To the University of Wyoming:

The members of the Committee approve the thesis of Ian M. Abernethy presented on 4/25/2011.

Dr. Anna Chalfoun, Chairperson

Dr. Elise Pendall, External Department Member

Dr. Matthew Kauffman

APPROVED:

Dr. Frank Rahel, Head, Department of Zoology and Physiology.

Dr. B. Oliver Walter, Dean, College of Arts and Sciences

Abernethy, Ian M., Independent and Interactive Effects of Habitat and Anthropogenic Disturbance on Small Mammals. M.S., Department of Zoology and Physiology, May 2011.

Ecosystems are experiencing anthropogenic disturbances at a global scale, resulting in widespread habitat loss, fragmentation, and alteration. Yet, we know little about how habitat attributes may interact with landscape-scale human disturbance to influence local wildlife communities. Sagebrush habitats range-wide have been particularly altered. In the past two decades, energy development has increased in sagebrush habitats in the Intermountain west of North America. While responses to energy development have been documented for game species such as the greater sage-grouse (Centrocercus urophasianus) and mule deer (Odocoileus hemionus), studies documenting responses of non-game mammals are lacking. We examined the effects of structural habitat characteristics in areas with and without energy development on the abundance and diversity of small mammals in sagebrush steppe. Small mammals were live-trapped across gradients of sagebrush cover and height in 2009 and 2010 within 2 natural gas fields and adjacent control areas in the Upper Green River Basin, WY, USA. Small mammal density varied marginally across gradients of sagebrush cover and height with species-specific patterns. The density of deer mice (Peromyscus maniculatus), western harvest mice (Reithrodontomys megalotis), and reproductive individuals increased with sagebrush cover and height. Conversely, grasshopper mouse (Onychomys leucogaster) and sagebrush vole (Lemmiscus curtatus) density was inversely related to sagebrush cover and height. In addition, the density of deer mice, western harvest mice, northern grasshopper mice, juvenile individuals, and species richness were higher at energy development sites. Population estimates of deer mice showed a significant interaction between sagebrush habitat treatment and energy development. In summary, our results suggest both independent and interactive effects of habitat and disturbance on the small mammal community. Therefore both must be considered in management actions related to human disturbance. Additionally, we performed a methodological assessment of live trap types. The ability of researchers to sample small mammal populations is affected by bias introduced by trapping methods. Havahart live traps captured significantly more small mammals than expected (> 25%), while Sherman live traps captured significantly fewer small mammals than expected (< 75%) in sagebrush steppe habitats. Havahart traps captured more than expected of most species and age classes of small mammals regardless of local habitat or the presence of natural gas development. Sherman live traps captured ten species and Havahart traps captured six species across three levels of sagebrush cover and height and between sites with and without natural gas development. Use of multiple trap types in small mammal studies may reduce bias associated with sampling methods.

INDEPENDENT AND INTERACTIVE EFFECTS OF ANTHROPOGENIC DISTURBANCE AND HABITAT ON SMALL MAMMALS

By

Ian M. Abernethy

A Thesis submitted to the Department of Zoology and Physiology
and the University of Wyoming
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE
in
ZOOLOGY AND PHYSIOLOGY

Laramie, Wyoming
May 2011

ProQuest LLC.
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106 - 1346

DEDICATION

To Kristy, without your support and motivation, I never would have been able to pursue this wonderful opportunity.

ACKNOWLEDGEMENTS

First, I thank Anna Chalfoun. Her mentorship and guidance have helped me grow as a person, a scientist, and a biologist.

I thank my wife, Kristy Palmer, and my parents, Rollin and Carolyn Abernethy for instilling in me, and sharing a love of the natural world. You have provided me with unwavering love and support in life and throughout graduate school.

Finally, I thank my friends and colleagues at the University of Wyoming for their friendship and thought provoking conversations. You all made this one of the greatest experiences of my life.

Table of Contents

CHAPTER ONE. INDEPENDENT AND INTERACTIVE EFFECTS OF HABITAT AND ANTHROPOGENIC DISTURBANCE ON SMALL MAMMALS.

ABSTRACT

Ecosystems are experiencing anthropogenic disturbances at a global scale, resulting in widespread habitat loss, fragmentation, and alteration. Yet, we know little about how habitat attributes may interact with landscape-scale human disturbance to influence local wildlife communities. Sagebrush habitats range-wide have been particularly altered. In the past two decades, energy development has increased in sagebrush habitats in the Intermountain west of North America. While responses to energy development have been documented for game species such as the greater sage-grouse (*Centrocercus urophasianus*) and mule deer (*Odocoileus hemionus*), studies documenting responses of non-game mammals are lacking. We examined the effects of structural habitat characteristics in areas with and without energy development on the abundance and diversity of small mammals in sagebrush steppe. Small mammals were live-trapped across gradients of sagebrush cover and height in 2009 and 2010 within 2 natural gas fields and adjacent control areas in the Upper Green River Basin, WY, USA. Small mammal density varied marginally across gradients of sagebrush cover and height with species-specific patterns. The density of deer mice (*Peromyscus maniculatus*), western harvest mice (*Reithrodontomys megalotis*), and reproductive individuals increased with sagebrush cover and height. Conversely, grasshopper mouse (*Onychomys leucogaster*) and sagebrush vole (*Lemmiscus curtatus*) density was inversely related to sagebrush cover and height. In addition, the density of deer mice, western harvest mice, northern grasshopper mice, juvenile individuals, and species richness were higher at energy development sites. Population estimates of deer mice showed a significant interaction between sagebrush habitat treatment and energy development. In summary, our results suggest both independent and interactive effects of habitat and disturbance on the small mammal community. Therefore both must be considered in management actions related to human disturbance.

INTRODUCTION

Anthropogenic disturbance that can result in habitat loss, fragmentation, and other changes in habitat quality is now a virtually ubiquitous aspect of managing wildlife populations (Saunders et al. 1991, Fahrig 2003). Consequently, human disturbance has been cited as one of the chief threats to global biodiversity (Wilcox and Murphy 1985, Saunders et al. 1991, Debinski and Holt 2000, Fahrig 2003). Simultaneously, landscapes generally consist of gradients of habitat structure, composition, and quality for wildlife species (Fretwell and Lucus 1970). And the occurrence and fitness consequences of habitat use for individual species can vary across these gradients (Chalfoun and Martin 2007, Grear and Burns 2007). Yet, while there is a growing body of research evaluating the consequences of habitat alteration on wildlife species, we lack a general understanding of how wildlife species respond to disturbance across local habitat gradients (Burns and Grear 2008). An important remaining question is whether local-scale habitat heterogeneity interacts with disturbance to either exacerbate or ameliorate effects generated by disturbance, or conversely, whether effects of disturbance and habitat are largely independent.

Small mammals are ideal for testing hypotheses about disturbance and habitat effects because they are locally abundant and have short generation times making it possible to detect changes in populations after relatively short time periods (Steele et al. 1984). Additionally, small mammals are an important focal assemblage because they contribute to local biodiversity, serve as a prey base for raptors, other mammals, and reptiles (Sureda and Morrison 1999), affect vegetation communities through seed dispersal and seed predation (Kaufman 1988, Kaufman 2000), and contribute to soil nutrient cycling though burrowing activities (Pearson et al. 2001).

There is clear evidence that habitat heterogeneity alters the distribution and abundance of small mammal species across a wide variety of ecosystems (O'Farrell 1980, Parmenter and MacMahon 1983, Kaufman 2000, Person et al. 2001, Reed et al. 2005, Burns and Grear 2008). Habitat influences critical resource availability such as food, burrow sites, and refugia from predators (Paramenter and MacMahon 1983), and the distribution of these resources and species-specific microhabitat requirements influence patterns of small mammal occurrence and abundance (O'Farrell 1980, Parmenter and MacMahon 1983). With habitat loss, the attributes and quality of remaining habitat patches change. And whether local-scale habitat attributes interact with large-scale disturbance effects to determine local small mammal community structure is unknown.

Changes in habitat caused by disturbance may lead to altered predation risk for small mammals (Brown and Kotler 2004). Temporal and spatial distribution of small mammal predators may change in response to anthropogenic disturbance (Richardson and Miller 1997, Kitchen et al. 2000 Mezquida et al. 2006, Martínez-Abraín et al. 2010).

Additionally, predation risk can vary with local habitat characteristics (Brown and Kotler 2004). Small mammals assess the predation risk of foraging in a particular habitat (Brown 1988, Brown and Kotler 2004). Ultimately, occupying an inherently risky habitat will result in decreased survival and fitness (Gilliam and Fraser 1987, Brown and Kotler 2004). The risk of predation perceived by a small mammal can be measured using Giving-Up Densities [GUDs] (Brown 1988, Brown and Kotler 2004). Giving-up Densities are the density of food resources remaining within a patch at which an individual stops foraging (Brown 1988). The GUD of an individual forager should correspond to a balance of the energy required for foraging, the predation cost, and the missed opportunity cost of not engaging in alternate behaviors such as territory maintenance and finding mates (Brown 1988). For example, an individual should deplete food resources more in a safe environment than in a risky environment. The abundance of food resources, predation risk, and other factors that influence habitat use vary with habitat heterogeneity. Similarly, GUDs should vary, depending on how individuals perceive the costs and benefits associated with foraging in a particular patch (Brown 1988, Schmidt and Ostfeld 2003). In a disturbed landscape, habitat structure, predator density, food availability, and other factors may differ from unaltered landscapes. Comparing GUDs among different patch types allows for an evaluation of the effects of habitat and disturbance the foraging behavior of small mammals, and may reveal biological mechanisms explaining patterns of abundance or distribution of small mammals (Brown 1988).

Sagebrush steppe is one of the most altered ecosystems in North America (Knick et al. 2003). Less than one percent of sagebrush steppe remains in pristine condition due to alteration for agriculture, urban development, energy extraction and other land uses (Paige and Ritter, 1999, Knick et al. 2003). Moreover, much of the remaining sagebrush steppe is now fragmented. Yet, little is known about the effects of these land use changes and associated human activity on sagebrush wildlife (Knick and Rottenberry 1995, Beever and Brussard 2004, Knick et al. 2003, Leu et al. 2008). More recently, natural gas and oil extraction has steadily increased across the Intermountain West, with many large-scale energy development projects occurring within sagebrush habitats (Knick et al. 2003, Bureau of Land Management 2005). In Wyoming, as of 2009, leases for more than 1.5 million ha were producing oil and natural gas while leases for more than 5 million ha had been approved for development (U.S. Department of the Interior [USDI] 2010*a, b*). Energy development inevitably results in habitat loss and fragmentation from the construction of roads, well pads, pipelines, and other infrastructure. Negative impacts of these projects have been documented in game animals like mule deer and sage grouse (Doherty et al. 2006, Sawyer et al. 2009, Harju et al. 2010) whereas other non-game taxa such as songbirds (but see Gilbert and Chalfoun 2011) and small mammals have received little attention.

We examined wildlife responses to anthropogenic disturbance across habitat gradients using small mammals occupying sagebrush steppe as a model system. We tested whether large-scale disturbance due to energy development interacted with local habitat attributes to influence the structure of the small mammal community. Our specific objectives were to quantify small mammal community composition and abundance across habitat gradients of low, medium, and high sagebrush cover and height within and outside of natural gas fields. Additionally, we performed a GUD experiment to examine percieved predation risk as a potential mechanism behind observed differences in small mammal abundance across habitat gradients and between energy development and control sites.

STUDY AREA

Our study was conducted within the Upper Green River Basin (42° 60’ N, 109° 75’ W) in western WY, USA. Sites were located within sagebrush habitats within the Pinedale Anticline and Jonah natural gas fields and adjacent areas away from energy development. The Pinedale Anticline and Jonah natural gas fields are among the most productive and concentrated energy development areas in North America (BLM 2006, 2008). The vegetation in the study area is primarly comprised of Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) with native forbs and grasses dominating the understory (Holloran et al. 2010). Annual precipitation averages 27.6 cm (Western Regional Climate Center 2011).

METHODS

Site Selection

To guarantee that sampling spanned a gradient of sagebrush cover and height, we established 3 a priori habitat treatment levels based on the range of sagebrush cover and height that exists within the study area. Shrub cover and height tend to covary within the study area, with the landscape ranging from low, sparse shrub cover to tall, high cover areas dominated by Basin big sage (*A. tridentata tridentata*), especially along moister areas with well drained soils such as ephemeral drainages. We stratified the study area into approximate cover classes which were: low (5 to 10% shrub cover and a height of less than 25 cm), medium (15 to 26% shrub cover and a height of 40 to 60 cm), and high (greater than 26% shrub cover and height greater than 100 cm) treatments. All sites were randomly selected across the study area using a high resolution (2 m) shrub cover map in a Geographic Information System [GIS] (USGS Fort Collins Science Center, Fort Collins, CO) and were ground-truthed prior to final site selection. We selected energy development sites with 2 to 4 natural gas well pads per 500 m moving window in a GIS (USGS Fort Collins Science Center, Fort Collins, CO). Control sites were located at least 1 km from natural gas activity. We sampled 3 sites within each habitat-energy development treatment combination in 2009 (total n = 18). In 2010, we trapped the same 18 sites examined in 2009 and added 2 replicates within each habitat-energy development treatment combination (total n = 30).

Small Mammal Abundance and Species Richness

At each site we quantified density by species, and species richness and diversity using mark-recapture techniques. We used 1 ha, 10 by 10 live-trapping grids with 10 m spacing between trapping stations. Because remaining stands of Basin big sagebrush in the study area are largely confined to narrow ephemeral channels; however, trapping grids at high sagebrush sites varied in shape to maintain trapping stations within this cover type. Paired sets of control and energy development sites of the same sagebrush habitat class were trapped concurrently. Each grid was trapped once between 15 May and 30 June and once between 1 July and 31 August to examine seasonal differences and account for potential temporal population fluctuations.

We used Sherman® (model LAFTG) and small Havahart® (model 1020) traps to sample small mammals. Havahart traps have mesh sides and doors at both ends of the trap. Some species may be more willing to enter this type of trap, and we wanted to maximize our odds of sampling the entire community (O'Farrell et al. 1994). Sherman traps comprised 75% and Havahart traps comprised 25% of all traps. In 2009, 2 traps were placed at each trapping station and alternated between 2 Sherman traps and 1 Sherman and 1 Havahart trap. In 2010, 1 trap was placed at each station with Havahart traps placed at every fourth station. Traps were baited with peanut butter and rolled oats and contained polyester bedding material for thermoregulation. Traps were opened at dusk each day and checked for captures at dawn the following day for 4 consecutive nights. Traps that were sprung but empty were recorded, and were counted as 0.5 trap-nights to adjust for trapping effort.

We identified each captured individual to species, recorded the sex, and measured mass, total length, and tail length. Because age class and the number of reproductively active individuals at a site can provide inference as to local habitat quality (Van Horne 1983), we also determined age class (juvenile or adult) and reproductive status for each individual. Female reproductive condition was classified as non-reproductive, swollen abdomen, lactating, and post lactating while males were considered either non-reproductive or scrotal. Juveniles were identified by pelage. All individuals were classified as either reproductive or juvenile for analysis. In 2009, individuals were marked by hair trimming. In 2010, individuals were marked in both ears with small Monel ear tags (model 1005-1, National Band and Tag Co.).

We used the number of unique individuals as an index for small mammal abundance for all species. We used the mean maximum distance moved (MMDM) of all species pooled from individually marked animals in 2010 to calculate the effective trapping area and converted abundance estimates to estimates of density for all species for both 2009 and 2010 (Wilson and Anderson 1985). We used the Shannon-Wiener Index to calculate diversity (Shannon and Weaver 1963). In 2010, we used program MARK to more rigorously estimate population sizes (White and Burnham 1999). However the only species for which had sufficient captures for these analyses were deer mice. Population estimates were made from mark-recapture data using the closed capture model. Model parameters were estimated collectively for sites within each sagebrush category for both natural gas and control sites during each trapping session due to small sample sizes (Converse et al. 2006). Our data did not allow us to evaluate multiple models with multiple parameters using an information-theoretic approach (Bagne and Finch 2010). Therefore, we chose to estimate a single model that estimated abundance while holding capture (*p*) and recapture (*c*) probabilities constant through time with minimal parameters to obtain the best possible population estimate.

All protocols followed American Society of Mammalogists guidelines (ASM 2007) and were approved by the University of Wyoming Institutional Animal Care and Use Committee.

Habitat Measurements

We quantified microhabitat characteristics to account for potential differences in small mammal assemblages due to local habitat variation. At each site, we measured shrub height, density, and percent cover of sagebrush shrubs. Additionally, we measured percent understory cover of bare ground, litter, rock, grass, and forbs. Prior to sampling, each grid was divided into 8 sections. A trap station within each section was randomly selected as a starting point for survey transects to ensure that the entire area was sampled. Transects were 15 m long and ran in a randomly selected direction. The line intercept method was used to estimate percent cover of shrubs (Lucas and Seber 1977, Bonham 1989). We estimated shrub density by counting all shrubs within 0.5 m of the 15 m transect within 5 height categories: 0 to 15cm, 15 to 30cm, 30 to 60cm, 60 to 90 cm, and >90cm. We used the point intercept method with points located every 0.3 m to estimate the percent cover of bare ground, litter, and rock, and percent cover and basal area of grass and forbs (Bonham 1989). We conducted habitat measurements randomly throughout the summer season to limit bias due to vegetation phenology, alternating between replicates inside and outside of energy development areas.

Giving-Up Densities

We collected GUDs using artificial food patches to assess perceived predation risk in 2010 (Brown 1988, 1989, Pusenius and Schmidt 2002, Brown and Kotler 2004). GUDs were measured once at each site concurrently with live trapping to account for small mammal density at the site. Artificial food patches were located within the same habitat type and energy development treatment as the adjacent live-trapping grid but were at least 250 m away to eliminate the possibility of drawing individuals away from the grid. Sites were selected by choosing a random direction from the grid center. Artificial food patches consisted of trays (30 cm in diameter) filled with 0.25 l of sand mixed with 15 g of unhusked millet seed (Brown 1989). Four food patches placed 30 m apart were set out near dusk and collected the following day near sunrise. The remaining millet seeds were then separated from the sand using a sieve. We obtained the mass of the millet seeds as our response variable for analyses.

Statistical Analyses

We analyzed the density of each species, species richness and diversity, the number of juveniles for all species, and the number of reproductive individuals for all species pooled across sagebrush habitat classes and between energy development and control sites via repeated-measures general linear mixed models (hereafter GLMMs) in SPSS 18 (SPSS Inc., Chicago, IL USA) using 2 main approaches. First, using the 18 sites sampled in both 2009 and 2010, we compared all response variables in order to document potential seasonal and year effects. Each trapping occasion was treated as a repeated measure on the experimental units (grids) and sagebrush habitat class and energy development treatment were included as fixed factors. Year and seasonal effects were evaluated using Bonferroni post-hoc tests. Secondly, we compared the same response variables using the complete set of spatial replicates trapped in 2010 (n = 30) to evaluate habitat and energy development effects. Again, each trapping occasion was treated as a repeated measure on the experimental units (grids), and sagebrush habitat class and energy development treatment were included as fixed factors.

We compared the density estimates obtained from the MARK analysis of deer mice using the 2010 trap data and repeated measures GLMMs. Trapping occasion was treated as the repeated measure on the grids. Sagebrush habitat class and energy development treatment were included as fixed factors. Dependent variables were density of deer mice, the number of juveniles, and the number of reproductive individuals.

We analyzed GUDs across habitat gradients of sagebrush cover and height and between natural gas development and control sites using GLMMs. Sagebrush height and cover class, and control or energy development were included as fixed factors. We also used Pearson correlations to relate small mammal densities to GUDs observed in each sagebrush class and between natural gas and control sites (Reed et al. 2005).

We selected microhabitat covariates in an a priori fashion using only metrics that were relevant for the natural history of each species. For sagebrush voles, we selected percent cover of forbs and grass because they are important food sources (Mullican and Keller 1985). We included percent bare ground as a covariate for northern grasshopper mice because evidence suggests decreased vegetation allows for more efficient foraging on invertebrates (Stapp 1997). Because least chipmunks, deer mice and western harvest mice are habitat generalists, we would expect the architecture of sagebrush shrubs to dictate densities of these species and did not include additional habitat metrics in these models (Parmenter and MacMahon 1983).

RESULTS

We obtained a total of 7,510 captures of 13 species in 56,712 trap nights. Of these, 2,856 individual small mammals were captured (Tables 1, 2). We obtained 3,158 and 4,352 total captures, with 1,350 and 1,506 unique individuals, in 2009 and 2010 respectively. Of these, deer mice were the most abundant species comprising 81.9% of total individuals (Tables 1, 2). The mean maximum distance moved for all species at all grids was 30.48 m, equating to an effective trapping area of 2.59 ha.

We did not observe significant differences in percent canopy cover ($F_{1,28} = 0.65$, $P = 0.43$) or shrub height ($F_{1,28} = 0.15$, $P = 0.70$) within each sagebrush habitat class between control and energy development sites. Understory habitat characteristics were also similar across energy development treatments (Table 3). Shrub canopy cover and height varied marginally from our predefined sagebrush habitat classes (Figure 1). However, sagebrush habitat classes had significantly different percent canopy cover ($F_{2,27} = 7.59$, $P < 0.01$) and shrub height ($F_{2,27} = 120.85$, $P < 0.01$) from each other (Figure 1).

Seasonal and Annual Variation in Density

We did not observe any significant time by sagebrush habitat class, time by energy development treatment, or time by sagebrush habitat class by energy development interactions for any response variable. Significant seasonal changes in density were observed for deer mice, northern grasshopper mice, western harvest mice, and least chipmunks, the number of juveniles and the number of reproductive individuals in at least one year of the study (Figure 2). Significant inter-annual differences in density were observed for the northern grasshopper mouse, western harvest mouse, least chipmunk, and the total number of reproductive individuals (Figure 2).

Energy Development and Sagebrush Habitat Class Interactions

We did not observe any sagebrush habitat class by energy development interactions for response variables using the number of unique individuals, indicating that these variables did not respond differently with respect to sagebrush habitat classes or energy development treatments.

Energy Development

The density of 3 species (deer mice, northern grasshopper mice, and western harvest mice), juveniles, and species richness were significantly higher at sites with energy development (Table 4). Densities of least chipmunks, sagebrush voles, reproductive individuals, and diversity were similar between natural gas and control sites.

Sagebrush Habitat Gradients

There were no significant differences between our response variables and sagebrush habitat class, but marginal differences in densities of 3 species and the densities of reproductive individuals were observed (Table 4). The density of deer mice and reproductive individuals increased marginally with increasing sagebrush cover and height. Sagebrush voles showed the opposite trend, with density marginally decreasing with increasing sagebrush class while accounting for percent cover of grass ($F_{1,24} = 5.94$, $P = 0.02$), and forbs ($F_{1,24} = 1.81$, $P = 0.19$) in the understory. Similarly, northern grasshopper mice decreased in density with increasing sagebrush class while accounting for percent cover of bare ground ($F_{1,24} = 1.45$, $P = 0.24$). Least chipmunks, western harvest mice, and the density of juveniles had similar densities across sagebrush habitat treatments. Both species richness and diversity were similar across sagebrush habitat treatments.

Density Estimates of Deer Mice From Program MARK

There was a significant time by sagebrush habitat class interaction (Wilks' $\Lambda = 0.76$; $F_{2,24} = 3.73$, $P = 0.04$). Low and medium sagebrush sites had lower densities of deer mice than the high sagebrush sites during the first trapping occasion, but during the second trapping occasion, the low and medium sagebrush gradients had higher densities than the high sagebrush sites. We also observed a significant sagebrush habitat class by energy development treatment level interaction ($F_{2,24} = 5.26$, $P = 0.01$). Densities of deer mice were higher at energy development sites at the high and low end of the habitat gradient whereas control sites had higher densities at the middle of the habitat gradient (Figure 3).

GUDs

We did not observe any significant differences in GUDs between energy development or control sites ($F_{1,21} = 1.86$, $P = 0.19$) or among sagebrush habitat classes ($F_{2,21} = 2.09$, $P = 0.15$). However, GUDs were consistently higher at control sites and at the lower end of the sagebrush habitat gradient (Figure 4). Local small mammal density was negatively correlated with GUDs ($r = -0.42$, $P = 0.02$).

DISCUSSION

Anthropogenic activities have altered most ecosystems, and changes in community composition, abundance, distribution, and behavior of wildlife have been attributed to these disturbances (Saunders et al. 1991, Gehring and Swihart 2004). Researchers have described disturbance effects for a diverse array of wildlife taxa. However, few of these have evaluated how populations respond to disturbance across local habitat gradients. Realizing that individual species may respond to disturbance differently depending on local habitat structure and composition is critical to successful wildlife management in the face of large-scale disturbance.

Declines in sage-grouse (Harju et al. 2010), mule deer (Sawyer et al. 2009), and sagebrush-obligate songbirds (Gilbert and Chalfoun 2011) in areas altered by energy development signal fundamental changes in habitat and wildlife communities reliant on sagebrush habitats. Similarly, small mammal communities were different at sites with natural gas development than at control sites. These differences can be attributed to disturbance effects rather than temporal fluctuations or site differences because observed patterns were consistent between years and microhabitat did not differ significantly between control sites and energy development sites within habitat classes.

Species-specific and population-level effects of natural gas development were observed. Sites with natural gas development had higher densities of deer mice, northern grasshopper mice, and western harvest mice. Control sites did not have higher densities of any species. However, differences in densities of rare species that occur at low densities on the landscape, such as the sagebrush vole, may have been difficult to detect due to low capture rates.

Changes in demographic rates and age structure of populations influenced by anthropogenic disturbance may signal changes in habitat quality. However, the density of a species may not accurately reflect local habitat quality (Van Horne 1983). The number of juvenile small mammals was higher at energy development sites, with the majority of juvenile individuals being deer mice. However, the density of reproductive (adult) individuals was similar between control and natural gas sites. Taken together, natural gas development may increase habitat quality for deer mice.

Generally, species richness is expected to decline in areas exposed to anthropogenic disturbance. Contrary to expectation, species richness was higher at natural gas sites than at control sites while diversity was similar between the two. However, other researchers in this and other systems have reported similar patterns. For example, small mammal diversity was similar near and away from Interstate 15 in Utah

USA (Bissonette and Rosa 2009). Similarly, in the Chihuahuan Desert, the number of species captured was higher at disturbed sites than away from disturbance (Stacey and Post 2009). These results have been attributed to increased habitat heterogeneity. Other studies have found that species richness in sagebrush steppe habitats decreases with high levels of fragmentation (Hanser and Huntly 2006). Natural gas fields are highly fragmented, and most will experience increased intensity of development in the future (BLM 2005). Altered small mammal communities are more likely as well densities increase, and as time since disturbance become greater.

Natural gas development inevitably results in habitat loss, fragmentation, edge effects, and other changes in habitat quality. Clearly, increased well densities and associated infrastructure result in more direct habitat loss, a greater degree of fragmentation, and intensified edge effects (Fletcher 2005, Sawyer et al. 2009). The density of wells examined in this study ranged from 2.5 to 5.1 wells/km^2. This represents a relatively low density of development across the study area (range: 0 to 22 wells/km^2) (Sawyer et al. 2009, Gilbert and Chalfoun 2011). Declines of sagebrush-obligate songbirds have been observed in the presence of natural gas development, with the greatest declines in areas with well densities higher than 8 wells/km^2 (Gilbert and Chalfoun 2011). Because development is increasing in the study area and across the Intermountain west (BLM 2005), wildlife communities, including small mammals, may similarly be impacted.

Heterogeneity of local habitat alters the distribution and abundance of small mammals (O’Farrell 1980, Swihart 2003, Burns and Grear 2008). Small mammal species were indeed partitioned differently along sagebrush habitat gradients. For example deer mouse density increased marginally with increasing sagebrush cover and height. Conversely, northern grasshopper mouse and sagebrush vole density decreased marginally with increasing sagebrush cover and height. Species specific-differences in distribution with respect to habitat structure indicate that habitat heterogeneity is important in maintaining regionally diverse small mammal assemblages (Grear and Burns 2007).

Interactive effects of local habitat structure and anthropogenic disturbances have been observed in some ecosystems (Manor and Saltz 2008, Manor et al. 2008). These interactions are complex and poorly understood. Furthermore, these patterns have not been investigated in many systems but may be extremely important in maintaining small mammal communities in disturbed habitats. In Mediterranean forests, research indicates that species' responses to anthropogenic disturbance differ based on local habitat structure (Manor and Saltz 2008). In our study, interactions between sagebrush habitat classes and natural gas treatments were observed when using population estimates of deer mice obtained from MARK. Deer mice densities were higher at low and high sagebrush sites with natural gas development, while they were marginally higher at medium sagebrush sites without natural gas development. Sites at the extremes of our habitat gradient (low and high sagebrush habitat classes) may be the most altered following disturbance. Sites in the low sagebrush habitat class initially had low vegetative cover. Following disturbance and subsequent re-colonization of native and exotic grasses and forbs, an increase of food resources available to deer mice at these sites may occur. Sites within the high sagebrush habitat class experience the highest degree of structural change in vegetation post-construction, reducing available refugia from predators. Management practices that take disturbance and habitat interactions into account may be vital for maintaining intact small mammal communities in the face of natural gas development.

Increases in a single generalist species may have widespread consequences for the entire wildlife community. The ability of a species to utilize a wide variety of food and habitat is a primary determinant of a species' ability to persist in human-altered landscapes (Swihart et al. 2003). Deer mice are one of the most widespread generalist species in North America, and were the most abundant species in our study. Densities of deer mice were higher at sites with natural gas development. This is consistent with other research in sagebrush habitats examining the effects of grazing (Beever and Brusard 2004), roads and windmills (Stacey and Post 2009), and exotic grass invasions (Longland 1994). The spatial distribution of small mammal populations is due in part to interspecific interactions (O'Farrell 1980, Bissonette and Rosa 2009). In unaltered ecosystems, both generalist and specialist species coexist with varying densities, largely regulated by competitive interactions (Manor and Saltz 2008). In human altered ecosystems, generalist species often out-compete specialist species because of altered habitat structure and food resources (Manor and Saltz 2008). Specialist species such as sagebrush voles (Beever and Brusard 2004) and red-backed voles (Lemaitre et al. 2010) may be displaced via interspecific competition with deer mice. Ultimately, small mammal communities in high disturbance areas may be dominated by a single generalist species, with local extinctions of specialist species (Manor et al. 2008).

Local habitat and the presence of energy development may alter the behavior of small mammals. Control sites had consistently higher GUDs than sites with natural gas development. Sites with low sagebrush cover and height had higher GUDs than sites with medium or high sagebrush cover. Higher GUDs indicate increased perception of predation risk by small mammals. Indeed, many raptor species, a primary predator of many small mammals, show avoidance patterns to anthropogenic disturbance (Richardson and Miller, 1997, Martínez-Abraín et al. 2010). Rodents are also a primary prey item of coyotes (*Canis latrans*) in sagebrush habitats (Mezquida et al. 2006). Coyotes often alter their activity patterns to minimize their contact with humans (Kitchen et al. 2000). Alteration of spatial distribution and behavior of predators may lead to changes in the abundance and distribution of prey. This pattern is consistent with our data. Small mammals in areas with natural gas disturbance may experience reduced predation allowing for increased foraging time, reproduction, and survival. This may be particularly evident in areas that have both natural gas development and high sagebrush cover, as increasing shrub height and cover reduces predation risk of small mammals (Kotler and Brown 1988, Ostoja and Schupp 2009). Deer mouse densities were highest in these areas, and may further alter species interactions.

In conclusion, we documented changes in a sagebrush small mammal community that included both independent and interactive effects of local habitat structure and natural gas development. Interactive effects of habitat and anthropogenic disturbance on wildlife populations are complex and poorly understood. Because changes in habitat associations and competitive interactions caused by disturbance change differently across habitat gradients, an understanding of species-specific responses is vital for effective management of altered systems.

MANAGEMENT IMPLICATIONS

Small mammals occupying sagebrush habitats are an important component of biodiversity and are vital for many community functions. We present evidence that natural gas development in sagebrush steppe ecosystems changes small mammal communities. Moreover, these impacts differed when accounting for variation in microhabitat structure. Furthermore, some small mammal species respond positively to disturbance while others may be negatively affected. While managers often consider and manage non-game species such as small mammals as a unit, habitat requirements are species-specific, and responses to disturbance may vary with local habitat structure and composition. Ultimately, it is important to take local habitat into account when planning future energy development projects and the placement of well pads, roads, pipelines, and other infrastructure. Management recommendations for reducing impacts for mule deer and sage-grouse include reducing surface disturbance and maintaining large areas of undeveloped sagebrush habitats that include a diversity of sagebrush canopy cover and heights (Sawyer et al. 2009, Holloran et al. 2010). These recommendations would likely benefit small mammal communities as well. In particular, we suggest avoiding placing natural gas infrastructure near or in areas with Basin big sagebrush. Basin big sagebrush has become a rare component of sagebrush habitats, and dramatic increases in deer mouse abundance when these areas are altered coupled with the potential for resulting altered trophic dynamics warrants caution for future developments.

ACKNOWLEDGEMENTS

Project funding was provided by the Wyoming Game and Fish Department. We thank the Wyoming Cooperative Fish and Wildlife Research Unit, especially M. Larson for logistical support. Input for study design was provided by S. Germain and M. Grenier. M. Ben-David graciously provided assistance with population modeling in MARK. Assistance with site selection and GIS was provided by M. O'Donnell of the USGS Fort Collins Science Center. Finally, we are grateful for the statistical assistance provided by S. Bieber and J. Weatherford.

LITERATURE CITED

American Society of Mammalogists Animal Care and Use Committee. 2007. Guidelines of The American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809-823.

Bagne, K.E., and D.M. Finch. 2010. Response of small mammal populations to fuel treatment and precipitation in a ponderosa pine forest, New Mexico. Restoration Ecology 18:409-417.

Beever, E.A., and P.F. Brussard. 2004. Community- and landscape-level responses of reptiles and small mammals to feral-horse grazing in the Great Basin. Journal of Arid Environments 59:271-297.

Bissonette, J. A., and S. A. Rosa. 2009. Road zone effects in small-mammal communities. Ecology and Society 14(1). http://www.ecologyandsociety.org/vol14/iss1/art27. Accessed 23 Jan 2010.

Bonham, C. D. 1989. *Measurements for terrestrial vegetation*. New York: Wiley.

Bureau of Land Management. 2005. Oil and gas activity on public lands in the United States and Wyoming. USDI-BLM, Wyoming State Office, Cheyenne, USA.

Bureau of Land Management. 2006. Final environmental impact statement: Jonah infill drilling project, Sublette County, Wyoming. Pinedale, Wyoming, USA.

Bureau of Land Management. 2008. Final supplemental environmental impact statement for the Pinedale Anticline oil and natural gas exploration and development project, Sublette, County, Wyoming. Pinedale Field Office, Pinedale, Wyoming USA.

Burns, C., and J. Grear. 2008. Effects of habitat loss on populations of white-footed mice: testing matrix model predictions with landscape-scale perturbation experiments. Landscape Ecology 23: 817-831.

Brown, J.S. 1988. Patch Use as an Indicator of Habitat Preference, Predation Risk, and Competition. Behavioral Ecology and Sociobiology 22:37-47.

Brown, J.S. 1989. Desert rodent community structure: A test of four mechanisms of coexistence. Ecological Monographs 59:1-20.

Brown, J.S. and B.P. Kotler. 1994. Hazardous duty pay and the foraging cost of predation. Ecology Letters 7:999-1014.

Chalfoun, A.D., and T.E. Martin. 2007. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. Journal of Applied Ecology 44:983-992.

Converse, S.J., G.C. White, and W.M. Block. 2006. Small mammal responses to thinning and wildfire in ponderosa pine-dominated forests of the southwestern United States. Journal of Wildlife Management 70:1711-1722.

Debinski, D.M. and R.D. Holt. 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology 14:342-355.

Doherty, K.E., D.E. Naugle, B.I. Walker, and J.M. Graham. 2006. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187-195.

Fahrig, L. 2003. The effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487-515.

Fletcher, R.J. 2005. Multiple edge effects and their implications in fragmented landscapes. Journal of Animal Ecology 74:342-352.

Fretwell, S.D., and H.L. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica 19:45-52.

Gehring, T.M., and R.K. Swihart. 2004. Home range and movement of long-tailed weasels in a landscape fragmented by agriculture. Journal of Mammalogy 85:79-86.

Gilbert, M.M. and A.D. Chalfoun. 2011. Energy development affects populations of sagebrush songbirds in Wyoming. Journal of Wildlife Management 75:in press.

Gilliam, J.F. and D.F. Fraser. 1987. Habitat selection under predation hazard: a test of a model with foraging minnows. Ecology 68:1856-1862.

Grear, J.S., and C.E. Burns. 2007. Evaluating effects of low quality habitats on regional population growth in *Peromyscus leucopus*: Insights from field-parameterized spatial matrix models. Landscape Ecology 22:45-60.

Hanser, S.E., and N.J. Huntly. 2006. The biogeography of small mammals of fragmented sagebrush-steppe landscapes. Journal of Mammalogy 87:1165-1174.

Harju, S.M., M.R. Dzialak, R.C. Taylor, L.D. Hayden-Wing, and J.B. Winstead. 2010. Thresholds and time lags in effects of energy development on greater sage-grouse populations. Journal of Wildlife Management 74:437-448.

Holloran, M.J., R.C. Kaiser, and W.A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65-72.

Kaufman, G.A., D.W. Kaufman, and B.K. Clark. 1988. Influence of fire and topography on habitat selection by *Peromyscus maniculatus* and *Reithorodontomys megalotis* in ungrazed tallgrass prairie. Journal of Mammalogy 69:342-352.

Kaufman, D.W., G.A. Kaufman, and B.K. Clark. 2000. Small mammals in native and anthropogenic habitats in the Lake Wilson area of north-central Kansas. The Southwestern Naturalist 45: 45-60.

Kitchen, A.M., E.M. Gese, and E.R. Schauster. 2000. Changes in coyote activity patterns due to reduced exposure to human persecution. Canadian Journal of Zoology 78:853-857.

Knick, S.T., D.S. Dobkin, J.T. Rotenberry, M.A. Schroeder, W.M. Vander Haegen, and C. Van Ripper III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. Condor 105:611-634.

Knick, S.T., and J.T. Rotenberry. 1995. Landscape characteristics of fragmented shrubsteppe habitats and breeding passerine birds. Conservation Biology 9:1059-1071.

Koehler, D.K., and S.H. Anderson. 1991. Habitat use and food selection of small mammals near a sagebrush/crested wheatgrass interface in southeastern Idaho. Great Basin Naturalist 51:249-255.

Kotler, B.P., and J.S. Brown. 1988. Environmental heterogeneity and the coexistence of desert rodents. Annual Review of Ecology and Systematics 19:281-307.

Lemaitre, J., D. Fortin, D.W. Morris, and M. Darveau. 2010. Deer mice mediate red-backed vole behavior and abundance along a gradient of habitat alteration. Evolutionary Ecology Research 12:203-216.

Longland, W.S. 1994. Seed use by desert granivores. Proceedings – Ecology and Management of Annual Rangelands. Pages 233-237 *in*. B.S. Monsen and S.G. Kitchen, editors. USDA Forest Service. Ogden, UT USA INT-GTR-313.

Leu, M., S.E. Hanser, and S.T. Knick. 2008. The human footprint in the west: A large-scale analysis of anthropogenic impacts. Ecological Applications 18:1119-1139.

Lucas, H.A., and G.A.F. Seber. 1977. Estimating coverage and particle density using the line intercept method. Biometrika 64:618-622.

Manor, R, O. Cohen, and D. Saltz. 2008. Community homogenization and the invasiveness of commensal species in Mediterranean afforested landscape. Biological Invasions 10:507-515.

Manor, R. and D. Saltz. 2008. Conservation implications of competition between generalist and specialist rodents in Mediterranean afforested landscape. Biodiversity Conservation 17:2513-2523.

Martínez-Abraín, A., D. Oro, J. Jiménez, G. Stewart, and A. Pullin. 2010. A systematic review of the effects of recreational activities on nesting birds of prey. Basic and Applied Ecology 11:312-319.

Mezquida, E.T., S.J. Slater, and C.W. Benkman. 2006. Sage-grouse and indirect interactions: potential implications of coyote control on sage-grouse populations. Condor 108:747-759.

Mullican, T.R., and B.L. Keller. 1985. Ecology of the sagebrush vole (*Lemmiscus curtatus*) in southeastern Idaho. Canadian Journal of Zoology 64:1218-1223.

O'Farrell, M.J. 1980. Spatial relationships of rodents in a sagebrush community. Journal of Mammalogy 61: 589-605.

O'Farrell, M.J., W.A. Clark, F.H. Emmerson, S.M. Juarez, F.R. Kay, T.M. O'Farrell, and T.Y. Goodlett. 1994. Use of a mesh live trap for small mammals: Are results from Sherman live traps deceptive? Journal of Mammalogy 75:692-699.

Ostoja, S.M., and E.W. Schupp. 2009. Conversion of sagebrush shrublands to exotic annual grasslands negatively impacts small mammal communities. Diversity and Distributions 15:863-870.

Paige, C., and S. A. Ritter. 1999. Birds in a Sagebrush Sea - Managing Sagebrush Habitats for Bird Communities. Partners in Flight - Western Working Group. Boise, Idaho.

Parmenter, R.R., and J.A. MacMahon. 1983. Factors determining the abundance and distribution of rodents in a shrub-steppe ecosystem: the role of shrubs. Oecologia 59:145-156.

Pearson, D.E., Y.K. Ortega, K.S. McKelvey, and L.F. Ruggiero. 2001. Small mammal communities and habitat selection in northern Rocky Mountain bunchgrass: Implications for exotic plant invasions. Northwest Science 75:107-117.

Pusenius, J. and K.A. Schmidt. 2002. The effects of habitat manipulation on population distribution and foraging behavior in meadow voles. Oikos 98:251-262.

Reed, A.W., G.A. Kaufman, and D.W. Kaufman. 2005. Rodent seed predation and GUDs: effect of burning and topography. Canadian Journal of Zoology 83:1279-1285.

Richardson, C.T., and C.K. Miller. 1997. Recommendations for protecting raptors from human disturbance: A review. Wildlife Society Bulletin 25:634-638.

Saunders, D.A., R.J. Hobbs, and C.R. Margules. 1991. Biological consequences of ecosystem fragmentation: A review. Conservation Biology 5:18-32.

Sawyer, J., M.J. Kauffman, and R.M. Nielson. 2009. Influence of well pad activity on winter habitat selection patterns of mule deer. Journal of Wildlife Management 73:1052-1061.

Schmidt, K.A., and R.S. Ostfeld. 2003. Mice in space: Space use predicts the interaction between mice and songbirds. Ecology 84:3276-3283.

Shannon, C.E. and W. Weaver. 1963. The mathematical theory of communication. University of Illinois Press, Urbana USA.

Stacey, C.A. and D.M. Post. 2009. Effects of disturbance by humans on small mammals in a Chihuahuan Desert ecosystem. Southwestern Naturalist 54:272–278.

Steele, B., R. Bayn, Jr., and V.C. Grant. 1984. Environmental monitoring using populations of birds and small mammals: analyses of sampling effort. Biological Conservation 30:157–172.

Stapp, P. 1997. Habitat selection by an insectivorous rodent: patterns and mechanisms across multiple scales. Journal of Mammalogy 78:1128-1143.

Sureda, M. and M.L. Morrison. 1999. Habitat characteristics of small mammals in southeastern Utah. Great Basin Naturalist 59:323-330.

Swihart, R.K., T.M. Gehring, M.B. Kolozsvary, and T.E. Nupp. 2003. Responses of 'resistant' vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. Diversity and Distributions 9:1-18.

U.S. Department of the Interior [USDI*a*]. 2010. Number of producible acres on federal lands, FY 1988-FY 2009. <http://www.blm.gov/wo/st/en/info/newsroom/Energy_Facts_07 /statistics.html>. Accessed 6 January 2011.

U.S. Department of the Interior [USDI*b*]. 2010. Total number of acres leased, FY 1984-FY 2009. <http://www.blm.gov/wo/st/en/info/newsroom/Energy_Facts_07/statistics.html>. Accessed 6 January 2011.

Van Horne, B., 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

Western Regional Climate Center. 2011. Western U.S. climate historical summaries page. <htpp://www.wrcc.dri.edu/summary/climeswy.html>. Accessed 6 Jan 2011.

Wilcox, B.A. and D.D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. American Naturalist 125:879-887.

White, G.C. and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 Supplement, 120-138.

Wilson, K.R., and D.R. Anderson. 1985. Evaluation of two density estimators of small mammal population size. Journal of Mammalogy 66:13-21.

TABLES

Table 1. Mean (± 1 SE) density of small mammal species captured during 2 occasions (top line 15 May – 30 June, bottom line 1 July – 31 August) in natural gas versus control sites and across sagebrush habitat treatments at 2 natural gas fields in western Wyoming, USA, 2009.

	Control			Energy		
Species	Low	Medium	High	Low	Medium	High
Deer Mouse	7.59(2.17)	6.05(1.31)	8.37(1.23)	7.21(1.10)	5.79(1.02)	9.78(1.95)
	8.49(2.53)	10.81(2.36)	14.54(1.61)	15.44(3.59)	8.75(2.57)	18.53(2.13)
W. Harvest	1.03(0.68)	2.57(1.45)	1.03(0.68)	2.70(0.67)	1.93(0.97)	2.45(1.90)
Mouse	2.06(1.14)	3.22(1.45)	5.92(1.10)	3.35(0.46)	1.16(0.00)	4.76(0.46)
Grasshopper	0.26(0.13)	0.64(0.64)	0.00(0.00)	0.77(0.22)	0.90(0.72)	0.77(0.77)
Mouse	2.06(0.68)	1.29(0.68)	0.64(0.46)	1.67(0.64)	2.57(1.29)	1.29(0.34)
Sagebrush	0.51(0.51)	0.13(0.13)	0.26(0.26)	0.00(0.00)	0.39(0.39)	0.13(0.13)
Vole	0.90(0.72)	1.54(0.80)	0.13(0.13)	0.26(0.26)	0.26(0.26)	0.39(0.39)

Table 1 Continued.

	Control			Energy		
Species	Low	Medium	High	Low	Medium	High
Red-Backed	0.00(0.00)	0.00(0.00)	0.13(0.13)	0.00(0.00)	0.00(0.00)	0.00(0.00)
Vole	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)
Least	0.39(0.22)	0.13(0.13)	1.29(0.68)	0.39(0.39)	0.64(0.13)	0.13(0.13)
Chipmunk	1.16(0.59)	1.16(0.22)	2.83(1.43)	1.29(1.29)	2.06(0.34)	1.03(0.56)
Number of	0.77(0.39)	1.93(0.77)	2.45(0.72)	2.19(0.84)	0.64(0.34)	1.67(0.72)
Juveniles	1.93(0.97)	2.32(0.97)	4.50(0.51)	4.50(1.80)	1.80(0.46)	3.60(0.93)
Number of	4.12(1.27)	2.70(0.80)	3.47(1.36)	3.47(0.22)	2.45(0.56)	4.25(0.80)
Reproductive	3.35(0.56)	4.89(1.69)	6.31(1.48)	4.63(1.56)	4.12(2.19)	7.46(2.24)

Table 2. Mean (± 1 SE) density of small mammal species captured during 2 occasions (top line 15 May – 30 June, bottom line 1 July – 31 August) in natural gas versus control sites and across sagebrush habitat treatments at 2 natural gas fields in western Wyoming, USA, 2010.

	Control			Energy		
Species	Low	Medium	High	Low	Medium	High
Deer Mouse	4.48(0.72)	6.56(2.28)	6.64(0.94)	8.65(1.94)	8.19(1.40)	12.51(1.19)
	9.58(1.27)	11.58(2.72)	11.81(0.98)	11.43(1.82)	13.75(3.51)	16.37(0.79)
W. Harvest Mouse	0.23(0.15)	0.31(0.14)	0.15(0.15)	0.54(0.15)	0.54(0.20)	0.77(0.37)
	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.15(0.09)	0.00(0.00)	0.08(0.08)
Grasshopper Mouse	0.08(0.08)	0.00(0.00)	0.23(0.15)	0.62(0.36)	0.46(0.28)	0.08(0.08)
	0.93(0.31)	0.62(0.31)	0.15(0.09)	1.00(0.29)	1.16(0.17)	0.46(0.23)
Sagebrush Vole	0.15(0.15)	0.15(0.09)	0.00(0.00)	0.31(0.14)	0.08(0.08)	0.00(0.00)
	0.00(0.00)	0.08(0.08)	0.00(0.00)	0.08(0.08)	0.00(0.00)	0.08(0.08)

Table 2 Continued.

	Control			Energy		
Species	Low	Medium	High	Low	Medium	High
Olive-	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.08(0.08)	0.00(0.00)	0.00(0.00)
Backed PM*	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)
Sorex spp.	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)
	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.08(0.08)
N. Pocket	0.00(0.00)	0.00(0.00)	0.08(0.08)	0.00(0.00)	0.00(0.00)	0.00(0.00)
Gopher	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)	0.00(0.00)
Least	2.08(0.86)	1.93(1.19)	1.70(0.78)	0.39(0.30)	2.01(0.33)	1.39(0.36)
Chipmunk	1.78(0.86)	1.24(0.67)	1.31(0.54)	0.54(0.54)	1.31(0.34)	1.31(0.47)
Number of	0.54(0.23)	1.39(0.50)	1.47(0.49)	2.16(0.86)	2.39(0.75)	3.63(0.70
Juveniles	3.78(0.49)	3.47(0.97)	2.39(0.51)	3.32(0.82)	3.32(0.40)	3.40(0.75)
Number of	2.39(0.31)	3.09(1.16)	3.78(0.60)	4.17(0.69)	4.09(0.95)	5.64(0.51)
Reproductive	1.85(0.62)	2.47(0.50)	3.24(0.64)	1.62(0.64)	2.32(0.65)	2.08(0.36)

*PM indicates pocket mouse

Table 3. Mean (± 1 SE) percent cover of understory habitat variables at control and energy development sites and among sagebrush habitat classes in western Wyoming, USA, 2009 and 2010.

Habitat	Control			Energy		
Variable	Low	Medium	High	Low	Medium	High
Grass	10.74(2.22)	12.71(1.33)	12.75(2.23)	13.60(2.66)	13.44(2.55)	17.04(3.65)
Forb	2.91(0.64)	2.19(0.38)	2.06(0.52)	2.45(0.40)	2.91(0.93)	5.13(1.49)
Grass Basal	2.29(0.62)	1.96(0.71)	1.33(0.28)	2.33(0.82)	2.25(0.88)	2.49(0.57)
Forb Basal	1.05(0.53)	0.33(0.13)	0.03(0.03)	0.60(0.23)	0.36(0.17)	0.20(0.09)
Bare	30.19(5.13)	26.20(3.81)	23.66(2.57)	27.18(4.52)	24.64(2.42)	19.03(2.03)
Litter	13.33(3.27)	20.63(3.09)	21.93(2.03)	13.96(1.85)	20.21(2.46)	19.50(2.10)
Rock	3.91 (2.40)	0.11 (0.07)	0.09 (0.05)	3.78 (2.32)	0.51 (0.38)	0.00 (0.00)

Table 4. *F* and *P* values from repeated measures general linear mixed models examining the effects of natural gas treatment and sagebrush habitat treatments on the density of unique individuals of small mammals at 2 natural gas fields in western Wyoming, USA, 2010 (*n* = 30 sites).

	Natural Gas Treatment		Habitat Treatment	
Species	*F*	*P*	*F*	*P*
Deer Mouse	6.48	**<0.01**	2.08	0.15
Northern Grasshopper Mouse	5.01	**0.03**	2.21	0.13
Sagebrush Vole	0.51	0.48	2.71	0.09
Western Harvest Mouse	7.62	**0.01**	0.07	0.93
Least Ground Squirrels	1.11	0.30	0.25	0.78
Juveniles	5.36	**0.03**	0.95	0.40
Reproductive Individuals	1.66	0.21	2.93	0.07
Species Richness	7.08	**0.01**	1.90	0.17
Diversity	1.98	0.17	1.04	0.37

FIGURES

Figure 1. Mean (± 1 SE) percent canopy cover (top panel) and mean height (bottom panel) of sagebrush shrubs at control and energy development sites and sagebrush habitat classes (low, medium, and high) in western Wyoming, USA, 2009-2010.

Figure 2. Mean (± 1 SE) density of deer mice, northern grasshopper mice, sagebrush voles, western harvest mice, least chipmunk, juveniles, and reproductive individuals during 4 live-trapping occasions (occasion 1, 15 May – 30 June, 2009; occasion 2, 1 July – 31 August, 2009; occasion 3, 15 May – 30 June, 2010; occasion 4, 1 July – 31 August, 2010) in sagebrush habitats in western Wyoming, USA, 2009-2010.

Figure 3. Mean (± 1 SE) density of deer mice calculated using Program MARK showing the interaction between natural gas treatment and sagebrush habitat classes (low, medium, and high sagebrush cover and height) at 2 natural gas fields in western Wyoming, USA, 2010.

Figure 4. Mean (± 1 SE) mass (g) of seeds remaining in artificial food patches from a Giving-Up Density experiment examining the perceived predation risk of small mammals at 2 natural gas fields in western Wyoming, USA, 2010.

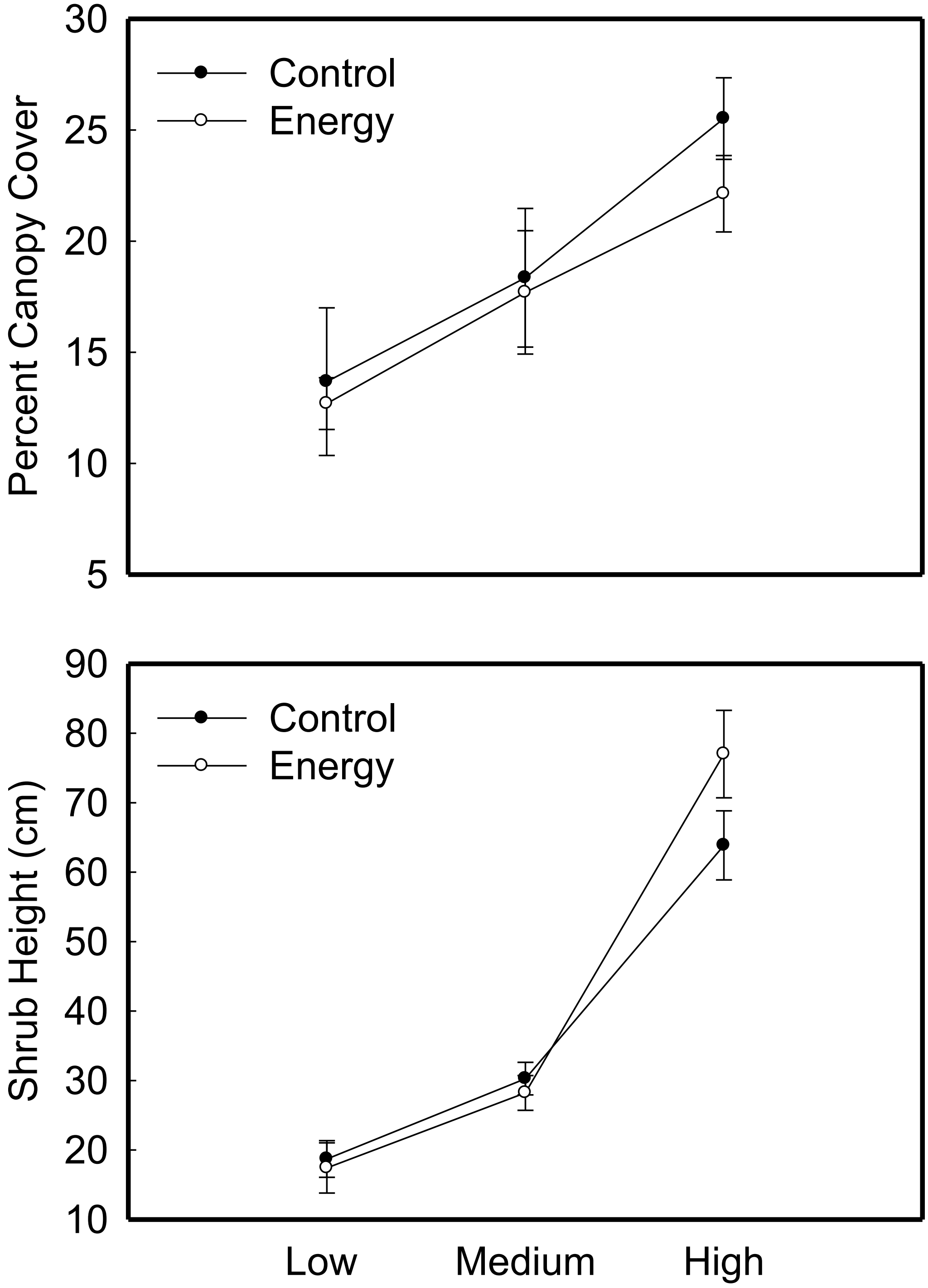
30
25
20
15
10
5
Percent Canopy Cover
Control
Energy
90
80
70
60
50
40
30
20
10
Shrub Height (cm)
Control
Energy
Low
Medium
High

Figure 1.

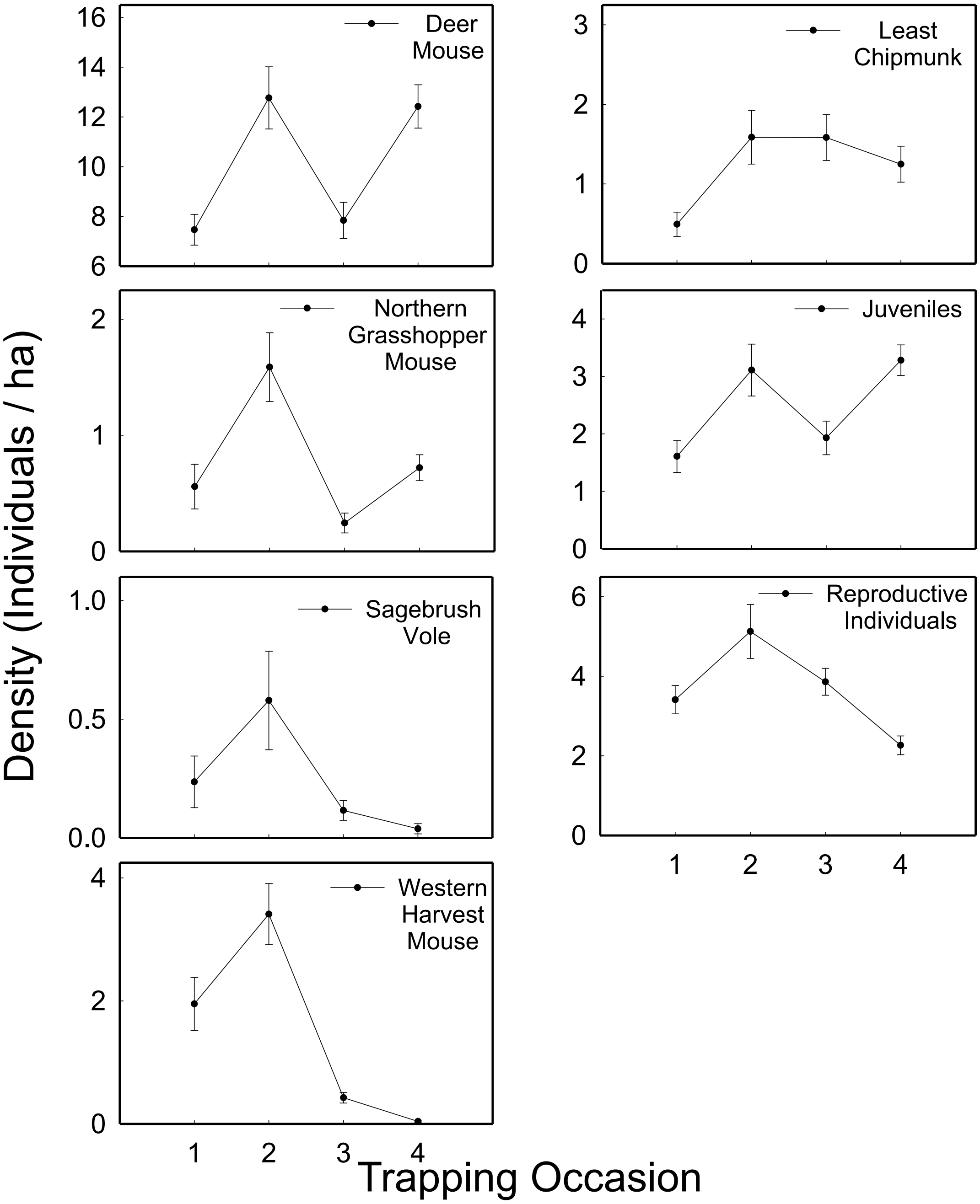
Deer Mouse
16
14
12
10
8
6
Least Chipmunk
3
2
1
0
Northern Grasshopper Mouse
2
1
0
Juveniles
4
3
2
1
0
Sagebrush Vole
1.0
0.5
0.0
Reproductive Individuals
6
4
2
0
1
2
3
4
Western Harvest Mouse
4
2
0
1
2
3
4
Density (Individuals / ha)
Trapping Occasion

Figure 2.

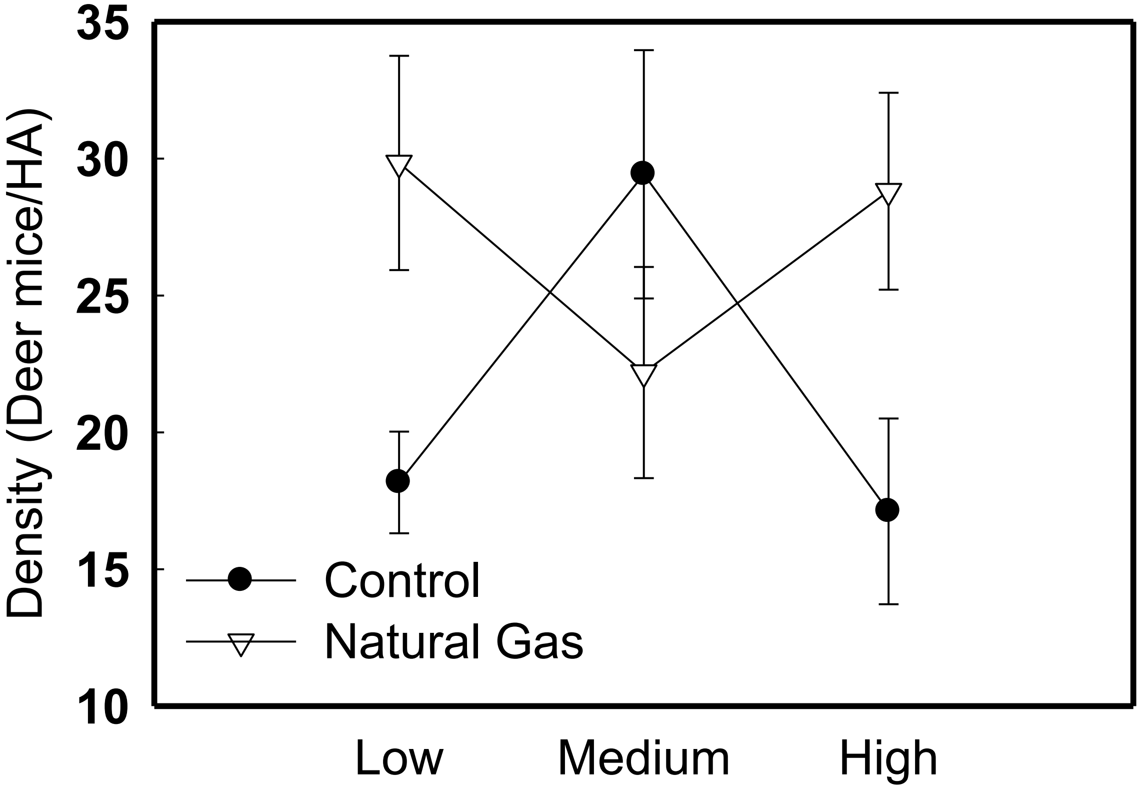
35
30
25
20
15
10
Density (Deer mice/HA)
Control
Natural Gas
Low
Medium
High

Figure 3.

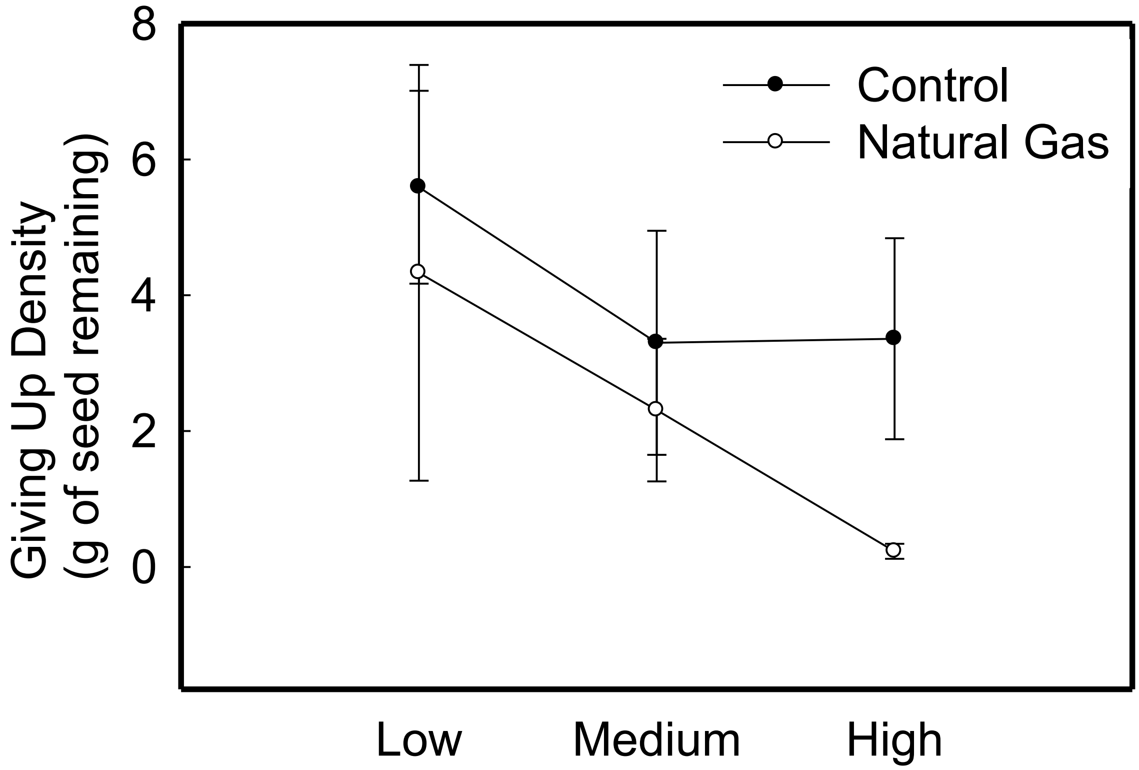
8
6
4
2
0
Giving Up Density
(g of seed remaining)
Control
Natural Gas
Low
Medium
High

Figure 4.

CHAPTER TWO. COMPARISON OF TWO LIVE TRAPS FOR SAMPLING SMALL MAMMALS IN SAGEBRUSH STEPPE.

ABSTRACT

The ability of researchers to sample small mammal populations is affected by bias introduced by trapping methods. Havahart live traps captured significantly more small mammals, while Sherman live traps captured significantly fewer small mammals than expected in sagebrush steppe habitats based on numbers of trap-nights and a chi-square distribution. Havahart traps captured more than expected of most species and age classes of small mammals regardless of local habitat or the presence of natural gas development. Sherman live traps captured ten species and Havahart traps captured six species across variation in sagebrush cover and height and between sites with and without natural gas development. Use of multiple trap types in small mammal studies may reduce bias associated with sampling methods, and ensure sampling a wider array of species.

INTRODUCTION

A problem common to all studies examining habitat associations and disturbance effects on small mammals is bias associated with trapping methods (Williams and Braun 1983, Slade et al. 1993, O'Farrell 1994). Generally, trapping is the only method of determining the community composition and abundance of small mammals occupying a site (Williams and Braun 1983). Regrettably, all trap types and trapping methods capture individuals, species, sexes, and age-classes with different probabilities, if at all (Smith et al. 1975, Catling et al. 1997). Furthermore, most methods do not provide thorough distribution and abundance data while simultaneously sampling a large number of species (Catling et al. 1997). Therefore, the use of multiple trap types may provide a mechanism to maximize the probability of sampling the entire small mammal community at a site (Maddock 1992). A remaining gap in our knowledge is how effective small Havahart® live-trap types are at sampling small mammals compared to the more conventionally used Sherman® traps.

Our ability to efficiently and accurately sample small mammal communities is vital when conducting ecological studies that may affect management decisions regarding large-scale anthropogenic disturbances (Blundel et al. 1999). Anthropogenic disturbances have influenced most ecosystems and have been cited as one of the primary threats to biodiversity (Debinski and Holt 2000, Fahrig 2003). Sagebrush steppe is one of the most altered habitats in North America, with most areas influenced by agriculture, urban expansion, energy extraction, and other land uses (Knick et al. 2003). In recent decades, natural gas and oil extraction has increased in western North America, largely within sagebrush habitats (Bureau of Land Management 2005).

Small mammals are ideal for testing hypotheses about disturbance and habitat effects because populations respond to disturbance after relatively short time periods (Steele et al. 1984). Additionally, small mammals are important for many community functions such as contributing to biodiversity, and serving as a prey base for raptors, other mammals, and reptiles (Sureda and Morrison 1999), as well as affecting vegetation communities through seed dispersal and predation (Kaufman 1988, Kaufman 2000), herbivory, and soil cycling (Pearson et al. 2001).

The objective of this study was to compare the efficacy of Sherman live traps and Havahart live traps in capturing small mammal species in sagebrush habitats. Sherman live traps have been widely used in small mammal research for decades while Havahart live traps have not been utilized despite differences in the design of the two traps. We assessed small mammal captures, richness, and demographic parameters across sagebrush habitat gradients of low, medium, and high sagebrush cover and height within and outside of natural gas fields in order to examine the consistency of trap performance in different landscape contexts.

MATERIALS AND METHODS

Study Site Our study was conducted near Pinedale, WY (42° 60’ N, 109° 75’ W) in western WY, USA. Sites were located within the Pinedale Anticline and Jonah natural gas fields and adjacent control areas away form energy development. The study area is primarily vegetated with Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) with an understory comprised of native forbs and grasses (Holloran 2010). Mean annual precipitation was 27.6 cm during the study (Western Regional Climate Center 2011).

Site Selection and Study Design We established three a priori habitat treatment levels based on the exiting range of sagebrush cover and height across the study area. Shrub cover and height covary across the study area; with the landscape ranging from low, sparse shrub cover to tall, high shrub cover areas. We categorized sagebrush habitat treatment levels as: low (5 to 10% cover with a height of less than 25cm), medium (15 to 26% cover with a height of 40 to 60cm), and high (greater than 26% cover with a height greater than 100cm). Sites were randomly selected across the study area using a 2 m resolution vegetation cover map in a Geographic Information System [GIS] (USGS Fort Collins Science Center, Fort Collins, CO). All sites were ground-truthed prior to final site selection. To investigate the effects of natural gas development on trap performance, we selected energy development sites that two to four natural gas well pads in a 500 m moving window in a GIS (USGS Fort Collins Science Center, Fort Collins, CO). Control sites were at least 1 km from natural gas development. Each sagebrush habitat class within and outside of natural gas development were examined across three replicates in 2009 (N=18) and five replicates in 2010 (N=30).

Trapping We quantified small mammal abundance, species richness, age class, and reproductive status. We used 1 ha, 10 by 10 live trapping grids with 10 m spacing between trapping stations at sites with low and medium sagebrush cover and height. Sites with high sagebrush cover and height in the study area are comprised of Basin big sagebrush (*A. tridentata tridentata*), which is now relegated to a few narrow ephemeral channels. Therefore, trapping grids at high sagebrush sites varied in size and shape to retain trapping stations within this cover type as much as possible. Control and energy development sites with the same vertical and horizontal sagebrush class were trapped concurrently. Each grid was trapped once between 15 May and 30 June and once between 1 July and 31 August to assess seasonal effects and account for potential temporal fluctuations in density.

We used Sherman traps (model LAFTG) and small Havahart (model 1020) traps. Sherman traps comprised 75% and Havahart traps 25% of all traps. In 2009, two traps were placed at each trapping station and alternated between two Sherman traps and one

Sherman and one Havahart trap. In 2010, one trap was placed at each station with Havahart traps placed at every fourth station. Traps were baited with peanut butter and rolled oats and contained polyester bedding material. Traps were opened at dusk and checked for captures at dawn the following day for four consecutive nights. Captured individuals were identified to species, age class, sex, reproductive status, and measured to obtain mass, total length, and tail length. Age class was classified as either juvenile or adult. Individuals were considered juvenile if they had juvenile pelage. All individuals were defined as either reproductive or non-reproductive for analysis. Females were considered reproductive if they had a swollen abdomen, were lactating, or showed evidence of lactation in the past. Males were considered reproductive if they had descended testes. In 2009, individuals were marked by hair trimming. In 2010, individuals were marked in both ears with small Monel ear tags (model 1005-1 National Band and Tag Co.). In both 2009 and 2010, we used the number of unique individuals as an index for small mammal abundance for all species. All protocols followed American Society of Mammalogists guidelines (American Society of Mammalogists 2007) and were approved by the University of Wyoming Institutional Animal Care and Use Committee.

Statistical Analyses Chi square tests were used to determine if the number of small mammals captured in Sherman and Havahart traps was different than expected for all species pooled, each individual species, juvenile and reproductive individuals, and the number of different species. The expected proportion of captures was 0.75 and 0.25 for Sherman and Havahart traps respectively.

RESULTS

We obtained a total of 5,540 captures of 11 small mammal species in 56,712 trap nights. Of these, 5,509 small mammals of 5 target species had adequate captures for these analyses. Sherman and Havahart traps had 3,503 and 2,006 captures respectively. We did not have adequate captures to perform analyses for shrews (*Sorex* spp.), northern pocket-gopher (*Thomomys clusius*), olive-backed pocket mouse (*Perognathus fasciatus*) southern red-backed vole (*Clethrionomys gapperi*), thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) and Wyoming ground squirrels (*S. elegans*).

All Pooled Havahart live traps captured significantly more small mammals than expected for all species pooled, for each individual species, and the number of juvenile and reproductive individuals (Figure 1, Table 1). This was the case for individuals captured for the first time and recaptures (Table 1). Sherman traps captured more species than Havahart traps overall. But Sherman traps had a single capture of northern pocket-gopher, olive-backed pocket mouse, shrew, southern red-backed vole, and 20 captures of Wyoming ground squirrels while Havahart traps had two captures of thirteen-lined ground squirrels. After accounting for these rare captures, the number of species captured in each trap type was similar regardless of energy development treatment or sagebrush habitat class.

Control versus Energy Development Sites At both control and energy development sites, Havahart traps captured significantly more small mammals than expected for all species pooled, deer mice, northern grasshopper mice, western harvest mice, and the number of juvenile and reproductive individuals (Table 2). At control sites, Havahart traps captured significantly more new and recaptured sagebrush voles than expected. At sites with natural gas development, Sherman and Havahart traps captured the expected number of new and recaptured sagebrush voles (Table 2).

Habitat Treatment Levels Across all habitat treatment levels, Havahart traps captured significantly more small mammals than expected for all species pooled, deer mice, western harvest mice, and the number of juvenile and reproductive individuals (Table 3). Captures of new and recaptured northern grasshopper mice and sagebrush voles in Havahart and Sherman Traps varied with sagebrush cover and height (Table 3).

DISCUSSION

Biased trap efficiencies may lead to erroneous inferences about small mammal populations (O'Farrell et al. 1994). The conclusion that using multiple trap types provides the best information on the entire small mammal community at a site was supported by our data (Maddock 1992, Slade et al. 1993, Catling et al. 1997). Havahart live traps performed better than expected overall, and better than expected in capturing most species and age classes of small mammals regardless of local habitat or the presence of large-scale disturbance.

Most studies of small mammals strive to sample the entire small mammal community to infer how species or demographic parameters may vary with habitat or land use (Manor et al. 2008). Captures of two relatively rare species, the northern grasshopper mouse and the sagebrush vole, were higher than expected under most conditions in Havahart traps. While captures of these species were still relatively low, more efficient sampling of these species allowed for stronger conclusions regarding habitat associations and the effects of disturbance on these species.

Contrary to many studies (Williams and Braun 1983, O'Farrell et al. 1994), Sherman traps captured more species overall, and across habitat and energy development treatments. Thirteen-lined ground squirrels were only captured in Havahart traps. Captures of a shrew, northern pocket-gopher, olive-backed pocket mouse, southern red-backed vole, and Wyoming ground squirrels, were only recorded in Sherman traps. Only one capture of each of these species was recorded over two years. These species were likely captured in Sherman traps simply because of the higher proportion of Sherman traps on our grids.

Age structure of small mammal species can be informative in assessing local habitat quality (Van Horne 1983). Higher than expected captures of reproductive and juvenile individuals in Havahart traps may allow for a more accurate assessment of how different age classes are distributed across the landscape. Similarly, data from marked individuals can be used to estimate density and demographic parameters (Lebreton et al. 1992, White and Burnham. 1999). Havahart traps captured more recaptured individuals than expected. These data allow for better population estimates and assessments of habitat quality from trapping data.

Sherman live traps have been utilized for over 50 years and are the most commonly used live traps in studies of North American small mammals (Slade et al. 1993). Sherman live traps are easy to maintain and can be efficiently set. Havahart model 1005 live traps have rarely, if ever, been used in small mammal studies. While Havahart traps performed better than expected, they do have potential drawbacks in a field research setting. Havahart traps have a very sensitive treadle mechanism and traps were frequently sprung during windy nights. During one night in 2009, all Havahart traps were sprung during a hailstorm. Additionally, Havahart traps have two gravity operated doors which are easily obstructed by vegetation, allowing captures to escape, thereby disabling the trap. However, the proportion of Havahart traps and Sherman traps sprung was similar. Finally, Havahart traps take considerably more time to properly set than Sherman traps (approximately 30 and 15 seconds respectively).

Researchers should strive to avoid capturing non-target species (American Society of Mammalogists 2007). A total of 40 birds including Brewer's sparrow (*Spizella breweri*), horned lark (*Eremophila alpestris*), sage sparrow (*Amphispiza belli*), and vesper sparrow (*Pooecetes gramineus*) were captured. Of these, 38 and 2 were captured in Havahart and Sherman traps respectively. All birds were held in traps for less than one hour and were released unharmed.

All animals are expected to have a range of behavioral responses to novel items placed in the landscape (O'Farrell et al 1994). Differences in design between Sherman and Havahart traps may elicit different behavioral responses from small mammals. Sherman traps consist of a metal box with only one door, and cannot be seen through. Havahart traps have one door on each end of the trap, and the sides consist of a sheet metal mesh. Our results are consistent with other research suggesting small mammals prefer mesh traps that can be seen through (O'Farrell et al. 1994). For example kangaroo rats have demonstrated antagonistic behavior towards Sherman traps by filling them with soil, but this behavior was not as prevalent with mesh traps (O'Farrell 1994).

In summary, Havahart traps accounted for more captures than expected in our study. The use of two live trap types increased the overall number of species observed. Additionally, increased captures of two rare species, and adult and juvenile individuals in

Havaharts provided data that may not have been obtained from one trap type alone. Utilizing multiple trap types in small mammal studies therefore provided more thorough sampling of a diversity of species.

ACKNOWLEDGMENTS

Funding was provided by the Wyoming Game and Fish Department. We thank the Wyoming Cooperative Fish and Wildlife Research Unit, especially M. Larson. M. O'Donnell of USGS Fort Collins Science Center provided GIS data and assistance with site selection. S. Bieber provided statistical assistance.

LITERATURE CITED

American Society of Mammalogists Animal Care and Use Committee. 2007. Guidelines of The American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809-823.

Bureau of Land Management. 2005. Oil and gas activity on public lands in the United States and Wyoming. USDI-BLM, Wyoming State Office, Cheyenne, USA.

Blundell, G.M., J.W. Kern, R.T. Bowyer, L.K. Duffy. 1999. Capturing River Otters: A comparison of Hancock and leg-hold traps. Wildlife Society Bulletin 27:184-192.

Catling, P.C., R.J. Burt, and R. Kooyman. 1997. A comparison of techniques used in a survey of the ground dwelling and arborial mammals in forests in north-eastern New South Wales. Wildlife Research 24: 417-432.

Debinski, D.M. and R.D. Holt. 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology 14:342-355.

Fahrig, L. 2003. The effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487-515.

Holloran, M.J., R.C. Kaiser, and W.A. Hubert. 2010. Yearling greater sage-grouse response to energy development in Wyoming. Journal of Wildlife Management 74:65-72.

Knick, S.T., D.S. Dobkin, J.T. Rotenberry, M.A. Schroeder, W.M. Vander Haegen, and C. Van Ripper III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. The Condor 105:611-634.

Lebreton, J. D., K.P. Burnham, J. Clobert, and D.R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals. A unified approach with case studies. Ecological Monographs 62:67-118.

Maddock, A.H. 1992. Comparison of two methods for trapping rodents and sherws. Israel Journal of Zoology 38:333-340.

Manor, R, O. Cohen, and D. Saltz. 2008. Community homogenization and the invasiveness of commensal species in Mediterranean afforested landscape. Biological Invasions 10:507-515.

O'Farrell, M.J., W.A. Clark, and F.H. Emmerson, S.M. Juarez, F.R. Kay, T.M. O'Farrell, T.Y. Goodlett. 1994. Use of a mesh live trap for small mammals: Are results from Sherman live traps deceptive? Journal of Mammalogy 75:692-699.

Pearson, D.E., Y.K. Ortega, K.S. McKelvey, and L.F. Ruggiero. 2001. Small mammal communities and habitat selection in northern Rocky Mountain bunchgrass: Implications for exotic plant invasions. Northwest Science 75:107-117.

Slade, N.A., M.A. Eifler, N.M. Gruenhagen, and A.L. Davelos. 1993. Differential effectiveness of standard and long Sherman livetraps in capturing small mammals. Journal of Mammalogy 74:156-161.

Smith, M.H., R.H. Gardner, J.B. Gentry, D.W. Kaufman, and M.J. O'Farrell. 1975. Desnity estimations of small mammal populations. PP. 25-54, *in* Small mammals: their productivity and population dynamics (F.B. Golley, K. Petrusewicz, and L. Ryszkowski, eds.). Cambridge Universtiy Press, London, United Kingdom, 451 pp.

Western Regional Climate Center. 2011. Western U.S. climate historical summaries page. <htpp://www.wrcc.dri.edu/summary/climeswy.html>. Accessed 6 Jan 2011.

White, G.C. and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 Supplement, 120-138.

Williams, D.F., S.E. Braun. 1983. Comparison of pitfall and conventional traps for sampling small mammal populations. The Journal of Wildlife Management 47:841-845.

Van Horne, B., 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

TABLES

Table 1. Chi-square and *P*-values comparing the observed and expected number of new and recaptured small mammals captured in Sherman and Havahart live traps in sagebrush habitats in western Wyoming, USA, 2009 and 2010.

Species		χ^2	*P*-value
All Species	New	184.90	<0.001
	Recapture	189.01	<0.001
Deer Mouse	New	85.50	<0.001
	Recapture	116.84	<0.001
Northern Grasshopper Mouse	New	16.80	<0.001
	Recapture	20.32	<0.001
Sagebrush Vole	New	5.44	0.020
	Recapture	5.77	0.016
Western Harvest Mouse	New	98.83	<0.001
	Recapture	80.38	<0.001
Least Chipmunk	New	23.84	<0.001
Juvenile	New	90.43	<0.001
	Recapture	71.98	<0.001
Reproductive	New	27.37	<0.001
	Recapture	23.06	<0.001
Species Richness	Species	1.33	0.248

Table 2. Chi-square and *P*-values comparing the observed and expected number of new and recaptured small mammals captured in Sherman and Havahart live traps at sites with and without natural gas development in sagebrush habitats at 2 natural gas fields in western Wyoming, USA, 2009 and 2010.

		Control		Energy	
Species		χ^2	*P*-value	χ^2	*P*-value
All Species	New	122.82	<0.001	68.51	<0.001
	Recapture	109.67	<0.001	82.19	<0.001
Deer Mouse	New	52.84	<0.001	34.83	<0.001
	Recapture	71.94	<0.001	47.54	<0.001
Northern Grasshopper Mouse	New	7.76	0.005	9.39	0.002
	Recapture	8.17	0.004	12.45	<0.001
Sagebrush Vole	New	8.17	0.004	0.00	1.000
	Recapture	10.67	0.001	0.67	0.796
Western Harvest Mouse	New	54.66	<0.001	44.70	<0.001
	Recapture	37.38	<0.001	43.01	<0.001
Least Chipmunk	New	21.46	<0.001	4.22	0.040
Juvenile	New	56.07	<0.001	36.42	<0.001
	Recapture	50.79	<0.001	50.79	<0.001
Reproductive	New	21.35	<0.001	8.09	0.004
	Recapture	25.17	<0.001	3.61	0.057
Species Richness	Species	38.35	<0.001	14.33	<0.001

Table 3. Chi-square and *P*-values comparing observed and expected number of new and recaptured small mammals in Sherman and Havahart live traps at low, medium, and high sagebrush canopy cover and shrub height in western Wyoming USA in 2009 and 2010.

		Low		Medium		High	
Species		χ^2	*P*-value	χ^2	*P*-value	χ^2	*P*-value
All Species	New	72.11	<0.001	46.42	<0.001	112.1	<0.001
	Recapture	63.19	<0.001	45.34	<0.001	81.34	<0.001
Deer Mouse	New	31.57	<0.001	24.33	<0.001	29.84	<0.001
	Recapture	36.01	<0.001	24.61	<0.001	57.19	<0.001
Northern Grasshopper Mouse	New	10.81	0.001	3.09	0.79	4.15	0.042
	Recapture	15.7	<0.001	11.52	0.001	0.86	0.355
Sagebrush Vole	New	5.07	0.024	0.78	0.378	0.67	0.414
	Recapture	NA	NA	0.67	0.414	NA	NA
Western Harvest Mouse	New	30.95	<0.001	25.33	<0.001	42.71	<0.001
	Recapture	22	<0.001	18.51	<0.001	40.00	<0.001
Least Chipmunk	New	11.85	0.001	4.91	0.027	8.26	0.004

Table 3 Continued.

Species		Low		Medium		High	
		χ^2	*P*-value	χ^2	*P*-value	χ^2	*P*-value
Juvenile	New	26.07	<0.001	21.97	<0.001	43.42	<0.001
	Recapture	31.95	<0.001	10.93	0.001	31.15	<0.001
Reproductive	New	15.38	<0.001	8.47	0.004	5.60	0.018
	Recapture	7.73	0.005	7.31	0.007	8.25	0.004
Species Richness	Species	3.01	0.078	2.46	0.117	0.86	0.355

FIGURES

Figure 1. Proportion of small mammals captured in Sherman (dark bars) and Havahart (light bars) live traps. The dashed line represents the expected proportion of captures in Sherman traps and the dashed and dotted line represents the expected proportion of captures in Havahart traps based on the number of each trap type available on trapping grids.

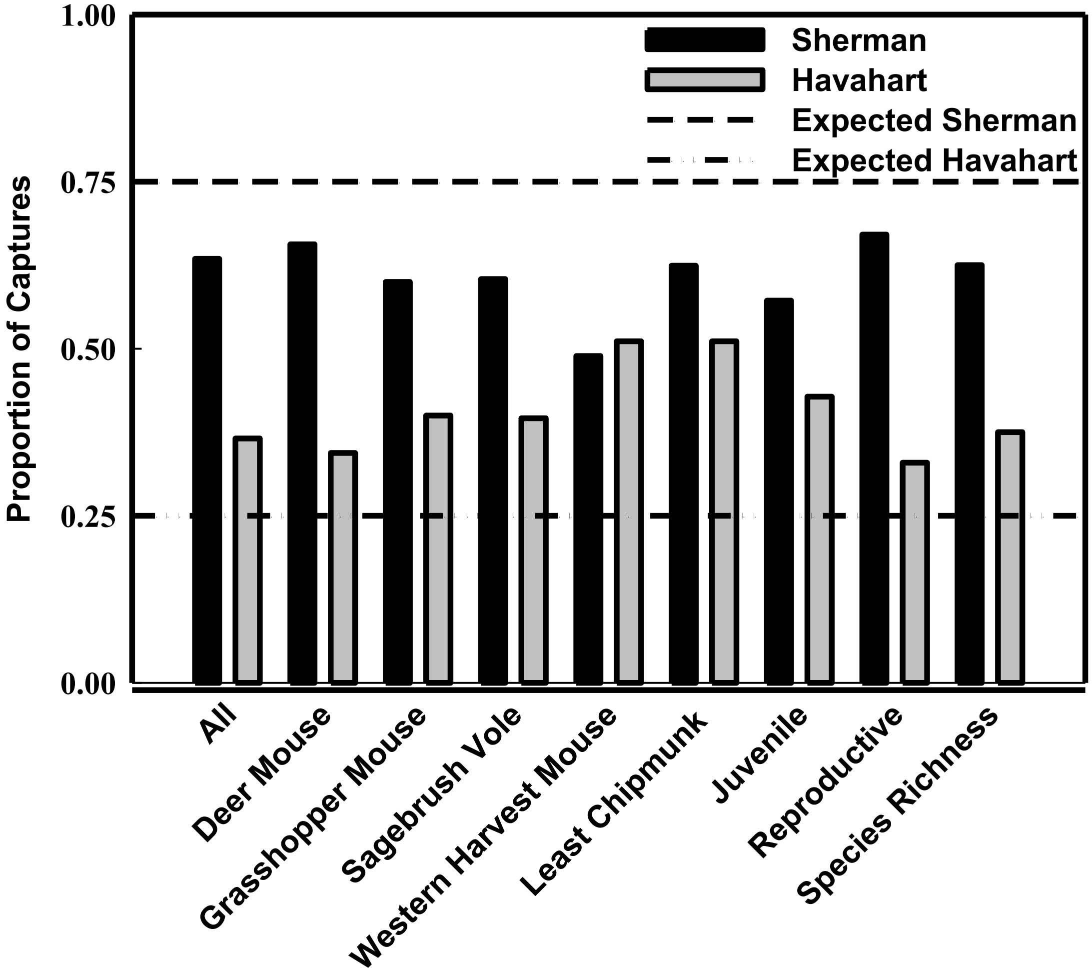
1.00
0.75
0.50
0.25
0.00
Proportion of Captures
Sherman
Havahart
Expected Sherman
Expected Havahart
All
Deer Mouse
Grasshopper Mouse
Sagebrush Vole
Western Harvest Mouse
Least Chipmunk
Juvenile
Reproductive
Species Richness

Figure 1.