However, it is difficult to predict the potential impacts that exotic plants may have on small mammal communities because little is known about small mammal ecology in intermountain grasslands. Our results emphasize the habitat specificity of montane voles and the habitat flexibility of deer mice in the low-elevation intermountain grasslands and lead us to hypothesize that generalist species such as deer mice may be favored over habitat and dietary specialists such as voles and shrews given invasions of such exotics as spotted knapweed, leafy spurge, and Eurasian toadflax species. Because small mammals play important species-specific roles in ecosystem functions, changes in small mammal species composition will likely affect predator communities and the ecological roles that small mammals play with regard to herbivory, seed and insect predation, seed dispersal, etc. This paper presents important baseline in-

formation on small mammal community composition, relative abundance, and habitat use in the rapidly dwindling native bunchgrass habitats of the Northern Rocky Mountains. However, additional research will be necessary to understand ecological roles of small mammals in native bunchgrass habitats, and comparative studies will be imperative to deciphering the complex ways in which small mammal community composition and small mammal roles are changing in these systems as a result of exotic plant invasions.

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