CHEATGRASS INVASION OF SAGEBRUSH STEPPE: IMPACTS OF VEGETATION STRUCTURE ON SMALL MAMMALS

by

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ABSTRACT

Nonnative plants can affect habitat quality for native animals directly, through changes in resources like cover or food, and indirectly, through changes in access to resources or predation risk. Understanding these effects is crucial to develop management techniques and maintain ecosystem processes. In sagebrush steppe, brome grasses such as cheatgrass (*Bromus tectorum*) can invade and form dense stands, increasing the depth and persistence of litter, as well as the density of standing vegetation. These structural changes alter abundance and composition of the small mammal community. We used a series of experiments to explore whether changes in vegetation structure associated with the invasion of cheatgrass would alter foraging and predation risk of small mammals, to better understand mechanisms driving documented population- and community-level effects. In the first experiment, we placed a measured amount of grain at stations with either increased litter or stem density, and examined how much grain was removed nightly. We found that adding litter reduced the amount of grain removed in 2 of our 3 study areas. In the second experiment, we timed animals fleeing a simulated predator through various depths of litter or densities of stems. We found that dense stems impeded movement more than litter. In the third experiment, we recorded animals moving through native sagebrush steppe and cheatgrass monocultures, and analyzed these recordings to detect differences in the volume of noise created, especially for frequencies detected by common predators. We found that animals moving through cheatgrass made more noise at high frequencies, compared to native sagebrush steppe. Based on these experiments, cheatgrass monocultures may reduce habitat quality for small mammals by decreasing foraging efficiency and increasing vulnerability to predators. Mitigation strategies should focus on reducing the density of standing vegetation where predation is a limiting factor and litter depth where small mammals are food-limited.

CHAPTER ONE

INTRODUCTION TO THESIS

Introduction

Species invasions can affect native plants and animals greatly, regardless of whether nonnative species are the drivers of observed changes or a symptom of ecosystem degradation (Didham et al. 2005, MacDougal and Turkington 2005). Introductions of nonnative organisms and their concomitant effects will continue to increase in the connected global environment, compounded further by anthropogenic climate change (Vitousek et al. 1996, Bradley et al. 2009). Altered climate patterns may provide the opportunity for additional introductions, as well as changes in the distributions of nonnative species that are already established (Walther et al. 2007, Bradley et al. 2009, Huang et al. 2011), through shifts in interaction between species (Janion et al. 2010, Fey and Cottingham 2011). Although we have documented the effects of several nonnative plants on many animal taxa, we still understand little about the driving mechanisms (Levine et al. 2003).

Vegetation structure can influence the community of animals that use an area as habitat and affect habitat quality and whether an animal chooses to settle in an area (Price and Brown 1983), which can lead to changes in abundance. Nonnative plants can alter native ecosystems (Vitousek et al. 1996, Simberloff 2005, Young and Larson 2011), by changing food and cover available for animals (Thompson 1982, Simmonetti 1989), as well as their risk of predation (Lima and Dill 1990). Such changes can result in shifts in community composition that can propagate through food webs (Power 1992), with complex effects.

Cheatgrass (*Bromus tectorum* L.) is an annual grass that was introduced to the western United States from Eurasia during the nineteenth century and has since become a ubiquitous invader (Mack 1981). Cheatgrass has the potential to alter the vegetation structure in the sagebrush-steppe ecosystem significantly, especially in the presence of fire (Mack 1981). After cheatgrass invaded sagebrush steppe burns, aggressive recolonization by cheatgrass displaces native plant species, leading to conversion of shrubland to annual grassland (Mack 1981). Currently, monocultures of cheatgrass are prevalent in the sagebrush-steppe vegetation zone in the Great Basin Desert, making establishment of native perennial plants in invaded areas nearly impossible (Knapp 1996). Changes in climate conditions over the next century are predicted to result in increased dominance by cheatgrass throughout the northern part of its range (Bradley et al. 2009).

Increased dominance by cheatgrass can result in changes to vegetation structure and composition (Rieder et al. 2010), with concomitant effects for native small mammals. Where cheatgrass is dominant, abundance of small mammals often is reduced and the composition of the small mammal community also may shift (Larrison and Johnson 1973, Gano 1982, Ostoja and Schupp 2009, Hall 2012). Several mechanisms for these changes in abundance have been proposed, including changes in food resources, the ability to move and perform necessary life history functions or avoid predators (Gano 1982, Ostoja and Schupp 2009, Hall 2012). We are aware of only one mechanism that has been tested formally, namely that increased density of vegetation associated with cheatgrass invasion impedes movements of rodents and lizards, possibly making them more vulnerable to predation (Newbold 2005, Rieder et al. 2010).

Through a series of experiments, we examined several mechanisms that could explain changes in populations of small mammals populations documented in areas dominated by nonnative plants, and provide information that will help guide restoration and mitigation efforts. In the first chapter, we tested whether changes in the physical structure or architecture of the vegetation associated with cheatgrass affect an animal's ability to access food resources. In the second chapter, we tested whether changes in vegetation structure associated with cheatgrass increase the vulnerability of deer mice to predators by reducing their ability to flee and making their movements more detectable to predators. Developing a mechanistic understanding of how cheatgrass and other nonnative plants affect populations of small mammals can help to develop restoration and management strategies to mitigate effects.

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CHAPTER TWO

EFFECTS OF CHEATGRASS INVASION ON FOOD ACCESSIBILITY FOR SMALL MAMMALS IN SAGEBRUSH STEPPE

Contributions of Authors and Co-Authors

Manuscripts in Chapters 2

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Contributions: Conceived and implemented the study design. Collected and analyzed the data.

Co-Author: Andrea R. Litt

Contributions: Assisted in conceptualizing this research, implementation of experiments, analysis of data, and development and review of this manuscript.

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Abstract

Composition and physical structure of the vegetation within an ecosystem provide food and cover for animals, which can influence habitat quality and selection. Changes in vegetation structure resulting from nonnative plant invasions can impact food resources indirectly, by access to food. Cheatgrass (*Bromus tectorum*) is a nonnative grass that can alter the vegetation structure of sagebrush steppe by creating dense, single-species stands in disturbed areas, with concomitant effects on small mammals. Changes in vegetation structure created by cheatgrass are hypothesized to affect access to food resources for small mammals, providing a potential mechanism for observed decreases in small mammal populations. To test whether cheatgrass impedes access to food resources, we placed a measured amount of grain at stations with either increased litter or stem density, and examined how much grain was removed by small mammals nightly. We found that adding litter at depths that approximate invasion reduced the amount of grain removed in 2 of our 3 study areas. Based on this experiment, the structural changes caused by the invasion of cheatgrass may impact small mammals by decreasing foraging efficiency and access to existing food litter depth in invaded areas to benefit small mammal species that are food limited.

Introduction

Composition and physical structure of the vegetation within an ecosystem provide food and cover for animals, which can influence habitat quality and selection (Rosenzweig 1973, Cody 1981, Arnan et al. 2007, Garden et al. 2007). Invasions by nonnative plants change plant diversity and vegetation structure, with potential consequences for native animals (Vilà et al. 2011). Although the effects of nonnative plants on animals have been well-studied in many systems, we know little about the driving mechanisms (Levine et al. 2003).

Invasion by nonnative plants can alter food resources for animals directly, especially when the nonnative plant creates a dense monoculture and displaces palatable native plants and arthropods (Vitousek et al. 1996, Litt and Steidl 2010). If animal populations are food limited (Power 2002), decreases in food resources may provide one explanation for decreased abundance of animals documented with some nonnative plants (Gano 1982, Rieder et al. 2010). Alternatively, some nonnative plants may provide additional food resources, such as fruits or palatable structures (Mattos et al. 2013), or contribute to increased abundance of other foods, such as arthropods (Ostoja and Schupp 2009).

Changes in vegetation structure resulting from plant invasions also can impact food resources indirectly, by altering risk of predation and access to food (Lima and Dill 1990). Animals may forage in areas that have fewer food resources, if the vegetation structure provides safety from predators (Kotler et al. 1991), and that anti-predator behaviors can impact demography and abundance (Creel and Winnie 2005). Dense vegetation structure associated with some nonnative plants could impede foraging, if foods are more difficult or energetically expensive to acquire. If vegetation structure makes accessing food more difficult, this could provide another potential mechanism for the effects of plant invasions on animals, although this idea has not been explored.

Cheatgrass (*Bromus tectorum*) is a nonnative grass that can alter the vegetation structure greatly by creating dense, single-species stands in disturbed areas (Rieder et al. 2010). This species is problematic in arid regions in the western United States; approximately 20% of the sagebrush-steppe vegetation zone in the Great Basin Desert is dominated by monocultures of cheatgrass, such that re-establishment of native perennial plants is nearly impossible (Knapp 1996). Native vegetation in sagebrush-steppe typically is characterized by heterogeneous structure created by a diversity of plant species such as bryophytes, forbs, and bunchgrasses (Young and Evans 1973). When cheatgrass invades sagebrush steppe, the vegetation structure typically is more homogeneous and dense, because the plant produces a persistent litter layer and dense stems that fill in the interspace between shrubs (Young and Evans 1973).

Abundance of small mammals in shrublands can decrease with increased cheatgrass (Larrison and Johnson 1973, Gano 1982, Ostoja and Schupp 2009, Hall 2012) and changes in abundance of food resources could provide one potential mechanism for these declines. Cheatgrass displaces native plants (Young and Evans 1973, Knapp 1996), but we know little about how these changes affect the diet of small mammals. Some small mammals consume cheatgrass in addition to other palatable plants and arthropods (Sieg et al. 1986), although this grass is not a preferred food resource (Kelrick et al.

1986). Invasion of cheatgrass is associated with increased abundance of some groups of arthropods, such as beetles (Rickard 1970) and ants (Ostoja and Schuppe. 2009), which are consumed by small mammals (Sieg et al. 1986), but effects on other arthropod groups or the implications of these changes on food resources for small mammals are less clear.

Changes in vegetation structure created by cheatgrass could affect access to food resources (Gano 1982, Rieder et al. 2010), providing another potential mechanism for decreases in small mammal populations. Increased stem density and litter depth associated with cheatgrass may contribute to the impediment of movement of small mammals documented in invaded areas (Rieder et al. 2010, Chapter 3). Changes in vegetation structure also may impede foraging by increasing the time and energy needed to find food, or increase the vulnerability of animals foraging away from shrubs to predators, and decreasing foraging away from this cover. In dense, homogeneous monocultures of cheatgrass, small mammals may not be able to find areas where foraging is facilitated.

If the changes in vegetation structure caused by the invasion of cheatgrass affect the ability of small mammals to access food resources, animals should have difficulty removing food placed in dense stems or deep litter. We explored this potential mechanism driving population changes in small mammals with an experiment focused on quantifying how increases in both stem density and litter depth affect foraging by small mammals. We predicted that increased density and homogeneity of structure found in cheatgrass invaded sagebrush steppe would impact animals ability to access food resources within invaded areas.

Methods

Foraging Trials

We performed foraging trials in 3 areas in southwestern and central Montana during the summers of 2012 and 2013. In 2012, we conducted trials on the Blacktail Wildlife Management Area (WMA) (hereafter Blacktail area), 50 km southeast of Dillon in southwestern Montana. In 2013, we conducted trials in 2 areas in central Montana: 1) approximately 40 km northeast of Roundup, Montana (hereafter Roundup area) and 2) on the Yellowstone WMA, east of Billings, Montana (hereafter Yellowstone area). All study areas had expanses of sagebrush steppe dominated by native plants. We randomly selected sites within each study area that were at least 100 m from roads or other vegetation communities to avoid edge effects. In 2012 at the Blacktail area we established 80 × 80 m sites, but changed our design in 2013 and instead established 30 × 40 m sites at the Roundup and Yellowstone areas (Figure 2.1).

Within each site, we established regularly spaced 10 × 10 m subplots. Within each subplot, we manipulated the vegetation structure using artificial materials in a single circular area (foraging station), 0.2 m in diameter, located 0.5 m from the center of the subplot in a randomly selected cardinal direction. We added artificial structure to stations to increase stem density, litter depth, or both. We did not add structure to some stations, which served as controls. In 2012 at sites in the Blacktail area, we systematically treated half of the subplots within each site with either stems at some sites or litter at others. In 2013 within each site we randomly allocated all structural treatments to 3 subplots within each site, leaving 3 subplots to remain as controls. We added 15-cm plastic whisker markers (Presco, Dallas, TX) to some stations to increase stem density to approximately 7,000 stems/m^2, which is similar to densities in areas invaded by cheatgrass (Rieder et al. 2010). We added landscape fabric (DeWhitt Company, Sikeston, MO), shredded to less than 0.5-cm wide, to some stations to increase litter depth to 3-cm deep, which is the litter depth we found in local stands of cheatgrass prior to this research (D. Bachen, unpublished data). Although we did not expect these artificial treatments to simulate cheatgrass structure exactly, we believe that their general structural characteristics and application at densities found in invaded areas allow us to draw inference about the general effects of each type of structure on foraging by small mammals.

We established a foraging station within the structural treatment in each subplot. Foraging stations consisted of a Petri dish to hold grain and a wire mesh cage to prevent foraging by larger mammals and birds. We placed wire mesh cages, made of cylinders of chicken wire (5-cm diameter) with a closed top and an open bottom (Figure 2.2), over each Petri dish (4.7-cm diameter, Fisherbrand, Hampton, NH). We positioned cages at foraging stations at least 2 weeks prior to initiating the experiments to allow animals to acclimate and we secured each cage in place with a nail.

To assess foraging, we quantified the amount of food animals could remove from each station overnight. We placed 8 g of grain at each station before dusk; we used sweet feed, a mixture of barley, corn, and wheat soaked in molasses. The next morning, we collected the remaining grain from each station and repeated this process for 5 consecutive nights. We allowed grain collected from each station to dry naturally before collection and recorded the weight to the nearest 0.1 g. We excluded data from stations exposed to precipitation overnight that were damp, to prevent bias.

In 2012, we conducted foraging trials at 17 sites selected within the Blacktail area and examined the effect of adding stems or litter, but not both combined. We randomly selected which sites would be treated with stem or litter additions; we added structure to every other station, leaving alternating stations as untreated control stations (i.e., 32 treated and 32 control stations per site).

In 2013, we tested the effects of adding stems, litter, and both combined on 14 total sites, with 7 sites in the Roundup area and 7 sites in the Yellowstone area. Based on the data collected during 2012, we performed a power analysis to investigate the number of sites, site size and number of subplots, and number of treatment replicated within each site needed to detect a change in removal of 1 g of grain each night from a foraging station (Figure 2.3, Appendix A). Based on the results of the power investigation we established 13 sites with 12 subplots each and 1 foraging station in each subplot. We assigned structure additions to stations based on a randomized complete block design where each site served as a block and subplots were the units within blocks to which treatments were assigned. At each site, we applied each of the 3 treatments (added stems, added litter, added stems and litter) to 3 stations (9 stations total) and retained 3 stations as untreated controls.

Characterizing Vegetation and Small Mammal Communities

We measured vegetation characteristics to: 1) quantify differences between native sagebrush steppe and cheatgrass monocultures and 2) to examine differences in native sagebrush steppe between study areas, to better understand results of the foraging trials. In 2012, we sampled vegetation in all subplots established within the 17 native sites in the Blacktail area (n = 1088 subplots). In 2013, we sampled vegetation in all 168 subplots at 14 native sites in the Roundup and Yellowstone areas. We also established 13 sites in cheatgrass monocultures, 7 sites in the Roundup area and 6 in the Yellowstone area, and 156 subplots within these sites; we measured vegetation characteristics within each subplot. We used measurements from native and invaded sites in Roundup and Yellowstone areas during 2013 to quantify differences in vegetation characteristics with invasion. We used all measurements in native sites collected in 2012 and 2013 to compare characteristics of native vegetation among study areas. Within each subplot, we randomly selected a 0.2 × 0.5-m quadrat and to the nearest 5% recorded cover of all grasses, cheatgrass, forbs, bryophytes, woody debris (dead wood on the ground), litter, and bare ground to the nearest 5% (Daubenmire 1959, Figure 2.1). We also measured litter depth, to the nearest mm, at the center and each corner of the quadrat.

We characterized the small mammal community found in native sagebrush steppe in each study area based on capture data from another experiment (Chapter 3), to determine whether we were making appropriate comparisons among geographically-separate areas and better understand results of the foraging trials. To capture animals, we established between 2 and 6 arrays of Sherman traps (7.5 × 8.8 × 22.7-cm folding, H.B.

Sherman Traps, Inc., Tallahassee, FL), totaling 250-400 traps, in areas of sagebrush steppe close to sites. Each trap was baited with sweet feed and set at dusk, then checked the following morning. The number of traps placed each night varied among sites and nights, and ranged from 120 to 400 traps. To prevent captures during the day, we closed all traps each morning. We identified each animal to species, released the individual at the point of capture, and sanitized the trap with a 20% Lysol solution (Montana State University Institutional Animal Care and Use Committee protocol 2012-12). We completed all trapping at least 2 weeks prior to initiating the foraging trials.

Analysis

Foraging Trials

To quantify the effect of structure on foraging, we estimated differences in mean amount of grain removed nightly from foraging stations among treatments using linear mixed models. The individual site and night (e.g. 1st of 5 nights) were modeled as random effects to account for repeated measures of foraging on subplots within sites repeated over multiple nights per subplot. Due to differences in study design we analyzed the data from the experiments conducted in 2012 and 2013 with separate models. We decided whether to include fixed effects by fitting a rich model, and removing interactions and covariates using a likelihood ratio test, when there was little support for including covariates or interactions (*sensu* Zuur et al. 2009). We considered a global model with treatment, study area (in the 2013 model), time (based on the 5 night considered for trials) and all possible interactions, as well as a quadratic relationship for time. Based on our *a priori* hypothesis we expected structural treatment to be included in the model. Because we expected animals to take time to find new resources, we expected that foraging would increase over the 5 nights the experiment was conducted at each site. To account for the repeated measurements of foraging over multiple nights within sites, we included random intercepts for each site, and random slopes for each night nested within site, and used the nlme package (Pinheiro et al. 2013) in program R (R Core Team 2013).

For foraging experiments on the Blacktail area in 2012, we selected a model with structural treatment and night, with night as modeled as a quadratic and their interactions as fixed effects. Foe foraging experiments in 2013 data we selected a model with structural treatment, area (Roundup or Yellowstone), night, as well as the interaction between structural treatment and area as fixed effects (Appendix B).

Characterizing Vegetation and Small Mammal Communities

We quantified differences in vegetation characteristics between native sagebrush-steppe and cheatgrass-invaded sites using linear mixed models to account for repeated measures of vegetation within each site. To compare native and invaded sites, we tested the effect invasion had on each vegetation characteristic by including the presence of a cheatgrass monoculture as a fixed effect. To account for multiple vegetation measurements collected within each site, we considered each site as a random effect with a separate intercept. We also assessed heterogeneity of vegetation cover and litter depth by calculating the coefficient of variation (CV) corrected for small sample size, calculated as:

$$\frac{s}{\bar{x}}\left(1+\frac{1}{4n}\right)$$

where s is the standard deviation, $\bar{x}$ the sample mean, and n the sample size. We calculated this value for each vegetation characteristic. We then used *t*-tests to compare vegetation heterogeneity between native and invaded sites, and ANOVA tests and linear models to test for differences between areas and quantify these differences.

To explore the differences in vegetation among areas we calculated average cover of vegetation attributes and average CV of these attributes for each site. We then plotted these averages to examine differences between areas and look for a pattern in cover among areas that may explain differences in foraging.

To compare the composition of the small mammal communities in each area, we quantified the number of individuals captured by species while trapping. We qualitatively compared the composition of the small mammal communities among study areas by examining relative dominance by species.

Results

Foraging Trials

Adding structure affected the amount of grain removed from foraging stations overnight, relative to untreated controls, although the direction and magnitude of the effect differed by study area (Tables 2.1 & 2.2, Figure 2.4). The mean amount of grain removed overnight decreased with the addition of litter in both the Blacktail and Yellowstone areas by an estimated 1.1 g/night and 0.8 g/night respectively (approximate 95% CIs = 0.7 to 1.4, 0.4 to 1.3 g/night), but the estimated amount of grain removed each night increased with litter additions by 0.5 g/night (0.1 to 1.0 g/night) on sites in the Roundup area. There is little evidence that adding stems affected the amount of grain removed each night (Tables 2.1 & 2.2, Figure 2.4). Although we did not find evidence that litter affected foraging, the effect of adding litter and stems in combination was intermediate to the application of either structure individually (Table 2.2, Figure 2.4). Quantifying the amount of grain that is biologically meaningful is difficult, as we are unsure of how many animals are foraging at each station every night. An adult deer mouse weighing 17 grams would be expected to consume 3.3 g of grain per day (Millar 1978), so the decrease in foraging we detected at stations treated with litter could represent a large portion of an individual animal's diet or a smaller portion of the diet of multiple animals.

Characterizing Vegetation and Small Mammal Communities

Cheatgrass-invaded sites were characterized by more grass cover and deeper litter, but less shrub cover and bare ground, relative to native sagebrush steppe (Table 2.3). Cover of all grasses was an estimated 39% higher (approximate 95% CI = 30 to 40%) and litter was 2.8 cm deeper (1.7 to 3.9 cm) in cheatgrass-invaded sites compared to native sagebrush steppe, whereas shrub cover 25% lower (19 to 30%) and cover of bare ground was 23% lower in invaded sites (18 to 30%). Vegetation in cheatgrass-dominated sites was more homogeneous than native sagebrush steppe for most cover classes, with the exception of cheatgrass, forbs, and bare ground (Table 2.4).

Average vegetation characteristics seemed to differ among area, but we did not observe consistant patterns in these differences (Figure 2.5). Small mammal communities were dominated by deer mice, but the presence and relative dominance of other species in the community differed by study area (Table 2.5).

Discussion

Foraging by animals is influenced by the amount of energy required to access food, the risk of predation while foraging, and the abundance and access to food (Brown 1988). Changes in vegetation structure associated with plant invasions could alter these tradeoffs (Robinson and Holms 1982). We found that sites dominated by cheatgrass had more grass and litter cover, as well as deeper litter and less bare ground, relative to native sagebrush steppe; we aimed to simulate these structural changes in our experiments, which affected foraging choices of small mammals.

Animals should prefer food sources that maximize energy and can be accessed with relatively little energy expended (Ydenberg et al. 1994). Vegetation structure can affect foraging efficiency and choices by animals (Diehl 1988, Butler and Gillings 2004, Butler et al. 2005). Access to food resources may be reduced further if animals completely avoid areas where vegetation structure inhibits foraging (Mittelbach 1981). We found that adding deep litter decreased foraging by small mammals in 2 of 3 study areas. Structural conditions created by litter may have increased the time and energy required to access food, reducing efficiency of foraging. In the Roundup area, where we found foraging increased with added litter, other factors may have made animals more willing to expend more energy while foraging (Mitchell et al. 1990). Vegetation differences may also have impacted foraging behavior, but because vegetation characteristics that we would expect to affect foraging (e.g. forbs, litter depth, and shrub cover) were not consistently different between as Roundup sites and Blacktail and Yellowstone area sites, we do not feel that vegetation can explain differences in foraging among areas (Figure 2.5).

Predators can influence foraging behavior greatly, as prey seek conditions that minimize risk, such as dense vegetation cover (Brown 1988, Lima and Dill 1990, Kotler et al. 1991, Chapter 3). Small mammals rarely forage away from shrub cover when risk of predation is high (Kotler 1984, Simonetti 1989, Kotler et al. 1991), even if food resources are more abundant in these risky places (Kotler et al. 1991). Although some small mammals use dense stems and deep litter as cover (Chapter 3), we found little evidence that increasing litter or stems increased foraging by small mammals for the majority of our study areas.

Prey species must consider much more than the mere presence of predators, including the abundance and composition of the predator community, when assessing predation risk (Rizzari et al. 2014, Creel et al. 2014). Although we did not quantify the predator community within each study area, we detected snakes regularly in the Roundup area and occasionally in the Yellowstone area (D. Bachen, personal observation). The presence and relative density of snake predators may make foraging within or under sagebrush more risky (Kotler et al. 1992, Bouskila 1995), relative to where avian and mammalian predators are more dominant. If our treatments alter cover for snakes, this could help explain increases in foraging at stations with added litter in the Roundup area. Increases in predation risk for small mammals under shrubs may make animals more likely to forage away from shrubs (Kotler et al. 1992, Bouskila 1995). If the structure of our treatments provided additional cover from predators (Chapter 3), animals may preferentially to forage within structural treatments, compared to the bare ground found in the interspace between shrubs.

The abundance and accessibility of food resources available in foraging areas also can influence how much effort animals will expend to access a given food resource, or the level of predation risk they will be willing to accept (Brown 1988). Diversity in both the composition and structure of the plant community affect food resources for animals (Brose 2003). We found that cheatgrass reduces heterogeneity of vegetation structure in invaded areas, which may affect the composition of food resources available to animals. These changes in available foods may force animals to exploit energetically-expensive or risky resources, with concomitant effects at the population level (Kotler and Brown 1988). Although we assume that the abundance and accessibility of food are relatively constant within sites due to their small size and placement on the landscape, and we account for site differences with our blocked design, differences in food resources among study areas also could explain differences in treatment effects.

Artificial structure has been used previously to experimentally test the effect of vegetation structure on behavior of small mammals (M'Closkey 1976, Simonetti 1989), and these materials can provide strong inference by reducing the potential for confounding factors. However, inferences also can be biased if artificial materials do not mimic the actual structure adequately. Although we did not formally test how well our treatments mimicked cheatgrass, we collected information from the literature and our own data in cheatgrass monocultures to inform our structural treatments by adding representative stem densities and litter depths.

Changes in structure associated with cheatgrass seem to alter foraging behavior of small mammals; establishing a definitive link between this mechanism and the population-level effects commonly documented with plant invasion (Larrison and Johnson 1973, Gano 1982, Ostoja and Schupp 2009, Hall 2012) would be an important advance in our understanding. Researchers have documented that invasion of nonnative plants alters plant and arthropod communities (Young and Evans 1973, D'Antonio and Vitousek 1992, van Hengstum et al. 2013, Litt et al. in press), but we do not know how these changes affect the quality and quantity of food resources for animals. Understanding how invasion alters abundance and composition of arthropod communities and the effect this has on food resources for other animals would be particularly informative, as some species groups can be an important components of the diets of small mammals (Seig et al. 1988) and birds (Wolda 1990).

Changes in access to food resources also should be considered forother vertebrate species in invaded sagebrush steppe. Cheatgrass affects movement of reptiles (Newbold 2005, Rieder et al. 2010). Species of concern in sagebrush steppe, such as greater sage-grouse (*Centrocercus urophasianus*) (Crawford et al. 2004), also could be impacted by dense vegetation structure. Sage grouse chicks are relatively small, but do not have sleek bodies that facilitate movement through cheatgrass structure (Rieder et al 2010). Because sage grouse chicks also are particularly vulnerable to decreases in food resources (Gregg and Crawford 2010), reducing their ability to access food could have potential implications at the population level. We need better understand whether the changes in vegetation structure cause by cheatgrass invasion can affect other species, particularly species of management concern.

Invasive plants continue to be introduced to novel ecosystems (Vitousek et al. 1997) and distributions of many invasive plants may change with altered climate patterns (Walther et al. 2002, Bradley 2009, Bradley et al. 2010, Huang et al. 2011). Many invasive plants are well-established (Vitousek et al. 1996) and removal or even reduction on a landscape scale is improbable or impossible, requiring novel approaches for management and conservation. Understanding the mechanisms by which the nonnative species affect wildlife may provide insight into alternative ways to reduce these impacts (Levine et al. 2003) and inform restoration and mitigation efforts.

Tables

Table 2.1. Parameter estimates from our inferential model quantifying the effect of structure on the amount of grain removed from foraging stations, Blacktail area, southwestern Montana, summer 2012. The model is parameterized with foraging stations in native vegetation as the reference level (intercept).

Covariate	**Estimate**	**95% CI**		**df**	***t***	***P***
(Intercept)	1.17	0.89	2.51	2838	4.09	<0.001
Litter	0.29	-0.19	0.76	2838	1.17	0.241
Stems	-0.35	-0.77	0.06	2838	-1.68	0.093
Time (Days)	-0.30	0.11	0.52	31	0.55	0.587
Time^2 (Days)	0.08	0.01	0.14	31	2.45	0.02
Litter × Time	-0.27	-0.40	-0.13	2838	-4.00	<0.001
Stems × Time	0.06	-0.06	0.18	2838	0.91	0.363

Table 2.2. Parameter estimates from our inferential model quantifying the effect of structure on the amount of grain removed from foraging stations, Yellowstone and Roundup areas, central Montana, summer 2013. The model is parameterized with foraging stations in native vegetation as the reference level (intercept).

Covariate	**Estimate**	**95% CI**		**df**	***t***	***P***
(Intercept)	1.64	1.03	2.25	631	5.30	0
Litter	0.51	0.07	0.95	631	2.29	0.023
Stems	0.35	-0.09	0.79	631	1.55	0.122
Litter & Stems	0.40	-0.04	0.84	631	1.80	0.073
Time (Days)	0.10	-0.06	0.22	38	1.76	0.086
Study Area	0.15	-0.66	0.97	12	0.49	0.690
Litter × Study Area	-1.34	-1.96	-0.73	631	-4.29	<0.001
Stems × Study Area	-0.51	-1.12	0.11	631	-1.62	0.105
Litter & Stems × Study Area	-0.80	-1.42	-0.19	631	-2.57	0.010

Table 2.3. Differences in vegetation characteristics (% cover and litter depth) between cheatgrass and native sagebrush steppe (difference = cheatgrass – native sagebrush, *n* = 27 sites, 324 subplots) obtained from the inferential model, central Montana, summer 2013.

	Difference	**SE**	***t***	***P***
Cheatgrass (%)	67	6	10.73	<0.001
Shrubs (%)	-25	3	-8.90	<0.001
All Grasses (%)	39	5	10.31	<0.001
Forbs (%)	1	2	0.56	0.580
Bryophytes (%)	-3	1	-4.33	<0.001
Woody Debris (%)	-2	1	-2.64	0.014
Litter (%)	15	4	3.49	0.002
Bare Ground (%)	-23	3	-7.76	<0.001
Litter Depth (cm)	2.8	0.5	5.17	<0.001

Table 2.4. Differences in heterogeneity of vegetation between cheatgrass and native sagebrush steppe (difference = cheatgrass – native sagebrush), as measured by CV (%, corrected for small sample size), central Montana, summer 2013. Negative values indicate invaded areas are more homogeneous.

	Difference (%)	**SE**	***t***	***P***
Cheatgrass	-56	30	-1.36	0.185
Shrubs	-81	9	-2.66	0.013
All Grasses	-47	36	-5.24	<0.001
Forbs	-39	36	-1.08	0.290
Bryophytes	-100	44	-2.82	0.009
Woody Debris	-172	27	-3.91	0.001
Litter	-86	33	-3.13	0.004
Bare Ground	-35	41	-1.05	0.305
Litter Depth (cm)	-71	14	-5.14	<0.001

Table 2.5. Composition of the small mammal community (animals captured in each area by species) in order of dominance for the 3 study areas, southwestern and central Montana, summers 2012 and 2013.

Species	**Blacktail**	**Yellowstone**	**Roundup**
Peromyscus maniculatus	114	3	27
Lemmiscus curtatus	50	0	0
Microtus ochrogaster	0	1	2
Reithrodontomys megalotis	0	1	1
Onychomys leucogaster	0	0	2
Perognathus fasciatus	0	0	1
Microtus montanus	1	0	0
Tamias minimus	1	0	0
Zapus princeps	1	0	0
Total captures	167	5	33

Figures

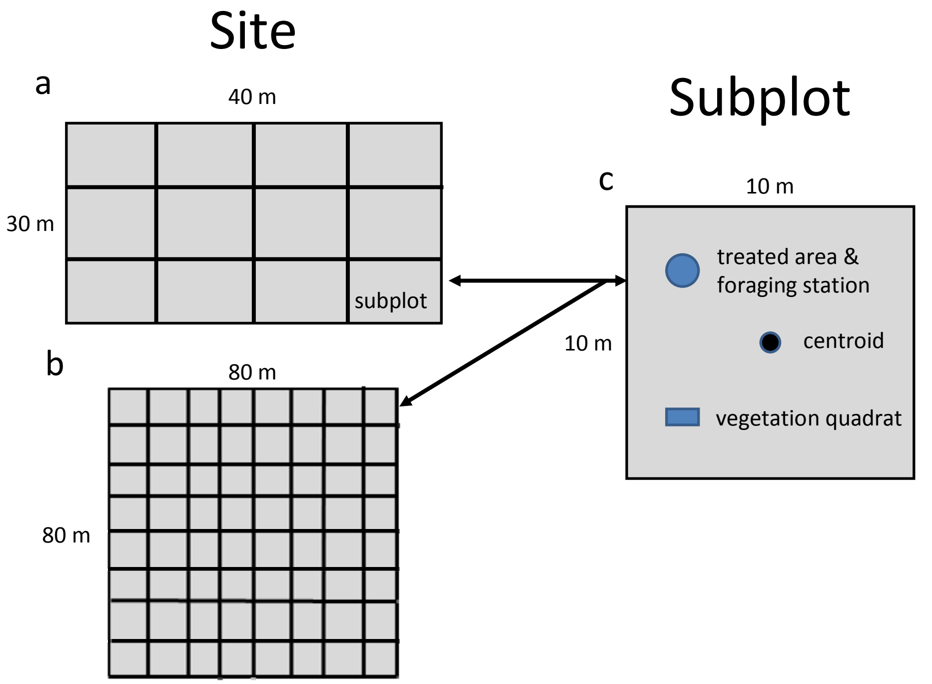

Figure 2.1. Site and subplot design for foraging experiments, southwest and central Montana, summers 2012 and 2013. We used 30 x 40 m sites (a), for both the Roundup and Yellowstone areas, and 80 x 80 m sites (b) fot the Blacktail area. We used the same subplot design (c) for all study areas. Within each subplot , we manipulated the vegetation structure in a randomly selected 0.2 x 0.2 m area, and established a foraging station established within this structure. We also quantified the vegetation characteristics within a 0.2 x 0.5 m quadrat, selected at random within the subplot.

Figure 2.2. A typical foraging station, placed in native vegetation. We placed grain in the Petri dish, and covered the dish with a cage to prevent foraging by larger mammals and birds.

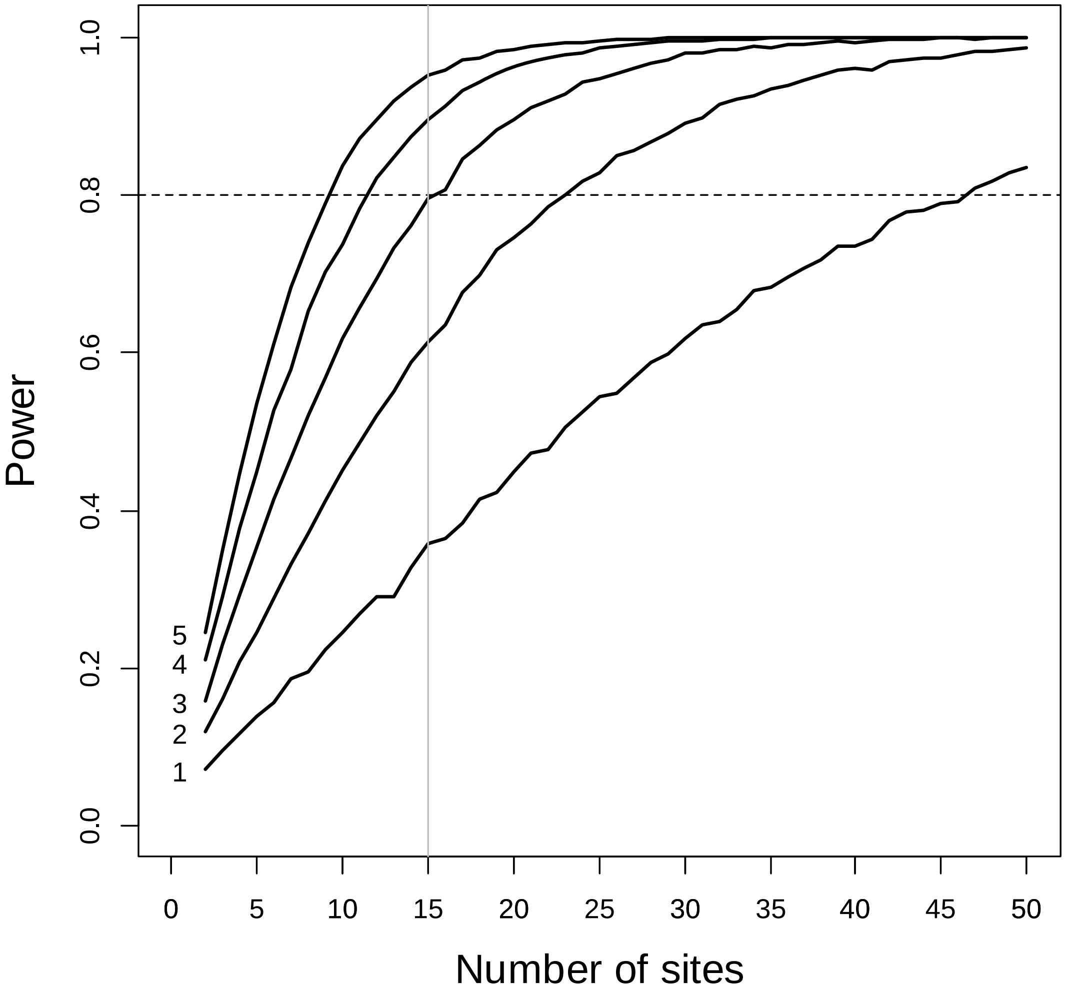

Figure 2.3. Simulated power curves based on foraging trials from 2012 to calculate a sample size for experiments in 2013. Lines represent the power to detect a difference of 1 g of seed removed over 1 night between an average treated foraging station and an average untreated station for a given number of sites (x-axis). Power curves differ based on the number of replicates of 3 treatments and 1 control within a site (number at the starting point of each curve), assuming 4 treatments/site. We chose power = 0.80 (β = 0.20) as a reference level for acceptable power (dashed line), as we felt this would give us a reasonable chance of detecting a treatment effect without committing a type-2 error. We sought to balance the minimum number of sites and replicates within sites needed to detect our chosen treatment effect with adequate power (gray line). See appendix A for further discussion.

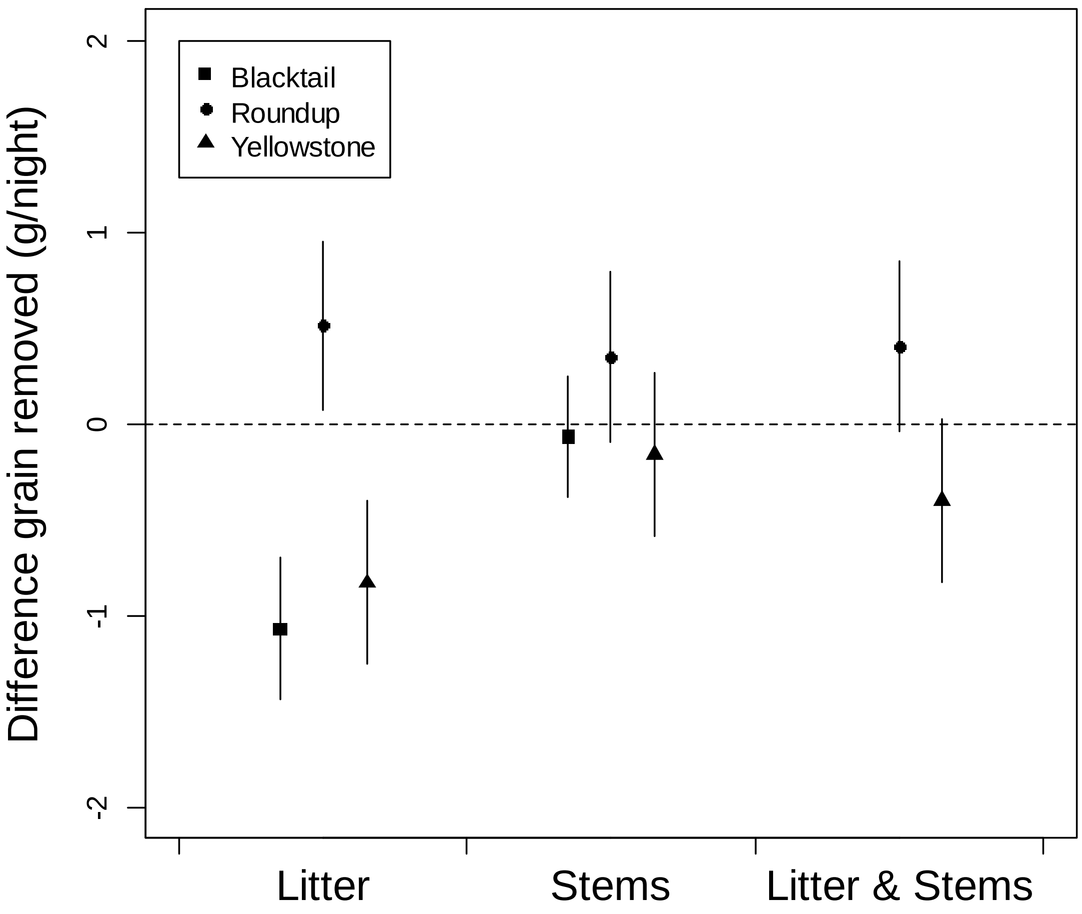

Figure 2.4. Differences in the amount of grain removed per night (average amount removed per night and approximate 95% CIs obtained from inferential models) with added structure, relative to untreated controls in native vegetation (reference line at 0). Values above the reference line indicate that small mammals removed more grain from treatment stations and values below the reference line indicate small mammals on average removed less grain from treatment stations, relative to control stations.

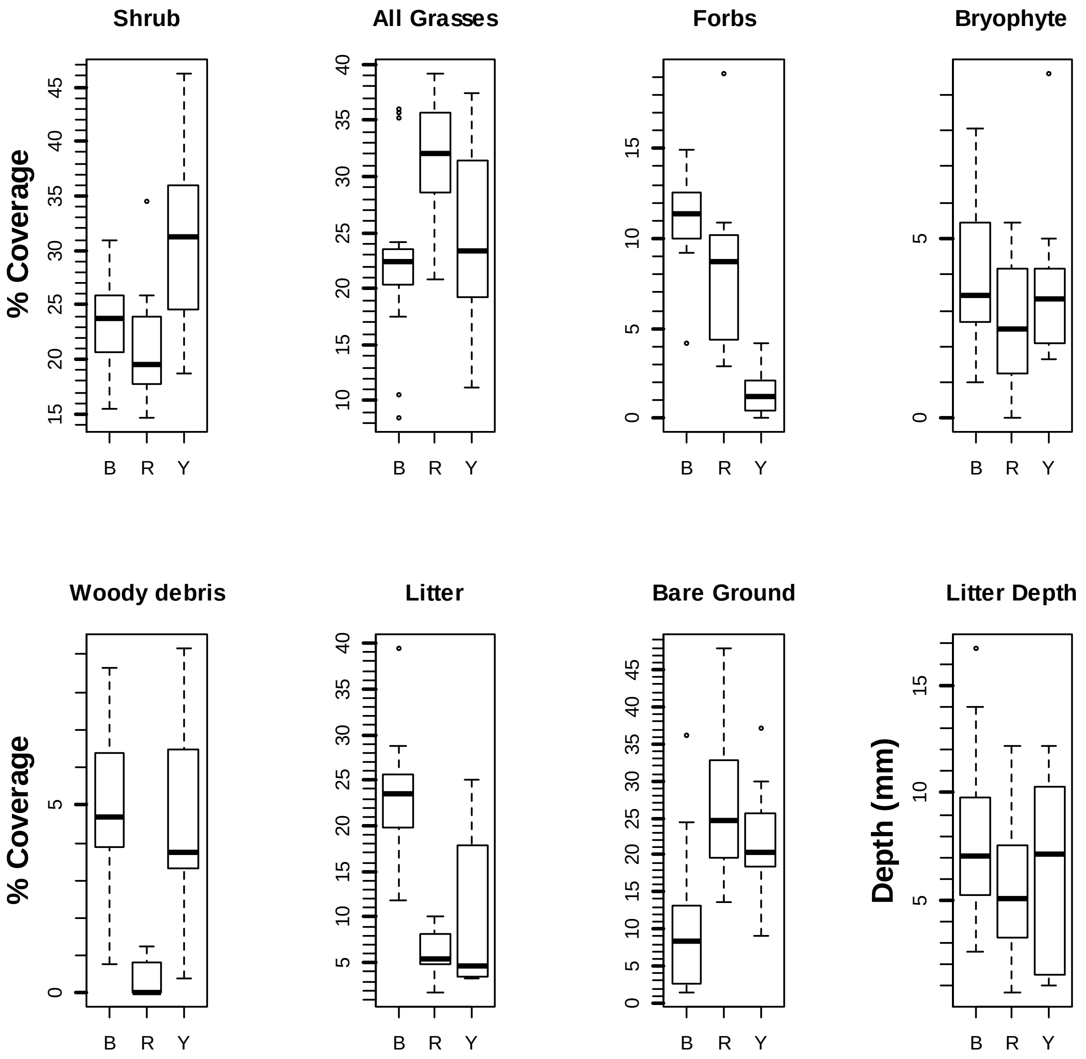

Figure 2.5. The distribution of the average vegetation characteristics on sites in Blacktail (B), Roundup (R), and Yellowstone (Y) areas by vegetation characteristic, southwestern and central Montana, summers 2012 and 2013.

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CHAPTER THREE

CHANGES IN PREDATION RISK FOR DEER MICE (*PEROMYSCUS MANICULATUS*) WITH PLANT INVASIONS: UNDERSTANDING MECHANISMS

Contributions of Authors and Co-Authors

Manuscripts in Chapter 3

Author: Daniel A. Bachen

Contributions: Conceived and implemented the study design. Collected and analyzed the data

Co-Author: Andrea R. Litt

Contributions: Assisted in conceptualizing this research, implementation of experiments, analysis of data and development and review of this manuscript

Co-Author: Claire Gower

Contributions: Assisted with conceptualizing this research, implementation of experiments and review of this manuscript.

Manuscript Information Page

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Abstract

Predation exerts a strong influence on behavior of prey, and the structure of vegetation can affect these interactions. The invasion of nonnative plants may change the vegetation structure of ecosystems with concomitant effects for animals. Although the effects of plant invasions on animals generally are well-documented, we know little about the mechanisms driving changes in presence and abundance, specifically whether plant invasion changes predators and prey interactions. In sagebrush steppe, brome grasses such as cheatgrass (*Bromus tectorum*) can invade and form dense stands, increasing the depth and persistence of litter, as well as the density of standing vegetation. These structural changes alter abundance and composition of the small mammal community. We used a series of experiments to explore whether changes in vegetation structure associated with the invasion of cheatgrass would alter predation risk of small mammals, to better understand mechanisms driving documented population- and community-level effects. In the first experiment, we timed animals fleeing a simulated predator through various depths of litter or densities of stems. We found that dense stems impeded movement more than litter. In the second experiment, we recorded animals moving through native sagebrush steppe and cheatgrass monocultures, and analyzed these recordings to detect differences in the volume of noise created, especially for frequencies detected by common predators. We found that animals moving through cheatgrass made more noise, compared to native sagebrush steppe. Based on these experiments, cheatgrass monocultures may alter the relationship small mammals have with their predators by impeding escape ability and increasing detectability.

Introduction

Predation exerts a strong influence on behavior of prey, as prey try to maximize the quality and quantity of resources, while minimizing interactions with predators (Hughes and Ward 1993, Holms 1991, Creel and Winnie 2005, Garrott et al. 2008). Animals using areas with abundant food resources and low predation risk are expected to experience little direct or indirect effects of predators on fitness due to predators (Lima and Dill 1990). If food resources are limited or low quality in areas with low predation risk, animals may not find sufficient food or may need to spend more time foraging, balancing the fitness consequences of reduced food intake and increased energy expenditure. Animals may change their behavior if predation risk is reduced temporarily (Werner et al. 1983, Travers et al. 1988, Creel et al. 2005), such as when rodents are able to forage in open areas when light is reduced due to cloud cover or moon phase (Clarke 1983, Price and Brown 1983, Kotler 1984, Simonetti 1989, Fanson 2010).

The structure of vegetation can affect interactions between predators and their prey (Lima and Dill 1990). Many animals use vegetation cover to avoid lethal interactions with predators (Werner et al. 1983, Travers et al. 1988, Kotler et al. 1991, Creel et al. 2005). Prey animals also mitigate predation risks by foraging near and within vegetation structure that maximizes their ability to escape (Heithaus et al. 2009).

Nonnative plants have become increasingly problematic worldwide (Vitousek et al. 1997) and result in changes in the structure and composition of vegetation (Vilà et al. 2011, Chapter 2). Invasions by nonnative plants provide an opportunity to explore the role of vegetation structure in predator-prey interactions as a natural experiment (*sensu*

Diamond 1983, HilleRisLambers et al. 2013). If nonnative plants provide more vegetation cover, predation risk may decrease and prey may increase in abundance in invaded areas (Malo et al. 2013). Conversely, changes in the complexity of vegetation structure associated with nonnative plants also may increase vulnerability of prey to predators or increase predator abundance (Pearson and Fletcher 2008), such that prey would be less abundant in invaded areas (Williams et al. 2013).

Cheatgrass is an annual grass that was introduced to the western United States from Eurasia during the nineteenth century (Mack 1981). Currently, approximately 20% of the sagebrush-steppe vegetation zone in the Great Basin Desert is dominated by monocultures of cheatgrass, such that establishment of native perennial plants is nearly impossible (Knapp 1996). Cheatgrass can alter structure of the vegetation by displacing native plants, typically resulting in an increase in the density of stems and depth of litter and homogeneity of dense cover in invaded areas (Chapter 3). Although sagebrush shrubs (*Artemisia* spp.) typically are the dominant plant in the sagebrush steppe, shrub cover is reduced or eliminated when stands of cheatgrass burn, resulting in conversion from shrubland to annual grassland (Mack 1981).

As with many plant invasions, increased dominance of cheatgrass has concomitant effects on native animals, including small mammals (Rieder et al. 2010). Small mammals often are less abundant with increased cheatgrass in sagebrush steppe; population sizes in these invaded areas may be 16 to 33% of that in native sagebrush or shrubland areas, even if the composition of the small mammal community changes little (Gano and Rickard 1982, Ostoja and Schupp 2009, Hall 2012). Community composition of small mammals also may shift with increased dominance by cheatgrass. For example, deer mice (*Peromyscus maniculatus*) are common, omnivorous rodents that tolerate a wide range of foods and physical conditions (Foresman 2001). Deer mice may be able persist in the novel environment created with cheatgrass and other plant invasions to become proportionally more abundant. However, animals with relatively narrow environmental tolerances or resource requirements may not find sufficient resources in invaded areas (Bateman and Ostoja 2012). In southern Idaho, small mammals were less abundant in dense monocultures of cheatgrass and the deer mouse and Great Basin pocket mouse (*Perognathus parvus*) dominated the community composition (Larrison and Johnson 1973).

Although the effects of plant invasions on animals generally are well-documented, we know little about the mechanisms driving changes in presence and abundance (Levine et al. 2003). Although cheatgrass greatly modifies vegetation characteristics in invaded areas (Chapter 2), many species of small mammals still can occur, suggesting that critical resources are available and invaded areas have not been modified beyond the environmental tolerances of species. Smaller populations of small mammals found in invaded areas may result from decreased abundance or access to food resources (Chapter 2) or increased predation risk due to an inability to escape predators (Rieder et al. 2010).

Animals may choose to avoid areas that reduce their ability to escape from predators (Lima and Dill 1990). Deer mice avoid areas with dense grasses (Pearson et al. 2001), which may be a behavioral response to reduce predation risk. Dense stems or deep litter created by cheatgrass have the potential to affect movement of small mammals, making them more vulnerable to predation by impeding the ability to flee between points of refuge (Rieder et al. 2010), but also could provide cover and decrease predation risk. Although cheatgrass generally slows movements of small mammals, we know little about which characteristics of vegetation structure affect movement, which would allow us to generalize about the potential influence of other nonnative plants.

Increased dominance by cheatgrass also could affect the ability of predators to detect prey. The noise an animal makes while moving may contribute to its risk of predation, as many predators of small mammals in sagebrush steppe such as owls, northern harrier hawks, foxes and coyotes use acoustic cues while hunting (Wells and Lehner 1978, Rice 1982). Mice avoid moving through relatively noisy substrates (Roche 1999), suggesting these animals modify their behavior to reduce their acoustic profile. Cheatgrass forms dense homogeneous stands (Chapter 2) that animals may have trouble avoiding; cheatgrass also senesces early in the year (Knapp 1996), creating dry vegetation that could increase the volume of noise animals make when moving, relative to native grasses.

The vegetation structure created by cheatgrass invasion may affect the predation risk of mice indirectly by 1) decreasing escape ability, and 2) increasing detectability of movement in invaded areas relative to native areas. We tested the effect of both mechanisms with a series of experiments. To test whether vegetation structure associated with cheatgrass impacts the ability of mice to move, we conducted experiments where we simulated a predation event and quantified the time it took for mice to flee through either dense stems or deep litter at various densities and depths. Based on previous research (Rieder et al. 2010) we expected structure to impede movement, but were unsure of the relative contribution of each structural component. To test if the amount of noise made by mice was greater in cheatgrass invaded sagebrush steppe relative to native sagebrush steppe, we recorded noise made by mice moving through cheatgrass and native sagebrush steppe. We predicted mice moving through cheatgrass would be louder than mice moving through native sagebrush steppe.

Methods

To better understand how changes in vegetation structure caused by cheatgrass invasion specifically affect small mammals, we conducted experiments to quantified the relationship between vegetation structure and the ability of small mammals to escape predators (escape ability experiments), and whether animals make more noise when moving through dense stands of cheatgrass, making them more detectable by predators (acoustic trials). We used similar methodologies to capture and assess responses of small mammals in both experiments. We focused on deer mice specifically, to maximize sample sizes.

We constructed enclosures (hereafter referred to as tracks) made of plywood (Figures 3.1 & 3.2). Tracks were 0.3-m wide and either 1.5 or 2-m long, depending on the experiment, and 0.5-m high, to prevent escape. The track included an opening at ground level on each narrow end, so we could place an animal at one end of the track and recapture that individual in a Sherman live trap (7.5 × 8.8 × 22.7 cm folding trap, H. B.

Sherman Traps, Inc., Tallahassee, FL) at the other end. To prevent escape of animals, we used natural materials to block openings along the base of the track.

We captured animals for both experiments in proximity to the track. At dusk, we set and baited 250-400 Sherman traps with sweet feed. We checked and closed all traps each morning, to prevent captures during the day. For each captured animal, we measured total body length (mm) with a ruler and mass with a spring scale (±1 g, PESOLA AG, Rebmattli 19, CH-6340, Baar, Switzerland). We determined age based on a combination of morphological characteristics (e.g., pelage color, head:body ratio) and weight. We determined sex and breeding condition visually by examining individuals for evidence of swollen testicles (males) or swollen nipples, distended abdomen, and increased weight (females) (McCravy and Rose 1992). We double marked each animal with a uniquely-numbered ear tag (Monel tag 1005-1, National Band and Tag Co., Newport, KY) and an ink mark on the ear (*sensu* Litt and Steidl 2011).

In each experiment, we released an individual animal into the track and encouraged them to run the length of the track (hereafter referred to as a race) using a padded stick to simulate a predator and provoke a flight response (*sensu* Djawdan and Garland 1988, Rieder et al. 2010). During the race, we kept the stick close to, but never in contact with the animal. After we completed all data collection, we released each animal at the point of capture and sanitized the trap with a 20% Lysol solution (Montana State University Institutional Animal Care and Use Committee protocol 2012-12).

Escape Ability Experiments:

We conducted this experiment over 12 days during summer 2012 on the Blacktail Wildlife Management Area, 50 km southeast of Dillon in southwestern Montana. We selected a site that had a level, even surface, devoid of vegetation, and was close to an area of sagebrush steppe where we could readily trap mice. We placed the 2-m long experimental track at this site for the duration of the experiment.

We explored the relationship between animal movement and changes in vegetation structure inherent with cheatgrass invasion (Chapter 2) by modifying stem density and litter depth. We used artificial materials to simulate changes in vegetation structure to draw stronger inferences, as the removal of stems or litter from natural areas would be problematic without disturbing the remaining vegetation architecture and variation among sites could confound results. Using artificial structure also may allow us to draw inference to other invasive grasses that cause an increase in stem density or litter depth. We simulated changes in stem density with 15-cm plastic whisker markers (Presco, Dallas, TX, Figure 3.3), and established 4 levels of stem density: 5,000, 10,000, 15,000 and 19,000 stems/m^2. We simulated grass litter with landscape fabric (DeWhitt Company, Sikeston, MO) shredded to less than 0.5-cm wide (Figure 3.4), and established 5 levels of litter depth: 1, 3, 5, 7, and 9 cm. We also tested bare ground, as a control, and tested 1 structural treatment per day. We started with bare ground on the first day and increasing litter depth or stem density each day. We tested all of the litter treatments first followed by all stem density treatments.

For each structural treatment, we timed the duration of each race to the nearest second. We started timing when the animal crossed the start line, demarcated by a piece of plastic flagging, and stopped timing when the animal entered the trap at the other end of the enclosure (Figure 3.1). For each treatment, we attempted to time each individual animal in 3 races, although this was not always possible. Some animals hid in the litter and either did not run or moved very slowly along the track as they attempted to hide repeatedly. We censored sprint times longer than 60 seconds and instead classified the race as one in which the animal hid (and failed to complete the trial). Animals were released each day; some individuals were recaptured on subsequent days and tested in multiple treatments.

Acoustic Trials

We conducted this experiment over 7 days between June and July 2013 in central Montana approximately 40 km northeast of Roundup, Montana (hereafter Roundup area). We established 8 native sites in the interspace between shrubs within native sagebrush steppe and 9 invaded sites within patches dominated by cheatgrass (17 total).

To conduct the experiment, we placed the 1.5-m track within either a randomly-selected native or invaded site. All sites were at least 10 m apart. We recorded animals running the length of the track and quantified the volume. We recorded each race using a Samson H2 Zoom audio recorder (Samson Technologies, New York), placed 0.5 m above the ground at the center of the track (Figure 3.2). The microphone was set to record downward at sampling rate of 4.1 kHz, the highest quality recording possible with this device. Each recording documented the average frequency and volume of each sampling occasion within the recording. We did not run experiments when the vegetation was wet or when there was wind to reduce potential bias. As with the escape ability experiments, animals were used in multiple races (from 1 to 13 races) and released each day; some individuals were captured on more than 1 day and were used in races on multiple days (from 1 to 6 days). Uniquely marked mice allowed us to keep track of specific individuals.

Analysis

For the escape ability experiments we sought to quantify the effect structure had on the movement ability of mice, which we measured as the time needed to run the length of the track. For the acoustic trials we sought to quantify and compare the volume of noise (dB) mice made while moving through native and invaded areas. For both experiments, we used generalized linear mixed effects models for analyses to account for repeated measurements, and used the MASS and nlme packages (Venables and Ripley 2002, Pinheiro et al. 2013) in program R (R Core Team 2013). For each experiment, we assessed the strength of fixed effects, starting with a model including all covariates describing attributes of the site or track (structural treatment for escape ability experiments, native/ invaded for acoustic trials), attributes of mice (age, sex), and attributes of races for acoustic trials race attributes (day of race and frequency of noise). We explored evidence for interactions of fixed effects and quadratic terms for continuous variables. We retained covariates and interactions when there was support, but we always retained experimental factors in the final model (*sensu* Zuur et al. 2009).

Escape Ability Experiments:

We modeled: 1) the probability of the animal running (and completing the trial) or hiding (and failing to complete the trial) using a generalized linear mixed model and 2) sprint time, as a function of vegetation structure using a linear mixed effects model; we fit models for stem density and litter depth treatments separately for both. We considered structural treatment as continuous covariate in both linear and quadratic forms (density of stems or depth of litter), age and sex of the animals, and all possible interactions as fixed effects. We accounted for multiple races in the same treatment by the same individual and included a random intercept for individual mice for a given treatment. To meet model assumptions of normality and constant variance, we log-transformed sprint times to account for increased variation with increased density of litter or stems.

Acoustic Trials:

We processed sound files from the acoustic trials with the digital audio editor Audacity (version 2.0.3, Audacity Team, 2013). Individual files, representing the noise made by 1 animal traveling the length of the enclosure, were first edited to remove noise made prior to and after the trial was conducted. We also removed noise made by other animals (e.g., birds and prairie dogs), by any wind that occurred during the experiment, and by people during the trial. By default the H2 Zoom split each recording into left and right channels. We completed all subsequent analysis using the right channel only as recordings from both channels were nearly identical. We extracted the volume and frequency of noise made at each sampling point within the recording.

To quantify the effect of vegetation type on the noise animals make while moving through the vegetation we used a linear mixed effects model. We accounted for multiple samples of volume taken during a single race and again included a random intercept for each individual mouse. We considered a model with vegetation type (native sagebrush steppe or patches dominated by cheatgrass), age and sex of the animals, date of the recording – as a proxy for variation in wind, and frequency of each sample within a recording in kHz, as well as interactions between frequency and vegetation type as fixed effects.

Results

Escape Ability Experiments:

Litter We recorded sprint times from 302 races by 32 individual deer mice with depths of litter between 0 and 9 cm. To quantify the probability of a mouse running or hiding, we selected an inferential model which parameterized as litter depth (Appendix B). The odds of a mouse completing the race changed with litter depth, but little evidence that age or sex of the animal were influential (Table 3.1). For every 1-cm increase in litter depth, the odds of a mouse running and completing the race decreased by an estimated 8% (95% CI = 5 to 12% decrease). Almost all mice completed the race when litter depth was low, but some individuals began to hide at litter depths of 5 cm, and even fewer animals completed races when litter was 7- and 9-cm deep (Figure 3.5a).

To quantify the effect litter had on sprint times for mice that chose to run, we used an inferential model where log sprint time was explained by the effects of litter depth and age of the animal (Appendix B). When animals ran and completed the race, there is evidence mean sprint time changed with litter depth and age, but sprint times were influenced little by sex of the animal (Table 3.1). For every 1-cm increase in litter depth, the sprint time of mice increased by an estimated 9% (95% CI = 7 to 13% increase, Table3.1, Figure 3.5b). Sprint times of juvenile mice were 40% greater than adults (2 to 95% increase). Adult mice (*n* = 108) weighed an average of 3.4 g (1.3 to 5.5 g) more than juveniles (*n* = 43).

Stem Density We recorded sprint times from 174 races by 27 individual mice with stem densities between 0 and 20,000 stems/m². To quantify the probability of a mouse running or hiding, we selected an inferential model that included stem density explaining log-odds of running as our inferential model (Appendix B). As we observed with litter, the odds of a mouse completing the race changed with the density of stems, but not based on age or sex of the animal (Table 3.2). For every additional 1000 stems/m², the odds of an animal completing a race decreased by an estimated 33% (95% CI = 20 to 44% decrease, Table 3.2); animals began to hide at stem densities of approximately 5,000 stems/m^2 (Figure 3.6a).

To quantify the effect stem density had on sprint times for mice that chose to run, we used an inferential model where log sprint time was explained by effects of stem density and age of the animal as parallel lines (Appendix B). Estimated mean sprint times for completed races changed with stem density and age and there was evidence of a curvilinear relationship between stem density and sprint time (Table 3.2, 3.6b). Sprint time increased up to approximately 15,000 stems/m^2, after which sprint times were likely relatively similar (Figure 3.6b). Sprint times of juveniles were estimated to be 87% greater than adults (95% CI = 23 to 184% greater, Figure 3.6b).

Acoustic Trials:

We recorded sound files for 28 individual mice from 160 trials (74 trials in native sites, 86 in invaded sites), resulting in 4000 observations between 1 and 22 kHz. Mice made more noise while moving through areas invaded by cheatgrass than through native sagebrush steppe ($F_{1,126} = 13.96$, $P < 0.001$ on 1/126 df); we did not find evidence that volume did not differ between mice of different ages or sexes. The volume created by a moving mouse differed not only between native and invaded areas, but also among recorded frequencies ($F_{21,39798} = 96.43$, $P < 0.001$ on 21/39798 df). Up to 10 kHz, we detected little difference in volume created by mice moving through native and invaded areas, but between 10 and 20 kHz, moving animals made more noise when moving through invaded areas (Figure 3.7). We found the greatest difference in volume between native and invaded areas for frequencies between 16 and 18 kHz, with estimated differences in mean volume of 3.4, 3.8 and 3.6 dB respectively (95% CIs = 3.1 to 3.7, 3.5 to 4.1, 3.3 to 3.9 dB).

Discussion

Predation can have a strong impact on how prey species interact with their environment (Kotler 1984, Gilliam and Fraser 1987, Brown et al. 1988, Simonetti 1989, Lima and Dill 1990, Creel and Winnie 2005,Garrott et al. 2008). Prey must balance resource acquisition with predation risk and tradeoffs can be altered by changes in vegetation structure associated with invasive plants (see also Chapter 2). Our findings suggest that changes in vegetation structure may impede the movement of animals, and increase the volume of noise animals make while moving. Both reduced movement ability and increased noise when moving can potentially alter the vulnerability of prey to their predators, providing potential mechanisms driving changes in abundance of small mammals found in sagebrush steppe invaded by cheatgrass (Larrison and Johnson 1973, Gano 1982, Ostoja and Schupp 2009, Hall 2012).

Animals can minimize predation risk by selecting areas where they are less detectable (Lima and Dill 1990). Noise created as prey move through vegetation can reveal their presence and location to predators, such that prey animals should minimize contact with vegetation that produces loud noise. Cheatgrass alters the ability of animals to avoid acoustic detection by predators, as mice make more noise. Animals may be unable to avoid this noisy, given that cheatgrass increases homogeneity and cover of vegetation structure and cover (Chapter 2). In addition, when mice move through cheatgrass, they make more noise at frequencies detectable by common mammalian and avian predators found in sagebrush steppe. Least weasels (*Mustela nivalis*), for example, hear best between 1 and 16 kHz (Heffner and Heffner 1987), but can still detect acoustic cues up to at least 32 kHz (Heffner and Heffner 1992); these frequencies overlap where we detected the increases in volume when mice moved through cheatgrass (10 to 20 kHz). If this frequency range is representative of the family Mustelidae, deer mice moving through cheatgrass also could be more vulnerable to predation by short-tailed weasels (*Mustela erminea*), long-tailed weasels (*Mustela frenata*), and badgers (*Taxidea* *taxus*). Coyotes and foxes (Canidae), owls (Strigiformes), and northern harrier hawks (*Circus cyaneus*), other predators of deer mice, also make use of auditory cues to detect prey (Wells and Lehner 1978) and likely hear at the frequencies where deer mice make more noise in invaded areas (Dijk 1972, Heffner and Heffner 1992).

In addition to reducing detectability by predators, prey also select microhabitat that maximizes their ability to escape predation (Lima and Dill 1990). Invasive plants can form dense stands, altering vegetation structure and heterogeneity, which can impact the ability of prey to escape predators by encumbering their movement (Rieder et al. 2010, Chapter 2). Dense vegetation structure hinders movement, and animals may be force to move through dense structure rather than avoid it as animals becomes more homogeneous. We confirmed that increased density and homogeneity of grass structure associated with cheatgrass impedes movement of mice, and further determined that movement was affected most by the increased density of stems.

Although we confirmed that dense grass slows movement of mice, we do not know if movements of predators also are impeded. Body size could affect the ability of animals to move through invaded areas, as adult mice, which were larger, were able to move faster through both litter and structure. Although short-tailed weasels are one of the smaller predators of deer mice, average mass still is 3-5 times greater than mice (Foresman 2001). Body morphology of predators could impact sprint velocity more than size; animals that are slender and quadrupedal move more quickly through cheatgrass than animals with other body types and modes of locomotion (Rieder et al. 2010). Given that most terrestrial predators of deer mice are larger than their prey and quadrupedal (e.g. coyote [*Canis latrans*], long-tailed weasel, badger), predators may be less impeded by dense vegetation structure, increasing predation risk for mice. Avian predators, such as owls and hawks (Accipitriformes), would have an even greater advantage over deer mice, as dense stems will not impede flight.

Prey do not need always need to flee and instead may hide to avoid predation, a decision based on a balance between movement ability and cover provided by the surrounding vegetation. Dense vegetation structure may provide refugia for prey to avoid capture by predators (Warfe and Barmuta 2004). We found that animals were more likely to hide as vegetation structure increased, which suggests that although dense vegetation impedes movement and increases acoustic detection, monocultures of invasive plants also could provide cover that decreases predation risk. In ecosystems with little vegetation cover, such as shortgrass prairie, changes associated with nonnative plants actually could be beneficial, subsequently resulting in increased densities of mice. Dense grass structure also could be perceived by prey as providing cover, but may not actually reduce predation risk if these areas also provide cover for predators such as snakes and weasels (Knight and Erickson 1976, Korpimaki et al. 1996, Kotler et al. 1992, Bouskila 1995).

Nonnative plants may create ecological traps in invaded areas by decoupling cues animals use to assess and mitigate predation risk from the realized risk of predation (Schlaepfer et al. 2002). Small mammals in North America do not share an evolutionary history with cheatgrass, so animals may not recognize that invaded areas increase predation risk. Although animals in some ecosystems presumably are familiar with dense native grasses, cheatgrass changes architecture of vegetation by decreasing heterogeneity of cover (Chapter 2), creating conditions that may differ from native plants. If animals assess predation risk incorrectly, mortality could be higher in invaded areas.

Predation clearly changes abundance of prey species, through both lethal and nonlethal effects (Lima and Dill 1990, Lima 1998). Vegetation structure may affect nonlethal interactions between predators and small mammals by altering predator avoidance behavior and lethal interactions if behavioral changes do not mitigate predation risk. We investigated multiple mechanisms by which cheatgrass may elevate the risk of predation for deer mice; establishing a link to population-level effects commonly documented with nonnative plants (Larrison and Johnson 1973, Gano 1982, Ostoja and Schupp 2009, Hall 2012) represents an important next step to understand invasions. Further exploration of the relative contribution of the lethal and nonlethal effects of predation and the relationship with vegetation structure will allow for better predictions of the effects of invasion by cheatgrass and other plants on small mammal populations. Distributions of many species of nonnative plants are predicted to change with altered climate patterns (Walther et al. 2007, Bradley et al. 2009, Bradley et al. 2010, Huang et al. 2011). Improving our understanding how invasive plants change ecosystems, the effects these changes have on animals, and strategies to mitigate negative impacts are essential for effective conservation and management.

Tables

Table 3.1. Inferential models 1) quantifying the probability of race completion for an average race (*n* = 308) and 2) time to complete the race (*n* = 292), for mice moving through varying depths of litter (0 to 9 cm), southwestern Montana, summer 2012.

Model	**Explanatory**	**Estimate**	**SE**	**df**	***t***	***P***
Race completion	(Intercept)	10.17	1.19	199	8.58	<0.001
	Litter depth (cm)	-0.84	0.16	74	-5.11	<0.001
Sprint time	(Intercept)	1.28	0.11	186	12.21	<0.001
	Litter depth (cm)	0.09	0.01	71	7.25	<0.001
	Age (A or J)	0.34	0.16	32	2.14	0.041

Table3.2. Inferential models 1) quantifying the probability of race completion (*n* = 174) 2) time to complete the race (*n* = 154), for mice moving through varying densities of stems (0 to 20,000 cm), southwestern Montana, summer 2012.

Model	**Explanatory**	**Estimate**	**SE**	**df**	***t***	***P***
Race completion	(Intercept)	8.16	1.29	116	6.31	<0.001
	Stem density (cm)	-0.40	0.09	27	-4.55	<0.001
Sprint time	(Intercept)	0.97	0.13	98	7.49	<0.001
	Stem density (cm)	0.29	0.03	24	10.22	<0.001
	Stem density^2 (cm)	0.62	0.20	24	-6.29	<0.001
	Age (A or J)	-0.01	0.001	28	3.05	0.005

Figures

Figure 3.1. Track used to assess movement ability of deer mice, shown with bare ground (control), southwestern Montana, summer 2012. We released animals through the opening at the far end and trials began when animals crossed the plastic flagging.

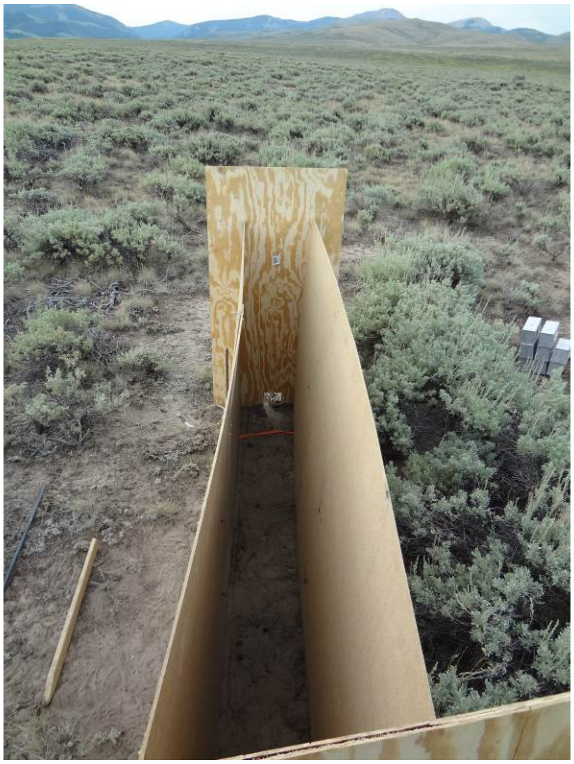

Figure 3.2. Track and the H2 Zoom unit used to record the noise made by deer mice moving through vegetation, shown in a cheatgrass-dominated site, central Montana, summer 2013.

Figure 3.3. Track used to assess movement ability of deer mice, shown with 1 wall removed to display artificial stems, southwestern Montana, summer 2012.

Figure 3.4. Track used to assess movement ability of deer mice, shown with 1 wall removed to display artificial litter, southwestern Montana, summer 2012.

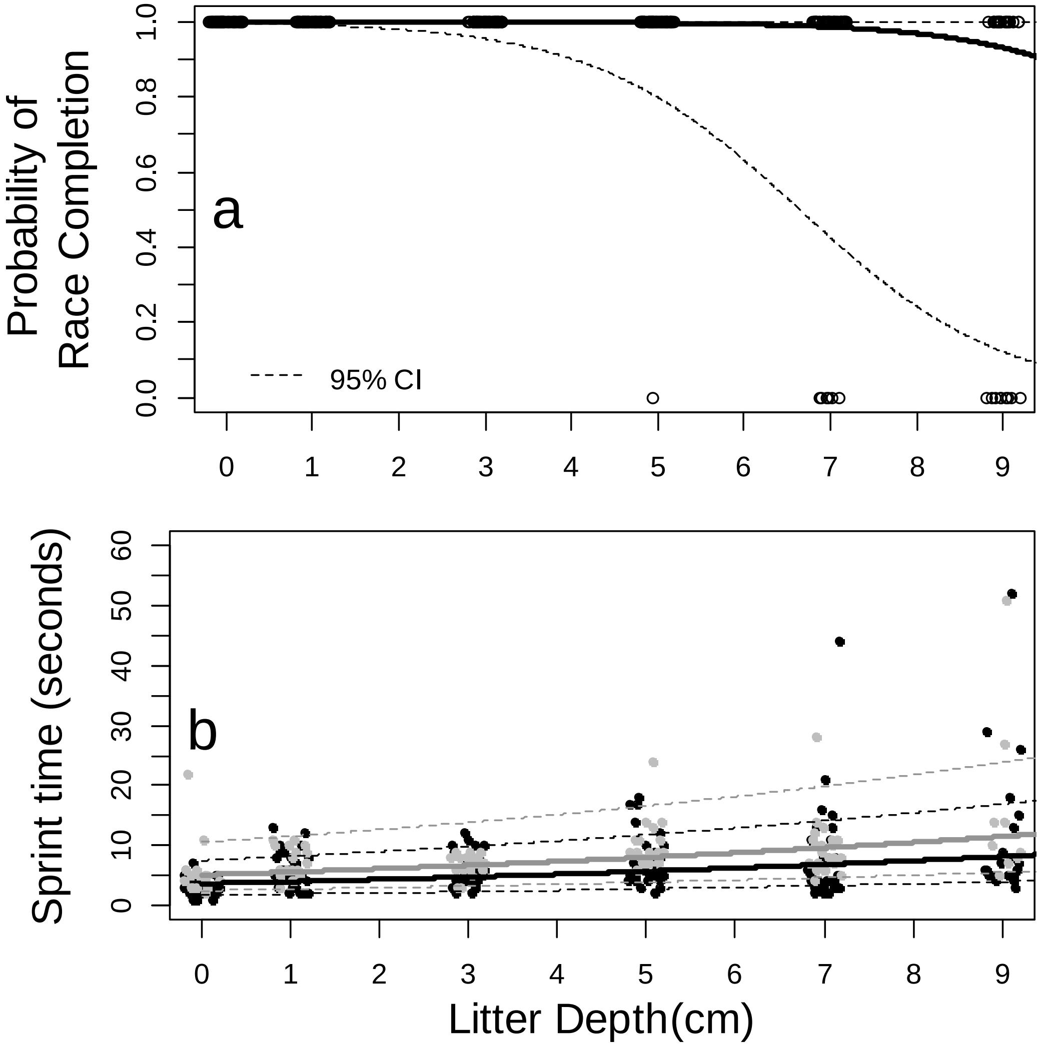

Figure 3.5. Relationship (and 95% CIs) between litter depth and (a) the probability of completing a race, and (b) sprint times of adult (black, *n* = 194 races) and juvenile (grey, *n* = 114 races) deer mice, southwestern Montana, summer 2012.

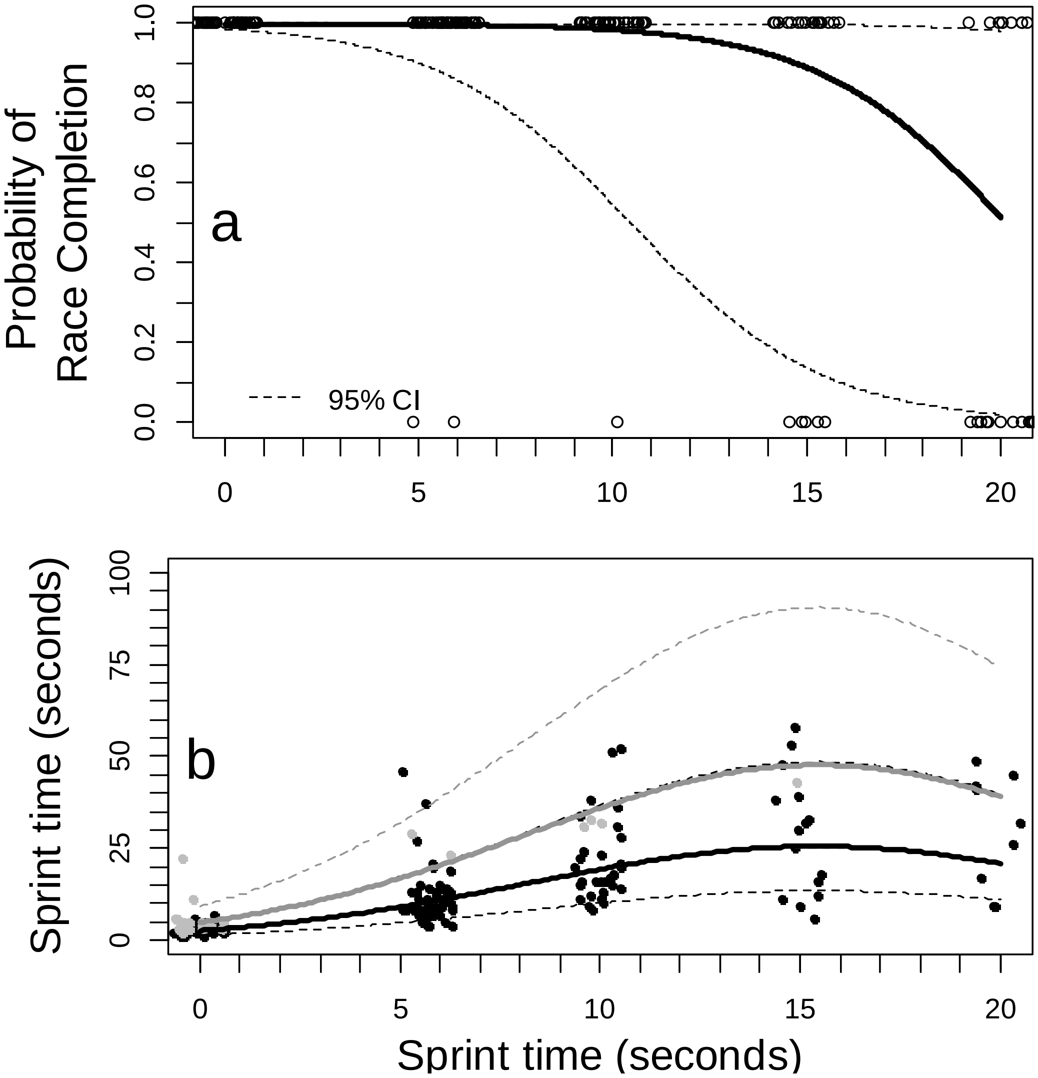

Figure 3.6. Relationship (and 95% CIs) between stem density and (a) the probability of completing a race, and (b) sprint times of adult (black, *n* = 147 races) and juvenile (grey, *n* = 14 races) deer mice, southwestern Montana, summer 2012.

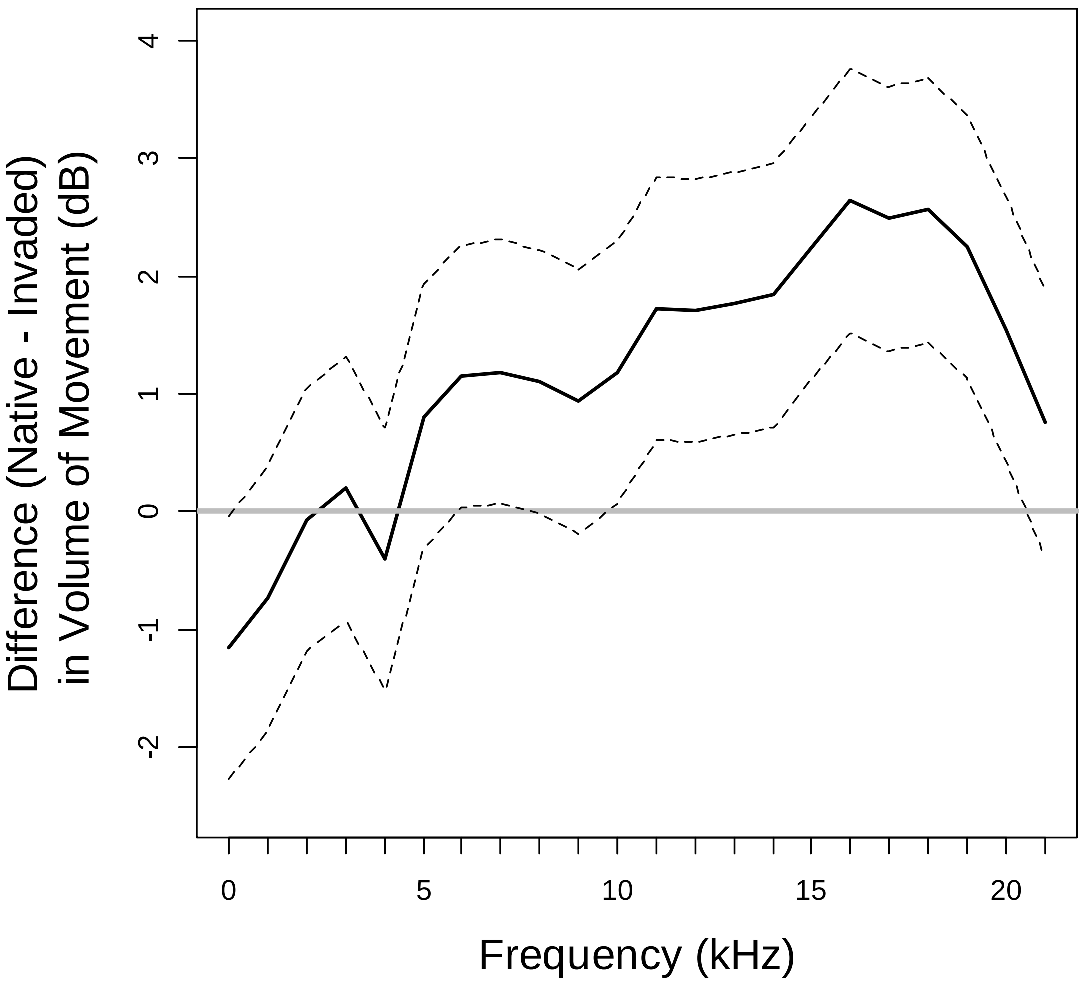

Figure 3.7. Differences in volume of noise (and 95% CIs) produced by deer mice moving through areas dominated by cheatgrass, relative to native sagebrush steppe (grey line), as a function of frequency. Difference calculated with a linear combination of the slope and intercept covariates representing the difference between noise made by movement of mice in native and invaded areas, covariance of these covariates was accounted for when calculating the variance for use in calculating confidence intervals. The reference line at zero represents no difference in the volume of noise made by movement of mice in native and invaded areas. Positive values indicate mice made louder noises when moving through areas dominated by cheatgrass and negative values indicate mice made louder noises when moving through native sagebrush steppe. We calculated differences based on a linear combination of the slope and intercept covariates representing native and invaded areas. We accounted for covariance of these covariates when calculating confidence intervals.

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CHAPTER FOUR

General Conclusions

Where cheatgrass dominates sagebrush-steppe ecosystems, small mammals may encounter reduced access to food and increased risk of predation, relative to native sagebrush steppe. We found that litter depth increased with cheatgrass invasion, which in turn, reduced access to food resources by small mammals (Chapter 2). We also confirmed that vegetation structure impedes movement of small mammals (Reider et al. 2010) and showed that dense stems decreased movement ability more than deep litter (Chapter 3). Finally, we determined that small mammals produce louder noises when moving through cheatgrass than in native dominated sagebrush steppe, possibly making them more detectable to predators (Chapter 2). These mechanisms may explain lower abundance of small mammals often found in invaded areas (Larrison and Johnson 1973, Gano 1982, Ostoja and Schupp 2009, Hall 2012).

Populations of species of small mammals in sagebrush steppe can be limited by either food resources or predation (Maron et al. 2010). Because cheatgrass seems to affect food resources as well as predation risk, cheatgrass invasion has the potential to affect diverse species. Establishing a link between these mechanisms and the population-level effects commonly documented with plant invasion (Larrison and Johnson 1973, Gano 1982, Ostoja and Schupp 2009, Hall 2012) will be important future research and represent an important advance in our understanding.

Management Implications and Future Research

Mechanisms by which invasive plants affect ecosystems are much less studied than the general effects of invasion, but exploration of these mechanisms can provide information useful for restoration (Levine et al. 2003). To increase effectiveness of treatments used to mitigate the impacts of invasive species and restore ecosystems, a stronger scientific basis for these treatments is needed (D'Antonio et al. 2004). We documented how dense litter and structure created by the invasion of nonnative grasses impact small mammals, which can be used to develop treatments specifically targeting the structural changes created by cheatgrass that affect small mammals. We could find little information on how treatments commonly used to control plant invasions, such as grazing and herbicide change vegetation structure. These management tools may not affect all structure characteristics (e.g. litter, stems, shrub cover) of vegetation equally. For instance, grazing may affect plant density plants, with little impact on the litter layer.

Shrubs provide important refugia from predation for small mammals (Kotler 1984, Simonetti 1989, Kotler et al. 1991), and may be less abundant when cheatgrass invaded sagebrush steppe (Mack 1981, Chapter 2). Decreased shrub cover commonly occurs as a result of fire in cheatgrass invaded sagebrush steppe (Mack 1981). Understanding how changes in refugia affect small mammals can provide further insight into decreases in the abundance of small mammals in cheatgrass invaded areas (Larrison and Johnson 1973, Gano and Rickard 1982, Ostoja and Schupp 2009, Hall 2012).

The use of artificial structure in experimental manipulations of vegetation structure can allow a more mechanistic understanding of the effects of plant invasions.

Thoughtful application of artificial structure (*sensu* Simonetti 1989) or the experimental manipulation of existing structure (*sensu* Pearson 2009) help researchers elucidate how the physical structure of vegetation influences animals.

Although our research focused on small mammals, changes in vegetation structure associated with cheatgrass invasion may affect other mammals (Larrucea and Brussard 2008), birds (Knick and Rotenberry 2000, Crawford et al. 2004), and reptiles (Newbold 2005, Rieder et al. 2010) in the sagebrush steppe. Some species are sagebrush obligates, such as greater sage grouse (Centrocercus *urophasianus*) and pygmy rabbit (*Brachylagus idahoensis*), that currently are decreasing in abundance (Crawford et al. 2004, Larrucea and Brussard 2008). Although the effects on both species have been documented when sagebrush dominated shrublands are converted to cheatgrass dominated grasslands (Knick and Rotenberry 2000, Crawford et al. 2004, Larrucea and Brussard 2008), no research has sought to explore how structural changes effect predation or food availability for either species. Future research into how cheatgrass structure affects these and other sensitive species found in sagebrush steppe could lead to the development of management techniques to help slow or reverse population declines.

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APPENDICES

APPENDIX A

OPTIMIZING SAMPLE SIZE FOR FORAGING EXPERIMENTS USING A POWER ANALYSIS

Purpose

In ecological studies, balancing the need to collect a large amount of data to draw precise conclusions about treatment effects with limited resources can be problematic. Power analyses provide a rigorous method to help guide study design by allowing researchers to calculate a sample size needed to detect a practically meaningful treatment effect under a set of assumptions: (1) a specified type-II error rate (or power), (2) a type-II error rate (or confidence level), (3) a specified practically meaningful difference, and (4) estimates of background variability for the model to be used. In one use of this technique, calculating the type II error rate across study designs allows a researcher to find a minimum number of replicates needed to discern a fixed treatment effect under the specified values used for calculations. The researcher can use this information, along with estimates of cost or time required, to estimate an adequate sample size for an experiment that will not exceed budget requirements.

We used a simulation based on data collected during foraging experiments over the summer of 2012 to conduct a power analysis and explore efficient study designs to maximize limited resources for experiments conducted in 2013 (Chapter 1 for study details).

Methods

Experimental design

In 2012, we established 17 sites with 64 foraging stations each spaced 10 m apart in a grid. Every other station within each site was systematically treated with artificial grass structure to increase either depth of litter or density of stems (32 stations); the remaining stations were left untreated as controls. Of the 17 sites, 6 were treated with stems, 5 with litter, and 6 served as controls. We placed a measured amount of grain at each station for 5 consecutive nights and we recorded the amount of grain removed by small mammals each night.

Although we were able to estimate treatment effects with the design used in 2012, we felt that we might be able to create a sampling design for 2013 that: 1) used sites with fewer foraging stations within sites, and 2) used fewer sites, but would still be able to detect a meaningful treatment effect. Reducing the number of sites and the foraging stations within sites would reduce project costs. In 2013, we also wanted to add an additional structural manipulation where litter and stems would be applied together. We thought that a randomized complete block design might help to reduce the number of stations and sites needed to detect a biologically relevant amount of grain from each foraging station, so we also a reasonable number of replicates of each treatment to use within each site (block).

Power analysis

We calculated the mean and variance of grain removed from a control station over 1 night, based on the data collected in 2012. Because foraging increased each night, we used the average amount removed on the 5th night, when animals were most familiar with the food resources to approximate how animals forage on natural food resources. After establishing a base foraging amount, we had to determine what difference in the amount of grain removed overnight between control and treated stations would be biologically meaningful. Deer mice (*Peromyscus maniculatus*), the dominant species of small mammal at our study sites, need approximately 3 g of food per day (Millar 1978), but because the number of animals foraging at a given station can vary with local abundance and other factors, establishing this threshold is difficult. We decided to set the minimum difference in amount of grain removed from treated stations when compared with control stations we wanted to detect at 1 g/night.

For this analysis, we used a simulation based on bootstrap iterations to calculate the power of designs with between 1 and 50 sites and between 1 and 5 replicates of the 4 treatments (litter, stems, litter and stems, control) within each site. For each iteration, we created data using the average and variance of the amount of grain removed from one foraging station placed in native vegetation during the 2012 experiment, drew weights from a normal distribution using a random normal number generator to simulate the amount of grain removed from a given foraging station in a given site. For the control stations, we drew from a distribution with a mean of 4.7 g removed/night. For treated stations, we assumed a treatment effect of 1 g, so we drew from a distribution with a mean of 3.7 g removed/night. We assumed the standard deviation on both distributions to be 1.7 g/night. We assumed no site effects in this simulation. Using a linear model with grain removed as a function of structural treatment and accounting for site (as a blocking variable), for each simulated data set, we recorded whether the true treatment effect (1 g) was actually detected according to the criteria of a p-value of greater than 0.05. This is equivalent to the 95% confidence interval excluding zero when there is a true treatment effect of 1 g, or not making a type II error. We repeated this process for 100,000 iterations per unique combination of number of sites and replication of treatments within site. After completing all iterations for a given number of sites and replicates of treatments within each site were run, we tallied the number of iterations where a treatment effect had been detected and divided this by the total number of iterations to calculate the percent of iterations where we corrected detected a treatment effect. This value is a simulation-based estimate of the power of a given design. We compared power for various designs by plotting the power of a given design by the number of sites and replicates of treatments within in site.

Results

As we expected, power to detect the 1 g difference between the average amount of grain removed from treated foraging stations and the average amount removed from control stations overnight, increased with the number of sites and the number of replicates within sites (Figure 2.3). We decided that power ≥ 0.8 would be appropriate. We could achieve this level of power with several combinations of sites and replicated: 12 sites with 5 replicates (240 foraging stations total), 15 sites with 4 replicates (240 foraging stations total), 15 sites with 3 replicates (180 foraging stations total), 22 sites with 2 replicates (176 foraging stations total), and 46 sites with no replication within sites (184 foraging stations total).

Implications

The number of replicates of the 4 treatments within each site decreased as the number of sites increased, but the number of stations generally decreased as the number of sites increased. Treating fewer sites could be beneficial by reducing time and costs associates with travelling between sites, and because finding sufficient area to adequately buffer many sites can be problematic. Treating fewer stations within each site is also desirable as this reduces material costs. We aimed to balance these two considerations by incorporating a design with a minimum of 15 sites, where we treated 3 replicates per site.

We did not account for sequential trials of this experiment over multiple nights in this analysis. By collecting data on more than 15 sites we would expect to increase power, and by collecting data collected over multiple nights, we would expect to increase power further. We considered the results of our analysis a minimum and if possible sought to increase the number of sites and survey sights over multiple nights.

Code for analysis

Note this function is written in R, and is intended to be applied to an $a \times 6$ matrix, where a is the number of unique combinations of foraging mean (for control), treatment effect size, variance of foraging mean, boot strap replications, sites, and replicates of treatment per block.

```
# Parameters:
########################
#t.u: Treatment mean
#diff: difference in treatment and control means (TE)
#sd: variance
#bs.rep: boot strap replicates
#sites: sites
#block.reps: number of replicates per block w/i site
################################
power.fxn<-function(x){
t.u<-x[1]
sd<-x[2]
diff<-x[3]
sites<-x[4]
block.reps<-x[5]
bs.rep<-x[6]
 stor.vec<-rep(0,bs.rep)
 for (i in 1:bs.rep){
	site.num<-rep(as.factor(sort(rep(1:sites,block.reps))),4)
	treat<-as.factor(c(rep("t1", (sites*block.reps)),rep("xtra1",
	(sites*block.reps)),rep("xtra2", (sites*block.reps)),rep("c", (sites*block.reps))))
	resp<-c(rnorm((sites*block.reps),t.u, sd),rnorm(((sites*block.reps)*3),(t.u - diff),
	sd))
	mod.out<-summary(lm(resp~treat+site.num))
	dv<-abs(mod.out$coefficients[2,1])
	dv.se<-mod.out$coefficients[2,2]
	t.star<-qt(.975,((sites*(block.reps*4))-(sites+3)))
	stor.vec[i]<-0<dv-dv.se*t.star
	}
sum(stor.vec)/bs.rep
}
```

Literature Cited

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APPENDIX B

MODEL SELECTION TABLES: CHAPTERS 2 and 3

Foraging experiments

Blacktail area, Summer 2012

Explanatory Variable	**df**	**L. Ratio**	***P***
Null	4		
Structure	6	29.73	<0.0001
Structure + Night	7	58.95	<0.0001
Structure + Night + (Structure × Night)	9	16.69	0.0002
Structure + Night + $Night^2$ + (Structure × Night) *	10	5.81	0.0160

Roundup and Yellowstone areas, Summer 2013

Explanatory Variable	**df**	**L. Ratio**	***P***
Null	4		
Structure	7	2.97	0.3961
Structure + Night	8	2.78	0.0954
Structure + Night +Area	9	2.66	0.103
Structure + Night +Area+ (Structure × Area) *	12	19.19	0.0003
Structure + Night + $Night^2$ + Area+ (Structure × Area)	13	2.87	0.0902
Structure + Night + Area+ (Structure × Area) + (Structure × Night)	15	1.21	0.5461
Structure + Night + $Night^2$ + Area+ (Structure × Area) + (Structure × Night)	16	2.85	0.0912

Escape ability experiments

Odds of Mice Hiding During Experiment: Litter Depth

Explanatory Variable	**Estimate**	**SE**	**df**	***t***	***P***
(Intercept)	10.56	2.28	199	4.62	<0.0001
Litter Depth (cm)	-0.62	0.77	73	-0.81	0.4220
Litter $Depth^2$ (cm)	-0.02	0.07	73	-0.36	0.7167
Age (Ad vs. Jv)	0.40	0.97	31	0.42	0.6797
Sex (M vs. F)	-1.08	0.98	31	-1.11	0.2777

Escape Ability Experiments: Litter Depth

Test for quadratic relationship of litter depth

Explanatory Variable	**df**	**L. Ratio**	***P***
Litter Depth	5		
Litter Depth^2	6	1.43	0.2322

Test for age and sex effects

Explanatory Variable	**df**	**L. Ratio**	***P***
Litter Depth	5		
Litter Depth + Age	6	4.57	0.0326
Litter Depth + Age + Sex	7	0.05	0.8222

Test for age and litter depth interactions

Explanatory Variable	**df**	**L. Ratio**	***P***
Litter Depth + Age	6		
Litter Depth + Age+ (Litter Depth × Age)	7	0.18	0.6756

Odds of Mice Hiding During Experiment: Stem Density

Explanatory Variable	**Estimate**	**SE**	**df**	***t***	***P***
(Intercept)	7.60	1.99	116	3.83	0.0002
Stem Density (1000/ m^2)	-0.28	0.33	26	-0.84	0.4109
Stem Density^2 (1000/ m^2)	-0.01	0.01	26	-0.53	0.6038
Age (Ad vs. Jv)	-2.89	1.83	27	-1.58	0.126
Sex (M vs. F)	1.24	1.24	27	1.00	0.327

Escape Ability Experiments: Stem Density

Test for quadratic relationship of stem density

Explanatory Variable	**df**	**L. Ratio**	***P***
Stem Density	5		
Stem Density^2	6	22.51	<0.0001

Test for age and sex effects

Explanatory Variable	**df**	**L. Ratio**	***P***
Stem Density^2	6		
Stem Density^2 + Age	7	9.13	0.0025
Stem Density^2 + Age + Sex	8	1.48	0.2245

Test for age class density interactions

Explanatory Variable	**df**	**L. Ratio**	***P***
Stem Density^2 + Age	7		
Stem Density^2 + Age + (Stem Density × Age)	8	0.02	0.8776

Acoustic Trials

Test for frequency effect, and how to model frequency (linear, curvilinear or categorical)

Explanatory Variable	**df**	**L. Ratio**	***P***
Invaded (Yes/ No)	5		
Invaded + Frequency (continuous)	6	71792.97	<0.0001
Invaded + Frequency^2	7	43.15596	<0.0001
Invaded + Frequency^3	8	11611.1	<0.0001
Invaded + Frequency (categorical)	26	10159.13	<0.0001

Test for effect of day

Explanatory Variable	**df**	**L. Ratio**	***P***
Invaded + Frequency (categorical)	26		
Invaded + Frequency (categorical) + Day	31	73.55321	<0.0001

Test for age and sex effects

Explanatory Variable	**df**	**L. Ratio**	***P***
Invaded + Frequency (categorical) + Day	31		
Invaded + Frequency (categorical) + Day + Age	32	1.116007	0.29078
Invaded + Frequency (categorical) + Day + Age + Sex	33	0.022533	0.880677

Test for frequency and invasion interaction

Explanatory Variable	**df**	**L. Ratio**	***P***
Invaded + Frequency (categorical) + Day	31		
Invaded + Frequency (categorical) + Day + (Frequency × Day)	52	1977.264	<0.0001