

GRANIVORES AND RESTORATION: IMPLICATIONS OF INVASION AND
CONSIDERATIONS OF CONTEXT-DEPENDENT SEED REMOVAL

By

Steven M. Ostoja

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Approved:

Eugene W. Schupp
Major Professor

James A. MacMahon
Committee Member

Karen H. Beard
Committee Member

Thomas A. Monaco
Committee Member

Christopher A. Call
Committee Member

Byron R. Burnham
Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

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ABSTRACT

Granivores and Restoration: Implications of Invasion and Considerations of
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by

Steven M. Ostoja, Doctor of Philosophy

Utah State University, 2008

Major Professor: Eugene W. Schupp
Department: Wildland Resources

Granivores are important components of sagebrush communities in western North America. These same regions are being altered by the invasion of the exotic annual *Bromus tectorum* (cheatgrass) that alters physical and biological dynamics in ways that appear to promote its persistence. This research directly relates to the restoration of *B. tectorum*-dominated systems in two inter-related ways. First, because these landscapes have large quantities of seeds applied during restoration, it is important to determine the major granivore communities in intact sagebrush communities and in nearby cheatgrass-dominated communities. Second, it is important to develop an understanding of patterns of seed harvest by granivores. In addition to the data chapters there are two review chapters; Chapter 1 highlights factors contributing to seed removal and Chapter 7 provides ecologically based techniques that could minimize the negative consequences of granivores during ecological restoration. Common groups of ants showed increased abundances; uncommon species and functional groups were generally negatively impacted by cheatgrass (Chapter 2). Conversely, rodents were negatively impacted by

conversion to cheatgrass (Chapter 4). Ant seed removal was highly context-dependent (Chapter 3), depending on the background vegetation (large-scale among-patch effects), foraging distance from the nest mound (small-scale among-patch effects), and the presence of other seed species in mixture (within-patch effects). In addition, cheatgrass provided associational resistance to native seeds in mixture, meaning the presence of cheatgrass increased native seed survival. In Chapter 5 a novel statistical technique in the ecological sciences showed that rodents have marked preferences for some seeds over others and that more seeds were removed in sagebrush compared to cheatgrass-dominated sites, although associational effects among seed mixtures were not detected. In Chapter 6 we show that the amount of seed harvested depended on both intraspecific and interspecific seed density. *B. tectorum* seeds had associational susceptibility (increased harvest) in the presence of native seeds. Although the reciprocal effect may occur, we did not find statistical support for it. These sets of studies are not only of basic ecological interests, but are also important for developing management strategies for restoration of these degraded lands.

(216 pages)

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CHAPTER 1

IMPORTANCE OF SEED CHOICE AND REMOVAL: SEED CHARACTERISTICS
AND ENVIRONMENTAL INFLUENCES¹**I. Abstract**

Granivorous animals are important components of many arid and semi-arid communities throughout North America. The important influence of selective seed predation and/or dispersal by granivorous animals on vegetation dynamics is well understood. Many sites throughout the Intermountain West that are home to these animals have been altered structurally and functionally by invasive species in ways that promote the sustained persistence of these invasive species. As such, the restoration of western arid- and semi-arid lands has been widespread to redirect disturbed and invaded landscapes toward a trajectory deemed desirable for wildlife and other ecological values and human interests alike. Because restoration often requires the application of seed, consideration of granivory in this process is critical. In so doing, it is important to consider factors both inherent to the seed as well as resource-wide characteristics that contribute to seed selection and/or removal by granivores in semi-arid and arid communities in North America. Using such a framework, we provide an overview of ant and rodent granivory, which may influence seed removal events and possibly mitigate potential negative impacts from granivory on ecological restoration. Additionally, we provide implications of these plant-animal interactions while considering managed systems where appropriate.

¹ Coauthored by Steven M. Ostoja and Eugene W. Schupp

II. Introduction

As in other environments, seeds have an important role in arid and semi-arid environments (Chambers & MacMahon, 1994). In these habitats the dominant plants in terms of vegetative cover and biomass are perennial shrubs, perennial grasses, and non-native annual grasses. The latter spend the majority of their life cycle as seeds scattered and hidden in the soil. This is obvious after precipitation when available moisture allows these seeds to germinate, grow, and ultimately set seed for the cycle to continue. Additionally, we know that seed production in North American deserts is strongly tied to precipitation events (Brown & Ernest, 2002), which influence annual variability in seed production and potentially affect seed consumer populations. In terms of total numbers, seeds of annuals dominate the seed bank in many sites in the eastern Great Basin (S. Ostoja, unpubl.) in both relatively intact sagebrush communities and non-native grasslands dominated by the exotic annual grass *Bromus tectorum* (cheatgrass).

Because the life history strategy of many plants demands a significant resource allocation to seed production, large quantities of seeds of many species can be found in the soil awaiting suitable conditions for germination while avoiding desiccation and predation (Chambers & MacMahon, 1994). Thus it is not surprising that many animals in North American arid and semi-arid environments have evolved a dependence on seeds. For animal consumers, seeds provide nutrition and a means of water extraction. Seeds are nearly always available in the soil environment to some degree and can be collected when abundant and stored for later use.

Granivores comprise a significant faunal biomass and are known to exert substantial impacts on ecosystems via direct seed predation and dispersal as well as through other activities associated with life in the habitat, such as burrow construction. More recently, granivory has received interest in managed systems as well (Hoffmann et al., 1995) because it may be one of the most important yet frequently overlooked processes affecting restoration (Whisenant, 1999). Janzen (1971) suggested that “seed eaters” should be considered for their potentially significant role in the development, structuring, and functioning of communities, and Majer (1989) has called attention to the potentially important but largely overlooked role of animals as agents of change in revegetation activities. And perhaps most convincingly, results from (Brown and Heske, 1990) show clearly how selective seed removal can alter plant community composition. Because seeds are an important food resource for desert granivores and restoration often involves the application of large quantities of seeds, xeric rangelands have been promoted as potentially good laboratories for exploring the integration of granivory and vegetation management (Kelrick & MacMahon, 1985; Archer & Pyke, 1991). The goals of this paper are (1) to provide a brief background of granivory within the North American arid and semi-arid regions and (2) to outline the important potential interactions between granivores and seeds that affect seed harvesting in both natural and managed environments, first by considering individual seeds as a resource and second by considering resource-wide qualities at the community level.

We use the term “seed” throughout this paper in reference to all non-ovarian reproductive tissues which to be botanically accurate are actually fruits. Because the differing tissues among these structures may either enhance or detract the seeds

desirability as a resource this distinction is thought to be a significant factor that could influence preference by a granivore (Kelrick & MacMahon, 1985).

III. Granivory – An Overview

Granivorous animals are critical components of many different ecosystems around the world (Brown et al., 1979, 1986; Davidson, 1977 a and b). However, unlike other arid and semi-arid regions, only in North America has granivory evolved in such a diverse faunal component (Mares, 1993; Kelt et al., 1996). Longland (1994) attributes the high abundance and diversity of granivorous animals to a greater availability and suitability of seeds as food compared to other types of plant materials in these plant communities. Based on the quantity of seed handled, the most important of these animals are rodents and ants (Davidson et al., 1980; Brown et al., 1979; Parmenter et al., 1984). Although seed-eating birds can be temporally important and at times locally abundant in North American arid and semi-arid communities (arid hereafter), few species are specialized granivores (Brown et al., 1979). Moreover, they have been shown to be generally only a small component of the granivore community in these environments (see Kelrick et al., 1986; Longland et al., 2001), and hence are not considered here.

Seed dispersal and seed predation by granivores are considered to be key processes affecting recruitment and survival of plants (Davidson et al., 1980; Hansen, 1978; Inouye et al., 1980; Schupp & Fuentes, 1995; Brown et al., 1986; Gibson et al., 1990; Wilson et al., 1990; Howe & Brown, 2001). Seed-eating animals can alter the composition of seed pools by preferentially harvesting some seeds over others (Brown et al., 1979) and can redistribute seeds by moving and caching them (Vander Wall, 1992a).

Both of these activities can have profound effects on plant populations and communities. In addition to these direct effects of granivory on seed pools, granivory and associated activities can have indirect effects by creating soil disturbances and affecting soil chemistry (Brown et al., 1979; MacMahon et al., 2000).

Considering ant granivores, two genera of harvester ants (*Pogonomyrmex* and *Veromessor*) within the family Formicidae are the dominant seed foragers in North American arid lands (Hobbs, 1985; Hölldobler and Wilson, 1990; Longland et al., 2001), although others are known to occur. Of these, the *Pogonomyrmex* spp. are the most common seed harvesting ants within the arid West (MacMahon et al., 2000; Chapter 2). Seed harvesting ants forage along trails that radiate from their mounds and are referred to as trunk-trail foragers. Foraging location and distance from the mound may vary due to biotic and abiotic interactions (MacMahon et al., 2000). Although harvester ants remove only a fraction of available seeds, and can only locate surface seeds, research suggests they are selective granivores and can have profound effects on the structure of plant communities (Hobbs, 1985; Inouye, 1991; Mull & MacMahon, 1997; MacMahon et al., 2000). Kelrick et al. (1986) showed that seed selectivity increases at a greater distance from the mound. Similarly, in a seed removal experiment with the harvester ant *P. occidentalis* (Mull & MacMahon, 1997), > 30% of seeds were removed within one day and removal rates varied with distance from the mound and among foraging trails.

Rodents also can have significant effects on the species diversity and composition of plant communities. In the Chihuahuan Desert kangaroo rats (*Dipodomys* spp.) are considered a keystone guild because they have major effects on plant species composition and biogeochemical processes via seed predation and soil disturbance (Brown & Heske,

1990). Unlike ants, rodents can locate seeds buried in the soil by chance, memory, tactile cues, and olfaction. Rodent species vary in the ability to find buried resources with olfaction (Vander Wall et al., 2003). Further, the detection of seeds by olfaction is greatly affected by both seed and soil water content (Vander Wall, 1998).

The process of seed dispersal, where plant propagules (“seeds”) are placed in suitable sites for germination and successful establishment, is of central importance in the fields of plant population, community, and restoration ecology (Wilson et al., 1990; Schupp & Fuentes, 1995; Schupp, 2007). Rodent seed moving behaviors have important implications not only for seed dispersal of many arid-land plants in natural systems, but perhaps also for plants in managed and restored systems. For decades, rodents generally have been considered to negatively affect seed resources due to direct seed predation. Although this is often true (see Vander Wall et al., 2005), research also demonstrates the positive role rodents can have in plant recruitment in arid environments through seed dispersal (West, 1968; McAdoo et al., 1983; McMurry et al., 1997; Vander Wall, 1990, 1992b, 1993, 1994; Longland et al., 2001; Theimer, 2005). Heske et al. (1993) have shown that in the Chihuahuan desert kangaroo rats have a greater impact on vegetation than do livestock because of high levels of seed predation and dispersal, as well as the soil disturbances that accompany such activities.

These animals disperse seeds in two important ways that differ in their potential effects on plant population ecology and potentially on the success of restoration through re-seedings when these animals are abundant. Rodents may place seeds either in one or a few central locations such as a burrow, which is called “larder-hoarding,” or in shallow holes around the surface of their home ranges, called “scatter-hoards,” or “caches.”

These caches of seeds are covered with soil and/or litter to conceal their locations. It is scatter-hoarded caches that contribute to seedling recruitment of certain plants, sometimes considerably. Successful germination can occur when rodents either fail to recover a cache at all or when they incompletely recover a cache and miss some seeds. Longland et al. (2001) reported that seedling recruitment of the native perennial bunchgrass *Achnatherum hymenoides* following initial caching by a single Merriam's kangaroo rat (*D. merriami*) was significantly greater than for seeds not harvested by granivores or for those harvested by ants. Because a diverse array of plant species are reported to emerge from scatter-hoards (Vander Wall, 1990, 1992b, 1994; Longland et al., 2001), this process may represent a critical mechanism of seed dispersal and subsequent establishment for many plant species (West, 1968; McAdoo et al., 1983; Vander Wall, 1994) and it may have an evolutionary basis (Voorhies, 1975; Vander Wall, 1990; Vander Wall et al., 2005). Specifically, some desert plants may have evolved to rely on rodents for seed dispersal via seed caching in microsites favorable for germination (Vander Wall, 1990; Longland & Bateman, 1998; Longland et al., 2001; Theimer, 2005).

IV. Relationships among Seed Preference and Seed Attributes

Because selective seed harvesting and consumption can strongly affect plant population and community development, it is prudent to consider factors leading to seed choice and selectivity in the context of seed application where granivorous animals are present. In particular, studies of seed characteristics are important when attempting to understand how both ants and rodents select seeds. Various characteristics have been

evaluated under natural and experimental conditions and subsequently identified as affecting preferential selection by granivores. Kelrick et al. (1986) suggest that granivores may select seeds on the basis of either the recognition of differences in the qualities of individual specific seed types or due to resource-wide qualities of the environment. A number of seed characteristics have been suggested as affecting the quality of individual seeds and therefore seed selection, including seed size (Price, 1983), nutritional composition (Kelrick et al., 1986; Jenkins, 1988; Crist & MacMahon, 1992), seed water content (Frank, 1988; Hulbert & MacMillen, 1988), seed anatomy and morphology (Lawhon & Hafner, 1981), seed chemistry and secondary compounds (Kelrick et al., 1986; Kerley & Erasmus, 1991), seed handling time (Bozinovic & Vasquez, 1999), and seed-microbial interactions (Crist & Friese, 1993). At a larger scale, resource-wide qualities may include overall seed availability and associated spatial and temporal dynamics of the resource (MacMahon et al., 2000; Crist & MacMahon, 1992), seed neighborhoods and seed mixtures (Veech, 2000, 2001; Veech & Jenkins, 2005), and soil and related edaphic effects (Price & Heinz, 1984) among others.

Because many characteristics can contribute to seed selection individually and synergistically, it is difficult to know what combination of seed characteristics and environmental conditions together drive seed selection and removal. Nevertheless, such factors, if understood, could help land managers minimize seed loss to granivorous rodents and ants by using specific seeds or seed combinations together with other techniques (e.g. altering seeding depth or timing of seeding – see Chapter 7). In the following section we summarize research findings that relate seed characteristics to seed selectivity and that may merit consideration in a restoration context.

A. SEED CHARACTERISTICS

1. Seed Nutritional and Water Contents

Because seeds are the primary food item of desert granivores their availabilities and nutritional contents are thought to drive, at least in part, which seeds are taken in what quantities. Price (1983) reported that six species of rodents selected significantly larger seeds in laboratory conditions than the sizes of seeds typically available in their desert environments and argued that this preference was driven by larger seeds having greater amounts of soluble carbohydrates. Her results also indicated a negative correlation with seed lipid content. This is consistent with Kelrick et al. (1986) who argued that seed preferences of desert granivores are strongly influenced by soluble carbohydrate content. Crist and MacMahon (1992) corroborated these conclusions with experimental data from *Pogonomyrmex occidentalis* (Western harvester ant), suggesting again that soluble carbohydrates were important in seed selectivity. It has also been suggested (Mattson, 1980) that the nitrogen content of seeds might influence dietary choice of some heteromyids, and this factor may be even more important in warm deserts (see West & Klemmedson, 1978).

Some genera of desert rodents preferentially select seeds with greater seed water content (Hulbert & MacMillen, 1988), and this selection is likely to vary with season, reproductive condition, and geographic region. Seeds with greater soluble carbohydrates also have greater metabolic water yields, which is critical to organisms living in arid systems (Frank, 1988). Kangaroo rats depend on pre-formed water in their diet and water that is produced metabolically when food is oxidized. Because the oxidation of different

nutrients produces different net amounts of metabolic water, diet selection becomes important for overall water balance of the organism (Frank, 1988). For example, in low humidity conditions, carbohydrate oxidation produces a net metabolic water gain, whereas lipid and protein metabolism result in net water loss. In high humidity conditions, carbohydrate oxidation is high and protein oxidation again results in water loss although lipid oxidation produces large water gains (Frank, 1988). In contrast, Kerley and Erasmus (1991) concluded that seed preferences of none of the South African mice species they studied were correlated directly with the free water content of seeds, although they did not consider metabolic water.

2. Seed Size

Results from rodent preference studies suggest that larger seeds are preferred relative to smaller seeds (Mares & Williams, 1977). As noted above, Price (1983) showed in laboratory experiments with six species of heteromyid rodents that the preferred seed size was 5 mg, which was much greater than the size of seeds the animals selected for naturally (0.22 mg). In contrast, ants appear to prefer smaller seeds due to ease of transport and handling (Crist & MacMahon, 1992; Davidson, 1993). Although seed size itself can affect selection by affecting handling, seed size alone may not fully explain size-based preferences. Optimal seed size for harvest might be predicted by applying foraging theory models (Charnov, 1976). For example, because size is correlated with energy availability larger seeds potentially have greater available carbohydrates and thus offer greater energy gain (Charnov, 1976; Kelrick et al., 1986).

3. Seed Anatomy, Morphology, and Secondary Chemistry

Differences in physical and chemical qualities of seeds can influence granivore preferences. Many plant species have seeds with physical features to either deter or encourage granivores (Janzen, 1969). The morphology as well as the anatomy of a given seed could greatly influence the handling time by the granivore, which would likely contribute to seed selectivity (Kelrick et al., 1986). We report (Chapter 5) that *Bromus tectorum* seeds were removed less than seeds of five native perennial grasses and the annual grass *Panicum miliaceum* (millet). A plausible explanation for the low preference of *Bromus tectorum* is the increased handling time needed to deal with non-nutritive tissues and persistent awns that reduce foraging efficiency (see Kelrick et al., 1986). A specific feature of seed morphology is shape, which might also play an important role in preference. Certain seed shapes (e.g. elongated) may be relatively difficult to transport and may be considered less desirable than other shaped seeds (e.g. round) which may promote harvest. The roles of shape and surface texture (round, elongate, smooth, textured) are largely unknown but potentially important and thus merit further research.

Important in the evolution of flowering plants was the biochemical coevolution of chemically-unrelated compounds (Davidson, 1993). Many of these compounds are thought to play a major role as attractants or repellants of certain plant parts including seeds (Janzen, 1969, 1971). These secondary chemical compounds can act as defense against seed eaters, and have been credited in determining relative food preferences of these animals. Secondary compounds may affect selection due to toxicity, taste, aversion, and/or interference with digestion. For example, tannins generally are not directly toxic,

but function as anti-nutritional substances because they make seeds less digestible and are thought to be the main chemical defense against many seed predators (Boesewinkel & Bouman 1995). Sherbrooke (1976) suggested that cyanogenic glucosides in the seeds of *Simmondsia chinensis* (jojoba), a common shrub in the Sonoran Desert, function as a defense against seed predation by some species of heteromyid rodents, while other rodents might have evolved detoxifying agents that allow them to tolerate these seeds. Perhaps this is the reason Kerley and Erasmus (1991) in South Africa found that for the mice used in their study the consumption of seeds was not correlated with the polyphenol content of the seeds.

The role of chemicals can be more complex. Fuller and Hay (1983) reported on the indirect effect of the production of a glue-like substance by desert annual seeds of *Salvia columbariae*, which significantly reduced predation by granivores. They suggested the mucilaginous substance on the seed coat when moistened allows sand particles to bind to the seed and it is the sand coating that reduces predation, further, they suggest that predation may be the selective pressure for the glue production. Additionally, as already noted seed characteristics likely interact in their effects on seed harvesting. For example, seed length combined with nitrogen content and the levels of saponins and non-protein amino acids accounted for nearly 70% of the seed preference of the kangaroo rat *D. ordii* (Henderson, 1990).

4. Fungal and Microbial Considerations

Microbes, especially bacteria and fungi, play critical roles in vegetation dynamics and plant-animal interactions in the arid west, although the extreme diversity and

difficulties of studying these organisms limits a full understanding of their function in natural communities (Janzen, 1969; Crist & Friese, 1993; Herrera et al., 1997). Some research from eastern Washington State indicates that soil bacteria are 2x more abundant and account for 20x active fungal biomass compared to bacteria (K. beard pers. comm.). Moreover we know that in arid soils fungi can be highly variable in abundance and diversity (Polis, 1991; Polis and Strong, 1996). Although there are conflicting reports some authors have reported fungi to be numerically less abundant than bacteria, fungi account for the majority of the microbial biomass in these soils (Skujins, 1984; Christensen, 1981; Kieft, 1991). Fungi play an important role in seed dynamics by affecting seed viability as well as interactions with seed consumers. Fungal pathogens, in addition to directly killing seeds (see Crist & Friese, 1993), might indirectly affect seed survival by affecting seed predator selectivity. Loss of seeds to pathogen attack can potentially shift seed predator selection to non-infected seeds even if they are less preferred. Further, if seed predators selectively avoid seeds infected with fungal pathogens that fail to kill the seeds, the seed theoretically is protected from predation by the fungus. Conversely, reports of increased selection of infected food items also exist (see Cork & Kenagy, 1989). As such, fungi associated with seeds can be beneficial or detrimental to plant establishment which can be mediated by the seed handling animal and may shift with varying levels and/or presence of fungal infection.

Given the degree to which granivore activity influences soil features, it is not surprising that both rodent and harvester ant burrows and mounds (i.e. nests) are associated with soil fungi (Herrera et al., 1997) and have even been promoted as hot spots for soil fungi (see Hawkins, 1996). Friese and Allen (1993) concluded that harvester ant

(*P. occidentalis*) mounds are places of microbial enrichment and that the ants promote the establishment of mutualistic mycorrhizal associations after mounds are abandoned.

Similarly, fungal colonies can be five times more abundant in kangaroo rat burrow soils than in soils away from burrows (Hawkins, 1996), and rodent dens appear to be areas of high microfungus diversity (Herrera et al., 1997).

Soil fungi can greatly affect soil seed pool reserves and thus plant establishment by either increasing or decreasing seed survival and/or rates of seed harvest by granivores. For example, some species of harvester ants reject seeds infected with spores of endophytic and saprophytic fungi, while others do not discriminate between infected and control seeds (Knoch et al., 1993). Crist and Friese (1993) placed seeds in fungal cultures obtained from soil seeds and presented moldy seeds along with control seeds to *P. occidentalis*, which harvested control seeds at nearly twice the rate of the moldy seeds; it was suggested that avoidance of moldy seeds may be due to the presence of the fungus *Penicillium* which is known to produce mycotoxins.

Many rodent species have evolved behaviors associated with food storing (Vander Wall, 1990), and given the ubiquity of fungal spores in soil environments it is not surprising that these animals may also have evolved strategies to take advantage of beneficial products of fungi while minimizing negative effects of the seed/fungus relationship. Kangaroo rats (*Dipodomys* spp.) are reported to prefer slightly moldy seeds over control and highly moldy seeds, suggesting they might be taking advantage of the beneficial effects of molds while avoiding the liabilities (Reichman & Rebar, 1985). Moreover, *Dipodomys spectabilis* actively manages seed reserves in what appears to be an effort to promote moderate amounts of fungal colonization (Reichman et al., 1986),

moving sterile seeds to places of high humidity while moving seeds with the “preferred” level of moldiness to areas of low humidity. In contrast, Eastern woodrats (*Neotoma floridana*) were more likely to consume food items that had high levels of fungal infection than food items with either no or intermediate levels of infection (Herrera & McDonald, 1997). Advantages resulting from the management and subsequent ingestion of moldy seeds include increased nutritional value and/or increased seed moisture content (Rebar & Reichman, 1983; Reichman et al., 1986). Thus, fungi can indirectly affect seed mortality due to predation by granivores, in addition to directly affecting mortality.

Some research suggests that plant-animal-microbe interactions are important at the population and community level within natural systems, which may have implications for restoration of these degraded systems. It is possible that this association could positively affect subsequent plant establishment thus influencing patterns of vegetation development in seeded areas where high densities of abandoned harvester ant mounds occur, as well as by altering rates of seed losses to predators. Recently, seeds coated with mycorrhiza inoculum have become commercially available for wildland restoration. How these seeds compare in granivore preference with un-coated native seeds is not known and merits investigation.

B. RESOURCE-WIDE QUALITIES

To better understand, predict, and potentially manage seed removal by granivores within the framework of arid-land restoration it is important to also consider resource-wide factors. The patterns of seed dispersion in time and space, the overall amount of seed present, the combinations of seed species available, and the characteristics of the

substrate all potentially influence the seed-seed consumer interaction. Here we consider the potential impact of such factors on seed removal in the heterogeneous arid-land environment. Understanding these effects in conjunction with the effects of factors unique to the seed will help predict outcomes and better establish management strategies for organisms in the context of reseeding events.

1. Seed Dispersion Patterns

Although seeds are available year round, and can lie dormant in the seed bank for one or more seasons, they generally come in annual pulses and can be variable spatially as well (Crist and MacMahon, 1994). These pulses of seed resources are parallel in many ways to the manner in which a reseeding event would occur. Seed application by drilling or broadcasting by plane or tractor in many instances pulses similar seed densities to what might occur in natural more intact systems (Longland et al., 2001). Therefore, evaluating how spatial and temporal seed dispersion patterns affect seed removal by granivores is prudent.

Different rodent species may use naturally or artificially available seed resources differently. Longland (1994) reported that heteromyid rodents harvested low density seed patches at similar rates to more dense seed patches. However, Reichman and Oberstein (1977) suggested that smaller pocket mice can effectively forage on a dispersed resource similarly to a clumped resource, unlike the larger heteromyid species evaluated. Given the nature of restoration seedings, species-specific foraging strategies might have important implications when the composition of the granivore community is known. When reseeding, seeds are ideally placed in a relatively regular pattern that minimizes

clumping. Thus, if smaller pocket mice or a diverse heteromyid community is present at the site of reseeded it is possible that large quantities of seeds could be lost to predation or secondarily dispersed (i.e. seed caching) by these animals. It is not clear how rodents might negotiate seeds sown by drilling that are in reality quite dense, but in a very long and thin linear clump.

Clumping creates variable seed densities at a small scale, with some patches having high densities of seeds (the clumps) and others with few seeds. Density-dependent foraging has been well demonstrated in both granivorous rodents and ants in North American deserts (Nelson & Chew, 1977; Price & Heinz, 1984; Mull & MacMahon, 1996; McMurray et al., 1997; Veech, 2001). Veech and Jenkins (2005) define density-dependent foraging as the harvest of a greater proportion of seeds from high-density patches than from low-density patches. Greater harvesting from higher density patches is presumed to be driven by greater energy gain per unit time (Charnov, 1976). In at least some cases the harvest rate increases uniformly with seed density (Price & Heinz, 1984), though such a regular pattern is unlikely to be universal. However, foraging decisions are not driven only by energy gain; for example, foraging behavior can be altered by the perceived risk of being eaten (Longland & Price, 1991). Optimal foraging theory (Charnov, 1976) suggests that animals should balance time spent foraging with associated costs. In this light, Bowers (1990) experimentally evaluated these tradeoffs at the scale of individual small-scale resource patches and showed that *Dipodomys merriami* accepts proportionately more risk at higher resource levels.

Beyond small-scale density effects within local seed patches, overall seed density within the foraging range of the organisms and satiation effects are also important,

especially within the context of reseeding events. Satiation is thought to be an evolved interaction among fruiting plants and the animals that eat them. The predator satiation hypothesis suggests that during mast years plants will produce more seeds than can be eaten by local seed predators so that some escape predation and germinate (Silvertown, 1980; Kelly & Sork, 2002). Implied in this hypothesis is that seed predators will starve or move elsewhere during non-mast years, when few or no seeds are produced (Ostfeld et al., 1996). It is unknown how seed supplementation through large-scale seedings affects seed survival in terms of seed predator responses in arid-land environments. This is an area of research that merits investigation. In particular, the effects of seeding densities on seed harvesting are critical to understand.

In addition to seed dispersion horizontally we must also consider how seeds are dispersed vertically (i.e. depth). In drill seeding (see Young & McKenzie, 1982), several factors are considered to determine seeding depth (e.g., seed material, soil texture, and seasonal precipitation). Although these variables are generally considered solely in terms of how they affect the germination, emergence, and establishment of seedlings, all of these can also influence seed detection by rodents. Rodents can detect seeds in the soil by olfaction as well as random searching. Deeper seeds should be in theory more difficult to find by either chance or by smell, although in reality the effect of depth on detection is complicated by soil texture and substrate moisture (see below). As an example, Indian ricegrass seeds were harvested in greater quantities by *Dipodomys* spp. when they were more shallowly buried (Longland, 1994). Ideally, then, depth of burial would consider both suitability for germination and emergence of the species as well as the effect of depth on seed losses to granivores (see Figure 1.1). Finding the optimal

depth that balances seeding depth where maximal seedling emergence can occur while considering the depth where seeds are essentially hidden from seed predators would be ideal. Along these lines, Vander Wall (1993) showed that an overlap occurred between chipmunk caching depth and the depth at which bitterbrush (*Purshia tridentata*) seedlings best establish. Such an approach could help determine suitable planting depths for restoration seeds while reducing the likelihood seeds will be located by foraging animals, thus helping management decisions. Note from the hypothetical example in Figure 1.1 that such a consideration may lead to a different ideal depth of drilling than would be selected based only on consideration of seedling emergence as a function of depth.

2. Seed Mixture Effects

Although seed removal studies are usually based on single seed-species experiments, seed mixtures are more representative of natural conditions as well as ecological restoration where multiple seed species are applied together on the landscape. Seeds in resource mixtures could be preferentially harvested or, conversely, could escape harvest as a function of the specific seed neighborhood they are in. Therefore, relative to monospecific seed arrays, the potential outcomes of seed mixtures are threefold: 1) an overall increase, 2) an overall reduction, or 3) no change in removal rate or preference of any given seed species. The context-dependent effects of outcomes 1 and 2 will alter relative preference, fate, and harvest rates of seeds, resulting in changed patterns of plant establishment and, potentially, vegetation structure.

First consider the case where mixed-seed neighborhoods increase the susceptibility of a specific seed species to harvesting. This negative result, considered by

some a form of “apparent competition” (sensu Veech 2000, 2001), occurs when an increased quantity of one seed species leads to a decrease in the abundance (increased harvest) of the second seed species. Veech (2000, 2001) and Veech and Jenkins (2005) demonstrated short-term apparent competition among seeds of desert plants fed on by Heteromyid rodents. For example, *Achnatherum hymenoides* had a negative indirect effect on *Astragalus cicer* because rodents foraged less in patches that only contained *Astragalus cicer* than they did in patches with both seeds present (Veech, 2001). Similarly, in forests of Chile, harvesting of the less-preferred *Nothofagus dombeyi* seeds increased in the presence of *Austrocedrus chilensis* seeds (Caccia et al., 2006). The alternative case, “apparent mutualism,” occurs if an increase in one species leads to an increase in the second species through reductions in seed harvesting in mixtures. Theoretically, a seed forager’s search image could become complicated or confused by seed mixtures so that they fail to find as many preferred seeds in mixture. The same outcome can come from a reduced efficiency of locating desirable seeds in diverse seed mixtures or among seeds that require increased handling time before the animal can perceive its relative desirability. In this light, the harvesting of several desirable perennial restoration seeds was reduced when present with seeds of cheatgrass (*Bromus tectorum*) relative to when present alone (Chapters 4 and 6). If preference drives these patterns such studies demonstrate that granivore-mediated indirect effects can affect seed survival patterns depending to the predators’ preferences for alternative seed types when present in mixed seed patches.

Previous work by Veech (2000, 2001) and Veech and Jenkins (2005) have used the ecological foundation of indirect effects (i.e. apparent competition and indirect

mutualism) as a theoretical framework for explaining the patterns of seed removal in the context of seed mixtures versus single seed patches (see Holt, 1977; Holt & Kotler, 1987; Caccia et al., 2006). They use apparent competition and apparent mutualism from the perspective of plant population responses, which we argue would be appropriate if the data indicate changes in plant population size(s) that are directly due to seed-seed interactions mediated by shared predators/dispersers. However, we suggest that a different, similar framework is more appropriate for considering context-dependent effects of seed mixtures on seed removal when considering the foraging process itself; that is, when the data deal only with the harvesting of seeds, which is the usual case, and not with the resultant demography of the plants. This framework follows the terminology used by many authors studying herbivory in monospecific versus mixed vegetation assemblages (see Tahvanainen & Root, 1972; Atsatt & O'Dowd, 1976; Rausher, 1981; Wahl & Hay, 1995; Callaway et al., 2005; Miller et al., 2007). In this framework, when more seeds are harvested from mixed patches than from monospecific patches there is evidence for “associational susceptibility” (sensu Tahvanainen & Root, 1972); the seed is more “susceptible” when it is associated with that particular heterospecific seed neighborhood. Other terms used to describe this outcome include “shared doom” and “associational damage” (see Thomas, 1986; Wahl & Hay, 1995). In contrast, when seeds have reduced harvesting when in mixture than when alone there is “associational resistance”; seeds in mixed patches are more resistant to harvesting in this context (see Chapter 3).

Context-dependent foraging is a broad area of ecological research including subjects ranging from humans to hummingbirds. Density-dependent foraging, granivore

preferences for alternative seed types, and prey switching have been suggested as potential behavioral mechanisms leading to indirect/associational interactions at the seed stage (see Veech, 2001). However, only a handful of studies have examined patterns of seed removal considering seed mixture as a context-dependent effect (Veech 2000, 2001; Veech & Jenkins, 2005; see Chapters 3, 5, and 6) for granivores in North American deserts. All previous studies have focused on rodents as the primary granivore, and to our knowledge these frameworks have been extended to ants only in this dissertation (Chapter, 3).

We argue for continued evaluation of context-dependent effects among seed mixtures, not only in the context of increasing our understanding of basic ecological interactions but also in the context of managing reseeded events as part of ecological restoration activities. Altering seed mixtures is potentially a relatively simple task managers could use to reduce seed harvesting by granivores. If the granivores are functionally seed predators, the desired outcome would be one of associational resistance among the seed materials chosen for reseeded, which would result in overall reductions of harvest and presumably increased probabilities of seed germination and seedling establishment (see Chapter 7). On the other hand, if seed dispersal (caching) by rodents is beneficial in restoration seedings perhaps a seed mixture that promotes associational susceptibility of the species would be desired. More research investigating how these behavioral processes operate in managed systems is suggested.

3. Soil and Related Edaphic Effects

Soil has an important role in seed-seed consumer dynamics as well as within the consideration of restoration and more specifically reseeded, because the soil is the medium where seed-seed remover interactions occur. Soil texture (Price & Heinz, 1984) may have important effects on both the distribution of desert rodents and ants and on the energetic costs of digging burrows and foraging for buried seeds. Soil texture influences the energetic costs associated with the separation of soil particles from the target particles (i.e. seeds) within the matrix (Price & Podolsky, 1989). Additionally, soil texture affects burrow humidity and potentially subsequent fungal infection (see above) of stored seeds for these fossorial organisms (see Kay & Whitford, 1978; Herrera et al., 1997). Understanding how soil texture might relate to predicted seed losses by granivorous animals could aid in determining seeding rates to account for expected removal.

Rake-sorting and gravity-sorting mechanisms are used by rodents to remove seeds from the soil matrix (see Price & Podolsky, 1989). When foraging animals move the forefeet forward and then down and back in a raking motion, the claws are spread open and larger particles are retained while smaller particles pass, hence “rake-sorting.” At the same time, the sides of the excavation pit cave in and gravity concentrates the larger and the less heavy particles on the surface near the bottom of the pit, hence “gravity-sorting.” Price and Podolsky (1989) showed that soil texture influences the size of seed selected. Moreover, rodents use different methods to extract seeds from soils of different textures and species differ in the influence of texture on seed extraction; nonetheless, all species evaluated were able to extract seeds best from fine-textured, heavy soils (Price & Heinz,

1984; Price & Podolsky, 1989). If seed size selection is in fact influenced by soil particle sizes, it may at times be prudent to choose smaller or larger seeds to reduce the removal of the target restoration seed by these animals. If, for example, high seed losses occur managers could select seeds that are either of similar or smaller sizes than the soil particles, thereby reducing the efficiency of rake-sorting seed extraction. Such application would likely only be an option in sandy or gravely large-particled soils. That is, selecting smaller-seeded species might be a good choice when seeding coarser textured soils to reduce losses to foraging animals.

4. Substrate Moisture

Seeds rapidly absorb water when the environment around them becomes moist. Soil moisture promotes the release of odorant molecules from seeds otherwise hidden from granivores in the soil (Vander Wall, 1994). For many rodent species, olfaction is a primary means for the detection of seeds in the soil. The North American deermouse (*Peromyscus maniculatus*), Great Basin pocket mouse (*Perognathus parvus*), and yellow pine chipmunk (*Tamias amoenus*) were able to detect seeds of three palatable species significantly better in moist (>99 % discovery rate) than in dry substrate conditions (overall a 13 % discovery rate) (Vander Wall, 1994). Vander Wall (1994) suggests this outcome is a consequence of the rodents' reduced ability to smell seeds in a dry substrate as opposed to a potential preference in conditions where seeds are simply easier to detect in moist substrates. However, the species studied differed in the ability to detect seeds in dry soil. *Perognathus parvus* found more seeds in the dry substrate than did the other

two rodent species, which may be evidence for shifting competitive relations among granivorous rodents as a function of soil moisture (Vander Wall, 1994).

V. Synthesis

Great Basin sagebrush communities are rapidly being converted to non-native annual rangelands and consequently occur where ecological restoration practices are presently being extensively conducted. However, the conversion of these landscapes is moving faster than the scientific advancement of the field of arid-land restoration. Ecologists struggle to find suitable restoration prescriptions to redirect the trajectory of degraded landscapes toward systems. At the same time ecologists realize how little we know about the many species that inhabit sagebrush communities let alone how they might be affected by these changes and how they might themselves influence the changes and the recovery. Restoration of these arid-lands will require a multi-pronged approach that must consider dynamics of undisturbed communities while understanding we are working toward a moving target. Granivory is one such dynamic; it has been shown to be an important and potentially even a keystone process in the arid west. As such, a continued research focus on granivory within the framework of ecological restoration is suggested.

VI. Preface to Dissertation Research

The research in this dissertation is centered on two inter-related themes related to granivory in the context of sagebrush community restoration. First we consider the community compositions and abundances of granivorous ants and rodents in intact big

sagebrush (*A. tridentata*) communities compared to those in converted cheatgrass (*B. tectorum*)-dominated annual grasslands. Because sites dominated by cheatgrass monocultures are in greatest need of ecological restoration, it is critical to understand the composition of granivore communities in these degraded sites relative to those found in more pristine sites because the granivore communities will ultimately influence the dynamics and patterns of seed removal (see below). Chapter 2, on ant assemblages in intact sagebrush and converted cheatgrass monoculture habitats, reports marked shifts in ant community structure, between the two vegetation types, primarily based on large changes in the abundance of species. Shifts in total species richness and diversity were not detected. Chapter 4, on rodent community assembles in Great Basin sagebrush communities and converted *Bromus tectorum* habitat types, shows even more extreme differences among vegetation types. This work corroborates the findings of others who have reported marked reductions in total abundance, species richness/diversity of rodent species in the cheatgrass-dominated monocultures relative to intact sagebrush.

The second theme of this dissertation is an exploration of factors influencing seed removal by ants and rodents. As such, the remaining data chapters report on three separate seed removal experiments (one for ants and two for rodents) with special attention to context-dependent effects. Chapter 3, on associational resistance and the importance of among- and within-patch characteristics on seed selectivity by Western harvester ants (*Pogonomyrmex occidentalis*), considers the effects of large scale and small scale among-patch factors as well as within-patch factors on seed removal patterns by this ubiquitous granivorous ant species. In chapter 5, we use a novel statistical approach in the ecological sciences, beta-distributed regression, to evaluate the presence

of associational interactions among seed mixtures in a rodent-specific seed removal experiment. In the final data chapter, chapter 6, we ask whether total seed densities and relative proportions of two co-occurring seed species affect seed preferences by granivorous rodents. In this chapter we report on evidence for the occurrence of associational effects among seed mixtures mediated by rodents. Chapter 7 provides both a template for summarizing this research and a review of granivory in the context of restoration that outlines the ecological foundations of granivory while considering the management implications.

VII. Literature Cited

- Archer, S. & D. A. Pyke.** 1991. Plant-animal interactions affecting plant establishment and persistence on revegetated rangelands. *J. Range Manage.* 44: 558-565.
- Atsatt, P. R., & D. J. O. Dowd.** 1976. Plant defense guilds. *Science* 193: 24-29.
- Bowers, M. A.** 1990. Exploitation of seed aggregates by Merriam's kangaroo rat: harvesting rates and predatory risk. *Ecology* 71:2334-2344.
- Bozinovic, F., and R. A. Vasquez.** 1999. Patch use in a diurnal rodent: handling and searching under thermoregulatory costs. *Functional Ecology* 13:602-610.
- Brown, J. H., & M. K. Ernest.** 2002. Rain and rodent: Complex dynamics of desert consumers. *BioScience* 52: 979-987.
- Brown, J. H. & E. J. Heske.** 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250: 1705-1707.
- Brown, J. H., D. W. Davidson, J. C. Munger, & R. S. Inouye.** 1986. Experimental community ecology: The desert granivore system. Pp. 41-61 *in* J. Diamond and T. J. Case (eds.), *Community ecology*. Harper and Row, New York.

- Brown, J. H., D. W. Davidson & O. J. Reichman.** 1979. An experimental study of competition between seed-eating desert rodents and ants. *American Zoologist* 19: 1129-1143.
- Brown, J. H., O. J. Reichman, & D. W. Davidson.** 1979. Granivory in desert ecosystems. *Ann. Rev. Ecol. Syst.* 10: 201-227.
- Caccia, F. D., E. J. Chaneton & T. Kitzberger.** 2006. Trophic and non-trophic pathways mediate apparent competition through post-dispersal seed predation in a Patagonian mixed forest. *Oikos* 113: 469-480.
- Callaway, R. M., D. Kikodze, M. Chiboshvili & L. Khetsuriani.** 2005. Unpalatable plants protect neighbors from grazing and increase plant community diversity. *Ecology* 86: 1856-1862.
- Chambers, J. E. & J. A. MacMahon.** 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. *Ann. Rev. Ecol. Syst.* 25: 263-292.
- Charnov, E. L.** 1976. Optimal foraging, the marginal value theorem. *Theor. Pop. Bio.* 9: 129-136.
- Christensen, M.** 1981. Species diversity and dominance in fungal communities. Pages 202-232 *in*: D. T. Wicklow and G. C. Carroll, (eds.), *The fungal community*. Marcel Dekker, New York.
- Crist, T. O. & J. A. MacMahon.** 1992. Harvester ant foraging and shrub-steppe seeds: interactions of seed resources and seed use. *Ecology* 73: 1768-1779.
- Crist, T. O. & C. F. Friese.** 1993. The impact of fungi on soil seeds: Implications for plants and granivores in a semiarid shrub-steppe. *Ecology* 74: 2231-2239.
- Crist, T. O. & J. A. MacMahon.** 1994. Harvester ant foraging and shrub-steppe seeds: interactions of seed resources and seed use. *Ecology* 73: 1768-1779.
- Cork, S. J. & G. J. Kenagy.** 1989. Nutritional value of hypogeous fungus for a forest-dwelling ground squirrel. *Ecology* 70: 577-586.
- Davidson, D. W.** 1977a. Species diversity and community organization in desert seed-eating ants. *Ecology* 58: 711-724.
- Davidson, D. W.** 1977b. Foraging ecology and community organization in desert seed-eating ants. *Ecology* 58: 725-737.
- Davidson, D. W.** 1993. The effects of herbivory and granivory on terrestrial plant succession. *Oikos* 68: 23-35.

- Davidson D. W., J. H. Brown & R. S. Inouye.** 1980. Competition and the structure of granivore communities. *Bioscience* 30: 233-238.
- Frank, C. L.** 1988. Diet selection by a heteromyid rodent: role of net metabolic water production. *Ecology* 69: 1943-1951.
- Friese, C. F. & M. F. Allen.** 1993. The interaction of harvester ants and vesicular-arbuscular mycorrhizal fungi in a patchy semi-arid environment: the effects of mound structure on fungal dispersion and establishment. *Funct. Ecology* 7:13-20.
- Fuller, P. J. & M. E. Hay.** 1983. Is glue production by seeds of *Salvia Columbariae* a deterrent to desert granivores? *Ecology* 64: 960-963.
- Gibson, D. J., C. C. Freeman & L. C. Hulbert.** 1990. Effects of small mammal and invertebrate herbivory on plant species richness and abundance in tallgrass prairie. *Oecologia* 84: 169-175.
- Hansen, S. R.** 1978. Resource utilization and coexistence of three species of *Pogonomyrmex* ants in an upper Sonoran grassland community. *Oecologia* 35: 109-117.
- Hawkins, L. K.** 1996. Burrows of kangaroo rats are hotspots for desert soil fungi. *J. Arid Envir.* 32: 239-249.
- Herrera, J. & M. W. McDonald.** 1997. Consumption by Eastern woodrats (*Neotoma floridana*) of food infected by fungi. *Am. Midl. Nat.* 137:282-289.
- Herrera, J., C. L. Kramer & O. J. Reichman.** 1997. Patterns of fungal communities that inhabit rodent food stores: effect of substrate and infection time. *Mycologia* 89: 846-857.
- Henderson, C. B.** 1990. The influence of seed apparency, nutrient content and chemical defenses on dietary preference in *Dipodomys ordii*. *Oecologia* 82: 333-341.
- Heske, E. J., J. H. Brown & Q. Guo.** 1993. Effects of kangaroo rat exclusion on vegetation structure and plant species diversity in the Chihuahuan Desert. *Oecologia* 95:520-524.
- Hobbs, R. J.** 1985. Harvester ant foraging and plant species distribution in annual grassland. *Oecologia* 67: 519-523.
- Hoffmann, L. A., E. F. Redente, and L. C. McEwen.** 1995. Effects of selective seed predation by rodents on shortgrass establishment. *Ecol. Appl.* 5: 200-208.

- Hölldobler, B., & E. O. Wilson.** 1990. *The Ants*. Belknap Press of Harvard University Press Cambridge, Massachusetts.
- Holt, R. D.** 1977. Predation, apparent competition, and the structure of prey communities. *Theor. Popul. Biol.* 12: 197-229.
- Holt, R. D., & B. P. Kotler.** 1987. Short-term apparent competition. *Am. Nat.* 130:412-430.
- Howe, H. F. & J. S. Brown.** 2001. The ghost of granivory past. *Ecol. Let.* 4: 371-378.
- Hulbert, A. J. & R. E. MacMillen.** 1988. The influence of ambient temperature, seed composition and body size on water balance and seed selection in coexisting heteromyid rodents. *Oecologia* 75: 521-526.
- Inouye, R. S., G. S. Byers & J. H. Brown.** 1980. Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology* 61: 1344-1351.
- Janzen, D. H.** 1969. Seed-eaters versus seed size, number, toxicity and dispersal. *Evolution* 23: 1-27.
- Janzen, D. H.** 1971. Seed predation by animals. *Annu. Rev. Ecol. Syst.* 2: 465-492.
- Jenkins, S. H.** 1988. Comments on relationships between native seed preferences of shrub-steppe granivores and seed nutritional characteristics. *Oecologia* 75: 481-482.
- Kay, F. R. & W. G. Whitford.** 1978. The burrow environment of the banner-tailed kangaroo rat, *Dipodomys spectabilis*, in south-central New Mexico. *Am. Midl. Nat.* 99: 270-279.
- Kerley, G. I. H. & T. Erasmus.** 1991. Chemical attributes of seeds of some economically important Karoo plants. *So. African J. Wildl. Res.* 21: 19-22.
- Kelly, D. & V. L. Sork.** 2002. Mast seeding in perennial plants: Why, how, where? *Ann. Rev. Ecol. Syst.* 33: 427-447.
- Kelrick, M. I. & J. A. MacMahon.** 1985. Nutritional and physical attributes of seed and some common sagebrush steppe plants: some implications for ecological theory and management. *J. Range Manage.* 38: 65-69.
- Kelrick, M. I., J. A. MacMahon, R. R. Parmenter & D. V. Sisson.** 1986. Native seed preferences of shrub-steppe rodents, birds and ants: the relationship of seed attributes and seed use. *Oecologia* 68:327-337.

- Kelt, D. A., J. H. Brown, E. J. Heske, P. A. Marquet, S. R. Morton, J. R. Reid, K. A. Rogovin & G. Shenbrot.** 1996. Community structure of desert small mammals: comparisons across four continents. *Ecology* 77: 746-761.
- Kieft, T. L.** 1991. Soil microbiology in reclamation of arid and semiarid lands. Pages 209-256 in J. Skujins, editor. *Semiarid lands and deserts: soil resource and reclamation*. Marcel Dekker, New York, USA
- Knoch, T. R., S. H. Faeth & D. L. Arnott.** 1993. Endophytic fungi alter foraging and dispersal by desert seed-harvesting ants. *Oecologia* 95:470-473.
- Lawhon, D. K. & M. S. Hafner.** 1981. Tactile discriminatory ability and foraging strategies in kangaroo rats and pocket mice (Rodentia: Heteromyidae). *Oecologia* 50: 303-309.
- Longland, W. S.** 1993. Desert rodents in disturbed shrub communities and their effects on plant recruitment. Pages 209-215 in B. Roundy, D. MacArthur, J. Haley, and D. Mann, (eds.), *Proceedings: wildland shrub and arid land restoration symposium*, Las Vegas, Nevada.
- Longland, W. S.** 1994. Seed use by desert granivores. Pp. 233-237 in B. S. Monsen and S. G. Kitchen, (eds.), *Symposium on ecology, management, and restoration of intermountain annual rangelands*. USDA Forest Service, Boise, Idaho.
- Longland, W. S. & S. L. Bateman.** 1998. Implications of desert rodent seed preferences for range remediation. *J. Range Manage.* 51: 679-684.
- Longland, W. S. and M. V. Price.** 1991. Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? *Ecology* 72:2261-2273.
- Longland, W. S., S. H. Jenkins, S. B. Vander Wall, J. A. Veech & S. Pyare.** 2001. Seedling recruitment in *Oryzopsis hymenoides*: Are desert granivores mutualists or predators? *Ecology* 82: 3131-3148.
- MacMahon, J. A., J. F. Mull & T. O. Crist.** 2000. Harvester ants (*Pogonomyrmex* spp.): Their community and ecosystem influences. *Ann. Rev. Ecol. Syst.* 31: 265-291.
- Mares, M. A. & D. F. Williams.** 1977. Experimental support for food particle size resource allocation in Heteromyid rodents. *Ecology* 58:1186-1190.
- Majer, J. D.** 1989. Fauna studies and land reclamation technology – a review of the history and need for such studies. Pp. 5-33 in J. D. Majer, (ed.), *Animals in primary succession: The role of fauna in reclaimed lands*. Cambridge University Press, New York.

- Mares, M. A.** 1993. Heteromyids and their ecological counterparts: a pandesertic view of rodent ecology and evolution. Pp. 652-714 in H. H. Genoways and J. H. Brown, (eds.), *Biology of the Heteromyidae*. American Society of Mammalogists, Special Publication No. 10.
- Mattson, W. J. Jr.** 1980. Herbivory in relation to plant nitrogen content. *Ann. Rev. Ecol. Syst.* 11: 119-161.
- McAdoo, J. K., C. C. Evans, B. A. Roundy, J. A. Young & R. A. Evans.** 1983. Influence of Heteromyid rodents on *Oryzopsis hymenoides* germination. *J. Range Manage.* 36: 61-64.
- McMurry, M. H., S. H. Jenkins & W. S. Longland.** 1997. Effect of seed density on germination and establishment of a native and an introduced grass species dispersed by granivorous rodents. *Am. Midl. Nat.* 138: 322-330.
- Miller, A. M., C. McArthur & P. J. Smethurst.** 2007. Effects of within-patch characteristics on the vulnerability of a plant to herbivore. *Oikos* 116: 41-52.
- Mull, J. F. & J. A. MacMahon.** 1996. Factors determining the spatial variability of seed densities in a shrub-steppe ecosystem: The role of harvester ants. *J. Arid Environ.* 32: 181-192.
- Mull, J. F. & J. A. MacMahon.** 1997. Spatial variation in rates of seed removal by harvester ants (*Pogonomyrmex occidentalis*) in a shrub-steppe ecosystem. *Am. Midl. Nat.* 138: 1-13.
- Nelson, J. F. and R. M. Chew.** 1977. Factors affecting seed reserves in the soil of a Mojave Desert ecosystem, Rock Valley, Nye County, Nevada. *Am. Midl. Nat.* 97:300-320.
- Ostfeld, R. S., C. G. Jones & J. O. Wolff.** 1996. Of mice and mast. *BioScience* 46: 323-330.
- Parmenter, R. R., J. A. MacMahon & S. B. Vander Wall.** 1984. The measurement of granivory by desert rodents, birds and ants: a comparison of an energetics approach and a seed-dish technique. *J. Arid Environ.* 7: 75-92.
- Polis, G. A.** 1991. Food webs in desert communities: complexity via diversity and omnivory. Pp. 383-437 in: G. Polis, (ed.), *The ecology of desert communities*. University of Arizona Press, Tucson, Arizona.
- Polis, G. A. & D. R. Strong.** 1996. Food web complexity and community dynamics. *Am. Nat.* 147: 813-846.

- Price, M. V.** 1983. Laboratory studies of seed size and seed species selection by Heteromyid rodents. *Oecologia* 60: 259-263.
- Price, M. V. & K. M. Heinz.** 1984. Effects of body size, seed density, and soil characteristics on rates of seed harvest by heteromyid rodents. *Oecologia* 61:420-425.
- Price, M. V. & R. H. Podolsky.** 1989. Mechanisms of seed harvest by heteromyid rodents - soil texture effects on harvest rate and seed size selection. *Oecologia* 81: 267-273.
- Rausher, M. D.** 1981. The effect of native vegetation on the susceptibility of *Aristolochia reticulata* (Aristolochiaceae) to herbivore attack. *Ecology* 62:1187-1195.
- Reichman, O. J. & C. Rebar.** 1985. Seed preferences by desert rodents based on levels of mouldiness. *Animal Behaviour* 33:726-729.
- Reichman, O. J., A. Fattaey & K. Fattaey.** 1986. Management of sterile and moldy seeds by a desert rodent. *Anim. Behav.* 34: 221-225.
- Sherbrooke, W. C.** 1976. Differential acceptance of toxic jojoba seed (*Simmondsia chinensis*) by four Sonoran desert Heteromyid rodents. *Ecology* 57: 596-602.
- Schupp, E. W.** 2007. Suitable sites for dispersal are context dependent. Pp. 445-46 in Dennis, A.J., E.W. Schupp, R.J. Green, and D.A. Westcott, (eds.), *Seed dispersal: theory and Its application in a changing world*. CAB International, Wallingford, UK.
- Schupp, E. W. & M. Fuentes.** 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* 2: 267-275.
- Silvertown J. W.** 1980. The evolutionary ecology of mast seeding in trees. *Biol. J. Linn. Soc.* 14: 235-250.
- Simon, E. W. & L. K. Mills.** 1983. Imbibition, leakage and membranes. Pp. 9-27 in C. Nozzolillo, P. J. Lea and F. A. Loewus, (eds.), *Mobilization of reserves in germination*. Plenum Press, New York.
- Skujins, J.** 1984. Microbial ecology of desert soils. *Adv. Micro. Ecol.* 7: 49-91.
- Tahvanainen, J. O. & R. B. Root.** 1972. The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia* 10:321-346.
- Theimer, T. C.** 2005. Rodent scatterhoarders as conditional mutualists. Pp. 283-296 in *Seed Fate*, P-M. Forget, J. E. Lambert, P. E. Hulme, and S. B. Vander Wall, (eds.), CABI.
- Thomas, C. D.** 1986. Butterfly larvae reduce host plant survival in vicinity of alternative host species. *Oecologia* 70: 113-117.

- Vander Wall, S. B.** 1990. Food hoarding in animals. University of Chicago Press, Chicago.
- Vander Wall, S. B.** 1992a. The role of animals in dispersing a "wind-dispersed" pine. *Ecology* 73: 614-621.
- Vander Wall, S. B.** 1992b. Establishment of Jeffrey pine seedlings from animal caches. *West. J. Appl. Forest.* 7: 14-20.
- Vander Wall, S. B.** 1993. A model of caching depth: Implications for scatter hoarders and plant dispersal. *Am. Nat.* 141: 217-232.
- Vander Wall, S. B.** 1994. Seed fate pathways of antelope bitterbrush: dispersal by seed-caching yellow pine chipmunks. *Ecology* 17:1911-1926.
- Vander Wall, S. B.** 1998. Foraging success of granivorous rodents: effects of variation in seed and soil water on olfaction. *Ecology* 79:233-241.
- Vander Wall, S. B., M. J. Beck, J. S. Briggs, J. K. Roth, T. C. Thayer, J. L. Hollander & J. M. Armstrong.** 2003. Interspecific variation in the olfactory abilities of granivorous rodents. *J. Mammal.* 84: 487-496.
- Vander Wall, S. B., K. M. Kuhn & M. J. Beck.** 2005. Seed removal, seed predation, and secondary dispersal. *Ecology* 86:801-806.
- Veech, J. A.** 2000. Predator-mediated interactions among the seeds of desert plants. *Oecologia* 124: 402-407.
- Veech, J. A.** 2001. The foraging behavior of granivorous rodents and short-term apparent competition among seeds. *Behav. Ecol.* 12: 467-474.
- Veech, J. A. & S. H. Jenkins.** 2005. Comparing the effects of granivorous rodents on persistence of Indian ricegrass (*Oryzopsis hymenoides*) seeds in mixed and monospecific seed patches. *West. N. Am. Nat.* 65: 321-328.
- Voorhies, M. R.** 1975. A new genus and species of fossil kangaroo rat and its burrow. *J. Mammal.* 56: 160-176.
- Wahl, M. & M. E. Hay.** 1995. Associational resistance and shared doom: effects of epibiosis on herbivory. *Oecologia* 102: 329-340.
- West, N. E.** 1968. Rodent-influenced establishment of ponderosa pine and bitterbrush seedlings in central Oregon. *Ecology* 49: 1009-1011.

West, N. E. & J. O. Klemmedson. 1978. Structural distribution of nitrogen in desert ecosystems. Pp. 1-16 *in* N. E. West and J. J. Skujins, (eds.), Nitrogen in desert ecosystems. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania.

Whisenant, S. K. 1999. Repairing damaged wildlands: a process-oriented, landscape-scale approach. Cambridge University Press, Cambridge.

Wilson, M. F., B. L. Rice & M. Westoby. 1990. Seed dispersal spectra: A comparison of temperate plant communities. *J. Veg. Sci.* 1: 547-562.

Young, J. A. & D. McKenzie. 1982. Rangeland drill. *Rangelands* 4: 108-113.

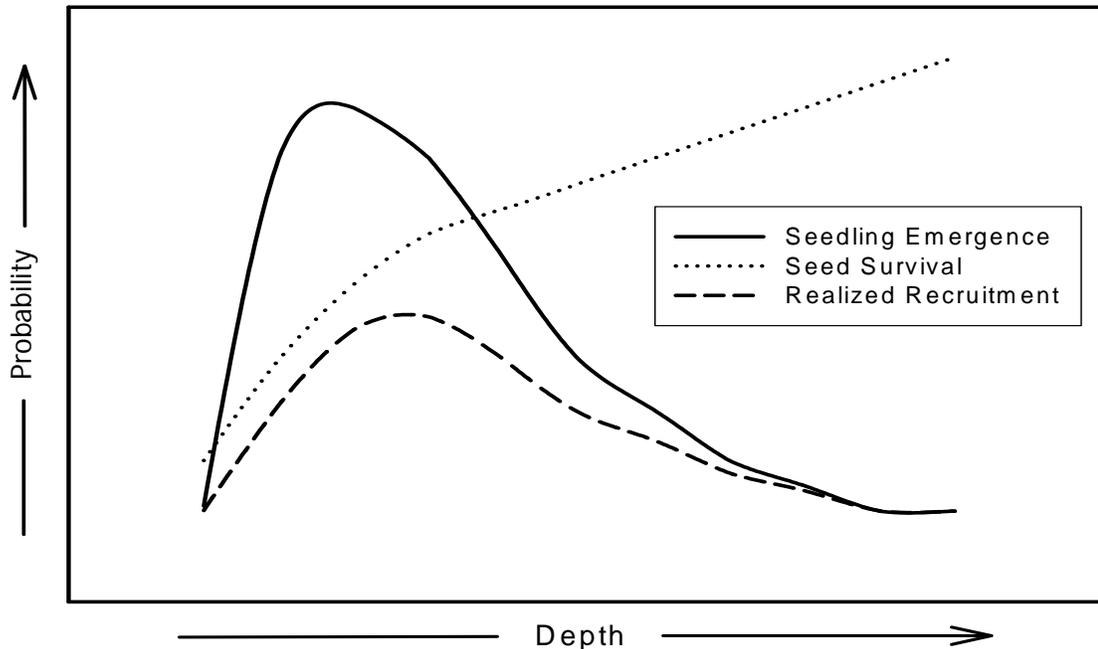


Figure 1.1. Theoretical depiction relating seeding depth to the probability of seedling emergence of surviving seeds based only on the effects of depth of seed germination and the ability of seedlings to emerge through the soil (solid line), the probability of seeds surviving in the soil un-detected by granivorous rodents (dotted line), and the probability of recruitment based on surviving and emerging which is the product of the first two lines (dashed line). Note that in this hypothetical example the best seeding depth considering the effects of rodents as well as the ability of a surviving seed to emerge as a seedling is deeper than would be predicted based only on the ability of a seedling to emerge.

CHAPTER 2

ANT ASSEMBLAGES IN INTACT SAGEBRUSH AND CONVERTED
CHEATGRASS-DOMINATED HABITATS IN RUSH
VALLEY, TOOELE COUNTY, UTAH, USA²

Abstract. Biological invasions are considered one of the greatest threats to native species in natural ecological systems. One of the most successful invasive species is *Bromus tectorum* (cheatgrass), which is having marked impacts on native flora and ecosystem processes. However, we know little about the effects of this invasion on native animal species in the Intermountain West. Because ants have been used to detect ecological change associated with anthropogenic land use, they seem well suited for a preliminary evaluation of the consequences of cheatgrass-driven habitat conversion. In the current study we assessed ant community assemblages in intact sagebrush and nearby cheatgrass-dominated vegetation using pit-fall traps. Ant abundance was about 10-fold greater in cheatgrass-dominated than in sagebrush plots although there was no indication that ant species diversity differed. There was a trend for functional group evenness to be more homogenous at sagebrush plots compared to cheatgrass-dominated plots, which is consistent with results from some other insect community shifts in similar habitat comparisons. Further, we noted a general trend that common species/functional groups increased in abundance while the un-common species/functional groups seemed to be negatively impacted but cheatgrass conversion. More specifically, most functional

² Coauthored by Steven M. Ostoja, Eugene W. Schupp, and Kelly Sivy

groups had greater abundances in cheatgrass-dominated plots, opportunists and cold climate specialists were more abundant in sagebrush plots. This initial survey of ant communities from intact native and altered vegetation types may be suggestive of similar trends of biodiversity shifts throughout the Intermountain West where cheatgrass has successfully replaced native species. The implications of ant communities on land management activities specifically in the context of arid-land ecological restoration are also discussed.

INTRODUCTION

Initially accidentally introduced in contaminated livestock feed, *Bromus tectorum* (cheatgrass) has become a very successful invader into novel habitats throughout the United States (Novak and Mack 2001). Climate change, overgrazing by livestock, and general poor management practices initially facilitated invasion by *B. tectorum* in sagebrush habitats (Billings 1990, Fleischner 1994). However the subsequent conversion of sagebrush habitat to annual grasslands dominated by the non-native *B. tectorum* is most closely tied to fires throughout the Intermountain West (D'Antonio and Vitousek 1992, Fleischner 1994, Brooks et al. 2004). It is estimated that about 40,000,000 ha have been invaded by or converted to near monocultures of *B. tectorum* within this region (see Link et al. 2006). Because of extensive fine fuels of *B. tectorum*, invaded communities are subjected to recurrent frequent fires that reinforce the conversion (Pellant 1989).

B. tectorum is proving to be one of the greatest threats to species diversity, threatening the historically-rich biotic diversity once a part of the Intermountain West (Vale 1975, Billings 1990). Many animals dependent on sagebrush and associated

vegetation are thought to have been greatly reduced or eliminated all together (Pimentel et al. 2000). Reports indicate that the conversion of sagebrush habitat to *B. tectorum* negatively impacts native animal species, such as sage grouse and small mammals (Yensen et al. 1992, Wirth and Pyke 2003, Chapter 4), but there is little understanding of the effects of conversion on less charismatic species like invertebrates. Although we assume that invertebrates respond similar to mammals and birds, there are few data evaluating this assumption.

Terrestrial invertebrates can be good indicators of ecological change associated with land use activities such as mining, restoration, and grazing (Andersen and Majer 2004). Specifically, ants have received much attention from ecologists as bio-indicators in land management and restoration because they are thought to respond in ecologically interpretable ways to environmental changes associated with disturbances (King et al. 1998, Hoffmann and Andersen 2003). Further, it is thought that ants are good indicators of the potential responses of a variety of species across very different taxonomic groups. For example, Andersen and Sparling (1997) found a relationship between aboveground ant activity and belowground decomposition processes at altered sites, and a negative correlation between ant species richness and soil microbial biomass across a range of undisturbed sites. This may be suggestive of the consequences of differentiating between within-habitat variation due to disturbance and variation across unique habitats when selecting for bio-indicators of ecological change (Andersen and Sparling 1997, Andersen 1997, Andersen et al. 2002). Thus, in the face of a changing sagebrush desert landscape throughout the Great Basin ants are appropriate groups to evaluate.

In this study, we evaluated ant communities of intact sagebrush and of adjacent areas converted to *B. tectorum* in the Great Basin of western Utah, USA. In addition to their value as bio-indicators, some species of ants harvest large quantities of seed. Because seed application is a frequent restoration strategy in these invaded habitats, ant communities was considered especially relevant for understanding the impacts of vegetation change. Our hypotheses were: (1) cheatgrass-dominated sites will differ in total ant abundance and species composition from nearby intact sagebrush sites, (2) conspicuous species (i.e. *Pogonomyrmex occidentalis*) will be more abundant in cheatgrass-dominated than in sagebrush sites. This second hypothesis is based on a previous finding that *P. occidentalis* mound densities is significantly higher in cheatgrass than in sagebrush locations (Ostoja *unpublished data*), coupled with the finding of significantly lower rodent species richness and abundances in cheatgrass monocultures (Chapter 4). Both hypotheses are relevant to ecological restoration.

METHODS

Study site and species

Study site - This study was conducted in Rush Valley in west-central Utah in an area referred to as Vernon Hills, Tooele County, Utah, USA (12 384335E 4438482N), approximately 155 km southwest of Salt Lake City, Utah. Six study plots were established; three 1.5-ha plots were in intact sagebrush vegetation (sagebrush hereafter) and three plots were in nearby annual non-native vegetation dominated by *B. tectorum* L (cheatgrass-dominated hereafter). Although perhaps not initially identical to the sagebrush plots, all cheatgrass-dominated plots were previously sagebrush-dominated

shrub stands that were converted to their current state by a fire in 1998; some of these plots were explored as potential field sites before the fire by the second author. In addition, all plots occur on the Hiko Peak soil series, where the potential plant community consists of about 45% perennial grasses, 15% forbs, and 40% shrubs, dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) (NRCS 2000). To our knowledge, no post-fire seeding or other attempts at restoration occurred (Dan Washington, Salt Lake Field Office, USDI Bureau of Land Management, pers.comm.).

Vegetation of sagebrush plots was typical of Wyoming big sagebrush communities of the Great Basin. In addition to *Artemisia tridentata* ssp. *wyomingensis* (Wyoming big-sagebrush), other shrubs such as *Atriplex canescens* (fourwing saltbush), *Gutierrezia sarothrae* (snakeweed), *Chrysothamnus viscidiflorus* (yellow rabbitbrush), and *Ephedra viridis* (Mormon tea) were present. The area between shrubs was dominated by the grasses *Achnatherum hymenoides* (Indian ricegrass), *Elymus elymoides* (bottlebrush squirreltail), *Poa secunda* (Sandberg bluegrass), *Hesperostipa comata* (needle-and-thread grass), *Leymus cinereus* (Basin wildrye), *Pseudoroegneria spicata* (bluebunch wheatgrass), and some *B. tectorum*. Cheatgrass-dominated plots were primarily *B. tectorum* ($\geq 90\%$ standing biomass, Ostoja unpublished data), but also had other weedy species including *Salsola* spp. (Russian thistle), *Sisymbrium altissimum* (tall tumbled mustard), and *Lepidium* spp. (peppercress).

Ant Sampling– In each plot, 25 pit-fall traps were placed in a 5 x 5 grid pattern with 20-m spacing between traps to sample the ant communities. A trap consisted of a

steel can (78 mm diameter) buried flush with ground level and with approximately 3 cm of 1:1 mixture of animal-safe propylene glycol (SIERRA[®] Antifreeze, Safe Brands Corporation) and water. Traps were baited with peanut butter placed near the inside rim of the can and on-quarter Pecan Sandie[®] cookie crumbled on the ground surface around the trap. Greenslade and Greenslade (1971) suggested that using bait with traps may bias capture rates due to variation in species-specific responses, however bait was used to increase the likelihood that of ants would encounter a trap (Marsh 1986). Trapping occurred from June 20-22 in 2004. Traps were set and then retrieved after 48 hr. This duration considered as the minimum trapping period to effectively characterize ant communities (Bestelmeyer et al. 2000, Borgelt and New 2006). Trapped animals were separated from the ethylene glycol solution, rinsed in purified water, and cold stored in 70% ethanol until identified.

Data analysis – Ants were identified to species using published keys, sorted, and counted. Identifications were verified by E. Sarnat at the Department of Entomology at the University of California at Davis. Voucher specimens were deposited at the Plant and Restoration Ecology Lab, Utah State University and at the Eastern Oregon Agricultural Research Center, Oregon State University. We were able to positively identify >99% of our specimens. All three “*Formica fusca*” specimens considered in our data analyses were identified to the *Formica fusca* group, but they could not be identified to species with total certainty due to missing critical taxonomic features.

Identified species were assigned to functional groups according to their species-group responses to environmental stress and disturbance following previous studies of

ants as bioindicators (Andersen 1997). These groups are dominant Dolichoderinae, subordinate Camponotini, hot-climate specialists, cold-climate specialists, cryptic species, opportunists, and generalized Myrmicinae. See Andersen (1997) for detailed descriptions of functional group designations.

Ant pitfall data were log-transformed at the trap level, and summed for each plot to minimize bias associated with variation in proximity of traps to nests, foraging strategies, and colony size (Suarez et al. 2000). Overall taxon abundances in pitfall traps were first assessed by summing the abundances of a species across the three plots in a vegetation type (i.e. cheatgrass-dominated or sagebrush). Simpson's, Shannon's, and McIntosh indices for diversity and Shannon's and McIntosh evenness indices were calculated for both vegetation types separately by species and by functional group. We used t-tests to compare ant species functional group richness, abundance, diversity, and evenness between vegetation types. Log-normal species abundance curves were used to visually compare proportional abundances between vegetation types. Additional t-tests allowed for the comparison of species and functional group abundances among the two vegetation types. All statistical analyses were conducted using SYSTAT 12 (SYSTAT 2007), unless otherwise noted in the text. Significance for all analyses was accepted at $\alpha = 0.05$. Taxa were treated at the species level for richness and other statistical analysis, unless treated as functional groups, allowing for ecological interpretation of taxon responses to vegetation type (Bestelmeyer 2005). Mean \pm standard errors (SE) are presented throughout. Because data were collected at the southern end of the Rush Valley region statistical inferences are limited to the study area (Wester 1992).

RESULTS AND DISCUSSION

Patterns of richness, diversity, and abundance

Surprisingly ant species richness was similar between the two vegetation types. Sixteen species were identified in this study, 15 in cheatgrass-dominated plots and 14 in sagebrush plots (Table 2.1). Thirteen of these species were trapped in both vegetation types. Measures of diversity and evenness for individual species and for functional groups were also similar in the two vegetation types (see Table 2.2). Although indices were consistently lower for the sagebrush plots, there were no statistically significant differences.

Although not well studied, limited research suggests cheatgrass-dominated sites are a less suitable habitat type for some other groups of animals (birds, Knick and Rotenberry 2000; small mammals, Gano and Rickard 1982, Chapter 3; lizards, Green et al. 2001, Newbold 2005*a* and *b*; snakes, Mull 2008, *in press*) in the Intermountain West. If the present results are suggestive of patterns across a broader geographic range, at least in terms of species diversity and evenness, ants may not respond negatively to sites dominated by cheatgrass. However, a closer consideration of shifting patterns in terms of species and functional group abundance(s) provides a more complete understanding of how cheatgrass conversion affects ant communities.

Species rank abundance curves indicate that ant communities from both cheatgrass-dominated and sagebrush plots follow a lognormal distribution (Fig. 2.1), a pattern also documented for North American desert ant communities in southeastern Arizona, USA (Chew 1977). Total ant abundance differed significantly between the two

vegetation types, being about 10-fold higher in cheatgrass-dominated plots (10342 ± 682) than in sagebrush plots (1075 ± 112), which was opposite the hypothesized pattern (Tables 2.1 and 2.3). In both cheatgrass-dominated and sagebrush plots the most abundant species was *Monomorium ergatogyna*, which was an order of magnitude more abundant than the second most common species (Fig. 2.2). Individual species were not equally abundant within either the cheatgrass-dominated ($F_{15,32} = 23.1$; $P < 0.0001$) or the sagebrush plots ($F_{15,32} = 15.9$; $P < 0.0001$) (Fig. 2.2). Moreover considering abundances at the functional group level, abundance did not differ significantly among groups in the sagebrush plots ($F_{6,41} = 2.05$; $P = .079$), although this difference was highly significant in the cheatgrass plots ($F_{6,41} = 4.94$; $P < 0.0001$).

Considering ant community differences in abundance in terms of the biology of the functional groups may provide additional insight into the patterns (see Fig. 2.3). For example, particularly in warmer climates of North America, the dominant Dolichoderinae (DD) are considered to be active and aggressive species while other functional groups (i.e. OPP, CCS) are reported to be subordinate and/or to occur where the DD are not abundant. With a marked relative increase in the abundance of DD in cheatgrass-dominated plots, all three species within the CCS had relatively lower abundances, as would be expected (Fig. 1). Similarly, although all species of Opportunists (i.e. OPP) had low abundances everywhere, one species, *Aphaenogaster unita*, was significantly more abundant in sagebrush than in cheatgrass-dominated plots. The GM, which are thought to be behaviorally dominate to the DD, were in fact more abundant than the GM functional group in both vegetation types (Andersen 1997). Thus, there is evidence that something about the biology of species interactions and resource uses of the functional

groups likely drives not only their community structuring in general, but also their responses to cheatgrass conversion. However, continued research is necessary to disentangle the suite of potential factors affecting the observed ant community changes. We suggest the results of this study be considered in the context of the experimental design and limited scope of the study area. A more comprehensive evaluation of invertebrate responses to cheatgrass conversion conducted over a larger spatial area and longer temporal period is suggested.

The greater overall ant abundance in cheatgrass-dominated plots may be related to differences in resource availability and/or to competitive release. Fielding and Brusven (1993) reported that grasshopper assemblages of sites dominated by annual vegetation (predominately cheatgrass) had relatively high densities of some species, which the authors attributed to a preference of these species for cheatgrass as a food item (also see Fielding and Brusven 1992). Not enough data are available on resource use and resource availability to make strong conclusions about the present system, though. However, at least for seed-harvesting ants such as *Pogonomyrmex* and *Pheidole* spp., competitive release from rodent granivores, which are less abundant and diverse in cheatgrass sites in this region (Chapter 3), might contribute to their greater abundances in cheatgrass-dominated plots. These seed-harvesting ants might increase in abundance due to increased resource acquisition potential in the absence of granivorous rodent competitors (Davidson et al. 1980). Arid-land ants and rodents are reported to have extensive diet overlap (Brown and Davidson 1977), a pattern corroborated in this dissertation using seed removal trials for both groups (see Chapters 4, 5, and 6).

Considering ant community differences in abundance in terms of the biology and associated features of the natural history of the functional groups may provide additional insight into the patterns (see Fig. 2.3). For example, the dominant Dolichoderinae (DD) are considered to be active and aggressive species while other functional groups (i.e. OPP, GM, CCS) are reported to be subordinate and/or to occur where the DD are not abundant. However, even with a marked increase in the abundance of DD in cheatgrass-dominated plots, all three species within the GM, which contains important seed-eating species, also had significantly greater abundances in cheatgrass-dominated plots (Fig. 2.2). Conversely, although all species of Opportunists (i.e. OPP) had low abundances everywhere, one species, *Aphaenogaster unita*, was significantly more abundant in sagebrush plots than in cheatgrass-dominated plots. Similarly, the CCS, represented by the genus *Temnothorax* at our sites, was as expected more abundant in the sagebrush plots (Figs. 2.2, 2.3). Likewise, the SC which is considered behaviorally submissive to DD was significantly more abundant in sagebrush plots. Thus there is evidence that something about the biology of species interactions and resource uses of the functional groups drives their responses to cheatgrass conversion. However, continued research is necessary to disentangle the suite of potential factors affecting the observed ant community changes. We suggest the results of this study be considered in the context of the experimental design and limited scope of the study area.

Conservation, restoration, and management implications

Cheatgrass-dominated sites are a major target of restoration in the semi-arid western USA. Because restoration often involves the application of large quantities of

seed, it is important to understand how seed harvesting species such as *Pogonomyrmex* spp. and *Pheidole* spp. are affected by conversion to cheatgrass. All species within these seed harvesting genera were more abundant in cheatgrass-dominated plots than in sagebrush plots. This can have important implications where aerial broadcast seeding is used. Some species of *Pogonomyrmex* are reported to remove 10% of the annual seed production, although they may remove 100% of more preferred seed types (Crist and MacMahon 1992, Mull and MacMahon 1997, MacMahon et al. 2000). Seed losses to harvester ant foraging could significantly impact the success of restoration.

Pogonomyrmex occidentalis is the most conspicuous ant in both habits, but numerically dominant in the cheatgrass-dominated versus the sagebrush plots. Moreover, this species has a greater mound density in cheatgrass-dominated habitats than in any of seven other vegetation types in the area, including intact sagebrush (Tyler Logan, *unpublished data*). Overall, these results suggest that predation of desirable seeds by ants might be a significant problem for aerial seeding efforts in cheatgrass-dominated sites. However, because ants can not locate and harvest buried seeds this should be less of a problem for drilled seeds (MacMahon et al. 2000).

The shifts in the ant communities found in this study could be happening at larger scales throughout the Intermountain West where cheatgrass conversion is occurring at an alarming rate. However, given the limited research on how cheatgrass conversion may be affecting other invertebrate groups it is difficult to assess whether these ant results represent what other groups are experiencing. Potentially, undetected rare ant species may be threatened by cheatgrass conversion, as the observations reported here suggest rarer species are more likely than commoner species to be negatively impacted by this

habitat conversion. Because other changes occur with cheatgrass conversion (i.e. soil morphology, soil microbial communities, and fire cycle), it is difficult to know which direct or indirect factors favor some species while harming others (Belnap et al. 2005). These results suggest that the effects of invasion on biodiversity may not be wholly negative but point to the continued need to assess animal communities in the face of a changing landscape.

REFERENCES

- Andersen, A. N. 1997. Functional groups and patterns of organization in North American ant communities: A comparison with Australia. *Journal of Biogeography* **24**:433-460.
- Andersen, A. N., and G. P. Sparling. 1997. Ants as indicators of restoration success: relationship with soil microbial biomass in the Australian seasonal tropics. *Restoration Ecology* **5**:109-114.
- Andersen, A. N., and J. Majer, D. 2004. Ants show the way down under: invertebrates as bioindicators in land management. *Frontiers in Ecology and the Environment* **2**:291–298.
- Andersen, A. N., B. D. Hoffmann, W. J. Muller, and A. D. Griffiths. 2002. Using ants as bioindicators in land management: simplifying assessment of ant community responses. *The Journal of Applied Ecology* **39**:8-17.
- Belnap, J., S. L. Phillips, S. K. Sherrod, and A. Moldenke. 2005. Soil biota can change after exotic plant invasion: does this affect ecosystem processes? *Ecology* **86**:3007-3017.
- Belnap, J., S. L. Phillips, and T. Troxler. 2006. Soil lichen and moss cover and species richness can be highly dynamic: the effects of invasion by the annual exotic grass *Bromus tectorum*, precipitation, and temperature on biological soil crusts in SE Utah. *Applied Soil Ecology* **32**:63-76.
- Bestelmeyer, B. T. 2005. Does desertification diminish biodiversity? Enhancement of ant diversity by shrub invasion in south-western USA. *Diversity and Distributions* **11**:45-55.

- Bestelmeyer, B. T., D. Agosti, L. E. Alonso, R. Roberto, C. Brandaeo, W. L. Brown Jr., J. H. C. Delabie, and R. Silvestre. 2000. Field techniques for the study of ground-dwelling ants. Pages 122-144 in D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz, (editors). *Ants. Standard Methods for Measuring and Monitoring Biodiversity*. Smithsonian Institution Press, Washington, DC.
- Billings, W. D. 1990. *Bromus tectorum*, a biotic cause of ecosystem impoverishment in the Great Basin. Pages 301-320 in G. M. Woodwell (editors). *The Earth in transition: patterns and processes of biotic impoverishment*. Cambridge University Press, New York, USA.
- Borgelt, A., and New, T. R., 2006. Pitfall trapping for ants (Hymenoptera, Formicidae) in mesic Australia: what is the best trapping period? *Journal of Insect Conservation* **10**: 75-77.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, & D. A. Pyke. 2004. Effects of invasive alien plants on fire regimes. *BioScience* **54**:677-688.
- Brown, J. H., and D. W. Davidson. 1977. Competition between seed-eating rodents and ants in desert ecosystems. *Science* **196**:880-882.
- Brown, Jr, W. L. 2000. Diversity of ants. Pages 45-79 in D. Agosti, D. J. Majer, L. Alonso and T. Schulz (editors). *Ants: standards methods for measuring and monitoring biodiversity*. Smithsonian Institution Press, Washington D.C, USA.
- Burge, D. O. 2005. Taxonomy, biology, and distribution of seed harvesting ants in the *Pheidole californica* complex (Hymenoptera: Formicidae). *Journal of Hymenoptera Research* **14**:137-150
- Chew, R. M. 1977. Some ecological characteristics of the ants of a desert shrub community in southeastern Arizona. *American Midland Naturalist* **98**:33-49.
- Crist, T. O., and J. A. MacMahon. 1992. Harvester Ant Foraging and Shrub-Steppe Seeds: Interactions of Seed Resources and Seed Use. *Ecology* **73**:1768-1779.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**:63-87.
- Davidson, D. W., J. H. Brown, and R. S. Inouye. 1980. Competition and the structure of granivore communities. *BioScience* **30**:233-238.
- Fielding, D. J., and M. A. Brusven. 1992. Food and habitat preferences of *Melanoplus sanguinipes* and *Aulocara elliotti* (Orthoptera, Acrididae) on disturbed rangelands in southern Idaho. *Journal of Economic Entomology* **85**:783-788.

- Fielding, D. J., and M. A. Brusven. 1993. Grasshopper (Orthoptera, Acrididae) community composition and ecological disturbance on Southern Idaho rangeland. *Environmental Entomology* **22**:71-81.
- Fleischner, T. L. 1994. Ecological costs of livestock grazing in western North America. *Conservation Biology* **8**:629-644.
- Gano, K. A., and W. H. Rickard. 1982. Small mammals of a bitterbrush-cheatgrass community. *Northwest Science* **56**:1-7.
- Greenslade, P., and Greenslade, P. J. M., 1971. The use of baits and preservatives in pitfall traps. *Journal of The Australian Entomological Society* **10**: 253-260.
- Green, G. A., K. B. Livezey, and R. L. Morgan. 2001. Habitat selection by northern sagebrush lizards (*Sceloporus graciosus graciosus*) in the Columbia Basin, Oregon. *Northwestern Naturalist* **82**:111-115.
- Hoffmann, B. D., and A. N. Andersen. 2003. Responses of ants to disturbance in Australia, with particular reference to functional groups. *Austral Ecology* **28**:444-464.
- King, J.R., A.N. Andersen, and A.D. Cutter. 1998. Ants as bioindicators of habitat disturbance: Validation of the functional group model for Australia's humid tropics. *Biodiversity and Conservation* **7**:1627-1638.
- Knick, S. T., and J. T. Rotenberry. 2000. Ghosts of habitats past: contribution of landscape change to current habitats used by shrubland birds. *Ecology* **81**:220-227
- Link, S. O., C. W. Keeler, R. W. Hill, and E. Hagen. 2006. *Bromus tectorum* cover mapping and fire risk. *International Journal of Wildland Fire* **15**:113-119.
- MacMahon, J. A., J. F. Mull, and T. O. Crist. 2000. Harvester ants (*Pogonomyrmex* spp.): their community and ecosystem influences. *Annual Review of Ecology and Systematics* **31**:265-291.
- Marsh, A. C., 1986. Ant species richness along a climatic gradient in the Namib Desert. *Journal of Arid Environments* **11**: 235-241.
- Mull, J. F., and J. A. MacMahon. 1997. Spatial variation in rates of seed removal by harvester ants (*Pogonomyrmex occidentalis*) in a shrub-steppe ecosystem. *American Midland Naturalist* **138**:1-13.
- Newbold, T. A. S. 2005a. Biotic and abiotic determinants of species distribution: desert horned lizards (*Phrynosoma platyrhinos*) and ants in a shrub-steppe ecosystem. Ph.D. dissertation Utah State University.

- Newbold, T. A. S. 2005b. Desert horned lizard (*Phrynosoma platyrhinos*) locomotor performance: The influence of cheatgrass (*Bromus tectorum*). *Southwestern Naturalist* **50**:17-23.
- Novak, S. J., and R. N. Mack. 2001. Tracing plant introduction and spread: genetic evidence from *Bromus tectorum* (cheatgrass). *BioScience* **51**:114-122.
- Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. *BioScience* **50**:53-65.
- SYSTAT. 2007. SYSTAT 12. *in*. SYSTAT software, Inc. Institute, San Jose, CA, USA.
- Suarez, A. V., J. Q. Richmond, T. J., Case, 2000. Prey selection in horned lizards following the invasion of Argentine ants in southern California. *Ecological Applications* **10**: 711-725.
- Vale, T. R. 1975. Pre-settlement vegetation in the sagebrush grass area of the Intermountain West. *Journal of Range Management* **28**:32-36.
- Ward, S. P. 2005. A synoptic review of the ants of California (Hymenoptera: Formicidae). *Zootaxa* **936**:1-86.
- Wester, D. B. 1992. Viewpoint: replication, randomization, and statistics in range science. *Journal of Range Management* **45**:285-290.
- Wilson, E. O. 2003. *Pheidole* in the New World, a hyperdiverse ant genus. Harvard University Press, Cambridge, Mass, USA.
- Wirth, A. T., and D. A. Pyke. 2003. Restoring forbs for sage grouse habitat: Fire, microsites, and establishment methods. *Restoration Ecology* **11**:370-377.
- Yensen, E., D. L. Quinney, K. Johnson, K. Timmerman, and K. Steenhof. 1992. Fire, vegetation changes, and population fluctuations of Townsend's Ground Squirrels. *American Midland Naturalist* **128**:299-312.

Table 2.1. Total numbers of ants of identified species from pitfall trap samples by vegetation type. Functional groups of species are based on Andersen (2002), Brown (2000), and Bestelmeyer (2005) are also shown.

Functional group/Species	Cheatgrass-dominated	Sagebrush
Dominant Dolichoderines (DD)		
Notes: Abundant, very active and aggressive species, favor hot and open habitats		
<i>Forelius pruinosus</i> (Roger)	8241	140
Cold Climate Specialists (CCS)		
Notes: Geographical distribution is cooler climates, occur where DD are not abundant.		
<i>Temnothorax nevadensis</i> (Wheeler)	20	25
<i>Temnothorax rugatulus</i> Emery	8	22
<i>Temnothorax</i> CA-10* Ward	9	10
Hot Climate Specialist (HCS)		
Notes: Associated with warm climates; demonstrate morphological, physiological, or behavioral specializations to aridity.		
<i>Pogonomyrmex occidentalis</i> Cresson	2673	899
<i>Myrmecocystus hammettensis</i> Cole	8	4
<i>Myrmecocystus testaceus</i> Emery	88	93
Cryptic Species (CrS)		
Notes: Small, often subterranean taxa which forage predominantly within soil and litter and interact little with other groups.		
<i>Solenopsis molesta</i> Say	3140	54
Opportunists (OPP)		
Notes: Submissive taxa that are subordinate to DD and GM, may be locally dominant where these taxa are poorly represented.		
<i>Aphaenogaster unita</i> Wheeler	9	69
<i>Formica fusca</i> Linnaeus ^g	--	3
<i>Formica manni</i> Wheeler	2	--
<i>Myrmica tahoensis</i> Wheeler	4	--
Generalized Myrmicines (GM)		
Notes: Mass recruiting taxa with lower tempo and are often subordinate to DD, may be dominant where latter are under represented.		
<i>Monomorium ergatogyna</i> Wheeler	14630	1686
<i>Pheidole creightoni</i> Gregg [†]	385	3
<i>Pheidole pilifera</i> Roger ^{††}	1476	103
Subordinate Camponotus (C)		
Notes: Co-occurring but behaviorally submissive to DD, large body size and often nocturnally foraging.		
<i>Camponotus vicinus</i> Mayr	3	46

Notes: “*” is an un-described species (but see Ward 2005), “g” indicates species designations were for the *Formica fusca* group and, “†” and “††” indicate that specimens from this taxonomically difficult complex (i.e. “california complex” for *P. creightoni*) and/or the larger group (i.e. “pilifera group”) were assigned with both major and minor workers (see Burge 2005, Wilson 2003).

Table 2.2. Means for Simpson's, Shannon's, and McIntosh diversity indices and Shannon's and McIntosh evenness indices by vegetation type for A) species and B) functional group (see Krebs 1999, Magurran 2004).

Index	Cheatgrass-dominated	Sagebrush
A) Species		
Simpson's diversity	0.69	0.62
Shannon's diversity	1.40	1.35
McIntosh diversity	0.43	0.37
Shannon's evenness	0.52	0.51
McIntosh evenness	0.58	0.49
B) Functional group		
Simpson's diversity	0.63	0.57
Shannon's diversity	1.16	1.10
McIntosh diversity	0.39	0.33
Shannon's evenness	0.60	0.56
McIntosh evenness	0.62	0.52

Table 2.3. Results of paired t-tests comparing cheatgrass-dominated and sagebrush plots for total ant abundance and for species richness, diversity and evenness indices by A) species and by B) functional group (df = 4 for each test).

	<i>SE</i>	<i>t</i>	<i>P</i>
A) Species			
Abundance	691.4	13.40	0.001
Richness	0.47	2.12	0.102
Simpson's diversity	0.06	1.34	0.249
Shannon's diversity	0.13	0.47	0.656
McIntosh diversity	0.05	1.22	0.290
Shannon's evenness	0.05	0.21	0.845
McIntosh evenness	0.07	1.26	0.271
B) Functional group			
Simpson's diversity	0.06	1.29	0.265
Shannon's diversity	0.21	-0.18	0.866
McIntosh diversity	0.05	1.16	0.310
Shannon's evenness	0.06	0.89	0.425
McIntosh evenness	0.08	1.32	0.257

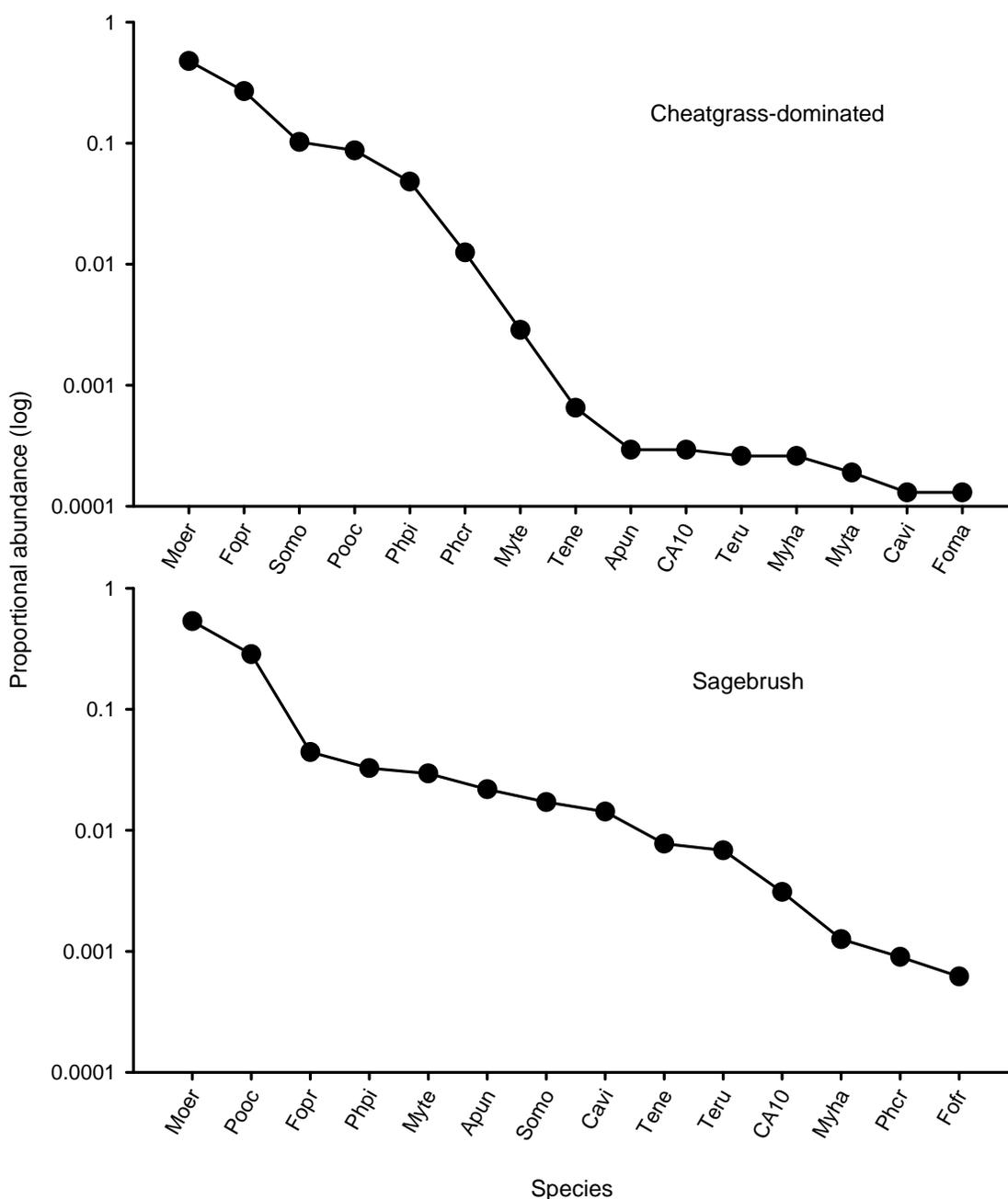


Figure 2.1. Rank abundance curves for ant species collected in (top) cheatgrass-dominated plots and (bottom) sagebrush plots. Thirteen species were identified in the cheatgrass-dominated and 14 in the sagebrush plots. Species codes are: Apun (*Aphaenogaster unita*), Cavi (*Camponotus vicinus*), Fopr (*Forelius pruinosus*), Fofu (*Formica fusca*), Foma (*Formica manni*), Moer (*Monomorium ergatogyna*), Myha (*Myrmecocystus hammettensis*), Myta (*Myrmica tahoensis*), Phcr (*Phiedole creightoni*), Phpi (*Phiedole pilifera*), Pogo (*Pogonomyrmex occidentalis*), Somo (*Solenopsis molesta*), Tene (*Temnothorax nevadensis*), Teru (*Temnothorax rugatulus*), and CA-10* (*Temnothorax* sp. CA-10).

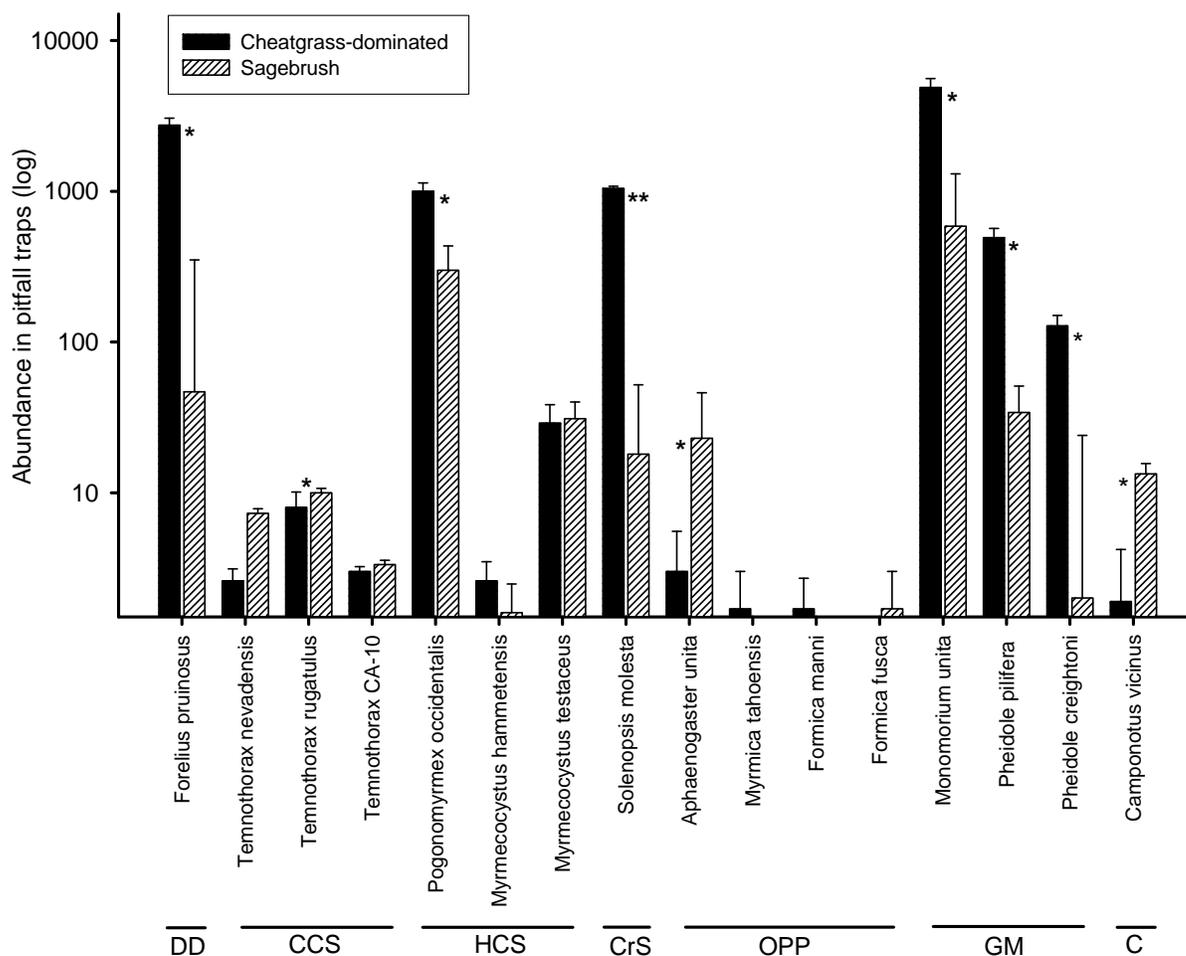


Figure 2.2 Means (\pm standard errors) of abundances in pitfall traps by species in cheatgrass-dominated (black) and sagebrush (stippled) plots. ** indicates $P \leq 0.001$, * indicates $P = 0.05$ for t-tests. Functional Groups: DD = Dominant Dolichoderinae, GM = Generalized Myrmicinae, C = Subordinate Camponotus, CCS = Cold Climate Specialists, CrS = Cryptic Species, HCS = Hot Climate Specialists, OPP = Opportunists; see Fig. 2.1 for descriptions of functional groups.

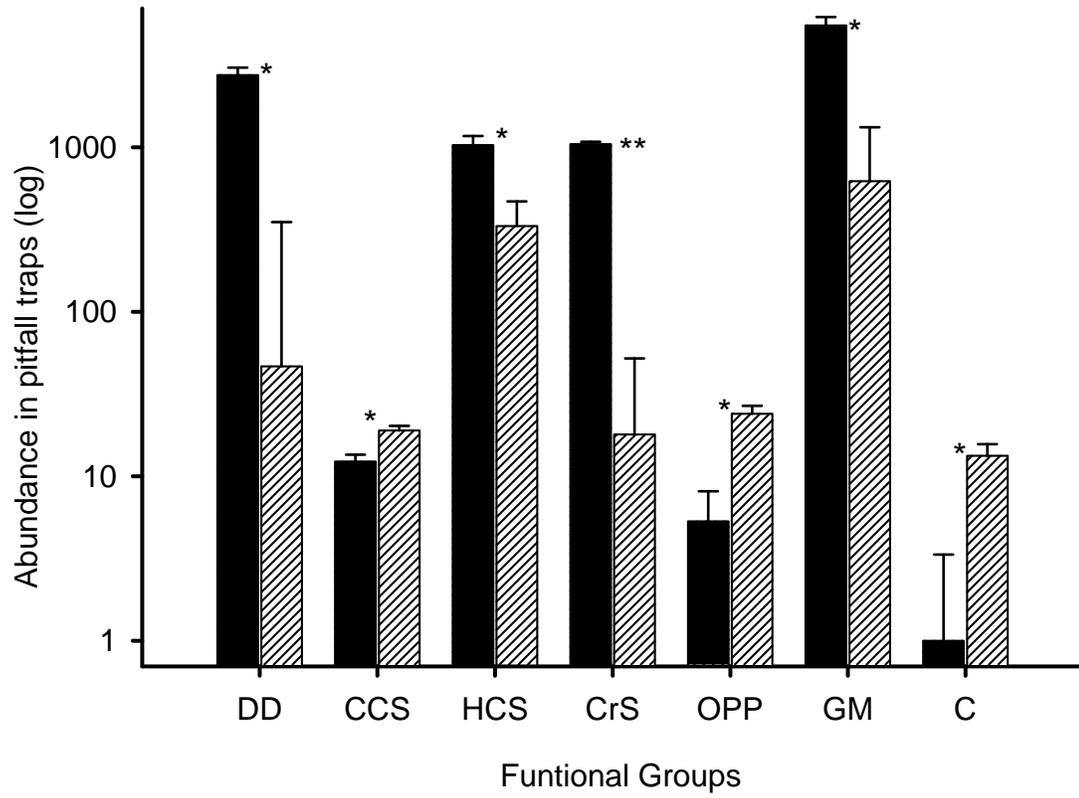


Figure 2.3 Means (\pm standard errors) of abundances in pitfall traps by functional group in cheatgrass-dominated (black) and sagebrush (stippled) plots. **indicates $P \leq 0.001$, * indicates $P = 0.05$ for t-test. See Fig. 2.2 for functional group abbreviations.

CHAPTER 3

ASSOCIATIONAL RESISTANCE AND THE IMPORTANCE OF AMONG- AND
WITHIN-PATCH CHARACTERISTICS ON SEED SELECTIVITY³

Abstract. The responses of granivorous animals to resource patches are a result of the combined influences of (1) the abundances of individual seed species in patches and their associated traits and (2) the overall availability of seed resources available to the granivores. In a field experiment we tested the importance of within- and among-patch characteristics on the removal of various seeds by Western harvester ants (*Pogonomyrmex occidentalis*). The within-patch effect considered the interactions among seed species in mixed seed patches with special attention to associational effects among the seed species in mixtures that are mediated by a shared consumer of those seeds. If a focal seed species incurs an increased rate of removal when present with a second seed species the outcome is termed “associational susceptibility.” Conversely, if the focal seed has a lower removal rate when present with the second seed species the outcome is “associational resistance.” Among-patch effects included small spatial scale effects of different distances from a focal ant mound and the larger spatial scale effects of different background vegetation communities. Selected species of seeds were presented in fixed quantities both alone (monospecific treatment) and in mixture with *Bromus tectorum* (cheatgrass) seed (mixed treatments) at four spatial locations with respect to active *P. occidentalis* mounds in adjacent sagebrush and cheatgrass-dominated communities in the eastern Great Basin of Utah, USA. Among-vegetation type

³ Coauthored by Steven M. Ostoja and Eugene W. Schupp

characteristics were important determinates of seed removal patterns and selectivity. We found greater levels of seed removal in sagebrush plots compared to cheatgrass-dominated plots for all seed types. Moreover, the smaller-scale among-patch effect was also important in that the spatial location with respect to the mound affected seed harvesting, particularly in the cheatgrass-dominated plots. Within-patch characteristics (i.e. seed mixture) were important, but importance differed among the seed types. Overall, however, we found a trend for associational resistance of cheatgrass seeds on the other species they were mixed with. These results demonstrate the importance of context, such as background vegetation, foraging distance, and seed mixture or resource availability, when considering seed removal patterns and rates.

INTRODUCTION

Large quantities of seed are consumed by granivores (Brown et al. 1979, Brown and Munger 1985, Crist and MacMahon 1992, Longland 1994), and selective seed predation in arid and semiarid communities can have important direct and indirect effects on vegetation (Brown et al. 1979, Davidson et al. 1980, 1985, Brown and Heske 1990). This seed-seed consumer interaction can alter probabilities of seed survival, affect seed pool reserves, and create shifting patterns of seedling recruitment for both annual and perennial plants. While total resource (i.e. seed) availability affects seed harvesting patterns by granivores, selectivity and consumption of individual seed species are strongly influenced by the morphological and chemical characteristics of seeds. In simple single-species seed choice experiments it is presumed that these attributes of individual seed species explain removal by granivores. However, the scenario is

complicated in situations where more than a single seed species is available, as is typical in natural environments (Atsatt and O'Dowd 1976, Veech 2001). Therefore, the likelihood of a seed being consumed is not only a function of its own characteristics, but also a function of the characteristics of co-occurring seeds in that patch. Moreover, unrealistic seed densities and/or the use of non-native seeds in choice experiments may produce results that are difficult to scale to an understanding of how ants influence seed pool dynamics in natural environments (Crist and MacMahon 1992).

Considering indirect interactions among plants, Atsatt and O'Dowd (1976) argued that susceptibility to attack is affected by the identity and proximity of neighbors. Potentially, a seed species subject to high rates of predation can gain protection when it is present with seeds deemed less desirable by generalist granivores. This effectively operates as an associational refuge, a form of the associational plant refuge theory (Pfister and Hay 1988, Milchunas and Noy-Meir 2002). This reduction in predation when in mixture with other species is termed "associational resistance," which has been widely documented in studies investigating how herbivores respond to focal plants in diverse vegetation patches. Alternatively, a given seed species can suffer increased harvesting when in mixed or diverse patches compared to when in single-species patches (i.e. attractant/decoy hypothesis, Atsatt and O'Dowd 1976). This has been called "associational susceptibility" (Brown and Ewel 1987), "associational damage," or "shared doom" (see Thomas 1986, Wahl and Hay 1995). Moreover, such associational susceptibility is likely more common than ecological reports indicate (see White and Whitham 2000).

Whether the outcome in mixed seed patches is associational resistance or associational susceptibility may depend on the relative desirability of co-occurring seeds, the likelihood of being found by potential seed predators and the scale at which predators select patches and seeds. While the relative palatability of co-occurring species can affect whether a given plant (or seed) receives associational resistance or associational susceptibility, the exact effect of relative palatability is uncertain. For example, an alga when present with more palatable species had increased susceptibility to herbivory, but when present with less palatable species it became resistant to attack (Wahl and Hay 1995). But the opposite results have been observed as well, with the presence of more desirable neighbors leading to lowered attack rates (i.e. attractant/decoy hypothesis, Atsatt and O'Dowd 1976). This suggests that other variables such as habitat characteristics, the scale of patchiness, factors associated with foraging behaviors, and the species-specific responses of predators to patchiness might be important as well. Consequently, the role of herbivore or predator preference in determining the directionality of associational patterns is not clear.

In addition to attempting to understand the outcomes of seed-granivore interactions from the perspective of the seed, the interaction can be further examined from the more direct perspective of the forager by incorporating optimal foraging theory, which states that animals should forage in ways that maximize energy intake while minimizing associated costs of travel, searching, and handling (Charnov 1976). Accordingly, harvester ants as single load central place foragers should concentrate resource acquisition at high-quality patches near the nest (see Davidson 1977), which effectively reduces travel time and predation risk, although such risk may vary as a

function of foraging strategy (Davidson 1977). It is possible, then, that outcomes not predicted by the plant-perspective hypotheses above (associational relations) can be more thoroughly explained by a simple set of foraging rules.

Western harvester ants, *Pogonomyrmex occidentalis* Cresson, are important granivores in semiarid systems throughout western North America (Mull and MacMahon 1997) that can remove up to one-quarter of the viable seed pool per year (Crist and MacMahon 1992). Via their selective seed predation they affect soil seed reserves and subsequent patterns of plant community establishment (Crist and MacMahon 1992, MacMahon et al. 2000). Sociality concentrates activity around a central space, the nest (Andersen 2001, MacMahon et al. 2000), which affects patterns of seed removal (see Crist and MacMahon 1992). Distance from the nest likely affects both the types of seeds harvested and the total amount of seed harvested. Theoretically, individual foragers may respond to fine-scale environmental factors (local food patches) whereas resource use variation between colonies could be influenced by differing vegetation structure or land use patterns (Crist and MacMahon 1991, Bestelmeyer and Wiens 2001).

In the current study we address two relevant issues with respect to resource patches. First, we assessed the effects of among-patch variation in the environment on patterns of seed preference and seed removal rates for five native grasses common to Great Basin sagebrush communities, for an annual exotic grass often used in seed selection experiments (*Panicum miliaceum*, millet), and for the annual exotic weed *Bromus tectorum* (cheatgrass). Among-patch factors were considered at two spatial scales. At the larger scale we considered the effects of vegetation type by comparing patterns of harvest in intact sagebrush communities versus adjacent highly degraded

cheatgrass-dominated communities. At the smaller scale we assessed the effects of distance from the focal mound. Second, we addressed how within-patch variation affected seed removal patterns, where a patch was a group of experimental seeds presented in a small constrained seed neighborhood such that the characteristics of the entire patch could be assessed rapidly by foragers. In particular, we compared the harvesting of seeds when in monospecific patches versus when in two-species seed mixtures. The focus of this part of the study was whether seed mixtures that included *B. tectorum* seed in a patch resulted in associational resistance or associational susceptibility for the other species in the mixture, and whether this result was influenced by the among-patch effects above. This study on ant-seed interactions relates to the general ecological question of how shifting patterns of vegetation (e.g., cheatgrass conversion) influence seed selectivity and rates of removal, both of which can have important implications for seed choice and thus successional patterns post-disturbance. This is of added interest given the apparent large differences in ant community composition in intact sagebrush communities and converted cheatgrass monocultures (see Chapter 2).

METHODS

Study site

This study was conducted around the Vernon Hills in Tooele County, west-central Utah, USA (12 384335 E 4438482 N). The site is approximately 155 km southwest of Salt Lake City, Utah. Six 1.2-ha study plots were established, three in intact sagebrush vegetation (sagebrush plots hereafter) and three nearby plots in annual non-native vegetation dominated by *Bromus tectorum* L. (cheatgrass; >90% standing biomass, S.M.

Ostoja, unpublished data; cheatgrass-dominated plots hereafter). Cheatgrass-dominated plots were previously sagebrush communities that were converted by a fire in 1996 (Bill Henderson, USDI BLM Salt Lake Field Office, pers. comm.). Perhaps not originally identical to the sagebrush plots, all cheatgrass-dominated plots were previously sagebrush-dominated shrub stands that were converted to their current state by a fire in 1998; some of these plots were explored as potential study sites before the fire by the second author. All six plots occur on the Hiko Peak series, where the potential plant community is composed of about 45% perennial grasses, 15% forb, and 40% shrubs, dominated by the shrub, *Artemisia tridentata wyomingensis* (Wyoming big sagebrush) (NRCS 2000). The cheatgrass-dominated plots also had other weedy species including *Salsola* spp. (Russian thistle) and *Lepidium* spp. (peppercress). Vegetation in sagebrush plots was typical of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) communities of the Great Basin. In addition to *A. tridentata* ssp. *wyomingensis*, other shrubs such as *Atriplex canescens* (fourwing saltbush), *Gutierrezia sarothrae* (broom snakeweed), *Chrysothamnus viscidiflorus* (yellow rabbitbrush), and *Ephedra viridis* (Mormon tea) were present. The understory was dominated by *Achnatherum hymenoides* (Indian ricegrass), *Elymus elymoides* (squirreltail), *Poa secunda* (Sandberg bluegrass), *Hesperostipa comata* (needle and thread), *Leymus cinereus* (basin wildrye), *Pseudoroegneria spicata* (bluebunch wheatgrass), and some *B. tectorum*.

Seed species

Seeds of the native perennial grasses *A. hymenoides*, *E. elymoides*, *P. spicata*, *P. secunda*, and *L. cinereus* were purchased from Granite Seed Company, Lehi, Utah, USA. *Panicum miliaceum* (millet), purchased from Cal Ranch Supply, Logan Utah, USA, Seeds of *B. tectorum* were collected in the vicinity of the research area by the author (SMO) in 2004 and 2005. *Bromus tectorum* seeds were mechanically cleaned and air blown to removal extra coreopsis material from the embryo in the laboratory at Utah State University. The native seed species were selected because they are used in reseeded/restoration projects in this region, few studies have used these seed species in the present context, and they are common to the west desert region of central Utah. The weed *B. tectorum* was selected because it is locally common, it is widespread and still expanding its range, it alters ecosystem processes (e.g. soil morphology, fire regimes, plant-animal diversity), and it might influence target seed choice by granivores (see Veech 2000 and 2001). *Panicum miliaceum* was also included because it has been used extensively in seed removal experiments (see Kelrick et al. 1986, Longland and Bateman 1998) and has been tested with some native species as a potential decoy seed in reseeded projects. In addition, results of seed preference studies for millet versus other desirable seed species (e.g. *A. hymenoides*) are inconclusive and/or vary as a function of seed predator type or vegetation type (see Kelrick et al. 1986, Longland and Bateman 1998).

We use the term “seed” throughout this paper in reference to all non-ovarian reproductive tissues which botanically speaking are fruits. Because the differing tissues among these two structures may either enhance or detract the seeds desirability as a

resource this distinction is thought to be a significant factor that could influence selectivity by a granivore (Kelrick and MacMahon 1985).

Seed trays

To quantify seed selection by ants and to determine whether the presence of cheatgrass seeds in a mixture affected harvesting of seed species, we designed a cafeteria-style seed removal experiment using ant-specific seed trays fashioned out of seven-day plastic pill boxes with a 10-mm diameter hole placed 5 mm above the bottom of each individual day compartment to allow access of ants to seeds while excluding rodents and birds (figure 3.1). In one set of trials seeds of all seven species were offered monospecifically (monospecific treatment). A seed patch was 2 g of one of the seed species placed randomly in one of the “day compartments” within the seven-day box. Thus all species were presented simultaneously and in very close proximity, but individual seed patches within compartments were of only a single species. In a second set of trials seeds of the five native grasses and of *P. miliaceum* were presented in mixture with *B. tectorum* seeds (mixture treatments). A seed patch consisted of 1 g of one of these six seed species combined with 1 g of cheatgrass seed. Each of these distinct mixed seed patch types was then placed randomly within one of the “day compartments” of the seven-day box, leaving one compartment empty. This resulted in 13 unique seed combinations overall.

Due to the nature of the experimental design and underlying research questions we used seed weights rather than seed density which resulted in different numbers of seeds available for removal among the different seed species. Approximate seeds

numbers/2 g quantity of seeds used were 512.8 seeds for *A. hymenoides*, 669.2 seeds for *B. tectorum*, 363.6 seeds for *E. elymoides*, 740.7 for *L. cinereous*, 338.9 seeds for *P. miliaceum*, 3333.3 seeds for *P. secunda*, and 454.5 seeds for *P. spicata*. Mean values are based on 100 randomly selected seeds of each species.

The exact consequences for the quantity of seeds removed are not completely clear. Ants remove seeds one at a time, so the absolute weight removed will be sensitive to some extent to individual seed size. But removal depends on many other characteristics besides weight, such as shape, surfaced texture, value as a resource, and more (MacMahon et al. 2000). In addition, the colony can recruit more individuals to harvest more resources when more are available and deemed desirable (MacMahon et al. 2000). Ultimately, however, because we were primarily interested in understanding if the ecological context in which seeds were encountered changed the way ants removed seeds our evaluation based on seed weight rather than density is not a large problem for this study; the absolute removal as not as important as changes in relative removal with changes in context.

In each of the six 1.2-ha plots a monospecific or a mixture tray was placed at one of four distances with respect to an active *P. occidentalis* mound (nest) in a random direction from the mound center. The distances were: (1) at the edge of the mound clearing (mound), (2) 1 m from the mound clearing (1 m), (3) 3 m from the mound clearing (3 m), and 4) 5 m from the mound clearing (5 m). Ants had access to seeds for 48 hrs and each seed treatment x distance combination was replicated ten times per plot during the months of August and September 2005. At the end of a 48-hr session seed

trays were collected and seeds were separated and reweighed by species to determine the amount of seed removed by species.

Ants

The only invertebrate species found using the seed trays was *P. occidentalis*. Results from an ant community survey indicate that although *P. occidentalis* was the most abundant seed harvester in both vegetation types, it was more abundant in cheatgrass-dominated plots than in sagebrush plots (see Chapter 2). Additionally, mounds of *P. occidentalis* were $> 40/\text{ha}$ in cheatgrass-dominated and $\text{ca. } \leq 20/\text{ha}$ in sagebrush plots (S.M. Ostoja unpublished data). However, it is possible that other species of ants occasionally encountered trays and removed seeds.

Statistical analyses

We conducted one-way analysis of variances (ANOVA) to compare seed harvest among the vegetation types and among seed types within each vegetation type, as well as among the distances within each vegetation type. Three-way ANOVAs of seed harvest were performed for all seed types combined in monospecific treatments, for non-*B. tectorum* seed harvest in mixture treatments, and for *B. tectorum* seed harvest in mixture treatments. Predictor variables were: distance from a focal mound (small scale among-patch effects), vegetation type (sagebrush or cheatgrass-dominated; large scale among-patch effects), the interaction between distance and vegetation type, and the trial. Response variables were the proportion of seeds removed for each of the seed species.

Seed harvest from trays was also analyzed with split-plot multivariate analyses of variance (MANOVA). The split-plot factor was vegetation type. We performed three

separate sets of analyses to assess the (1) amount of seed harvested in monospecific treatments, (2) the amount of non-*B. tectorum* seed harvested in mixture treatments, and (3) the amount of *B. tectorum* seed harvested in mixture treatments. Individual MANOVAs tested for differences among seed species in harvest from monospecific seed patches. In the second set of analyses separate MANOVAs tested for differences in harvest among non-*B. tectorum* seed species when in mixture with *B. tectorum*. In the third set of analyses separate MANOVAs tested for differences in *B. tectorum* among the different non-*B. tectorum* background seed species. In all cases the response variables were the proportion of seeds removed. The predictor variables were: distance from a focal mound (small scale among-patch effects), vegetation type (sagebrush or cheatgrass-dominated; large scale among-patch effects), the interaction between distance and vegetation type, and the trial. The error term for the vegetation effect (main plot) was trial within vegetation type, while the error term for the other effects was distance x trial within vegetation type.

ANOVAs were used to evaluate the harvest of each non-*B. tectorum* species in mixed seed patches relative to the harvest of *B. tectorum* in the mixture. The response variable was the ratio between the proportion of non-*B. tectorum* seeds removed and the proportion of *B. tectorum* seeds removed. The predictor variables and error terms were the same as for the MANOVAs. In all cases the proportions of seeds removed were arcsine transformed in order for the data to conform to the assumptions of ANOVA. Significance for all analyses was declared at $\alpha \leq 0.05$. Lastly, we qualitatively evaluated the mean proportional shift in removal for each non-*B. tectorum* seed species between monospecific and mixture treatments to assess the potential occurrence of associational

interactions among the seed species tested. All analyses were conducted with SYSTAT 11 (SYSTAT, 2006).

RESULTS

Seed harvest in monospecific treatments

Results of a one-way ANOVA indicated that more seed overall was removed in sagebrush plots than in cheatgrass-dominated plots ($F_{1,558} = 240.3$, $P < 0.001$). One-way ANOVAs further indicated that the quantity of seed harvested differed among species in both the cheatgrass-dominated ($F_{6,273} = 2.99$; $P < 0.007$) and the sagebrush ($F_{6,273} = 10.4$; $P < 0.001$) plots. In both vegetation types the most preferred seeds were *A. hymenoides* and *P. miliaceum* whereas the least preferred seed type was *B. tectorum*. Results from the three-way ANOVA for all seed species combined indicated that the interaction between distance and vegetation type were significant (Table 3.1 A). Moreover, the seed type x distance x vegetation type interaction was also significant (Table 3.1 A), indicating that both scales of among-patch characteristics interact to influence seed removal patterns in the monospecific treatments and that the seed species respond differently to these characteristics (Table 3.1 A).

Considering seed species separately, results from the MANOVA indicate that the general trend in cheatgrass-dominated plots was for less seed to be harvested at increasingly greater distances from mounds (Fig. 3.2), although the greatest amount of *B. tectorum* seed was removed at the greatest distance from the mounds (Table 3.2, Fig 3.2). In contrast to the general results from cheatgrass-dominated plots, seed harvest in sagebrush plots tended to be greatest at the mound and at 5 m from the mound, with

generally less removal at intermediate distances (see Fig. 3.2). The main effects distance and vegetation type were significant for all species while the vegetation type x distance interaction was significant for all except *B. tectorum* seed (Table 3.2).

Non-B. tectorum seed harvest in mixture treatments

Similar to the patterns for seed harvest in monospecific treatments, one-way ANOVA results indicated that non-*B. tectorum* seed harvest from mixtures was generally greater in sagebrush than in cheatgrass-dominated plots, although the pattern was not nearly as strong ($F_{1,478} = 4.32$, $P = 0.04$). In contrast to the monospecific results, seed species did not differ in the proportion harvested in either cheatgrass-dominated ($F_{5,234} = 2.19$, $P = 0.055$) or in sagebrush plots ($F_{5,234} = 0.935$; $P = 0.46$). Results from the three-way ANOVA in the mixture treatments indicated that removal of non-*B. tectorum* seeds in mixture treatments varied due to the main effects of seed type, distance, and vegetation type (Table 3.1 B). In addition, all interactions were significant except for the seed type \times vegetation (see Table 3.1 B), and in the overall analysis the seed type \times distance \times vegetation interaction was significant (Table 3.1), indicating again the complexities of seed harvesting.

Using MANOVA to evaluate seed harvest by species, the main effect of vegetation type in mixture treatments was only significant for *L. cinereus* (Table 3.3), a very different result than found in monospecific treatments and in the complete model with all species together. In the mixture treatment the main effect of distance was significant for all non-*B. tectorum* seeds except *P. secunda* (Fig. 3.3, Table 3.3). In contrast to monospecific results the greatest seed harvesting occurred at 1 m, especially in

cheatgrass-dominated plots (Fig. 3.3). The effect of distance on removal in the sagebrush plots appears to be primarily due to less seed harvested at 3 m (Fig. 3.3) than at other distances, an interesting and surprising result that produced a different pattern of removal compared to the monospecific treatments. Similar to the monospecific treatment, the distance x vegetation interaction was significant for all species except *P. secunda* (Table 3.3).

B. tectorum seed harvest in mixture treatments

The one-way ANOVA showed that seed harvest of *B. tectorum* in mixture treatments was significantly greater in sagebrush than in cheatgrass-dominated plots ($F_{1,478} = 179.4, P < 0.001$). Harvest of *B. tectorum* did not differ as a function of which seed species it was mixed with in sagebrush plots ($F_{5,234} = 0.133; P = 0.984$). However, seed species did affect *B. tectorum* harvest in cheatgrass plots ($F_{5,234} = 2.37, P = 0.04$). This result is like driven the increased harvest of *P. secunda* seeds compared to the relatively low harvest of the other non-*B. tectorum* seeds in mixture. Similarly, results from the three-way ANOVA suggest that the distance x vegetation interaction was significant for all species except *P. secunda* (Table 3.4). There was no significant effect of seed type in the mixture on the harvest of *B. tectorum* (Table 3.1 C). The seed type \times distance \times vegetation interaction was not significant (Table 3.1 C) for *B. tectorum* seed harvest.

Results from the MANOVA analyses indicated that *B. tectorum* seed harvest in mixture was significantly affected by vegetation in all seed species mixtures and was significantly affected by distance when mixed with all species other than *E. elymoides* and *P. secunda* (Table 3.4). Overall, more *B. tectorum* seed was harvested from mixtures

at 1 m from a mound than at other distances in cheatgrass-dominated plots (Fig. 3.4), except for maybe when *B. tectorum* was present with *P. secunda* seeds where harvest of the weed seed appeared to be relatively similar at the three closest distances to the mound. In sagebrush plots, however, the greatest *B. tectorum* seed harvest was either at the mound or at 5 m from the mound while the least harvest was at 3 m (Fig. 3.4), and this trend was consistent for all seed combinations (Fig. 3.4, Table 3.4).

*Harvest from monospecific versus mixture treatments – evidence for
associational resistance*

A major interest in the current research was how seed removal by ants might be influenced by the seed neighborhood in which a given seed occurred. In particular, we were interested in whether the within-patch effect of seed neighborhood on seed removal varied as a function of the among-patch levels of spatial context; that is, vegetation type and distance from a mound. However, in the current experimental framework, statistical comparison of the quantity of seed removed from monospecific treatments with 2 g of seed available and from mixture treatments with only 1 g of seed available is not straightforward. To address this issue we used two approaches. Our first approach was to analyze least square means of the ratio of non-*B. tectorum* seed removal to *B. tectorum* seed removal in the mixture treatments. Means and standard errors of this analysis for each seed combination are in Figure 3.5. If the point is above zero, then more of that non-*B. tectorum* seed type was removed than was *B. tectorum* seed, whereas if the point is below zero then proportionally more of *B. tectorum* seed was removed.

Patterns for this analysis are similar for four of the six seed types, *A. hymenoides*, *E. elymoides*, *P. miliaceum*, and *P. spicata*. All of these species were disproportionately harvested relative to *B. tectorum* seeds in the cheatgrass-dominated plots whereas *B. tectorum* was disproportionately harvested in the sagebrush plots (Fig. 3.5, Table 3.5). There appeared to be no discrimination either for or against *L. cinereus* relative to *B. tectorum* and neither the effect of vegetation nor distance significantly affected the pattern of relative harvest (Fig. 3.5, Table 3.5). A unique pattern emerged in the *P. secunda*/*B. tectorum* combination treatment, where consistently less *P. secunda* was removed compared to *B. tectorum*. The ratio of harvest did not differ among vegetation types or at varying distances from the mound, although the interaction between these two was significant (Fig. 3.5, Table 3.5).

For our second approach we compared the proportion of non-*B. tectorum* seed removed (i.e. percent of total) from the monospecific treatments to the proportion of the same seed removed from the mixture treatments, despite the potential importance of density dependence of seed harvesting (see Price and Heinz 1984, Chapter 6). Because of the shortcomings of this approach (see Chapters 5 and 6), we only consider three possible qualitative alternative outcomes of ecological interest: 1) no difference in proportional removal between the two treatment types (neutral effect), 2) proportionally more non-*B. tectorum* seed removed from mixtures than from monospecific treatments (associational susceptibility), or 3) proportionally less non-*B. tectorum* seed removed from mixtures than from monospecific patches (associational resistance). Seed harvest for all species suggests associational resistance, especially in the sagebrush plots (Figure 3.6). Interestingly, ants harvested a smaller proportion of the seed when there was less of

it initially available (that is, from the mixture treatments), strongly suggesting that the results are not due to satiation and that density-dependent harvesting is not biasing the results.

DISCUSSION

Generally, it is thought that seed removal patterns for seed harvesting ants like *P. occidentalis* follow two general patterns consistent with foraging theory (Charnov 1976). First, because they are trunk-trail or central place foragers more seeds are thought to be collected nearer the mound than further from the mound (Crist and MacMahon 1991, Anderson and MacMahon 2001). Second, ant foraging is expected to be concentrated in high-density seed patches (Mull and MacMahon 1997, MacMahon et al. 2000). Although we did not test the density-dependent expectation, we did show that seed removal by harvesting ants varied as a function of distance from the mound, a small scale among-patch effect. In addition we showed that harvesting varied as a function of background vegetation, a large-scale among-patch effect, and as a function of seed neighborhood, a within-patch effect. Indeed, the fate of a seed was very dependent on the spatial context of the seed in multiple ways.

Seed preferences

There was a clear preference for the native seeds, especially *A. hymenoides*, and for *P. miliaceum*, over the non-native *B. tectorum* seeds, a result consistent with other findings (Kelrick et al. 1986, Crist and MacMahon 1991). Note that these preference rankings were not clearly related to weight. The low harvest rate of cheatgrass seeds was

likely a combined function of low nutritional value and persistent awns which make handling difficult. Interestingly, *B. tectorum* went virtually un-harvested from seed trays in cheatgrass-dominated plots. Although we found greater harvest of *B. tectorum* in sagebrush than in cheatgrass-dominated plots, our results reiterate that cheatgrass is a relatively undesirable seed for ants. Mull and MacMahon (1996) reported that *B. tectorum* accounted for the majority of seed harvested by *P. occidentalis* in a sagebrush habitat in Wyoming. Because cheatgrass can be by far the most abundant seeds present in such sites (Humphrey and Schupp 2001), one might predict that the search image for cheatgrass seed would be keen and that their ubiquitous nature would drive increased harvest. However, the low relative value of *B. tectorum* seeds and its overwhelming abundance in the background seed pool (Crist and MacMahon 1991, 1992, Humphrey and Schupp 2001) might help explain the low harvest rates, especially from the seed trays in cheatgrass-dominated plots.

Of the *B. tectorum* seeds that are harvested by *P. occidentalis*, large numbers are later discarded in refuse piles, and many of these seeds are partially eaten and effectively removed from the seed pool (Mull 2003). For surviving discarded *B. tectorum* seeds the effectiveness of dispersal by harvester ants is a function of how many seeds are subsequently relocated from refuse piles to favorable sites for establishment (Schupp 1993). In this light, despite the low preference of cheatgrass seeds it has been argued that harvester ant activities could indirectly facilitate increased densities of *B. tectorum* near their mounds (see Mull and MacMahon 1997). Which may be due to the open conditions near the mound that are suitable for germination and growth and the high densities of

discarded *B. tectorum* seeds that are dispersed especially to sites (also see Nowak et al. 1990) where resources are relatively abundant in a patchily distributed resource matrix.

Large-scale among-patch effects: vegetation type

In the monospecific treatments more seed was harvested in the sagebrush plots than in the cheatgrass-dominated plots for nearly all seed types and treatments. Differences in harvester ant population sizes do not explain the differences in removal among the vegetation types. The most abundant seed harvesting ant species in our sites was *P. occidentalis*, which was three-times more abundant in pitfall traps in the cheatgrass-dominated plots than in the sagebrush plots (Chapter 2). In addition, harvester ant mound density was approximately twice as high in the cheatgrass-dominated plots as in the sagebrush plots (see Chapter 2). So why were more seeds in general being harvested in the sagebrush plots despite there being fewer harvester ants? The explanation is not completely clear, but it is likely that the seed resources in the background seed pool indirectly influenced what was removed from the seed trays. More seeds in general are likely available in cheatgrass-dominated plots compared to native sagebrush plots, even though the quality of the resource was relatively poor (i.e. dominated by *B. tectorum*).

Differences in competitive interactions between the two community types may also influence patterns of seed harvest. Because rodent granivores are greatly reduced in cheatgrass-dominated plots (Chapter 4), ants are likely the most important granivore in these degraded communities. Potentially then, in the face of cheatgrass conversion, this may shift the competitive interactions for seed resources from an intense ant-rodent to

less intense ant-ant one. It seems logical, then, to think that ants are likely to have the dominant impact on seed mortality in cheatgrass-dominated sites, while rodents are likely the most important granivores in sagebrush sites. Evidence for such an interaction is noted by Brown and Davidson (1977) who pointed to the important role rodent granivores can have in limiting the abundance of seed harvesting ants through resource competition. In the face of intense competition in the sagebrush plots seed harvesting ants might forage more efficiently on a per colony basis than those living in cheatgrass-dominated locations. Further work assessing the relationship among inter- and intra-specific competition among granivores in the context of cheatgrass conversion would help understand patterns noted in this research.

Small-scale among-patch effects: distance from mounds

To some degree our results indicate seed removal decreased at increasingly greater distances from the mound, although this result was most evident in the cheatgrass-dominated plots. Similar patterns of removal were demonstrated in sagebrush habitats in Wyoming (see Mull and MacMahon 1997, Anderson and MacMahon 2001). However, in our sagebrush plots the greatest amount of seed removed was at the mound clearing and again at 5 m away from the mound. Why would there be a difference in distance effects between sagebrush and cheatgrass-dominated communities? It is possible that the increased density of *P. occidentalis* in cheatgrass-dominated vegetation could potentially produce an increased inter-colony competition for resources effectively shifting foraging behavior to locations closer to the central mound in contrast to a more diffuse foraging effort in the sagebrush.

The nature of the vegetation in each vegetation type may further explain patterns. Because *P. occidentalis* foragers have greater running speeds and net energetic gain when using trunk trails, they tend to use cleared paths over vegetated areas (Fewell 1988). Because cheatgrass can thickly reinvade cleared ant trails annually, it likely impedes the utility of foraging trails in areas with high cheatgrass densities. In contrast, trails likely remain clear for longer periods with less maintenance in native vegetation. Foraging trails radiating from central mounds in cheatgrass-dominated sites are very difficult to locate at distances of ≥ 2 -3 m, while they are still easily located at distances of ≥ 5 m in sagebrush plots (S. M. Ostoja pers. observ). Furthermore, ant workers decline exponentially with distance along trunk trails from their central mound (Crist and MacMahon 1991). As a result, seed harvesting decreases with increasing distance from the main foraging trail (Mull and MacMahon 1997), and the greater the distance from the ant mound, the more likely a seed is to be far from a trunk trail further reducing harvest at increasingly greater distances.

Lastly, it is possible that the true general patterns of seed harvest in terms of distance effects were not detected due to limitations of the experimental design. The distances from a focal mound used in the current study might not have been sufficient to detect the expected distance-dependent patterns of foraging in our sagebrush sites. Others have found that harvest and/or selectivity shifted at distances > 9 m (Kelrick et al. 1986), 7 m (Crist and MacMahon 1991), and > 10 m (Davidson 1978), from the mound. Unfortunately, we were constrained to a 5 m limit in this study due to the very high mound densities in cheatgrass-dominated plots.

Combined influence of large and small-scale among patch effects

The loss of shrubs in cheatgrass plots could further explain the reduction of seed removal at more distant locations from focal mounds found in cheatgrass-dominated plots but not in sagebrush plots. Shrub structure is thought to provide visual references for foraging individuals of this species (Crist and MacMahon 1991). Once sagebrush sites are converted to cheatgrass monocultures most if not all shrub “references” would be lost, which may indirectly affect foraging patterns, especially with increasing distance from the mound. The combined effect of foraging trails clogged with dense cheatgrass and the loss of shrub references could effectively constrain seed harvesting in cheatgrass sites to areas near the mound. This alteration in foraging patterns could feed back into vegetation structure by altering the spatial scale at which seeds are being harvested in the community.

Overall, it appears that foraging by *P. occidentalis* is strongly influenced by community-wide characteristics. Others have found that seed removal patterns by *Messor* harvester ants in Spain are affected by the spatial structure of the ecosystem (Azcárate and Peco 2003). Structural changes in communities invaded by cheatgrass can contribute to other ecosystem wide changes (e.g. reductions in other granivore groups). Invasion of cheatgrass may lead to a mosaic of microhabitat types differing not only in vegetation structure but also microclimate, soil properties, water and nutrient availability, productivity, and seed availability. Such factors can effectively result in foraging behaviors and patterns of seed selectivity and intensity of harvesting by ants in cheatgrass-dominated systems that are unique from patterns found in native vegetation. How such altered foraging behavior might contribute to plant community development

post invasion and/or contribute to the maintenance of *B. tectorum* persistence is presently unknown.

Within-patch effects: seed neighborhoods

Generally, the patterns for removal of non-*B. tectorum* species when present with *B. tectorum* seeds were not similar to the patterns of removal for the focal seeds in monospecific treatments, suggesting seed neighborhoods matter greatly. Moreover, in most cases noticeably lower proportion of the seeds were removed when in combination with *B. tectorum* compared to when they were alone in monospecific patches (see associational effects section below). To our knowledge this is the first study looking at within-patch effects (i.e. heterospecific seed mixtures) on seed removal by seed harvesting ants, although several researchers have addressed this issue with rodent granivores (see Veech 2000, 2001, Caccia et al. 2006, and Chapters 5 and 6). For example, Veech (2001) found a negative indirect effect of the highly preferred *Oryzopsis hymenoides* (*A. hymenoides*) seeds on the less preferred *Astragalus cicer* seeds due to rodents having a lower foraging effort in patches containing only *A. cicer* seeds than in patches containing a mixture of seeds. However the interaction was non-reciprocal, in that *Astragalus cicer* did not affect harvest of *O. hymenoides*. In contrast, in the present study it was the least preferred seed, *B. tectorum*, which had a negative effect on the more highly preferred seeds.

In addition to the larger scale among-patch qualities of the environment like background vegetation, seed availability, and relative abundance of associated heterospecific granivores, the relative preference or palatability of the associated seeds

may also play a critical role in influencing the outcome of associational effects among seeds in mixed neighborhoods. In cheatgrass-dominated plots, ants were more likely to remove non-*B. tectorum* seeds than seeds of *B. tectorum* from the mixed seed patches, at least for the most preferred seed types. In contrast, in the sagebrush plots ants took more *B. tectorum* seed than they took seeds of *A. hymenoides*, *P. miliaceum*, and *P. spicata*, although the pattern was affected by distance as well (see Fig. 3.5). These outcomes suggest that among-patch factors can affect how these seed foraging ants respond to within-patch mixed seed neighborhoods. Moreover these results also suggest that monospecific preference trials alone may not be an appropriate proxy for predicting how seeds will be perceived by harvester ants in mixed seed neighborhoods, reiterating the importance of the context-dependence of seed harvesting.

Combined among- and within-patch effects

We noted differing patterns between the vegetation types of seed harvest of the non-*B. tectorum* seeds when comparing removal from the monospecific treatments to harvest from mixtures. Interestingly, the effects of distance on non-*B. tectorum* seed removal were different among the treatment types. Specifically, the removal of non-*B. tectorum* seeds from cheatgrass-dominated plots in mixture treatments was by far the greatest at 1 m from the mound (except for *P. secunda*), with less seed harvested at greater distances. In contrast, patterns from the monospecific treatments showed a more gradual decline in harvesting with distance in cheatgrass-dominated plots. In sagebrush plots, harvest of non-*B. tectorum* seeds in monospecific treatments was greatest near and distant from the mound, and lowest at intermediate distances. Whereas seed removal in

the mixture treatment in the sagebrush plots, we noted the relatively uniform pattern of seed harvest for all the non-*B. tectorum* seeds across the distances from the mound.

These spatial patterns, especially evident in the cheatgrass-dominated plots, indicate a greater concentration of foraging for select food items near the mound. But this result was highly dependent on whether it was monospecific or a mixture treatment. It is uncertain why the seed trays at the mound had less non-*B. tectorum* seed removed than did the ones located 1 m from the mound in mixture treatments. In general, the patterns of harvest of non-*B. tectorum* seeds from mixtures in sagebrush plots were generally similar to the patterns seen in monospecific treatments when visually compared to the dissimilar pattern that occurred in the cheatgrass-dominated plots.

Associational effects

It has been noted that the susceptibility of a seed species to attack by granivores often depends on conditions of the local environment, on its abundance and associated traits, and on the availability of other seed types (Veech 2000, Azcárate and Peco 2003). The present study further corroborates these results. In addition, our results indicate the importance of neighbor identity in influencing associational effects. The effects of neighbors could be due simply to taxon-specific attributes of the neighbors (Atsatt and O'Dowd 1976). Theoretically, predation on highly desired seeds could be reduced when in an unpalatable seed neighborhood that effectively repels seed predators (McNaughton 1978, Atsatt and O'Dowd, Hay 1986), resulting indirectly in protection from predation. Such associational resistance (Tahvanainen and Root 1972), has been documented in herbivory studies (Holmes and Jepson-Innes 1989, Callaway et al. 2005), and now for

seed harvesting ants. Overwhelmingly in this study the harvest of non-*B. tectorum* seeds was lower in mixture with *B. tectorum* seeds than when in monospecific patches, demonstrating associational resistance. However, as noted already the characteristics of the seed alone do not completely explain patterns of removal in mixed-patch seed neighborhoods, where among-patch factors appear to also be important.

But what produces the strong degree of associational resistance as demonstrated in the results of the current research? There are several potential explanations based on the biology of this ant species that may shed light on understanding these patterns. Given the chemical sensitivity of ants, it is possible that target seeds simply were less detectable when in mixture with cheatgrass seeds. Alternatively, cheatgrass with their persistent awns might increase the handling time of the more desirable seeds in mixture, diminishing their desirability, as predicted by foraging theory (Charnov 1976). In this scenario the seed patch as a whole would be less preferred if handling time increased due to the presence of cheatgrass in the patch.

Interestingly, associational resistance was greater in sagebrush plots than in cheatgrass-dominated plots, a result that points to the importance of among-patch context in terms of evaluating the strength of within-patch interactions. This is likely related to the overall background seed communities. Cheatgrass-dominated plots clearly had much greater quantities of cheatgrass seed in the background seed neighborhood than did sagebrush plots. Thus, in cheatgrass-dominated communities all available desirable seeds are likely to be mixed with many cheatgrass seeds so that ants abandoning such mixed seed patches are unlikely to gain by encountering a more pure desirable seed patch. In contrast, such mixed patches involving many cheatgrass seeds are probably less

widespread in sagebrush communities and abandoning these mixed patches should be more likely to lead to encountering higher quality patches with a greater relative abundance of the more desirable seeds.

Although to our knowledge no information exists indicating that associational effects among seed patches mediated by granivores could produce otherwise differing patterns of plant establishment, it is reasonable to imagine how such dynamics could occur. If the likelihood of germination were greater for some seed types in a mixed patch simply due to its resistance derived from the reduced probability of predation in that patch, then differing patterns among the plant populations could occur. The relative contribution seed predators might have in producing community wide patterns in terms of plant community structure is unknown but such information would be of interest.

Summary

Our results document the importance of both among- and within-patch characteristics for determining patterns of seed harvest. In cheatgrass-dominated annual grasslands, seed harvest rates were generally lower than in sagebrush communities, even though seed-eating ant abundance was far greater there (Chapter 2). The importance of distance from a mound for seed removal differed among the community types which may be largely a function of differing granivore communities, variations in resource availability, and the direct negative effect of *B. tectorum* on the foraging ability of *P. occidentalis*. Moreover, the influence of seed mixture was not as great in cheatgrass communities where that seed type would be the most abundant seed resource for the ants occupying those sites; although the directionality of associational susceptibility was

consistent between the two vegetation types, the magnitude was much greater in sagebrush communities. In sum, results of this study suggest that the dynamics of seed removal by harvester ants may be largely context-dependent

Conservation and management implications

The differential selection and removal of one seed type over another when in mixture can have important implications in both natural and managed systems. If ants disproportionately harvest native seeds the implications for native plant reestablishment are great, especially when removal results in direct predation. Considering that native seed abundances in cheatgrass-dominated systems are very low (Humphrey and Schupp 2001) compared to in healthy native systems and native seeds are preferentially harvested, the potential for post-disturbance recovery of native plants could be greatly hindered. If desirable native seeds were harvested at greater rates when present in mixed seed patches with seeds of low preference the implications for plant establishment into degraded landscapes would be especially dire. However, in the current study the desirable native seeds were removed less when in a mixed patches with *B. tectorum* than when in single species seed-patches. Thus, although there are still great negatives associated with an abundant seedbed of cheatgrass, at the least the associational susceptibility should increase seed survival in the face of ant predation.

Associational effects might have further consequences as well. In a restoration context where broadcast re-seeding is used to increase native species diversity in cheatgrass-infested rangelands that can not be drill-seeded due to edaphic difficulties or regulations, selecting the appropriate seed mixture might help reduce rates of seed

predation by ants. Obviously, seeding desirable seeds with *B. tectorum* seeds is not suggested, but it is possible that some other less harmful species, perhaps even native ones, might also provide associational resistance to the desired restoration species. Species like *P. secunda*, which was second only to *B. tectorum* in its low preference by ants, might also provide associational resistance to other native restoration species. However, more research using other seed types directed toward the application of this framework is needed before it can become useful to management (see Longland and Bateman 1998).

REFERENCES

- Anderson, C. J., and J. A. MacMahon. 2001. Granivores, exclosures, and seed banks: harvester ants and rodents in sagebrush-steppe. *Journal of Arid Environments* **49**:343-355.
- Atsatt, P. R., and D. J. O'Dowd. 1976. Plant defense guilds. *Science* **193**:24-29.
- Azcarate, F. M., and B. Peco. 2003. Spatial patterns of seed predation by harvester ants (*Messor Forel*) in Mediterranean grassland and scrubland. *Insectes Sociaux* **50**:120-126.
- Bestelmeyer, B. T., and J. A. Wiens. 2001. Ant biodiversity in semiarid landscape mosaics: the consequences of grazing vs. natural heterogeneity. *Ecological Applications* **11**:1123-1140.
- Brown, B. J., and J. J. Ewel. 1987. Herbivory in complex and simple tropical successional ecosystems. *Ecology* **68**:108-116.
- Brown, J. H., and D. W. Davidson. 1977. Competition between seed-eating rodents and ants in desert ecosystems. *Science* **196**:880-882.
- Brown, J. H., and E. J. Heske. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* **250**:1705-1707.
- Brown, J. H., and J. C. Munger. 1985. Experimental manipulation of a desert rodent community: food addition and species removal. *Ecology* **66**:1545-1563.

- Brown, J. H., O. J. Reichman, and D. W. Davidson. 1979. Granivory in desert ecosystems. *Annual Review of Ecology and Systematics* **10**:201-227.
- Caccia, F. D., E. J. Chaneton, and T. Kitzberger. 2006. Trophic and non-trophic pathways mediate apparent competition through post-dispersal seed predation in a Patagonian mixed forest. *Oikos* **113**:469-480.
- Callaway, R. M., D. Kikodze, M. Chiboshvili, and L. Khetsuriani. 2005. Unpalatable plants protect neighbors from grazing and increase plant community diversity. *Ecology* **86**:1856-1862.
- Crist, T. O., and J. A. MacMahon. 1991. Foraging patterns of *Pogonomyrmex occidentalis* (Hymenoptera, Formicidae) in a shrub-steppe ecosystem - the roles of temperature, trunk trails, and seed resources. *Environmental Entomology* **20**:265-275.
- Crist, T. O., and J. A. MacMahon. 1992. Harvester ant foraging and shrub-steppe seeds: interactions of seed resources and seed use. *Ecology* **73**:1768-1779.
- Crist, T. O., and J. A. Wiens 1994. Scale effects of vegetation on forager movement and seed harvesting by ants. *Oikos* **69**:37-46.
- Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* **9**:129-136.
- Davidson, D. W. 1977. Foraging ecology and community organization in desert seed-eating ants. *Ecology* **58**:725-737.
- Davidson, D. W. 1978. Experimental tests of the optimal diet in two social insects. *Behavioral Ecology and Sociobiology* **4**:35-41.
- Davidson, D. W., J. H. Brown, and R. S. Inouye. 1980. Competition and the structure of granivore communities. *BioScience* **30**:233-238.
- Davidson, D. W., D. A. Samson, and R. S. Inouye. 1985. Granivory in the Chihuahuan desert: interactions within and between trophic levels. *Ecology* **66**:486-502.
- Fewell, J. H. 1988. Energetic and time costs of foraging in harvester ants, *Pogonomyrmex occidentalis*. *Behavioral Ecology and Sociobiology* **22**:401-408.
- Hay, M. E. 1986. Associational plant defenses and the maintenance of plant diversity: turning competitors into accomplices. *The American Naturalist* **128**:617-641.
- Holmes, R. D., and K. Jepson-Innes. 1989. A neighborhood analysis of herbivory in *Bouteloua Gracilis*. *Ecology* **70**:971-976.

- Humphrey, L.D., and E.W. Schupp. 2001. Seedbanks of *Bromus tectorum*-dominated communities in the Great Basin. *Western North American Naturalist* **61**:85-92.
- Kelrick, M. A., and J. A. MacMahon. 1985. Nutritional and physical attributes of seed of some common sagebrush steppe plants: some implications for ecological theory and management *Journal of Range Management* **38**:56-69.
- Kelrick, M. I., J. A. MacMahon, R. R. Parmenter, and D. V. Sisson. 1986. Native seed preferences of shrub-steppe rodents, birds and ants: the relationships of seed attributes and seed use. *Oecologia* **68**:327-337.
- Longland, W. S., and S. L. Bateman. 1998. Implications of desert rodent seed preferences for range remediation. *Journal of Range Management* **51**:679-684.
- Longland, W. S. 1994. Seed use by desert granivores. Pages 233-237 in B. S. Monsen and S. G. Kitchen, editors. *Symposium on ecology, management, and restoration of intermountain annual rangelands*. USDA Forest Service, Boise, Idaho, USA.
- MacMahon, J. A., J. F. Mull, and T. O. Crist. 2000. Harvester Ants (*Pogonomyrmex* spp.): their community and ecosystem influences. *Annual Review of Ecology and Systematics* **31**:265-291.
- McNaughton, S. J. 1978. Serengeti ungulates: feeding selectivity influences the effectiveness of plant defense guilds. *Science* **199**:806-807.
- Mull, J. F., and J. A. MacMahon. 1996. Factors determining the spatial variability of seed densities in a shrub-steppe ecosystem: The role of harvester ants. *Journal of Arid Environments* **32**:181-192.
- Mull, J. F., and J. A. MacMahon. 1997. Spatial variation in rates of seed removal by harvester ants (*Pogonomyrmex occidentalis*) in a shrub-steppe ecosystem. *American Midland Naturalist* **138**:1-13.
- Mull, J. F. 2003. Dispersal of sagebrush-steppe seeds by the western harvester ant (*Pogonomyrmex occidentalis*). *Western North American Naturalist* **63**:358-362.
- Nowak, R. S., C. L. Nowak, T. DeRocher, N. Cole, and M. A. Jones. 1990. Prevalence of *Oryzopsis hymenoides* near harvester ant mounds: indirect facilitation by ants. *Oikos* **58**:190-198.
- Pfister, C. A., and M. E. Hay. 1988. Associational plant refuges: convergent patterns in marine and terrestrial communities result from differing mechanisms. *Oecologia* **77**:118-129.

- Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* **107/108**:15-29.
- Tahvanainen, J. O., and R. B. Root. 1972. The influence of vegetation diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia* **10**:321-346.
- Thomas, C. D. 1986. Butterfly larvae reduce host plant survival in vicinity of alternative host species. *Oecologia* **70**:113-117.
- Veech, J. A. 2000. Predator-mediated interactions among the seeds of desert plants. *Oecologia* **124**:402-407.
- Veech, J. A. 2001. The foraging behavior of granivorous rodents and short-term apparent competition among seeds. *Behavioral Ecology* **12**:467-474.
- Wahl, M., and M. E. Hay. 1995. Associational resistance and shared doom: effects of epibiosis on herbivory. *Oecologia* **102**:329-340.
- White, J. A., and T. G. Whitham. 2000. Associational susceptibility of cottonwood to a box elder herbivore. *Ecology* **81**:1795-1803.



Figure 3.1. Ant specific seed tray fashioned from 7-day pill box. 10-mm entry holes were drilled into both outside walls of each compartment 5 mm from the base to allow free access by ants to seeds yet prevent the spilling of seeds out of the compartment and denying access to rodents.

Table 3.1. Three-way factorial analysis of variance (ANOVA) of seed harvest in A) monospecific treatments, B) non-*B. tectorum* seed harvest in mixture treatments, and C) *B. tectorum* seed harvest in mixture treatments.

A) Seed in monospecific treatments				
Source	df	MS	F	P
Seed type	6	4.51	15.81	≤ 0.001
Distance	3	10.40	35.56	≤ 0.001
Vegetation	1	112.30	394.04	≤ 0.001
Seed type × distance	18	0.87	3.05	0.000
Seed × vegetation	6	0.31	1.10	0.359
Vegetation × distance	3	9.90	34.74	0.000
Seed type × distance × vegetation	18	0.69	2.42	0.001
Error	504	0.29		
B) Non- <i>B. tectorum</i> seed in mixture treatments				
Source	df	MS	F	P
Seed type	5	0.225	2.515	0.029
Distance	3	3.809	42.487	≤ 0.001
Vegetation	1	0.571	6.366	0.012
Seed type × distance	15	0.225	2.512	≤ 0.001
Seed × vegetation	5	0.193	2.152	0.058
Vegetation × distance	3	1.664	18.558	≤ 0.001
Seed type × distance × vegetation	15	0.164	1.827	0.029
Error	432	0.090		
C) <i>Bromus tectorum</i> seed harvest in mixture treatments				
Source	df	MS	F	P
Seed type	5	0.040	0.648	0.663
Distance	3	0.763	12.422	≤ 0.001
Vegetation	1	12.851	209.224	≤ 0.001
Seed type × distance	15	0.024	0.392	0.981
Seed × vegetation	5	0.039	0.633	0.675
Vegetation × distance	3	1.410	22.948	≤ 0.001
Seed type × distance × vegetation	15	0.029	0.469	0.955
Error	432	0.061		

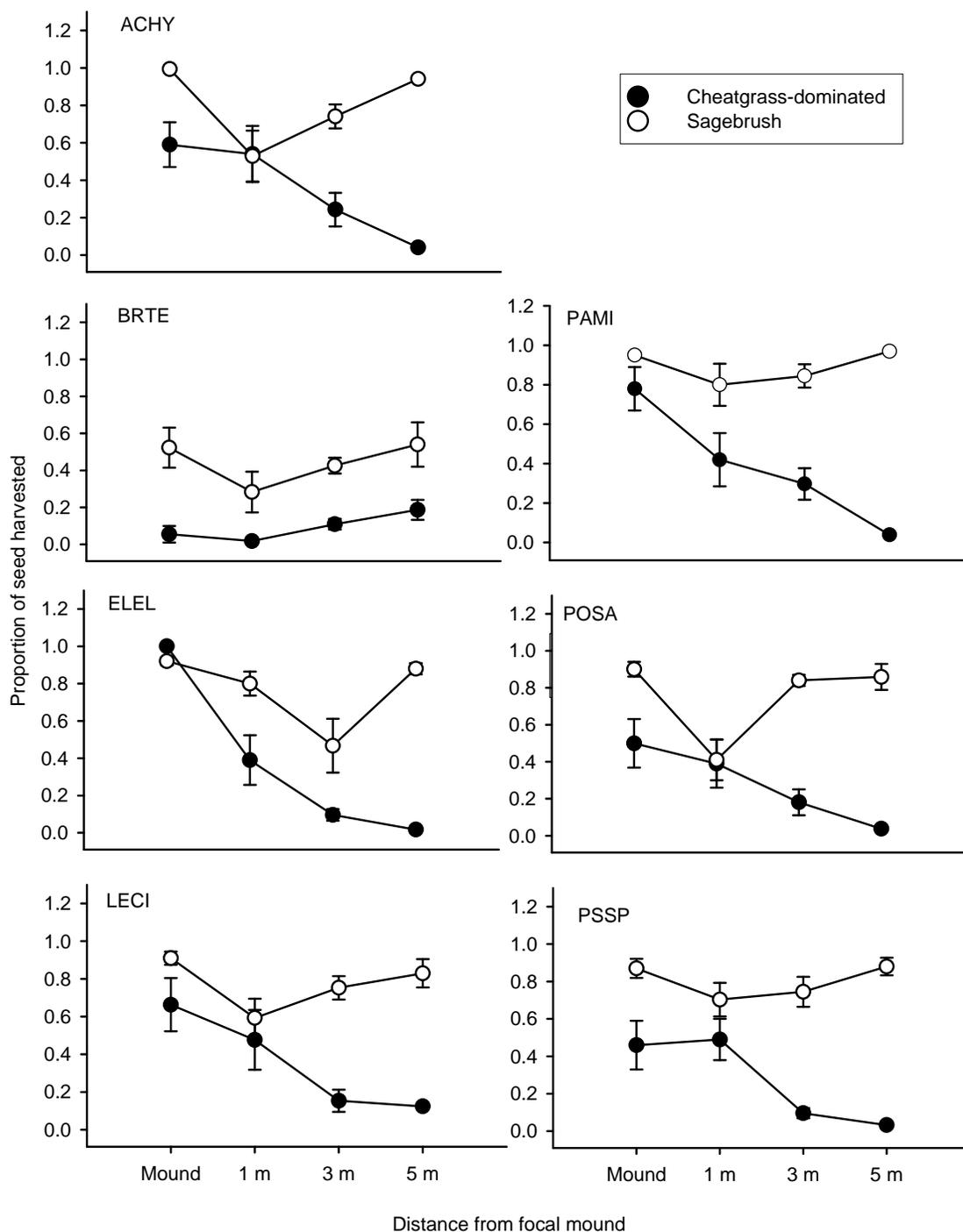


Figure 3.2. Mean (± 1 SE) of the weight of seeds harvested in monospecific treatments at each of the sampled distances from focal mounds. See Table 3.2 for statistical results. Species codes are ACHY, *Achnatherum hymenoides*; BRTE, *Bromus tectorum*; ELEL, *Elymus elymoides*; LECI, *Leymus cinereus*; PAMI, *Panicum miliaceum*; POSA, *Poa secunda*; and PSSP, *Pseudoroegneria spicata*.

Table 3.2. MANOVA results of the seed-dish experiment examining removal of seeds in monospecific treatments including vegetation type (cheatgrass-dominated versus sagebrush) and distance from a focal mound.

Source of Variation	df	MS	F	P
<i>A. hymenoides</i>				
Vegetation	1,18	3.78	72.46	≤ 0.001
Distance	3,54	0.35	3.43	0.023
Vegetation × distance	3,54	0.71	7.01	≤ 0.001
<i>B. tectorum</i>				
Vegetation	1,18	2.47	27.20	≤ .0001
Distance	3,54	0.16	3.46	0.022
Vegetation × distance	3,54	0.04	0.82	0.489
<i>E. elymoides</i>				
Vegetation	1,18	3.08	64.90	≤ 0.001
Distance	3,54	1.68	27.62	≤ 0.001
Vegetation × distance	3,54	0.74	12.19	≤ 0.001
<i>L. cinereus</i>				
Vegetation	1,18	3.93	72.42	≤ 0.001
Distance	3,54	0.53	5.32	0.003
Vegetation × distance	3,54	0.51	5.04	0.004
<i>P. miliaceum</i>				
Vegetation	1,18	5.20	104.57	≤ 0.001
Distance	3,54	0.50	7.02	≤ 0.001
Vegetation × distance	3,54	0.50	7.27	≤ 0.001
<i>P. secunda</i>				
Vegetation	1,18	4.51	92.28	≤ 0.001
Distance	3,54	0.34	3.99	0.012
Vegetation × distance	3,54	0.60	7.03	≤ 0.001
<i>P. spicata</i>				
Vegetation	1,18	5.578	103.08	≤ 0.001
Distance	3,54	0.273	4.08	0.011
Vegetation × distance	3,54	0.390	5.815	0.002

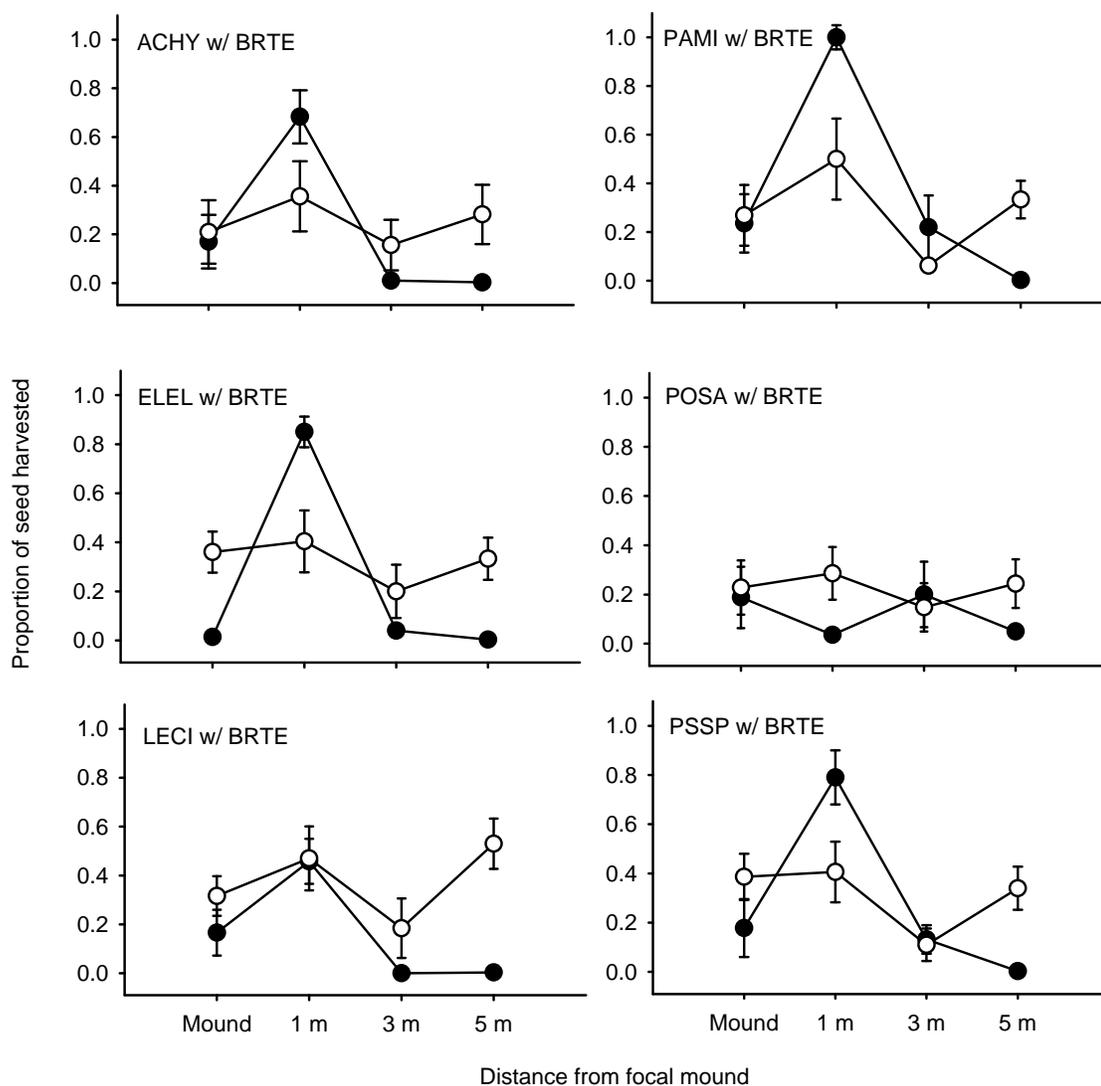


Figure 3.3. Mean \pm 1 (SE) of the weight of non-*B. tectorum* seed harvested in mixture treatments in cheatgrass-dominated (black circles) and sagebrush (open circles) plots at each of the distances from focal mounds. See Table 3.3 for statistical results. Species codes are ACHY, *Achnatherum hymenoides*; BRTE, *Bromus tectorum*; ELEL, *Elymus elymoides*; LECI, *Leymus cinereus*; PAMI, *Panicum miliaceum* POSA, *Poa secunda*; and PSSP *Pseudoroegneria spicata*.

Table 3.3. MANOVA of the seed-dish experiment to examining removal of non-*B. tectorum* seeds in mixture treatments by vegetation type (cheatgrass-dominated versus sagebrush) and distance from focal mound.

Source of Variation	df	MS	F	P
<i>A. hymenoides</i> w/ <i>B. tectorum</i>				
Vegetation	1,18	0.03	0.23	0.636
Distance	3,54	0.76	6.75	≤ 0.001
Vegetation × distance	3,54	0.34	2.98	0.039
<i>E. elymoides</i> w/ <i>B. tectorum</i>				
Vegetation	1,18	0.18	3.87	0.065
Distance	3,54	1.13	18.17	≤ 0.001
Vegetation × distance	3,54	0.71	11.32	≤ 0.001
<i>L. cinereus</i> w/ <i>B. tectorum</i>				
Vegetation	1,18	0.97	11.06	0.004
Distance	3,54	0.47	5.73	0.002
Vegetation × distance	3,54	0.24	2.92	0.042
<i>P. miliaceum</i> w/ <i>B. tectorum</i>				
Vegetation	1,18	0.11	1.55	0.229
Distance	3,54	1.63	14.14	≤ 0.001
Vegetation × distance	3,54	0.60	5.24	0.003
<i>P. secunda</i> w/ <i>B. tectorum</i>				
Vegetation	1,18	0.23	2.39	0.140
Distance	3,54	0.01	0.14	0.939
Vegetation × distance	3,54	0.07	0.98	0.408
<i>P. spicata</i> w/ <i>B. tectorum</i>				
Vegetation	1,18	0.02	0.23	0.641
Distance	3,54	0.92	10.84	≤ 0.001
Vegetation × distance	3,54	0.50	5.85	0.002

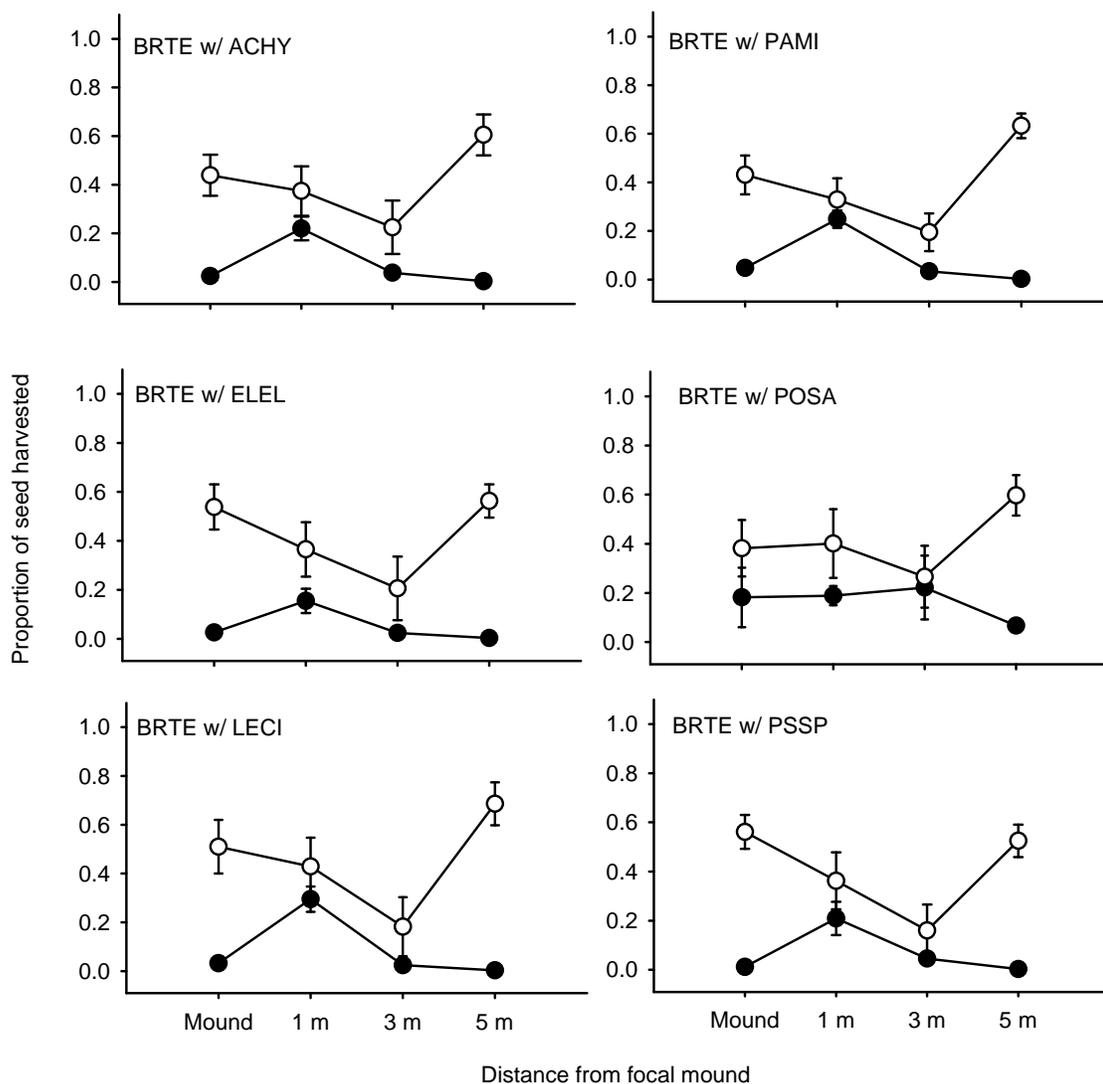


Figure 3.4. Mean ± 1 (SE) of the weight of *B. tectorum* seed harvested in mixture treatments in cheatgrass-dominated (black circles) and sagebrush (open circles) plots at each of the distances from focal mounds. See Table 3.4 for statistical results. Species codes are ACHY, *Achnatherum hymenoides*; BRTE, *Bromus tectorum*; ELEL, *Elymus elymoides*; LECI, *Leymus cinereus*; PAMI, *Panicum miliaceum*; POSA, *Poa secunda*; and PSSP *Pseudoroegneria spicata*

Table 3.4. MANOVA of the seed-dish experiment examining removal of *Bromus tectorum* seed in mixture treatments by vegetation type (cheatgrass and sagebrush) and distance from focal mound.

Source of Variation	df	MS	<i>F</i>	<i>P</i>
<i>B. tectorum</i> w/ <i>A. hymenoides</i>				
Vegetation	1,18	2.29	31.17	≤ 0.001
Distance	3,54	0.13	2.85	0.046
Vegetation × Distance	3,54	0.22	4.91	0.004
<i>B. tectorum</i> w/ <i>E. elymoides</i>				
Vegetation	1,18	2.68	31.18	≤ 0.001
Distance	3,54	0.13	2.71	0.054
Vegetation × Distance	3,54	0.20	4.06	0.011
<i>B. tectorum</i> w/ <i>L. cinereus</i>				
Vegetation	1,18	2.65	22.25	≤ 0.001
Distance	3,54	0.28	5.78	0.002
Vegetation × Distance	3,54	0.35	7.27	≤ 0.001
<i>B. tectorum</i> w/ <i>P. miliaceum</i>				
Vegetation	1,18	1.97	45.42	≤ 0.001
Distance	3,54	0.16	5.89	≤ 0.001
Vegetation × Distance	3,54	0.31	11.11	≤ 0.001
<i>B. tectorum</i> w/ <i>P. secunda</i>				
Vegetation	1,18	1.22	9.18	0.007
Distance	3,54	0.03	0.25	0.861
Vegetation × Distance	3,54	0.21	1.97	0.129
<i>B. tectorum</i> w/ <i>P. spicata</i>				
Vegetation	1,18	2.24	31.19	≤ 0.001
Distance	3,54	0.16	3.81	0.015
Vegetation × Distance	3,54	0.27	6.57	≤ 0.001

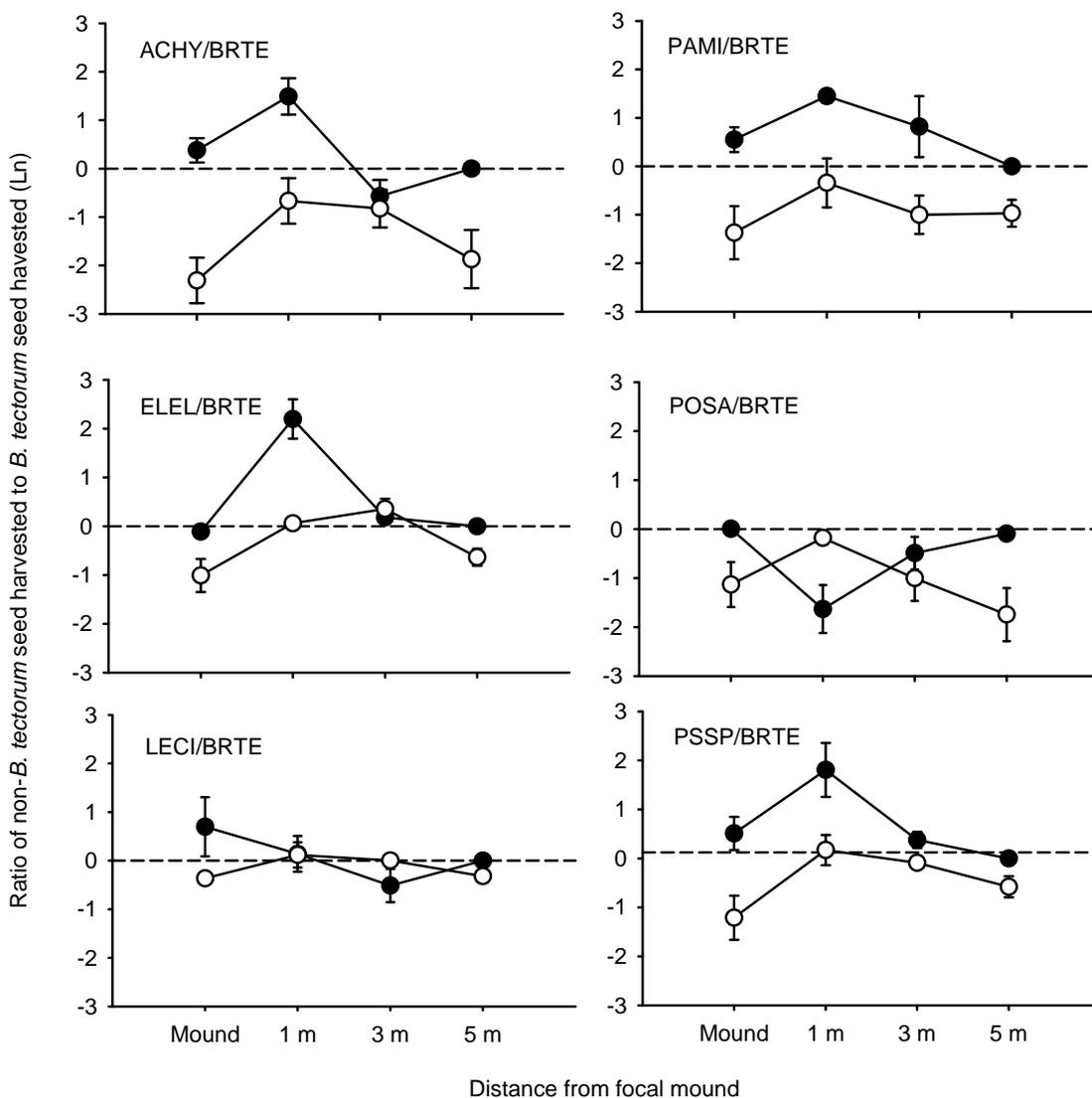


Figure 3.5. Mean ratio of the amount of non-*B. tectorum* seed harvested to *B. tectorum* seed harvested (± 1 SE) for cheatgrass-dominated (black circle) and sagebrush (open circles) plots at each of the four distances from a given focal mound. Values greater than zero indicate more non-*B. tectorum* seed relative to *B. tectorum* seed was harvested. Conversely, values below zero indicate that the amount of non-*B. tectorum* seed harvested was less than the amount of *B. tectorum* seed harvested. See Table 3.5 for statistical results. Species codes are ACHY, *Achnatherum hymenoides*; BRTE, *Bromus tectorum*; ELEL, *Elymus elymoides*; LECI, *Leymus cinereus*; PAMI, *Panicum miliaceum* POSA, *Poa secunda*; and PSSP *Pseudoroegneria spicata*

Table 3.5. ANOVA of the seed-dish experiment examining the ratio of the amount of non-*B. tectorum* seed harvested to the amount of *B. tectorum* seed harvested in mixture treatments by vegetation type (cheatgrass and sagebrush) and distance from focal mound.

Source of Variation	df	MS	F	P
<i>A. hymenoides</i> / <i>B. tectorum</i>				
Vegetation	1,18	60.94	43.51	≤ 0.001
Distance	3,54	8.48	5.02	0.004
Vegetation × distance	3,54	5.51	3.26	0.028
<i>E. elymoides</i> / <i>B. tectorum</i>				
Vegetation	1,18	15.25	31.27	≤ 0.001
Distance	3,54	11.30	22.91	≤ 0.001
Vegetation × distance	3,54	4.59	9.30	≤ 0.001
<i>L. cinereus</i> / <i>B. tectorum</i>				
Vegetation	1,18	1.00	1.69	0.210
Distance	3,54	0.88	0.88	0.459
Vegetation × distance	3,54	2.17	2.15	0.104
<i>P. miliaceum</i> / <i>B. tectorum</i>				
Vegetation	1,18	53.20	42.36	≤ 0.001
Distance	3,54	4.49	2.58	0.063
Vegetation × distance	3,54	0.98	0.56	0.643
<i>P. secunda</i> / <i>B. tectorum</i>				
Vegetation	1,18	4.28	2.67	0.119
Distance	3,54	0.56	0.43	0.773
Vegetation × distance	3,54	9.20	7.03	≤ 0.001
<i>P. spicata</i> / <i>B. tectorum</i>				
Vegetation	1,18	24.40	29.32	≤ 0.001
Distance	3,54	7.65	7.08	≤ 0.001
Vegetation × distance	3,54	2.23	2.08	0.115

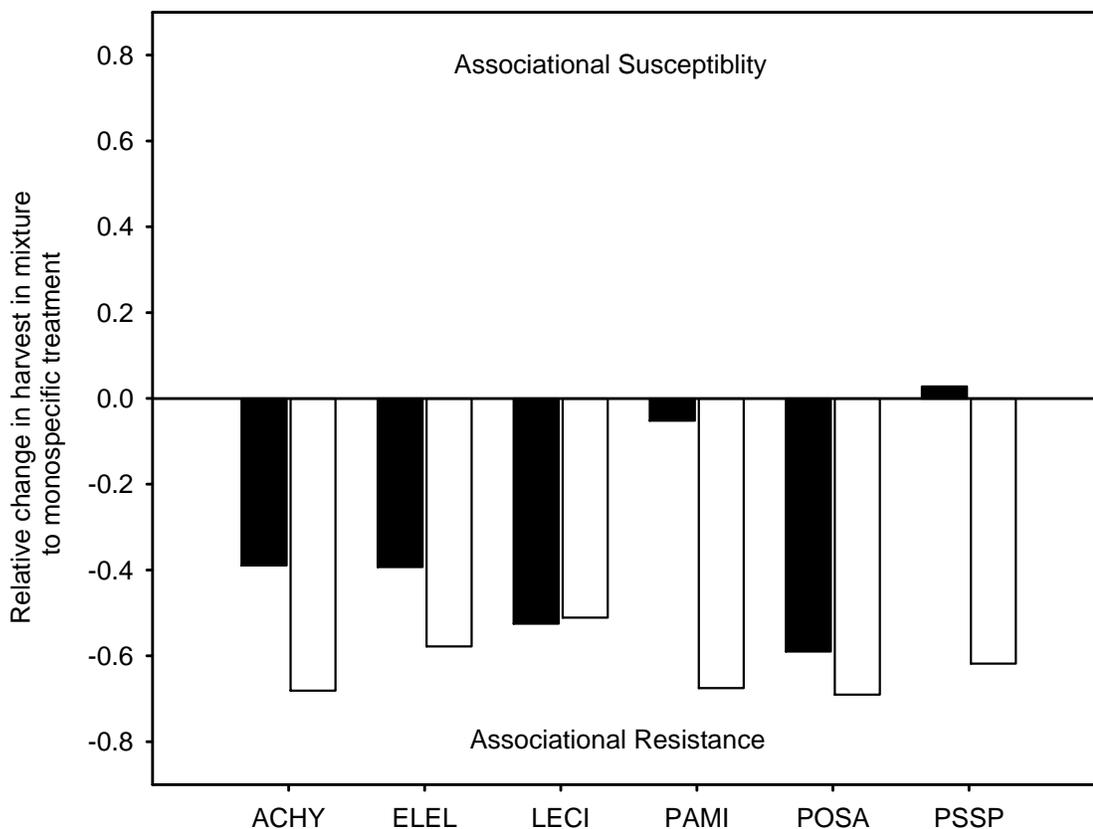


Figure 3.6. Relative change in seed harvest in mixture compared to seed harvest in monoculture in cheatgrass (black bars) and sagebrush (open bars) plots combining all distances. Relative change was measured as the ratio of mean proportion of a non-*B. tectorum* seed species harvested from a mixture treatment to the proportion of that seed harvested in the monospecific treatment. Positive values indicate an overall increase in harvest in mixture compared to monospecific treatments (associational susceptibility). Conversely, negative values indicate an overall reduction in harvest when in mixture compared to monospecific harvest (associational resistance).

CHAPTER 4

RODENT ASSEMBLAGES IN GREAT BASIN SAGEBRUSH COMMUNITIES AND
CONVERTED BROMUS TECTORUM HABITAT TYPES⁴

Abstract. Cheatgrass (*Bromus tectorum*) is fast replacing native sagebrush communities throughout the Great Basin and nearby regions, impacting native plant and animal communities as well as altering fire regimes, which may be contributing to the long term persistence of this weedy species. In Tooele County, Utah, USA, we investigated with Sherman live trapping whether intact sagebrush vegetation and nearby converted vegetation dominated by *Bromus tectorum* differed in rodent community composition, diversity, and abundance. Both rodent abundance and species richness were considerably greater in sagebrush plots than in cheatgrass-dominated plots. Nine species were captured in sagebrush plots; five of these nine were also trapped in cheatgrass plots, all at much lower abundances than in the sagebrush. Cheatgrass-dominated plots had no species that were not found in sagebrush. This initial survey of rodent communities in native sagebrush and in converted cheatgrass-dominated vegetation suggests that diversity and abundance of rodents may be shifting, potentially at the larger spatial scale of the entire Great Basin where cheatgrass continues to invade and ultimately dominate more landscape at an unprecedented rate.

⁴ Coauthored by Steven M. Ostoja and Eugene W. Schupp

INTRODUCTION

Non-native species invasions not only threaten ecosystem processes but are considered one of the most significant components of global ecological change (D'Antonio and Vitousek 1992). *Bromus tectorum* L. (cheatgrass) is one of the most successful invasive species of the Intermountain West. This annual Eurasian grass was first identified in North America in the late 1800s in areas of Washington, Oregon, and Utah (Knapp 1996, Novak and Mack 2001). The invasion of cheatgrass is generally thought to be promoted by disturbances such as overgrazing, but invasion can be associated with poorly managed sites in general, such as abandoned fields, eroded areas, and recently burned rangelands; it is now estimated to cover about 40,000,000 ha (Knapp 1996, Novak and Mack 2001, Rimer and Evans 2006). Once cheatgrass becomes a significant understory component of sagebrush communities it provides continuous fine fuels allowing fires to easily carry and destroy the native vegetation (Brooks et al. 2004). Often all that re-establishes post-fire are near monocultures of cheatgrass effectively creating a feedback of a shortened fire return interval that further promotes continued annual weed persistence and makes native plant re-establishment virtually impossible. The prevalence of *B. tectorum* raises concerns regarding its potential effects on ecosystem structure and function. Although much effort has focused on the effects of *B. tectorum* invasion on native vegetation and ecosystem processes (e.g., Knapp 1991, Belnap et al. 2005, 2006, Rimer and Evans 2006), the impacts on native fauna of conversion from sagebrush communities to cheatgrass-dominated mixed weedy communities remain poorly explored.

For most native fauna we have a limited understanding of both short-term and long-term effects of weed invasion. Although it is assumed that all weed invasions are harmful to native animal species (Randall 1996), this may not always be true. For example, species richness might increase with the introduction of non-native vegetation due to enhanced habitat or resource availability or because of a reduction in predators. In this light, Ellis et al. (1997) reported greater rodent species richness in exotic riparian vegetation than in native vegetation and attributed this to the presence of plant species not found in non-invaded habitat. Conversely, small mammal species captures were lower in cheatgrass than in several other native habitat types in Washington State (Gitzen et al. 2001). Similarly, Longland (1994) reported marked differences in abundances of four rodent species between undisturbed sagebrush and disturbed habitat dominated by the non-native annual grass Medusahead (*Taeniatherum caput-medusae*). Three of four species were less abundant while one species, *Peromyscus maniculatus*, was more abundant in the annual grass-dominated system. However, to date only limited work has addressed the potential shifts in diversity and/or abundances of native rodents as a consequence of habitat conversion in the Great Basin, where sagebrush communities are rapidly being converted to cheatgrass monocultures (Link et al. 2006). Indeed, we can find no report of rodent communities from intact undisturbed sagebrush vegetation and disturbed vegetation dominated by *B. tectorum* (i.e. cheatgrass monoculture) from this region.

Because rodents can have significant effects on community structure and ecosystem processes through seed dispersal, seed consumption, and associated soil disturbances (Heske et al. 1994, Gitzen et al. 2001), understanding rodent communities in

both intact sagebrush and cheatgrass-dominated communities should have important implications for the management and restoration of these systems. In the current study we had the specific goal of quantifying rodent community assemblages in sagebrush and nearby converted cheatgrass-dominated stands. Because this research is part of larger set of studies investigating seed-granivore interactions in ecological restoration, granivorous rodents are our primary emphasis.

METHODS

Study site and species

Study Site - This study was conducted in Tooele County, west-central Utah, USA, in locations referred to as Vernon Hills (12 384335E 4438482N) and Simpson Springs (12 350537E 4437129N). These areas are, respectively, approximately 155 and 172 km southwest of Salt Lake City, Utah. At Vernon Hills, six study plots were established, three in typical Wyoming big sagebrush vegetation (*Artemisia tridentata wyomingensis*; sagebrush hereafter) and three in nearby annual non-native vegetation dominated by *Bromus tectorum* L. (cheatgrass-dominated hereafter). At Simpson Springs four study plots were selected, two in sagebrush vegetation and two in nearby cheatgrass-dominated vegetation (Total n = 10 plots, 5 sagebrush and 5 cheatgrass-dominated).

At both Vernon Hills and Simpson Springs cheatgrass-dominated plots were previously sagebrush-dominated shrublands that were converted by fire in 1998 and 1988, respectively, to non-native mixed weed communities dominated by *B. tectorum* (>90% standing biomass; S.M. Ostoja, unpublished data), but with other weedy species

including *Salsola* spp. (Russian thistle) and *Lepidium* spp. (peppergrass). One of the Simpson springs cheatgrass-dominated plots burned again in 2005. All six Vernon Hills plots were on the Hiko Peak soil series, where the potential plant community is about 45% perennial grasses, 15% forbs, and 40% shrubs (NRCS 2000). The four Simpson Spring plots were on the Taylorsflat soil series, where the potential plant community is 50% perennial grasses, 14% forbs and 35% shrubs. In both soil series the dominant shrub in non-disturbed areas is Wyoming big sagebrush (NRCS 2000). The area near the cheatgrass plots at both sites were also explored by the author EWS in 2002.

Vegetation of sagebrush plots was typical of Wyoming big sagebrush desert of the Great Basin. In addition to *Artemisia tridentata* ssp. *wyomingensis*, the shrubs *Atriplex canescens* (fourwing saltbush), *Gutierrezia sarothrae* (snakeweed), *Chrysothamnus viscidiflorus* (yellow rabbitbrush), and *Ephedra viridis* (Mormon tea) were present. Interspaces were dominated by the grasses *Achnatherum hymenoides* (Indian ricegrass), *Elymus elymoides* (bottlebrush squirreltail), *Poa secunda* (Sandberg bluegrass), *Hesperostipa comata* (needle-and-thread grass), *Leymus cinereus* (Basin wildrye), *Pseudoroegneria spicata* (bluebunch wheatgrass), with some *B. tectorum*.

Rodents - In each of the 10 plots a 10 x 10 trapping grid with 10-m spacing was established. Sherman live traps (3" x 3-1/2" x 9") were baited with mixed bird seed and rolled oats for three consecutive nights on four occasions, twice in 2004 and twice in 2005 for a total of 3800 trap nights. The first trapping session for each plot was conducted between the months of April and June and the second was conducted between the months of July and October. The second trapping session/year in a plot was

conducted at least two months following the first session. A 2004 trapping event for one cheatgrass-dominated plot and one sagebrush plot took place for only two nights due to inclement weather. Trapped animals were identified to species, weighed, sexed, individually identified with ear tags, and released at the location of capture.

Data analyses

Species richness was the number of species recorded in a given vegetation type summed across all plots and sessions. Mean species abundance was the mean of the number of individuals captured per session per vegetation type. Because trapping at different times within and between the years we combined all data into one analysis. We used one-way ANOVA was used to compare mean rodent species abundance between vegetation types, where vegetation type was the independent variable and MNKA was the dependent variable. These analyses were performed with $\alpha \leq 0.05$ for significance. Species abundance curves (percent of total) were created using the total combined capture data for each vegetation type. Site and rodent species (mean number known to be alive/trapping grid) were arranged based on a non-metric multi-dimensional scaling analysis (nMDS), which is suggested for descriptive and/or exploratory purposes only (see De'ath 1999).

RESULTS AND DISCUSSION

Patterns of assembly and diversity

The rodent community was composed of nine species in sagebrush plots and five species in cheatgrass-dominated plots; all species in cheatgrass were also found in

sagebrush. Not only were sagebrush plots more species rich, they also had a much greater overall abundance of rodents (Table 4.1). Considering total captures, 6.1-times more rodents were captured in sagebrush plots than in cheatgrass-dominated plots. In both sagebrush and cheatgrass the rodent community was numerically dominated by *P. maniculatus*, which accounted for >50% of all individuals captured (Table 4.1, Fig. 4.1). All species found in both vegetation types were captured in greater numbers in sagebrush than in cheatgrass-dominated plots, four species significantly so (Table 4.2).

These large differences in rodent communities likely reflect an overall reduction in habitat suitability of cheatgrass when compared to nearby sagebrush habitat. Intact sagebrush vegetation provides a diversity of microhabitats for rodents. Sagebrush habitat is characterized physiognomically by shrubs in the genus *Artemisia* occurring in a relatively regularly-spaced arrangement with an herbaceous understory of perennial grasses and forbs in shrub interspaces (West 1983, 2000). It is thought that such a diversity of microhabitats may partially explain rodent diversity and species co-existence in this and similar community types where native vegetation remains intact (Davidson et al. 1980). For example, studies of heteromyid rodents have concluded that bipedal genera (kangaroo rats, *Dipodomys* spp., and kangaroo mice, *Microdipodops* spp.) tend to use open areas such as sparsely-vegetated shrub interspaces whereas quadrupedal genera (e.g., pocket mice, *Chaetodipus* and *Perognathus* spp.) tend to forage mostly under shrubs or in areas of abundant grass, forb, or rock cover (see Davidson et al. 1980, Price and Brown, 1983; Reichman and Price 1993).

In this light, we used a nMDS to assess how individual plots and vegetation types account for observed differences in species abundances. Species abundances based on

the mean number known alive (MNKA)/plot are most closely associated with plots where majority of captured occurred. The first axis depicts a clear separation of the cheatgrass-dominated and the sagebrush plots as a function of characteristics associated with the respective community types (Fig. 4.2). This axis explained 61% of the total variation in the rodent communities and demonstrates that most of the differences in rodent communities were due to differences between the two vegetation types rather than due to differences among plots within vegetation types. On the other hand, the second axis separated the replicate plots within each vegetation type based on rodent community composition. The tighter cluster of cheatgrass-dominated plots than of sagebrush plots suggests a greater homogeneity of the rodent communities in these disturbed, highly altered habitats (Fig. 4.2). Further this result may allow insight to the greater habitat heterogeneity among sagebrush plots, resulting in greater variation in rodent communities among these plots.

The removal of shrub structure might account for much of the vast reduction in species diversity and abundance within the cheatgrass sites. Shrub structure might help maintain diverse desert rodent communities (see Davidson et al. 1980) by minimizing overlap in habitat and/or resource use (Brown et al. 1979). This is supported by the above interpretation of axis two of the MDS analysis in that the less variable cheatgrass-dominated plots were homogeneously devoid of shrub structure while the more variable sagebrush plots were more variable in structure.

However, shrub structure alone does not appear to completely explain the results. For example, nine of 15 *D. ordii* captured in cheatgrass-dominated plots in 2005 were within 0.5 m of an active *Pogonomyrmex occidentalis* (Western harvester ant) mound,

These mounds are characterized by large clearings devoid of vegetation and debris (ca. 2 m diameter at our sites with reports of >5 m in extreme cases; see MacMahon et al. 2000), strongly suggesting these rodents were selecting more open areas within the cheatgrass, conditions these species are also known to prefer in sagebrush habitat types (i.e. shrub interspaces). With mound densities reported to be 15-20/ha (we recorded > 40 mounds/ha in one cheatgrass-dominated plot), harvester ant mounds might facilitate rodent species that prefer open areas like *D. ordii* by producing a substantial area cleared of vegetation. Similarly, recent research suggests (see Mathis et al. 2006) that shrub removal alone does not adversely impact small mammal populations as severely as does the presence of dense stands of cheatgrass as concluded in other studies (Larrison and Johnson 1973). Lastly, Parmenter and MacMahon (1983) concluded that removal of shrubs did not directly negatively impact rodent species other than least chipmunks (*Tamias minimus*).

Similar to our results, in Washington State (Gano and Rickard 1982, Gitzen et al. 2001) and in Idaho (Larrison and Johnson 1973) total rodent abundances were greatly reduced in areas where cheatgrass dominated compared to nearby native habitat. These authors concluded that it was the combined effect of a lack of shrub structure for predator avoidance and the difficulty in moving through the thick herbaceous cover that was responsible for the overall paucity of small mammals in sites dominated by cheatgrass. Conversely, Wood (1969) reported that rodent populations were greater in annual weed communities than in native mesquite or black grama grass communities. Ultimately, it is not really known how such factors (shrub removal and/or cheatgrass dominance) might together either directly, or perhaps more importantly indirectly, impact native small

mammal populations. Nonetheless, when sagebrush communities are converted to cheatgrass monoculture the combined impacts of shrub loss and of cheatgrass dominance could be greater than expected from additive effects. Clearly, more work is needed to understand the mechanisms behind the present results.

Conservation, restoration, and management implications

Once ubiquitous, sagebrush communities throughout the Great Basin are now threatened by both annual grassland conversion and tree encroachment (Johnson and Miller 2006). The degree to which our results might represent wider ranging shifts in rodent community structure as a function of ongoing vegetation changes at the landscape level is not known. However, if these results do accurately reflect large-scale changes in rodent communities at the regional level the implications are major. Many rodent species via selective seed removal and associated seed handling behaviors are known to affect plants and consequently vegetation structure. Direct seed predation by rodents can clearly negatively impact plant populations. However, rodent granivores can positively influence establishment of some desert plant species when un-recovered seed caches germinate and establish (see West 1968, Longland et al. 2001, Vander Wall 1993). Therefore, the reduction or even loss of these seed predator/dispersal agents might have large impacts on some plant populations. These shifts in rodent communities and vast reductions in abundances of more specialized species, like heteromyids, could ultimately have wide reaching negative consequences that could potentially be felt system wide (see Longland et al. 2001).

A better understanding of the interrelationships among rodents and plant seeds could have important management implications for the reestablishment of native flora into degraded plant communities. In some instances rodents might be managed to help “re-seed” sites to increase plant species diversity. Further, because cheatgrass-dominated communities support some rodents that are dependent on seeds native plant reestablishment in these invaded sites could either be promoted or hindered depending on the direction of the net effect of the interaction between seeds and granivores. Of primary importance is whether the rodents act primarily as seed dispersers or as seed predators. Further, associational effects among seed species might alter the outcome of the granivore-seed interaction. It is possible that native seeds might suffer greater rates of predation when present in a seed neighborhood dominated by weedy, less preferred seeds (Chapters 5 and 6), further hindering the potential for native plant re-establishment. Conversely it is possible that native seeds would escape detection in a background of less desirable heterospecific seed mixtures, effectively escaping predation (Chapter 3) thereby increasing the germination and subsequent establishment of native seeds.

Highly degraded sites like those dominated by cheatgrass are frequently restored through re-seeding. Thus, a consideration of the rodent community is prudent, especially when the community is dominated by heteromyid rodents which are mainly granivorous and which surface cache seeds abundantly (Longland et al. 2001). There is limited research investigating the interaction between re-seeding efforts and rodent granivory in the Great Basin. Although it is often assumed that rodent seed predation has significant negative impacts on seedlings through seed consumption (see Sullivan and Sullivan 1982, 2002), this might not always be true (Ostojka, Schupp, and Longland unpublished data).

Sown seed that is harvested can potentially be re-dispersed and cached, resulting in seedling germination and establishment, ultimately aiding restoration success. Several researchers have either promoted theoretical models or applied appropriate techniques to minimize seed losses in reseeding events (e.g. diversionary food supplementation) (see Sullivan 1979, Kelrick and MacMahon 1985, Archer and Pyke 1991). If rodent harvesting might ultimately be beneficial for some species, these efforts might not be warranted. More research is needed not only to evaluate the many potential outcomes of sown seed/granivore interactions on management landscapes but also to explore novel approaches to maximizing success in arid land restoration in the context of native rodent communities.

REFERENCES

- Andersen, D. C., and S. M. Nelson. 1999. Rodent use of anthropogenic and 'natural' desert riparian habitat, lower Colorado River, Arizona. *Regulated Rivers-Research & Management* **15**:377-393.
- Archer, S., and D. A. Pyke. 1991. Plant-animal interactions affecting plant establishment and persistence on revegetated rangeland. *Journal of Range Management* **44**:558-565.
- Belnap, J., S. L. Phillips, and T. Troxler. 2006. Soil lichen and moss cover and species richness can be highly dynamic: The effects of invasion by the annual exotic grass *Bromus tectorum*, precipitation, and temperature on biological soil crusts in SE Utah. *Applied Soil Ecology* **32**:63-76.
- Belnap, J., S. L. Phillips, S. K. Sherrod, and A. Moldenke. 2005. Soil biota can change after exotic plant invasion: does this affect ecosystem processes? *Ecology* **86**:3007-3017.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *BioScience* **54**:677-688.

- Brown, J. H., D. W. Davidson, and O. J. Reichman. 1979. An experimental-study of competition between seed-eating desert rodents and ants. *American Zoologist* **19**:1129-1143.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**:63-87.
- Davidson, D. W., J. H. Brown, and R. S. Inouye. 1980. Competition and the structure of granivore communities. *BioScience* **30**:233-238.
- De'ath, G. 1999. Extended dissimilarity: a method of robust estimation of ecological distances from high beta diversity data. *Plant Ecology* **144**:191-199.
- Ellis, L. M., C. S. Crawford, and M. C. Molles. 1997. Rodent communities in native and exotic riparian vegetation in the middle Rio Grande Valley of central New Mexico. *Southwestern Naturalist* **42**:13-19.
- Gano, K. A., and W. H. Rickard. 1982. Small mammals of a bitterbrush-cheatgrass community. *Northwest Science* **56**:1-7.
- Gitzen, R. A., S. D. West, and B. E. Trim. 2001. Additional information on the distributions of small mammals at the Hanford Site. Washington. *Northwest Science* **75**:350-362.
- Heske, E. J., J. H. Brown, and S. Mistry. 1994. Long-term experimental study of a Chihuahuan Desert rodent community: 13 years of competition. *Ecology* **75**:438-445.
- Kelrick, M. A., and J. A. MacMahon. 1985. Nutritional and physical attributes of seed of some common sagebrush steppe plants: Some implications for ecological theory and management. *Journal of Range Management* **38**:56-69
- Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert - history, persistence, and influences to human activities. *Global Environmental Change-Human and Policy Dimensions* **6**:37-52.
- Larrison, E. J. and D. R. Johnson. 1973. Density changes and habitat affinities of rodents of shadscale and sagebrush associations. *Great Basin Naturalist* **33**:255-264.
- Link, S. O., C. W. Keeler, R. W. Hill, and E. Hagen. 2006. *Bromus tectorum* cover mapping and fire risk. *International Journal of Wildland Fire* **15**:113-119.
- Longland, W. S. 1994. Seed use by desert granivores. Pages 233-237 in B. S. Monsen and S. G. Kitchen, editors. *Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands*. USDA Forest Service, Boise, Idaho.

- Longland, W. S., S. H. Jenkins, S. B. V. Wall, J. A. Veech, and S. Pyare. 2001. Seedling recruitment in *Oryzopsis hymenoides*: are desert granivores mutualists or predators? *Ecology* **82**:3131-3148.
- MacMahon, J. A., J. F. Mull, and T. O. Crist. 2000. Harvester ants (*Pogonomyrmex* spp.): their community and ecosystem influences. *Annual Review of Ecology and Systematics* **31**:265-291.
- Mathis, V. L., W.G. Whitford, F.R. Kay, and P.U. Alkon. 2006. Effects of grazing and shrub removal on small mammal populations in southern New Mexico, USA. *Journal of Arid Environments* **66**:76-86.
- Novak, S. J., and R. N. Mack. 2001. Tracing plant introduction and spread: genetic evidence from *Bromus tectorum* (cheatgrass). *BioScience* **51**:114-122.
- Parmenter, R. R., and J. A. MacMahon. 1983. Factors determining the abundance and distribution of rodents in shrub-steppe ecosystem: the role of shrubs. *Oecologia* **59**:145-156.
- Price, M. V., and J. H. Brown. 1983. Patterns of morphology and resource use in North American desert rodent communities. *Great Basin Naturalist Memoirs* **7**:117-134.
- Randall, J. M. 1996. Plant invaders: how non-native species invade and degrade natural areas. Pages 45-78 in J. M. Randall and J. Marinelli (editors). *Invasive plants: weeds of the global garden*. Brooklyn Botanic Garden, Brooklyn, New York.
- Reichman, O. J., and M. V. Price. 1993. Ecological aspects of heteromyid foraging. Pages 539-574 in H. H. Genoways and J. H. Brown, (editors). *Biology of the Heteromyidae*. The American Society of Mammalogists.
- Rimer, R. L., and R. D. Evans. 2006. Invasion of downy brome (*Bromus tectorum* L.) causes rapid changes in the nitrogen cycle. *American Midland Naturalist* **156**:252-258.
- Sullivan, T. P. 1979. The use of alternative foods to reduce conifer seed predation by the deer mouse, (*Peromyscus maniculatus*). *Journal of Applied Ecology* **16**:475-495.
- Sullivan, T. P., and D. S. Sullivan. 1982. The Use of Alternative Foods to Reduce Lodgepole Pine Seed Predation by Small Mammals. *Journal of Applied Ecology* **19**:33-45.
- Sullivan, T. P., and D. S. Sullivan. 2004. Influence of a granivorous diversionary food on population dynamics of montane voles (*Microtus montanus*), deer mice (*Peromyscus maniculatus*), and western harvest mice (*Reithrodontomys megalotis*). *Crop Protection* **23**:191-200.

- Vander Wall, S. B. 1993. A Model of Caching Depth: Implications for Scatter Hoarders and Plant Dispersal. *American Naturalist* **141**:217-232.
- West, N.E. 1968. Rodent-influenced establishment of ponderosa pine and bitterbrush seedlings in central Oregon. *Ecology* **49**:1009-1011.
- West, N. E., 1983. Western Intermountain Sagebrush-steppe. Pages 351-374 *in* Temperate Deserts and Semi-Deserts, (editors). N. E. West, Elsevier Scientific Publishing Company, The Netherlands.
- West, N. E., 2000. Synecology and disturbance regimes of sagebrush steppe ecosystems. Pages 15-26 *in* P.G. Entwistle, A. M. DeBolt, J. H. Kaltenecker, and K. Steenhof (eds.), Proceedings: Sagebrush steppe ecosystems symposium. Bureau of Land Management Publication No. BLM/ID/PT-001001, Boise Idaho, USA.
- Wood, J. E. 1969. Rodent populations and their impact on desert rangelands. *New Mexico Agricultural Experiment Station Bulletin* **555**. 17 pages.

Table 4.1. The total number of individuals captured per species per vegetation type per year, and the abundance of each species as a proportion of the total rodents captured that year in that vegetation type ($n = 5$).

Family <i>Species</i>	Cheatgrass-dominated				Sagebrush			
	2004		2005		2004		2005	
	Abundance	Proportion	Abundance	Proportion	Abundance	Proportion	Abundance	Proportion
Cricetidae								
<i>Lemmyscus curtatus</i>	2	.071	5	.102	6	.025	9	.037
<i>Onychomys leucogaster</i>	0	--	0	--	2	.008	3	.012
<i>Peromyscus maniculatus</i>	15	.535	22	.448	119	.512	124	.516
<i>Peromyscus truei</i>	0	--	0	--	1	.004	3	.013
<i>Reithrodontomys megalotis</i>	3	.074	5	.102	9	.038	11	.045
Heteromyidae								
<i>Dipodomys ordii</i>	7	.250	15	.306	61	.262	58	.241
<i>Perognathus parvus</i>	1	.035	2	.041	29	.125	26	.108
Sciuridae								
<i>Ammospermophilus leucurus</i>	0	--	0	--	4	.017	3	.012
<i>Tamias minimus</i>	0	--	0	--	1	.004	3	.012
Total Abundance	28		49		232		240	
Total Number of Species	4		5		9		9	

Table 4.2. Means (± 1 SE) and standard errors for the number of individuals captured/session combining 2004 and 2005 data over all cheatgrass-dominated and sagebrush plots. Values with different letter in the same row are statistically different ($P \leq 0.05$, $n = 5$).

Family <i>Species</i>	Vegetation Type	
	Cheatgrass- dominated	Sagebrush
Cricetidae		
<i>Lemmyscus curtatus</i>	0.30 \pm 0.12	0.71 \pm 0.86
<i>Onychomys leucogaster</i>	--	0.22 \pm 0.52
<i>Peromyscus maniculatus</i>	1.85 \pm 0.47 ^a	12.1 \pm 2.80 ^b
<i>Peromyscus truei</i>	--	0.20 \pm 0.52
<i>Reithrodontomys megalotis</i>	0.42 \pm 0.13 ^a	1.23 \pm 0.22 ^b
Heteromyidae		
<i>Dipodomys ordii</i>	1.10 \pm 0.31 ^a	5.85 \pm 1.92 ^b
<i>Perognathus parvus</i>	0.15 \pm 0.11 ^a	2.75 \pm 1.37 ^b
Sciuridae		
<i>Ammospermophilus leucurus</i>	--	0.35 \pm 0.16
<i>Tamias minimus</i>	--	0.21 \pm 0.11

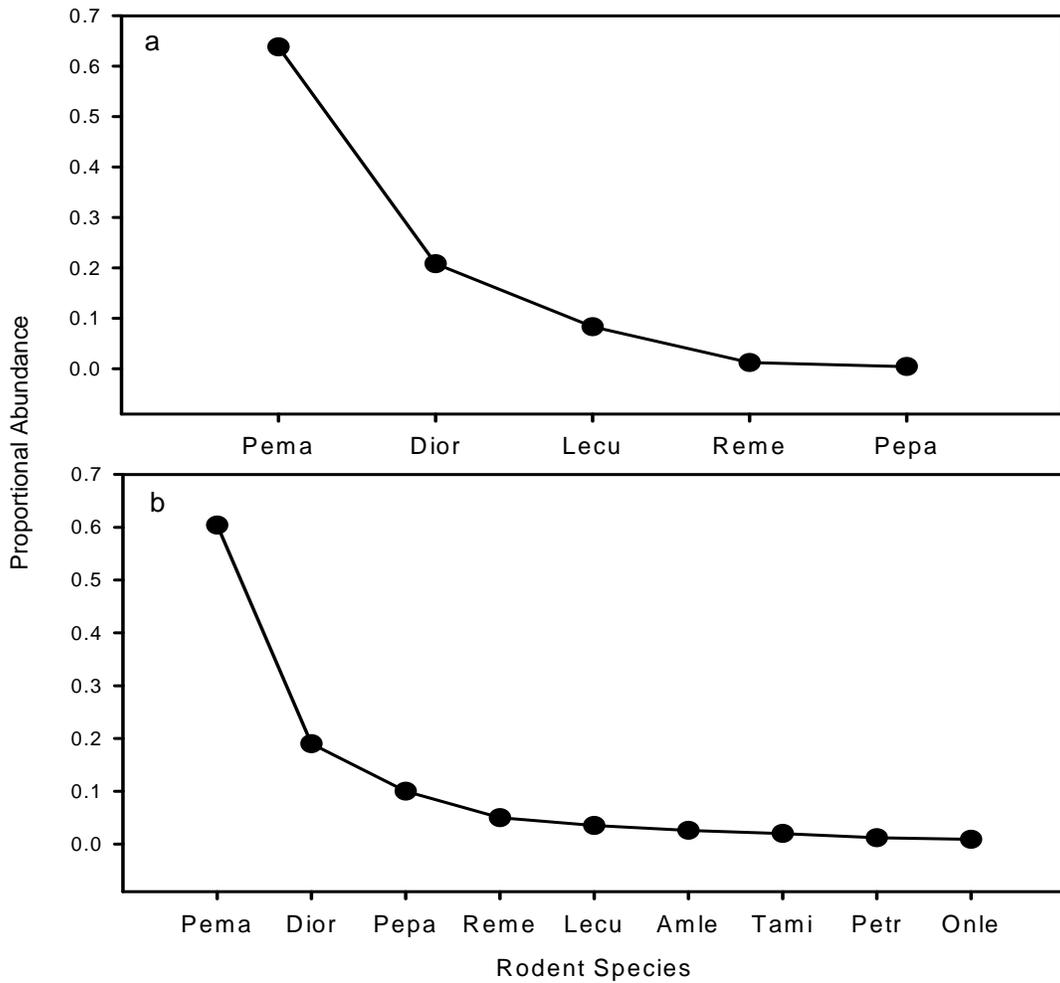


Figure 4.1. Rank abundance curves for rodents species captured in cheatgrass-dominated plots (a) and sagebrush plots (b) for both years combined. Species codes are: *Peromyscus maniculatus* (Pema) *Dipodomys ordii* (Dior), *Perognathus parvus* (Pepa), *Reithrodontomys megalotis* (Reme), *Lemmys curtatus* (Lecu), *Ammospermophilus leucurus* (Amle), *Tamias minimus* (Tami), *Peromyscus truei* (Petr) and *Onychomys leucogaster* (Onle).

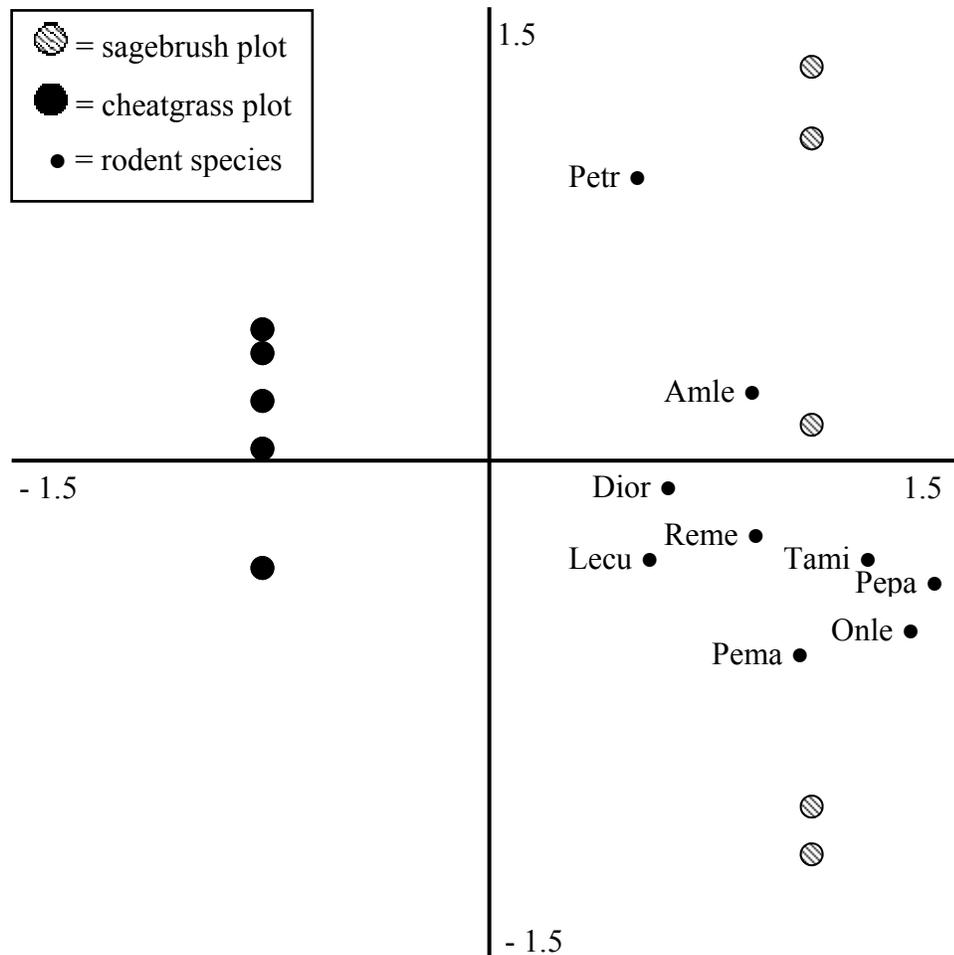


Figure 4.2. Non-metric multidimensional scaling analysis of rodent species composition in two vegetation types in the Great Basin of western Utah. The analysis was based on mean rodent captures (MNKA) at five trapping grids in each of the two community-types; cheatgrass-dominated plots are denoted by black circles and sagebrush plots are denoted by hatched circles. The first axis, which explains 61% of the variation in community structure, separates the two vegetation types, whereas the second axis indicates the relative heterogeneity among replicate plots within respective given vegetation type. Each species point represents its relative association among the ten trapping grids based on the MNKA for that grid. Abbreviations for species codes are shown in the legend for figure 4.1.

CHAPTER 5

ASSOCIATIONAL INTERACTIONS WITHIN SEED MIXTURES: BETA-DISTRIBUTED REGRESSION AS AN ALTERNATIVE TO TRADITIONAL STATISTICAL TECHNIQUES⁵

Abstract. Relative heterogeneity of a resource patch can be an important influence on patterns of seed removal by seed-eating rodents. In natural environments, seeds are not distributed homogeneously but rather are embedded in a heterogeneous seed matrix that varies spatially and temporally in overall seed density as well as in the species composition of local seed neighborhoods. Similarly, in an ecological restoration context reseeded generally applies seed mixtures rather than single species to the landscape. Although the understanding of seed removal in mixed species patches compared to monospecific patches is critical, seed removal experiments most often use homogeneous resource patches. In this study, we investigated whether seed preference rankings and/or removal rates by rodents changed for five native perennial grasses, the exotic annual invasive grass *Bromus tectorum*, and the domesticated annual grass *Panicum miliaceum* when they were presented in mixture versus when available alone in two vegetation types in the eastern Great Basin, USA. Seed removal experiments with fixed seed densities often produce data that fail to meet distributional assumptions of traditional parametric regression techniques that presume a normal distribution of the response. To accommodate the distributional characteristics of our data, we used a beta regression approach which can be well-suited for analyses of ecological response variables that are

⁵ Coauthored by Steven M. Ostoja, Susan Durham and Eugene W. Schupp

restricted to values between 0 and 1 and that may have asymmetric distributions. We present results from normal-distributed regression and from beta-distributed regression. Both approaches suggested that rodents demonstrated a marked ranking of preference of the 7 seed types when they were available alone. When combined with *B. tectorum*, the ranking of preferences of the non-*B. tectorum* seed species shifted. Additionally, the different statistical approaches suggested alternative conclusions about the importance of seed mixtures on the removal of target seeds. We compare results of the two approaches in terms of ecological conclusions and management decisions, and we discuss beta regression as an alternative statistical approach with special attention to the importance of the variance that is inherent in ecological experimental designs with similar approaches to the current study.

INTRODUCTION

Ecological framework

Many factors contribute to seed selectivity and subsequent removal by granivores. In addition to characteristics of the seeds themselves (i.e., size and nutritional and chemical traits), seed removal experiments also have considered the importance of contexts in terms of seed selection by granivores. Context-specific seed removal studies have most often focused on temporal and spatial variability of seed resources at single or multiple scales. For example, DeCasenave and coauthors (1998) found that seasonality and microhabitat were important in explaining patterns of seed removal in the northern Monte desert, Chile. Recently, context dependence in terms of mixed species seed patches, or neighborhoods, also has begun to be investigated. The framework for this

consideration is critical because seeds are not available in the environment in a single species homogenous manner, but rather are found within a highly variable mixed-species matrix, and the mixture of seeds available can alter foraging decisions and thus seed fates (Veech 2001, Veech and Jenkins 2006). As a result, rodents potentially induce indirect or associational effects among seed species present in mixture. Thus, the impacts of seed predation and/or secondary dispersal by rodents may vary as a function of the context of the seed mixture available to rodent seed removers. Direct and indirect interactions among seeds mediated by rodent granivores may ultimately be as important as direct and indirect interactions among plants themselves (e.g., resource competition) in determining plant community structure and spatial patterns.

Indirect effects result when one species impacts another through the presence of a third species. Seeds of co-occurring plant species do not compete for resources, but they may interact indirectly when present in mixed species patches in the presence of polyphagous granivores. In mixed-species patches, seed neighbors can theoretically decrease harvesting of a given target seed species by causing the granivore either to fail to locate or to reject a seed that would have been harvested in isolation. Therefore, in a multi-species seed neighborhood the presence of some seed species could confer an “associational resistance” from seed predators on other seed species in the mixture (Tahvanainen and Root 1972, Rand 1999, Chapter 1). Conversely, mixed-seed patches can also increase the susceptibility of a focal seed to harvesting by rodent granivores, an interaction referred to as “associational susceptibility” (Chapter 1). Thus, the effects of rodent seed harvesting on seed pool composition and plant recruitment might not be predictable from simple knowledge of seed preferences developed from typical

monospecific cafeteria-style experiments. To our knowledge, no data presently exist showing how variations in associational effects among seeds in mixtures mediated by seed predators might differentially be displayed at the plant population level. In fact, only three studies (Veech 2000, 2001, Caccia et al. 2006) have shown evidence of indirect effects within a trophic pathway (see Caccia et al. 2006) for seed removal experiments; all three studies focused on rodents as the seed remover. Some other studies have shown mixed-species seed patches do not affect foraging patterns of granivores in terms of producing associational interactions among co-occurring seeds (see Hulme and Hunt 1999). Thus, additional studies on the consequences of seed mixtures may prove important, especially in terms of the consideration of consequences for patterns of plant establishment.

Biotic interactions involving indirect effects among pairs of species have important impacts on both ecological and evolutionary patterns in natural and human-affected systems. In a recent review of biotic indirect effects, White et al. (2006) noted that multi-species interactions are often not considered in studies of interactions between alien and native species. In this context, we have two reasons for attempting to better understand seed removal patterns of native seed species common to Great Basin sagebrush communities and for seeds of the non-native invasive annual grass *Bromus tectorum* (cheatgrass). *B. tectorum* is fast becoming the dominant annual species across the entire Great Basin, successfully invading natural communities and effectively displacing native vegetation and altering ecosystem processes in ways that promote its continued persistence. Thus, understanding how seed removal of desirable native seeds is affected by the presence of *B. tectorum* has important implications for the conservation

and potential re-establishment of native species where *B. tectorum* occurs. If the presence of *B. tectorum* seeds alters the patterns of harvesting of native seeds then this dynamic has implications for native plant population reestablishment and dynamics in communities undergoing invasion. Second, an understanding of how seed mixtures affect seed harvesting can have important implications for restoration because seed is applied in multi-species mixtures and the actual mixture used can be selected to some extent by the land manager. These applied seeds are available to granivores and in theory these granivores could negatively impact restoration through direct seed predation or positively affect restoration through effective secondary dispersal and caching. In this context understanding associational interactions among seeds might be important for developing seed mixtures that maximize survival and establishment of the most desirable species.

The current study specifically addressed the following issues: (1) preferences by granivorous rodents for seeds of five native grass species, for *Panicum miliaceum* (millet), and for *B. tectorum* in both intact Wyoming big sagebrush (*Artemisia tridentata*) communities and in converted cheatgrass-dominated communities; (2) the occurrence and type of associational effects of *B. tectorum* seeds on seeds of the native grasses and of *P. miliaceum*; and (3) whether there is a temporal component to seed removal for the seed species considered. These objectives were addressed with two alternative modeling approaches, one based on a normal distribution for the response and the second on a beta distribution.

Statistical framework

The primary powerhouse of traditional applied statistics for many ecological data sets is the general linear model (LM), which encompasses regression, analysis of variance, and analysis of covariance models and assumes that the response variable follows the normal distribution. Although the general LM is suitable in many scenarios, the assumption of a normal distribution is not universally appropriate for all ecological data. One approach to the problem of non-normality is to trust in the legendary robustness of the general LM to deviations from normality. A less trusting, but common and more sensible solution is to apply a transformation to the response data such that the rescaled response better meets the normality assumption. However, even in the best case the use of a suitable transformation still leads to problems with interpretation and inference (due to hypothesis testing on the new scale; McArdle and Anderson 2004) and with back-transformation of estimates to the original scale; in the worst cases transformation may be an inadequate solution.

As an alternative to making less than satisfactory or, worse, perfunctory attempts at molding data to normal-distribution models, we can use a *generalized* linear model (GLM; McCullagh and Nelder 1989). The GLM allows the probability distribution of the response to be discrete (e.g., binary, multinomial, Poisson) or continuous (e.g., normal, lognormal, beta); as such, the LM is a special case of the GLM with a normal distribution. In the GLM, the population mean is determined by a linear function of the predictor variables (i.e., the linear predictor) through a nonlinear link function. The link function identifies the transformation of the mean (as opposed to a transformation of the data) that “links” the linear predictor to the mean. Consequently, a GLM is able to

accommodate data with non-normal distributions, to restrict predictions to the natural range of values, and to allow various relationships between the mean and the variance of the data other than the LM assumption of constant variance.

Analyses in seed choice experiments often use proportions as response variables. Proportion data have several characteristics that make a normal-distribution model potentially problematic. First, proportion data are restricted to values between (and including) zero and one. The range of the normal distribution is between negative and positive infinity, and an LM may produce predictions outside of the $[0, 1]$ range. Second, the variance of proportion data is a function of the mean: maximum variance occurs when the mean proportion is 0.5, and variance approaches zero as the mean approaches either zero or one. The LM assumes that variances are constant for all means. Third, the distribution of proportion data may be asymmetric (e.g., skewed left or right, or even bimodal). Normally-distributed data are symmetric, with the mode at the mean.

Examples of the application of a generalized linear model with a beta distribution (hereafter, beta regression) to the analysis of proportion data are found in economics, public management, and psychology (see Brehm and Gates 1993, Paolino 2001, Smithson and Verkuilen 2006). Here we extend the application to an ecological data set and compare the results to those from a general linear model (hereafter, normal regression). The two-parameter beta distribution provides a flexible class of models that can effectively accommodate a wide range of distributions including extreme skewing, general bimodality, and symmetry not unlike a normal distribution (see Fig. 5.1 for examples). The main assumptions of two-parameter beta distributions are that the response variable is continuous, interval-level, and bounded between zero and one, not

including the endpoints. As such, the beta regression model with modifications for zero and one (see below) is very useful for proportions, as result from seed or food choice experiments. We point readers to Smithson and Verkuilen (2006) and the companion white paper (Smithson and Verkuilen 2005) for a detailed theoretical and quantitative explanation of regression with beta-distributed response variables. Additional discourses on beta regression can be found in Kieschnick and McCullough (2003) and Ferrari and Cribari-Neto (2004).

METHODS

Study site and species

This study was conducted in northeastern Utah in two sites known as Vernon Hills (UTM Zone 12, 384335 East, 4438482 North) and Simpson Springs (UTM Zone 12, 350537 East, 4437129 North), which are in Tooele County, Utah, USA, approximately 155 and 172 km southwest of Salt Lake City, Utah, respectively. At the Vernon Hills site, six 1.2-ha study plots were established; three plots were in typical Wyoming big sagebrush vegetation (*Artemisia tridentata wyomingensis*; sagebrush hereafter) and three plots were in nearby annual non-native vegetation dominated by *B. tectorum* (cheatgrass-dominated hereafter). At the Simpson Springs site four study plots were selected: two in sagebrush, and two in nearby cheatgrass-dominated vegetation. In each of the 10 plots, six 120-m parallel transects (20 m between transects) with seven permanent points per transect (20 m between points on a transect) were established for the seed trials.

At both Vernon Hills and Simpson Springs the cheatgrass-dominated plots were all previously shrublands that were dominated by sagebrush that were converted by fire to a non-native mixed annual weed community dominated (>90% standing biomass, S.M. Ostoja unpubl data) by *B. tectorum* (Bill Henderson, BLM Salt Lake Field Office, pers. comm.). It is possible that the cheatgrass plots were not identical to the sagebrush plots before disturbance events that promoted their current state. All six Vernon Hills plots occur on the Hiko Peak series, where the potential plant community on this soil is about 45% perennial grasses, 15% forb, and 40% shrubs (NRCS 2000). While all four Simpson Spring plots occur on the Taylorsflat series, where the potential plant community is 50% perennial grasses, 14% forbs and 35% shrubs. The important shrub in non disturbed areas on each series is Wyoming big sagebrush (NRCS 2000).

The sagebrush plots had vegetation typical of Wyoming big sagebrush communities of the Great Basin. In addition to *Artemisia tridentata* ssp. *wyomingensis*, other shrubs present include *Atriplex canescens* (fourwing saltbush), *Gutierrezia sarothrae* (snakeweed), *Chrysothamnus viscidiflorus* (green rabbitbrush) and *Ephedra viridis* (Mormon tea). The interspaces between shrubs were dominated by the perennial native grasses *Achnatherum hymenoides* (Indian ricegrass), *Elymus elymoides* (bottlebrush squirreltail), *Poa secunda* (Sandberg bluegrass), *Hesperostipa comata* (needle-and-thread grass), *Leymus cinereus* (Basin wildrye), and *Pseudoroegneria spicata* (bluebunch wheatgrass), along with scattered *B. tectorum*. Cheatgrass-dominated plots consisted mainly of *B. tectorum* but also had other annual weedy exotic species including *Salsola* spp. (Russian thistle) and *Lepidium* spp. (peppercress).

Granivorous rodents live-trapped at Vernon Hills and Simpson Springs in 2004 and 2005 were *Dipodomys ordii*, *Perognathus parvus*, *Reithrodontomys megalotis*, and *Peromyscus maniculatus* (Chapter 4). The rodent community is diverse at the research sites but is numerically dominated by *P. maniculatus*, which accounted for >50% of all individuals captured, followed by *D. ordii* and *P. parvus* (Chapter 4). Moreover, sagebrush plots had greater rodent diversity and abundance than did cheatgrass-dominated plots (Chapter 4).

Seeds of the native grasses *A. hymenoides*, *E. elymoides*, *P. spicata*, *P. secunda*, and *L. cinereus* were purchased from Granite Seed Company, Lehi, Utah, USA. Seeds of *Panicum miliaceum* were purchased from Cal Ranch Supply, Logan Utah, USA. Seeds of *B. tectorum* were collected in the vicinity of the research sites by one of the authors (SMO) in 2005. All *B. tectorum* seeds were mechanically cleaned and air blown to removal extra coreopsis material from the embryo. These native seed species were selected because they are common in reseeding/restoration projects in this region, few studies have used these seed species in this context, and they are dominant grasses in the west desert region of central Utah. The weed species *B. tectorum* was selected because it is locally common and/or widespread, has been shown to alter ecosystem processes (e.g., soil morphology, fire regimes, plant-animal diversity), is increasing in range, and may influence seed choice by granivores (see Veech 2000, 2001, Knapp 1996, Brooks et al. 2004, Chapter 2, 4). *P. miliaceum* was included because it has been used extensively in seed selection experiments (see Longland and Bateman 1998) and has been tested with some native species as a potential decoy seed in reseeding projects.

We use the term “seed” throughout this paper in reference to all non-ovarian reproductive tissues which botanically speaking are fruits. Because the differing tissues among these two structures may either enhance or detract the seeds desirability as a resource this distinction is thought to be a significant factor that could influence selectivity by a granivore (Kelrick and MacMahon 1985).

Seed trays

To evaluate seed selection by rodents in monospecific patches and in mixture with cheatgrass we designed a cafeteria-style seed removal experiment using rodent-specific seed trays. Seeds of the five native grasses and *P. miliaceum* (hereafter, target seed species) were presented for removal either alone (monospecific hereafter) or in mixture with *B. tectorum* seeds; in addition, *B. tectorum* seeds were presented alone. This resulted in 13 unique seed combinations. Monospecific treatments consisted of 3 g of an individual seed species per seed tray, and mixture treatments consisted of 1.5 g of one of the non-*B. tectorum* seed mixed with 1.5 g of *B. tectorum* seed per seed tray. In a given plot each of the 13 seed combinations was replicated three times during a trial night, resulting in 39 seeds trays available during a given night. The 39 seed trays were placed randomly at the permanent points along the transects; three transects had six trays and the remaining three had seven trays. Trays were plastic Petri dishes (14-cm diameter, 1.5-cm deep). The seed trays were made available for seed removal at sunset and any remaining seeds were recovered at or before sunrise the following morning. Ant seed predation was prevented because ants were not active while seed trays were open. Seeds were separated by species and re-weighed to determine the amount removed by species.

Because the underlying research questions were centered on understanding potential variations in relative preferences and if context-dependent effects among mixed seed neighborhoods occur, seed weight rather than seed density was used. Consequently this resulted in a differing number seeds available for removal among the seed species used in the research which, is not a problem given the current experimental design and statistical analysis. We calculated the mean seed weight for each species by weighing 100 randomly selected seeds. The approximate seeds numbers/3 g quantity of seeds of each of the seeds species used was; 769.2 seeds for *A. hymenoides*, 1053.8 seeds for *B. tectorum*, 545.4 seeds for *E. elymoides*, 1111.1 for *L. cinereous*, 508.35 seeds for *P. miliaceum*, 4999.9 seeds for *P. secunda*, and 681.8 seeds for *P. spicata* respectively. Because seed harvest by rodents is complex and can vary as a function of seed number or availability, seed size and shape, resource value, and more, it is difficult to predict the exact consequences of this choice for determining the absolute quantity of seed harvested (Price 1983, Kelrick et al. 1986). However, our primary focus was not on the absolute amount harvested and the use of seed weight rather than number allowed for an easy comparison of relative seed harvesting as a function of vegetation type, time period, and seed neighborhoods.

From February through September 2005 three trials were conducted in three of the cheatgrass-dominated and three of the sagebrush plots each month. Two trials were omitted from analyses due either to precipitation events or to damage to most (>50%) of the seed trays from wild or feral animals. This experimental design resulted in 46 trials for all plots combined (22 for sagebrush and 24 for cheatgrass-dominated plots).

Seed tray experiments may overestimate absolute rates of seed harvest if the animals “learn” to use trays as foraging cues (see Veech and Jenkins 2005). However, as noted above, we were primarily interested in assessing the relative preferences among the seed species and, especially, in the difference in relative preference between monospecific and mixed seed patches. Our design may not be an appropriate proxy for the assessment of natural seed harvest rates, but addresses our objectives sufficiently.

Data analyses

Inspection of data suggested that removal generally was low early in the study, peaked in early summer, and then waned. To accommodate this temporal trend in a simple form, trial nights were assigned to one of three periods, with the first from 2 February 2005 through 26 April 2005, the second from 27 April 2005 through 27 June 2005, and the third from 28 June 2005 through 30 September 2005. Dates defining periods were selected to provide reasonable balance in sample sizes. The mean amount of seed removed for each treatment for each plot for each trial night was computed over the three seed trays for each seed species, and then these values were used to compute means for each treatment for each period over the multiple trial nights within a period for each seed species. The proportion of seed removed was calculated as the mean amount of seed removed divided by the amount of seed presented in a seed tray (3 g / species monospecific, 1.5 g / species mixture). These proportions were used as response data in the analyses.

Due to the $(2 \times 6 + 1)$ treatment structure and to the use of both proportion of non-*B. tectorum* seed removed and proportion of *B. tectorum* removed as response variables in mixture treatments, three distinct subsets of data were analyzed:

(1) The effects of vegetation type, time period, and seed species (a categorical fixed-effects factor with 7 levels: 5 native species, *B. tectorum*, and *P. miliaceum*) on the proportion of seeds removed when presented in monoculture were assessed using an analysis of variance of a three-way factorial in a split-split plot design. Plots, as defined above, served as whole plots and were the experimental units for the whole-plot factor, vegetation type. Repeated measurements on plots (subplots) were the experimental units associated with the subplot factor, time period. Multiple measurements on plots in each period (sub-subplots) were the experimental units associated with the sub-subplot factor, seed species.

(2) The effects of vegetation type (a categorical fixed-effects factor with 2 levels: cheatgrass-dominated or sagebrush), time period (a categorical fixed-effects factor with 3 levels), and seed species (a categorical fixed-effects factor with 6 levels: 5 native grass species plus *P. miliaceum*) on the proportion of *B. tectorum* removed when presented in mixture with non-*B. tectorum* seeds were assessed using an analysis of variance of a three-way factorial in a split-split plot design as described above.

(3) The effects of vegetation type, time period, presentation (a categorical fixed-effects factor with 2 levels: monospecific and in mixture with cheatgrass), and seed species (a categorical fixed-effects factor with 6 levels: 5 native species plus *P. miliaceum*) on the proportion of non-*B. tectorum* target seed removed were assessed using an analysis of variance of a four-way factorial in a split-split plot design. Plots

served as whole plots and were the experimental units for the whole-plot factor, vegetation type. Repeated measurements on plots (subplots) were the experimental units associated with the subplot factor, time period. Multiple measurements on plots in each period (sub-subplots) were the experimental units associated with two sub-subplot factors, presentation and seed species.

Both normal and beta regression models were fit to each subset. The factorial treatment and experimental design structures of both modeling approaches were identical. For statistical analyses using a normal regression model, proportions of seed removed were transformed using an arcsine-square root transformation prior to analysis, a common method to improve the agreement of proportion data with assumptions of normality and homogeneity of variances (Sokal and Rohlf 1981). The analyses were generated using the MIXED procedure in SAS/STAT software, Version 9.1.3 of the SAS System for Windows.

For analyses using a beta regression model, proportions of seed removed were transformed from the closed unit interval $[0, 1]$, which includes 0 and 1, to the open unit interval $(0, 1)$, which excludes 0 and 1, using

$$\frac{p \times (N - 1) + 0.5}{N}$$

where p is the proportion and N is the sample size, as recommended by Smithson and Verkuilen (2005, 2006). Analyses were generated using the GLIMMIX procedure, production version dated June 2006, in SAS/STAT software, Version 9.1.3 of the SAS System for Windows.

RESULTS

Model selection

Although statistical results are reported for both normal regression model (PROC MIXED) and beta regression model (GLIMMIX) analyses, we emphasize the latter of these two models as best representing the results of this experiment. The beta regression model fit the assumptions vastly better. Fig. 5.2 provides an example from the monospecific data set of means and associated standard errors. The high errors that were clearly associated with our data set were better modeled in the beta regression while the constrained assumption of homogeneity of variance of normal- regression (PROC MIXED) is demonstrated by the unrealistically small standard errors (see Fig. 5.2).

Monospecific seed removal

Differential seed selectivity among the seed species when available in monospecific presentations was evident (see Table 5.1). Removal proportions varied among seed species (Table 5.1, main effect of seed species). Based on least square mean comparisons, the most preferred seed species were *A. hymenoides* and *P. miliaceum* while the least preferred were *B. tectorum* and *P. secunda* (Fig. 5.3, left column). Note these rankings are not clearly related to seed size. More seed was removed from sagebrush plots than from cheatgrass-dominated plots (Table 5.1, main effect of vegetation type; Fig. 5.3, left column). Additionally, there was a suggestive effect of time period (Table 5.1).

Importantly, we reach some different conclusions in the interpretation of results depending on whether we accept the normal or the beta regression model (Table 5.1). Based on the normal regression model, which indicated a very significant interaction between vegetation type and seed species, we would have concluded that preference rankings of seed species differed between sagebrush and cheatgrass-dominated plots. However, the more appropriate beta regression model provided absolutely no statistical support for this interaction.

Mixture seed removal – Bromus tectorum

Only vegetation type significantly affected *B. tectorum* removal from mixture treatments (Table 5.2); more seeds were removed in the sagebrush than in the cheatgrass-dominated plots. Removal of the weed seed did not vary as a function of which non-*B. tectorum* it was present with in mixture in either vegetation type (Fig. 5.4). The main effect of presentation was not significant, nor was any two-, three-, or four-way interactions with presentation significant. Therefore, there was no evidence for an associational effect of any species on *B. tectorum* seed removal (Table 5.2).

Mixture vs. monospecific seed removal – non-B. tectorum

The final model compared non-*B. tectorum* seed removal in monospecific to that in mixture treatments. Here we were primarily interested in evidence that seed removal varied as a function of presentation type (monospecific vs. mixture). In this model seed removal was significantly affected by the main effects of vegetation type, time period, and seed species (Table 5.3). The main effect of presentation was not significant, nor

was any two-, three- or four-way interactions with presentation significant, indicating associational effects did not occur.

Comparing the results from the two models again demonstrates that model selection can have a very important effect on the conclusions reached. The main effect of time period was not significant with the normal regression model but was with the beta regression model. However, more interesting was that the seed species \times presentation interaction was not significant in the more appropriate beta regression model even though it was highly significant in the normal regression model. If this interaction was significant it would demonstrate that the species differed in how presentation affected their harvest and thus suggest that species differed in associational effects in some manner. The lack of significance of any effect that contains presentation in this analysis clearly shows that there were no detectable associational effects.

DISCUSSION

Patterns of seed removal

Given the greater diversity and abundance of the rodent community in the intact sagebrush plots compared to the converted cheatgrass-dominated plots (see Chapter 4), it is not surprising that more seed were removed from the sagebrush plots. Despite the strong difference in overall removal the patterns of relative seed preferences were very similar for the two vegetation types, especially in the monospecific seed presentations. As noted, the differential seed selectivity among the seed species when available monospecifically was likely driven by the combined influence of vegetation type, which affects the rodent community, and the inherent seed preferences of the rodents present.

Many authors have demonstrated apparent preferences for specific food items by granivorous animals of North American deserts (Johnson 1961, Kelrick et al. 1986, Anderson and MacMahon 2001, Chapter 3). Veech (2001) tested the preferences of the heteromyid rodents *Dipodomys merriami* and *Perognathus longimembris* for eight plant species and concluded that the rodents exhibited distinct but variable preferences for some seeds and avoidance of others. Kelrick and MacMahon (1985) pointed to the importance of nutritional as well as physical seed characteristics in predicting harvest (but see Jenkins 1988). Others have argued that differences among rodent species in seed preference might be understood not only by morphological constraints on seed handling but also by variable toxicity sensitivity and nutritional requirements (Jenkins and Ascanio 1993). Our results are consistent with other research indicating the high desirability of *A. hymenoides* and *P. miliaceum* seeds; both species have high soluble carbohydrates and have a high ratio of energy gain to handling time (Kelrick et al. 1986, Veech 2001). Additionally, at least for *A. hymenoides*, a long standing evolutionary history with seed-caching rodents may further contribute to its overall high relative desirability (Longland et al. 2001). Nonetheless, with the exception of *P. secunda*, all of the native grass seeds were removed in substantial quantities. Because we did not investigate underlying mechanisms that might be driving differential harvest we are unable to conclude which factor or suite of factors produced the results reported.

Although there are few studies we can compare our results to, results of seed harvest in mixtures have ranged from a lack of associational effects (Hulme and Hunt 1999) through weak evidence for them (Chapter 3, 6) to strong evidence for such effects (Veech 2001). Visual inspection of the results suggests a slight shift in relative

preference for some of the target seeds when presented in mixture versus monospecifically. For example, visually, seeds of *P. secunda* were removed at greater relative proportion in mixture than when alone. Note that when alone, *P. secunda* had a significantly lower proportional removal than did the other native grasses and *P. miliaceum*, but in mixture removal of *P. secunda* was similar to the other seeds and even greater than *L. cinereous*. In addition, it appears that *A. hymenoides* and *L. cinereous* realized slight reductions in removal in mixture treatments compared to monospecific treatments. Overall, however, the evidence for a change in species preferences in seed mixtures was weak. The interaction of seed species \times presentation (monospecific versus mixture) was significant for the normal regression model but it was not significant in the more appropriate beta regression model. Thus, despite the visual changes described, associational effects were at best very weak in this study.

Veech (2000) found that apparent competition (*sensu* associational susceptibility) most likely resulted among the species whose seeds were the most heavily harvested (e.g. *A. hymenoides*), whereas we found marginal evidence for it with the species that had the lowest rates of predation (e.g. apparently increased removal of *P. secunda* when present with *B. tectorum*). In another study Veech (2001) found a negative indirect effect of *A. hymenoides* on *Astragalus cicer* caused by rodents having a lower foraging effort in patches that only contained *A. cicer* seeds than in patches that also contained *A. hymenoides* seeds. The results from Chapter 3 and 6 and the weak patterns in the current study suggest something other than the overall preference for seeds may explain patterns of associational interactions. In addition to seed preferences, density-dependent foraging and prey switching have been suggested as potential behavioral mechanisms leading to

associational effects among seeds which may help explain resultant patterns (see Veech 2001, Wootton 1994). However, the results of the current study (and see Chapter 3 and 6) and those of similar design from others (see Veech 2000, 2001) point to potentially different causes for resultant patterns. Factors of the environment, including the scale of the patch (spatial) as well as a shifting background seed resource temporally may further explain patterns reported here.

Within-season variation in seed removal by rodents has also been shown by other researchers (Veech and Jenkins 2005). Although we were not able to confirm temporally shifting patterns of seed removal for the monospecific treatments, we did in the mixtures. Also, we noticed a general trend for increasing removal in the cheatgrass-dominated plots over time while seed removal in the sagebrush plots peaked in the middle sampling period. It is possible that some of the apparent differences in temporal patterns of seed removal among the two vegetation types are a function of differences in background seed resources. Presumably, the sagebrush plots had a more diverse seed resource background that also differed temporally in patterns of availability compared to cheatgrass-dominated plots. While overall seed availability in the cheatgrass-dominated plots is likely greater than in the sagebrush due to the abundant seed production of *B. tectorum* (Humphrey and Schupp 2001), especially early in the season when their seeds are released, the desirability of those seeds is low. Furthermore, changing behavioral strategies in terms of seed handling could also produce varying temporal patterns of seed harvest. There is some indication that heteromyid rodents shift from predominantly scatter-hoarding seeds in shallow caches throughout their home range early in the season to larder-hoarding, whereby seeds are more deeply buried in one or a few burrows for use later in the season

(Vander Wall 1990, William S. Longland personal communication). Potentially, then, these rodents may be less “choosy” of the types of seeds they select later in the season when they are not exposed to the added predation risk associated with caching and subsequent re-caching of seeds. In addition, over time as more and more of the year’s seed production is harvested the overall pool of available resources decreases which may also contribute to reduced selectivity and overall increased harvest from our trays. Therefore, a comprehensive consideration of seed availability, inherent seed desirability, the role of both space and time and natural cues influencing behaviors associated with seed selection should be assessed in an experimental framework to identify a causal relationship, if one exists.

Management implications

Outside of *B. tectorum* and *P. miliaceum*, the seeds considered in this research have been and will be used for ecological restoration. Many of the degraded sites within the Intermountain West that will have seed applied as part restoration are also habitats for organisms that can consume large quantities of seed. The consideration of granivory in the context of ecological restoration has been promoted to maximize success of management actions (Kelrick and MacMahon 1985, Archer and Pyke 1991, Hoffmann et al. 1995). An understanding of the granivores present and their relative seed preferences could be an important first step in reducing direct seed losses to granivory (see Chapter 1). Although in these cafeteria trials all native grass seeds except *P. secunda* were removed in substantial quantities, how rodents might harvest these seeds in a natural large-scale reseedings is generally unknown but merits investigation.

Consequences of model selection

We included a comparison of the alternative models to point to the importance of model selection criteria in understanding patterns revealed by the data while maintaining ecological relevance. Like many ecological data sets ours did not fit a central tendency or normal distribution assumed for traditional approaches such as normal regression modeling as in PROC MIXED. Due to the nature of the study design and the biology of the study organism(s), the resultant data set was bimodal and proportional in nature. It was not uncommon for seeds in a seed tray to be either completely un-removed or else completely or nearly completely removed. The shape of our proportional data distribution was better suited for regression with a beta-distributed dependent variable than with a normally distributed dependent variable, which did not meet associated assumptions. We have shown that the use of this alternative statistical approach is important for differentiating the biologically important effects revealed by the data, which would have otherwise drawn our attention to the statistically significant occurrence of associational interactions (i.e. associational resistance and/or associational susceptibility). We contend beta regression approach may have a frequent place in the evaluation of ecological data where traditional approaches fall short.

REFERENCES

- Anderson, C. J., and J. A. MacMahon. 2001. Granivores, exclosures, and seed banks: harvester ants and rodents in sagebrush-steppe. *Journal of Arid Environments* **49**:343-355.
- Archer, S., and D. A. Pyke. 1991. Plant-animal interactions affecting plant establishment and persistence on revegetated rangelands. *Journal of Range Management* **44**:558-565.
- Brehm, J., and S. Gates. 1993. Donut shops and speed traps: evaluating models of supervision and police behavior. *American Journal of Political Science* **37**: 555-581.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *BioScience* **54**:677-688.
- Caccia, F. D., E. J. Chaneton, and T. Kitzberger. 2006. Trophic and non-trophic pathways mediate apparent competition through post-dispersal seed predation in a Patagonian mixed forest. *Oikos* **113**:469-480.
- DeCasenave, J. L., V. R. Cueto, and L. Marone. 1998. Granivory in the Monte desert, Argentina: is it less intense than in other arid zones of the world? *Global Ecology and Biogeography Letters* **7**:197-204.
- Ferrari, S. L. P., and F. Cribari-Neto. 2004. Beta regression for modelling rates and proportions. *Journal of Applied Statistics* **31**:799-815.
- Hoffmann, L. A., E. F. Redente, and L. C. McEwen. 1995. Effects of selective seed predation by rodents on shortgrass establishment. *Ecological Applications* **5**:200-208.
- Hulme, P. E., and M. K. Hunt. 1999. Rodent post-dispersal seed predation in deciduous woodland: predator response to absolute and relative abundance of prey. *Journal of Animal Ecology* **68**:417-428.
- Humphrey, L. D., and E. W. Schupp. 2001. Seed banks of *Bromus tectorum* dominated communities in the Great Basin. *Western North American Naturalist* **61**:85-92.
- Jenkins, S. H. 1988. Comments on relationships between native seed preferences of shrub-steppe granivores and seed nutritional characteristics. *Oecologia* **75**:481 - 482.

- Jenkins, S. H., and R. Ascanio. 1993. A Potential nutritional basis for resource partitioning by desert rodents. *American Midland Naturalist* **130**:164-172.
- Johnson, D. R. 1961. The food habits of rodents on rangelands of Southern Idaho. *Ecology* **42**:407-410.
- Kelrick, M. A., and J. A. MacMahon. 1985. Nutritional and physical attributes of seed of some common sagebrush steppe plants: some implications for ecological theory and management *Journal of Range Management* **38**:56-69.
- Kelrick, M. I., J. A. MacMahon, R. R. Parmenter, and D. V. Sisson. 1986. Native seed preferences of shrub-steppe rodents, birds and ants: the relationships of seed attributes and seed use. *Oecologia* **68**:327-337.
- Kieschnick, R., and B. D. McCullough. 2003. Regression analysis of variates observed on (0,1): percentages, proportions and fractions. *Statistical Modeling* **3**:193-213.
- Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert - history, persistence, and influences to human activities. *Global Environmental Change-Human and Policy Dimensions* **6**:37-52.
- Longland, W. S., and S. L. Bateman. 1998. Implications of desert rodent seed preferences for range remediation. *Journal of Range Management* **51**:679-684.
- Longland, W. S., S. H. Jenkins, S. B. V. Wall, J. A. Veech, and S. Pyare. 2001. Seedling recruitment in *Oryzopsis hymenoides*: are desert granivores mutualists or predators? *Ecology* **82**:3131-3148.
- McArdle, B. H., and M. J. Anderson. 2004. Variance heterogeneity, transformations, and models of species abundance: a cautionary tale. *Canadian Journal of Fisheries and Aquatic Sciences* **61**:1294-1302.
- McCullagh, P., and J. A. Nelder. 1989. *Generalized linear models*, 2nd ed. Chapman & Hall, London.
- Paolino, P. 2001. Maximum likelihood estimation of models with beta-distributed dependent variable. *Political Analysis* **9**:325-346.
- Price, M. V., and J. H. Brown. 1983. Patterns of morphology and resource use in North American desert rodent communities. *Great Basin Naturalist Memoirs* **7**:117-134.
- Rand, T. A. 1999. Effects of environmental context on the susceptibility of *Atriplex patula* to attack by herbivorous beetles. *Oecologia* **121**:39-46.

- Smithson, M, and J. Verkuilen. 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variable. *Psychological Methods* **11**: 54-71.
- Smithson, M. and Verkuilen, J. 2005. Beta regression: practical issues in estimation. Available at: <http://psychology.anu.edu.au/people/smithson/details/betareg/Readme.pdf>.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. W. H. Freeman. San Francisco, California, USA.
- Tahvanainen, J. O., and R. B. Root. 1972. The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia* **10**:321-346.
- Vander Wall, S. B. 1990. *Food hoarding in animals*. University of Chicago Press, Chicago.
- Veech, J. A. 2000. Predator-mediated interactions among the seeds of desert plants. *Oecologia* **124**:402-407.
- Veech, J. A. 2001. The foraging behavior of granivorous rodents and short-term apparent competition among seeds. *Behavioral Ecology* **12**:467-474.
- Veech, J. A., and S. H. Jenkins. 2005. Comparing the effects of granivorous rodents on persistence of Indian ricegrass (*Oryzopsis hymenoides*) seeds in mixed and monospecific seed patches. *Western North American Naturalist* **65**:321-328.
- Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* **25**:443-466.

Table 5.1. Type 3 tests of fixed effects for the proportion of seed removed in monospecific treatments for normal regression and beta regression models. Vegetation type compares cheatgrass-dominated to sagebrush plots, time period represents the early, mid, and late sample periods, and seed species refers to the seven species of seeds used in trials. ^a highlights differences in statistical significance between the normal and beta regression models.

Normal regression				
Effect	df	<i>F</i>	<i>P</i>	
Vegetation type	1,8	50.71	< 0.001	
Time period	2,11	2.92	0.096	
Vegetation type × time period	1,11	1.05	0.382	
Seed species	6,114	9.89	< 0.001	
Vegetation type × seed species	6,114	3.67	0.002 ^a	
Time period × seed species	12,114	0.82	0.634	
Vegetation type × time period × seed species	12,114	0.29	0.989	
Beta regression				
Effect	df	<i>F</i>	<i>P</i>	
Vegetation type	1,35	38.59	< 0.001	
Time period	2,28	3.79	0.057	
Vegetation type × time period	1,28	2.25	0.152	
Seed species	6,114	3.10	0.009	
Vegetation type × seed species	6,114	0.34	0.918 ^a	
Time period × seed species	12,114	0.51	0.909	
Vegetation type × time period × seed species	12,114	0.22	0.997	

Table 5.2. Type 3 tests of fixed effects for the proportion of *B. tectorum* seed removed in mixture treatments for normal and beta regression models. Vegetation type compares cheatgrass-dominated to sagebrush plots, time period represents the early, mid, and late sample periods, and seed species refers to the six target seed species used in trials which were present with the *B. tectorum* seeds.

Normal regression				
Effect	df	<i>F</i>	<i>P</i>	
Vegetation type	1,8	13.12	0.007	
Time period	2,11	0.59	0.572	
Vegetation type × time period	2,11	0.49	0.626	
Seed species	5,95	0.70	0.624	
Vegetation type × seed species	5,95	0.87	0.504	
Time period × seed species	10,95	0.56	0.839	
Vegetation type × time period × seed species	10,95	0.63	0.784	
Beta regression				
Effect	df	<i>F</i>	<i>P</i>	
Vegetation type	1,8	15.42	0.004	
Time period	2,11	1.93	0.192	
Vegetation type × time period	2,11	1.71	0.225	
Seed species	5,95	0.62	0.684	
Vegetation type × seed species	5,95	1.12	0.356	
Time period × seed species	10,95	0.97	0.476	
Vegetation type × time period × seed species	10,95	0.92	0.523	

Table 5.3 Type 3 tests of fixed effects for the proportion of non-*B. tectorum* seed removed in monospecific and mixture treatments for normal and beta regression models. Vegetation type compares cheatgrass-dominated to sagebrush plots, time period represents the early, mid, and late sample periods, and seed species refers to the six target seed species used in trials. ^a and ^b highlight differences in statistical significance between the normal and beta regression models.

Normal regression				
Effect	df	<i>F</i>	<i>P</i>	
Vegetation type	1,8	59.67	< 0.001	
Time period	2,11	2.70	0.113 ^a	
Vegetation type × time period	2,11	0.50	0.622	
Presentation	1,209	0.14	0.704	
Vegetation type × presentation	1,209	0.48	0.490	
Time period × presentation	2,209	0.50	0.609	
Vegetation type × time period × presentation	2,209	2.59	0.078	
Seed species	5,209	12.58	< 0.001	
Vegetation type × seed species	5,209	1.58	0.166	
Time period × seed species	10,209	1.16	0.323	
Vegetation type × time period × seed species	10,209	0.30	0.982	
Seed species × presentation	5,209	3.80	0.003 ^b	
Vegetation type × seed species × presentation	5,209	0.75	0.587	
Time period × seed species × presentation	10,209	0.37	0.958	
Vegetation type × time period × seed species × presentation	10,209	0.55	0.849	
Beta regression				
Effect	df	<i>F</i>	<i>P</i>	
Vegetation type	1,8	53.46	<0.001	
Time period	2,11	4.93	0.039 ^a	
Vegetation type × time period	2,11	2.27	0.150	
Presentation	1,209	0.01	0.914	
Vegetation type × presentation	1,209	0.26	0.612	
Time period × presentation	2,209	0.21	0.811	
Vegetation type × time period × presentation	2,209	1.92	0.151	
Seed species	5,209	6.52	<0.001	
Vegetation type × seed species	5,209	0.23	0.949	
Time period × seed species	5,209	0.79	0.645	
Vegetation type × time period × seed species	10,209	0.17	0.998	
Seed species × presentation	10,209	1.50	0.194 ^b	
Vegetation type × seed species × presentation	5,209	0.15	0.980	
Time period × seed species × presentation	10,209	0.41	0.942	
Vegetation type × time period × seed species × presentation	10,209	0.39	0.950	

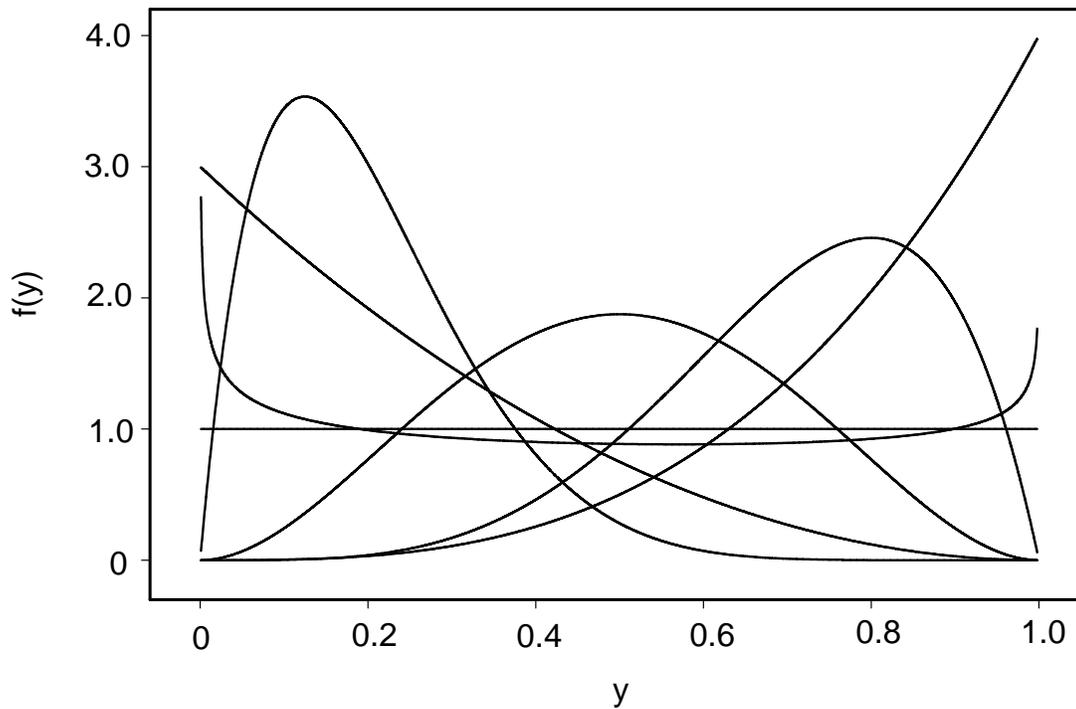


Figure 5.1. Probability density curves demonstrating some of the great variety of data distributions that beta regression can accommodate. The horizontal axis represents the values of the random variable (often denoted y ; in the case of the current study, proportion). The vertical axis represents the "density" associated with each values of the random variable (y); it is scaled such that the area under the curve is equal to one. The data in the present study are most similar to the "bath tub" curve that is relatively flat in the middle and peaks at each end.

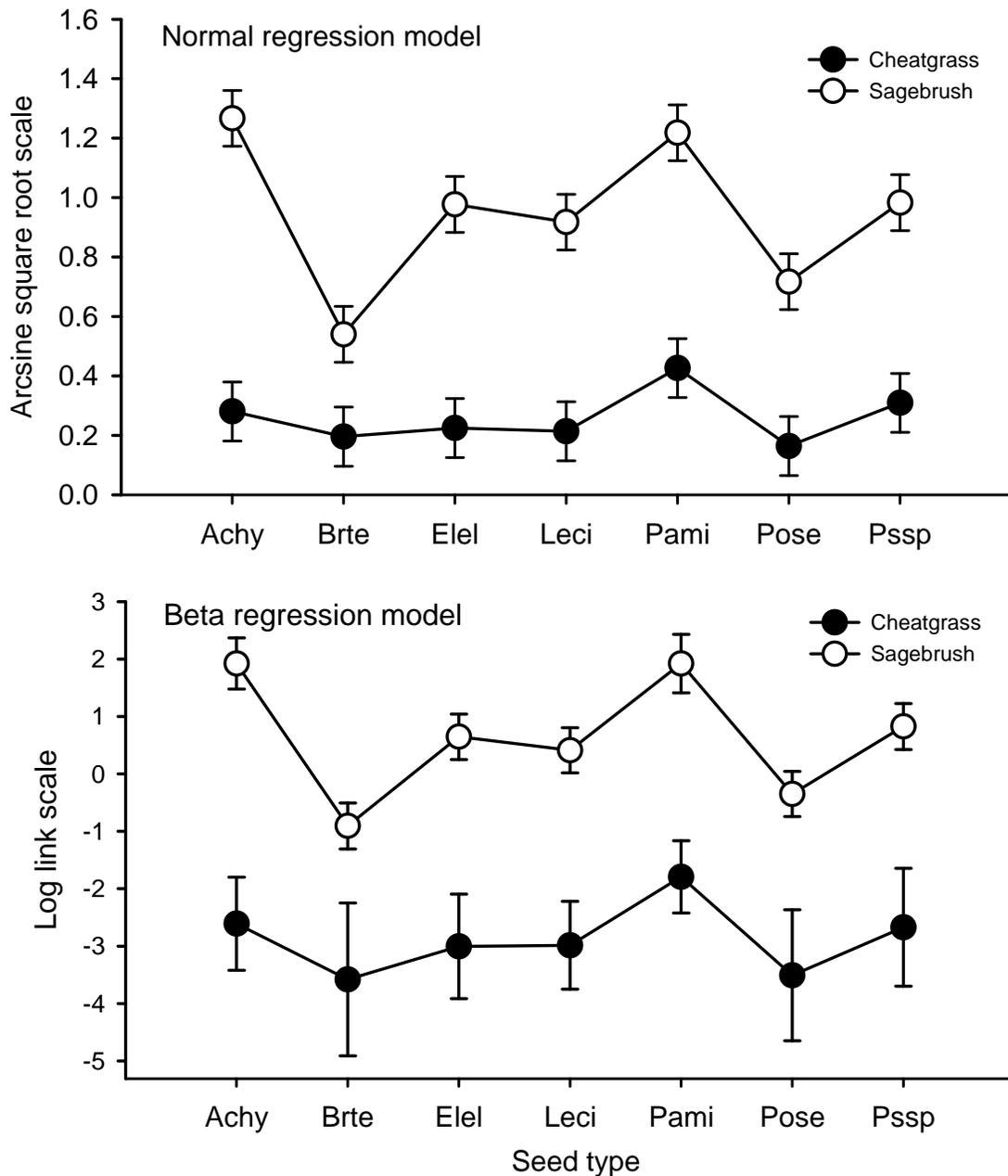


Figure 5.2. Means \pm standard errors from the normal regression model based on a normal distribution with homogenous errors (a) and from the beta regression model based on a beta distribution (b). The treatment of the means does not differ among the two models, but the standard errors are markedly different. Species abbreviations are Achy, *Achnatherum hymenoides*; Brte, *Bromus tectorum*; Elel, *Elymus elymoides*; Leci, *Leymus cinereous*; Pami, *Panicum miliaceum*; Pose, *Poa secunda*; Pssp, *Pseudoroegneria spicata*.

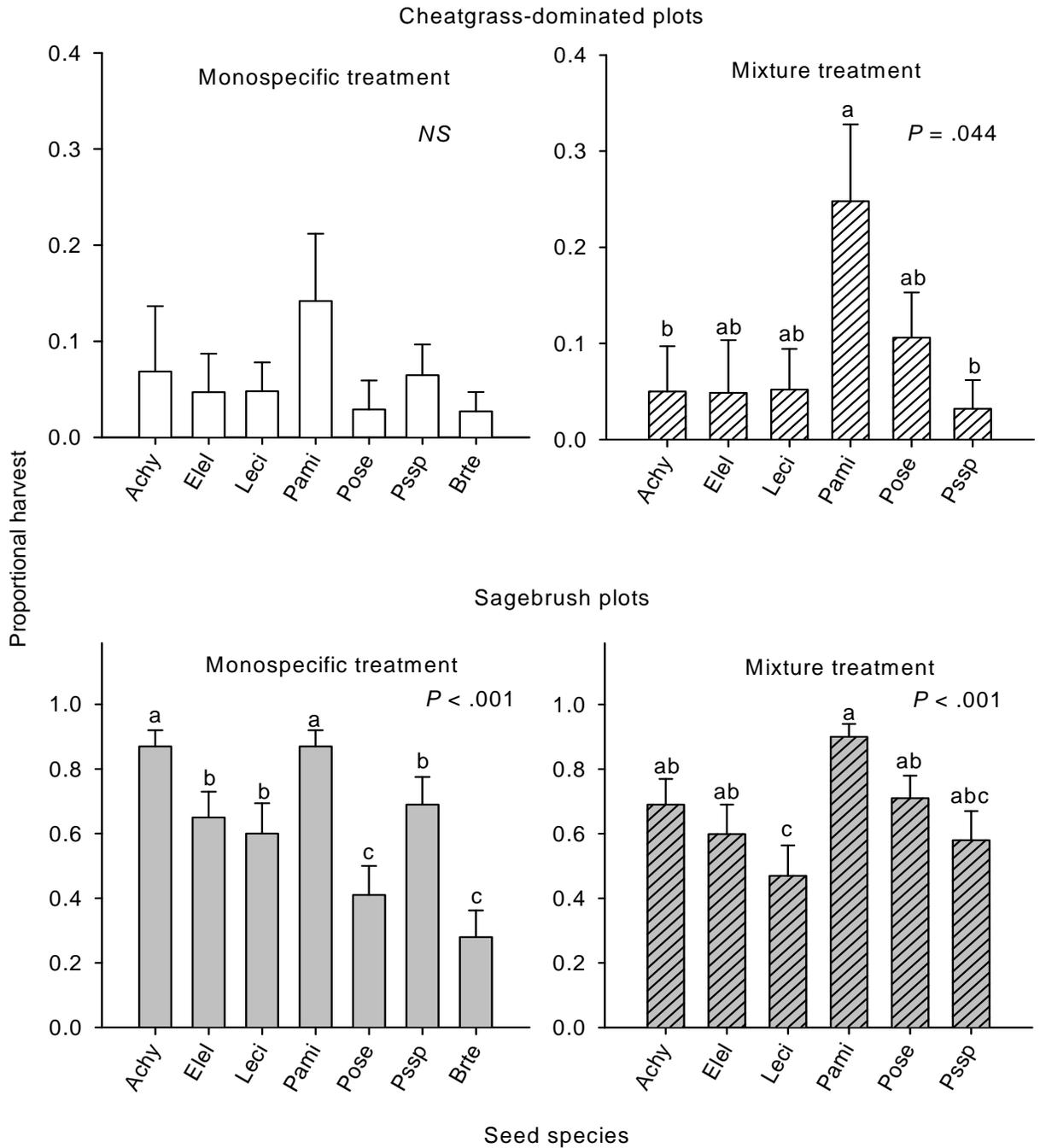


Figure 5.3. Least-square means \pm standard errors of proportional seed removal of target seed in cheatgrass-dominated plots in monospecific (open bars) and mixture (hashed bars) treatments and in sagebrush plots in monospecific (gray bars) and mixture treatments (gray hashed bars). Different letters indicates mean seed removal differed significantly ($\alpha = 0.05$) among species within that vegetation type – seed presentation treatment combinations. See figure 5.2 for species abbreviations.

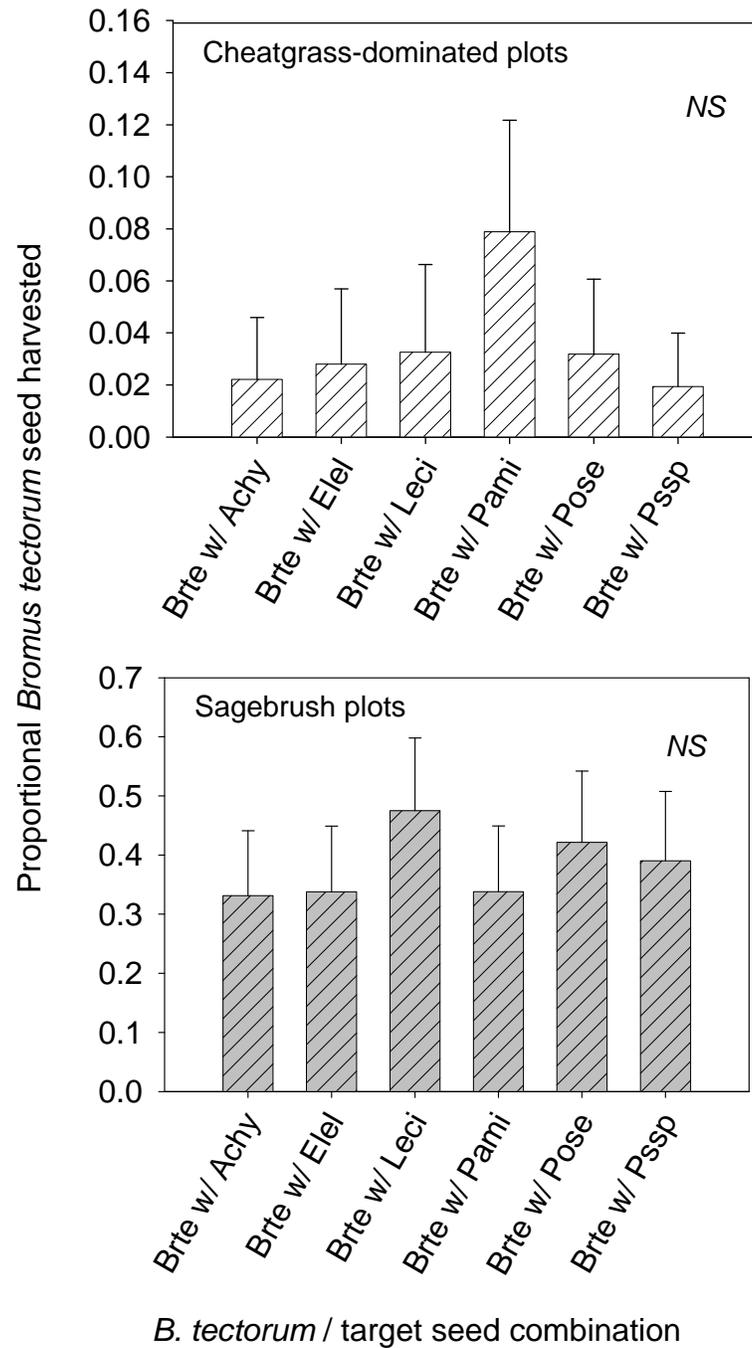


Figure 5.4. Least-square means \pm SEs of proportional seed removal of *Bromus tectorum* seed in mixture treatments in cheatgrass-dominated plots (open-hashed bars) and in sagebrush plots (gray hashed bars). *NS* indicates that *B. tectorum* seed removal did not differ ($P = 0.05$) as a function of the species in was in mixture with. See figure 5.2 for species abbreviations.

CHAPTER 6

INTER- AND INTRA-SPECIFIC SEED DENSITIES AFFECT SEED
PREFERENCES BY GRANIVOROUS RODENTS⁶

Abstract. Rodents are known to forage in a density-dependent manner, increasing harvesting in patches with greater seed densities. In addition, at a set overall density, seed harvesting may be context-dependent, with the fates of seeds depending on the species identities of other individuals in the seed neighborhood. That is, in mixtures of different species, indirect or associational effects may strongly influence species-specific seed harvest. If seed harvest for one species increases due to the association of a second seed species the outcome is considered an associational susceptibility for seed species one. In contrast, if the seeds of the first species are harvested less because they are in that mixed species patch or in association with a second species the resultant pattern is termed associational resistance. To evaluate the occurrence of density-dependent foraging by rodent granivores and associational effects among seeds in mixtures we conducted rodent seed removal experiments in the eastern portion of the Great Basin desert in west-central Utah, USA. Our experimental approach used a completely additive design patterned after a two-species competition experiment using either the seeds of *Achnatherum hymenoides* (Indian ricegrass), *Leymus cinereus* (Basin wildrye), or *Pseudoroegneria spicata* (bluebunch wheatgrass) as the native seed species combined with seeds of the non-native exotic annual grass *Bromus tectorum* (cheatgrass). The experiment involved placing 0, 1, 2, 3, 4, or 5 g of the native seeds mixed with 0, 1, 2, 3, 4, or 5 g of *B. tectorum* seeds,

⁶ Coauthored by Steven M. Ostojia, Eugene W. Schupp, and Susan Durham

resulting in 35 weight (our proxy for density) combinations, omitting the 0, 0 combination. We detected density-dependent foraging on the three target seeds and on cheatgrass when in monocultures. The presence of *B. tectorum* with *A. hymenoides* or *L. cinereus* seeds did not significantly affect removal of either native species. However, results indicate that the presence of *B. tectorum* with *P. spicata* seeds may increase rates of removal of this native seeds. Harvest of *B. tectorum* seeds was greater when in combination with all of the native seed species, indicating an associational susceptibility of *B. tectorum* seeds when present with these native seeds. These results demonstrate that seed fate is determined by both total seed density and the local seed environment, suggesting that associational effects between native seeds and cheatgrass can occur in field conditions.

INTRODUCTION

At the most basic level the seed-granivore dynamic is a two-way interaction involving seeds of a single species and an individual consumer of those seeds (Janzen 1971, Howe and Brown 2001, Longland et al. 2001). Seeds are a resource for the granivore, and the granivore, although a seed consumer, is also a potential dispersal agent for seeds (West 1968, Janzen 1971, Price and Jenkins 1986, Chambers and MacMahon 1994, Price and Waser 1985, Hulme 1994, Longland et al. 2001, Theimer 2005, Schupp 2007). The intensity of seed harvesting and the resultant consequences for the dynamics of plant populations can be complex and often dependent on characteristics of the local biotic and abiotic environment (Schupp 1988, Schupp and Frost 1989). For example, species composition, diversity, and structure of vegetation influence seed availability and

quality and thus the granivore community and resulting competitive interactions among seed eaters (Brown 1973, Brown et al. 1979, Brown 1999, Caccia et al. 2006, Chapter 3 and 5), which in turn potentially influence seed removal patterns (Schupp and Fuentes 1995, Caccia et al. 2006). Moreover, the intensity of seed harvesting among microsites in the same community (Price 1979, Jorgensen et al. 1995, Longland 1994, Chapter 3) or among nearby plant communities (Brown et al. 1986, Bowers 1990) can be drastically different. The physical environment also influences elements of seed removal.

Moonlight and lunar cycles (Hay 1986), seasonality (Brown et al. 1979), edaphic effects (Price and Podolsky 1989), and soil moisture (Vander Wall 1998) all can affect patterns and amounts of seed removal in natural settings (see Chapter 1). In addition, inherent seed characteristics such as chemistry, morphology, and nutrient content might influence “choice” by granivores and overall patterns of removal (Kelrick and MacMahon 1985, Kelrick et al. 1986). These biotic and abiotic influences of granivory, combined with foraging patterns and seed handling behaviors, all influence granivore exploitation of seed resources and in turn affect plant populations (Brown and Heske 1990, Howe and Brown 2001).

Density-dependent foraging has been well-demonstrated for granivorous rodents in North American deserts (Nelson and Chew 1977, McMurray 1997, Veech and Jenkins 2005). Veech and Jenkins (2005) define density-dependent foraging as the harvest of a greater proportion of seeds (of a given seed species) from high-density patches than from low-density patches, and “overall” seed density as the combined density of seeds of all species in a patch. In this light, Price and Heinz (1984) showed that the number of seeds harvested per second increases with seed density. Density-dependent foraging is

predicted by optimal foraging theory (Charnov 1976), which suggests that animals should spend more time foraging at more dense resource patches, maximizing gain while reducing associated costs of foraging. Foraging decisions likely involve balancing energy gain with the perceived risk of being eaten (Longland and Price 1991). For example, Bowers (1990) showed that *Dipodomys merriami* accept proportionately more risk at higher resource levels.

In addition to total seed density, the patterns of seed dispersion in time and space and the combinations of species of seeds available in particular resource patches can potentially influence these seed-granivore interactions. Because seeds are not homogeneously distributed in the environment and generally occur in mixed species patches, interactions between seed species are likely critical. In seed neighborhoods with mixtures of seeds some seed species may confer an “associational resistance” (sensu “apparent mutualism” Holt 1977) from seed predators on other seed species (Tahvanainen and Root 1972, Hay 1986, Veech 2000, 2001). Associational resistance would occur if a granivore’s foraging on one seed species was diminished by the presence of other seed species in the local neighborhood. In its simplest form this might lead to linked plant population dynamics where an increase in one species leads to an increase in another species (Holt 1977, Veech 2000). Although not as well documented for seed removal experiments, plants growing in dense or diverse vegetation are frequently less susceptible to herbivory than are isolated plants or plants growing in monospecific stands (Tahvanainen and Root 1972, Bach 1980, Rausher 1981, Callaway et al. 2005). Theoretically, a seed forager’s search image could become “confused” by mixed-species seed patches, hindering the ability to find its seed prey. Protection from

removal also may result from a reduced foraging efficiency on desirable seeds in diverse seed aggregations or with seeds that require increased handling time before the animal can perceive its relative desirability.

Being in a seed mixture also might increase the susceptibility of a specific seed species to predation. This “associational susceptibility” (sensu “short-term apparent competition” Holt and Kolter 1987, Veech 2000, 2001, Caccia et al. 2006) occurs when an increase in the quantity of the seed of one species leads to a decrease in the abundance of the seed of another species. Veech (2001) and Veech and Jenkins (2005) have demonstrated short-term apparent competition among seeds of desert plants fed on by heteromyid rodents. For example, Veech (2001) reported a negative indirect effect of *A. hymenoides* on *Astragalus cicer* due to a lower foraging effort in patches with only *A. cicer* compared to patches with both seed species. A dependence of seed harvest on the mixed-species context could alter selection and change the fate of all seeds present, which could change patterns of germination and establishment and produce patterns of vegetation structure different from what would be expected based on responses of rodents to monospecific seed patches.

Thus, total seed densities and relative proportions of different seed species in mixed species neighborhoods can affect seed harvesting and might potentially serve as better predictors of seed harvest than traditional monospecific seed density experiments. However, the effects of relative proportions and of total seed density on foraging behavior and seed removal are largely unexplored to date. Moreover, to our knowledge no study has investigated seed-seed interactions between native and non-native seed species. In this study, we examined the importance of seed density and of relative

proportions of seed species in mixtures on the intensity of seed removal of three common native perennial grasses (*Achnatherum hymenoides*, *Leymus cinereus*, and *Pseudoroegneria spicata*) and one non-native annual grass (*Bromus tectorum*) by rodent granivores in a Great Basin sagebrush community. The objectives of this seed removal experiment were: (1) to determine whether harvesting of seeds of the three native grasses and of the exotic grass was density-dependent (i.e. intra-specific foraging effects), using seed weight as a proxy for density and (2) to determine whether associational effects (i.e. associational resistance or associational susceptibility) occur between seeds of the weed *B. tectorum* and, individually, the three native perennial grasses (i.e. interspecific effects).

METHODS

Study sites and species

The study was conducted in west-central Utah, USA, at sites referred to as Vernon Hills (12 384335E 4438482N) and Simpson Springs (12 350537E 4437129N), which are, respectively, about 155 and 172 km southwest of Salt Lake City, Utah, in Tooele County. The vegetation is typical of Wyoming big sagebrush communities in the Great Basin. Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) is dominant, although other shrubs such as fourwing saltbush (*Atriplex canescens*), broom snakeweed (*Gutierrezia sarothrae*), yellow rabbitbrush (*Chrysothamnus viscidiflorus*) and Mormon tea (*Ephedra viridis*) are present. The understory is dominated by the grasses Indian ricegrass (*Achnatherum hymenoides*), bottlebrush squirreltail (*Elymus elymoides*), Sandberg bluegrass (*Poa secunda*), needle and thread grass (*Hesperostipa*

comata), basin wildrye (*Leymus cinereus*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and cheatgrass (*Bromus tectorum*).

Native grass species used in this study were *A. hymenoides*, *L. cinereus*, and *P. spicata*. Seeds of these species were purchased from Granite Seed Company, Lehi, Utah, USA. Seeds of *B. tectorum* were collected in the vicinity of the research areas by the senior author in 2005. The rodent community is diverse at the study sites but is numerically dominated by *P. maniculatus*, which accounted for >50% of all individuals captured (Chapter 4). Other nocturnal granivorous rodents trapped at Vernon Hills and Simpson Springs in 2005 were *Dipodomys ordii*, *Perognathus parvus*, *Reithrodontomys megalotis*, and *Peromyscus maniculatus* (Chapter 4).

Seed trays

To assess the intraspecific and interspecific effects on removal rates and relative preferences by granivorous rodents in two-species seed mixtures we used a cafeteria-style seed removal experiment. Our experimental approach was a completely additive design modeled after a two-species plant competition experiment using seeds of one of the native species above in combination with *B. tectorum*. We placed 0, 1, 2, 3, 4, or 5 g of the native species' seeds with 0, 1, 2, 3, 4, or 5 g of *B. tectorum* seeds, resulting in 35 weight (density) combinations (omitting the 0, 0 combination). Each of seven 1.2-ha plots had six parallel 120-m transects (20 m spacing between transects) with six permanent points on each transect. Six of the 35 seed combinations were randomly placed at permanent points along each of five transects and the remaining 5 combinations

were randomly placed along the last transect. Each native species-cheatgrass treatment was replicated 15 times during the period 4 May to 9 September 2005.

Because we were primarily interested in how variation in total resource availability might affect patterns of seed harvest in mixed seed species neighborhoods we used constant seed weight categories rather than constant seed density categories. Seed harvest by rodents is complex and affected by seed number, size, shape, nutritional and toxic characteristics, and more, so no single experimental approach is necessarily better or more realistic for assessing harvest rates (Kelrick et al. 1986). However, the use of seed weight rather than number does provide an easy and suitable way to assess changes in the relative quantities of resources harvested among the different seed mixtures, and it is such relative changes rather than absolute harvest rates that are the primary focus of this study.

As a consequence of this experimental approach the numbers of seeds available for removal differed among the seed species. We weighed 100 randomly selected seeds for each of the species to determine mean seed weight. The approximate seeds numbers/1 g quantity of seeds of each of the seeds species used was; 256.4 seeds for *A. hymenoides*, 334.6 seeds for *B. tectorum*, 370.4 for *L. cinereous*, and 227.3 seeds for *P. spicata* respectively.

Plastic Petri dishes (14 cm diameter, 1.5 cm deep) were used to offer seeds to rodents. Seed-tray experiments have been widely used for more than a decade to evaluate seed harvest by North American desert rodents. Seed-tray experiments may overestimate absolute rates of seed harvest if the animals “learn” to cue in on trays as foraging opportunities. However, because we were interested in the effects of seed

neighborhood on relative intensity of harvest rather than absolute quantity of seed harvested this should not be a problem. Seed trays were set out at sunset and collected at or before sunrise the following morning, denying granivorous ants access to the trays. Seeds remaining in a tray were separated by species (native versus cheatgrass) and reweighed to determine the amount removed. Trays that were destroyed or damaged by pronghorn antelope or wild horse trampling were omitted from the analyses.

Analyses

We used a multiple linear regression with one categorical predictor (target species), two continuous predictor variables (native seed density and cheatgrass seed density), and their interactions. Two separate sets of analyses were conducted. First, we analyzed the entire data set with the native species combined to assess the interactions between “native seeds” and cheatgrass. Second, we conducted three separate analyses, one for each individual native species-cheatgrass combinations, to assess species-specific interactions. In all cases, we analyzed the effect of both native seeds and cheatgrass seeds on native seed harvest and the effects of both native seeds and cheatgrass seeds on cheatgrass harvest, using the weight of seed harvested as the response variable. Due to blocking and the nature of the study design this multiple regression approach is embedded in a mixed design (because individual data points are not independent). Graphical analysis of residuals was used to assess assumptions of linearity, normality, and homogeneity of variance. The MIXED procedure in SAS/STAT for Windows Release 9.1.2 was used for model fitting.

Model predictions of seed harvest are portrayed using topographical isocline plots, which depict the projection of the 3-D response surface onto the 2-D (i.e. native and cheatgrass) seed density plane using S-Plus. These figures illustrate how seed harvest of either the native species or of *B. tectorum* is influenced by varying seed densities of both species. For example, refer to *P. spicata* in the bottom panel of Fig. 6.1. The 3.2 g isocline depicts all combinations of initial quantities of *P. spicata* seeds and of *B. tectorum* seeds that result in 3.2 g of the native seed *P. spicata* being consumed. Looking at it slightly differently, the figure shows that just under 3.2 g of *P. spicata* seed was harvested when 4 g of *P. spicata* was available alone (0 g of *B. tectorum*), but only about 2.8 g of *P. spicata* was harvested when the 4 g of *P. spicata* was available with 4 g of *B. tectorum*. Specifically, the isoclines have positive slopes when a reduction of target seed harvest (y-axis, in this example the native species) occurs with increasingly greater amounts of the second seed species (x-axis, in this example *B. tectorum*); that is, with increasing quantities of the second species, more of the target species must be initially available for the same amount of it to be harvested. Such patterns when significant are termed associational resistance (Fig 6.1). Conversely, negative slopes to isoclines signify an increase in target seed harvest (y-axis) occurs with increasingly greater quantities of the second seed species (x-axis), a pattern termed associational susceptibility.

RESULTS

Native seed harvest

In the overall analysis including all three native species in the model, the weight of native seeds removed increased greatly as the initial amount of native seeds increased

(Table 6.1A), as shown by the isoclines rapidly increasing in value up the y-axis for all native species (Table 6.1A, Fig. 6.1). This suggests that intra-specific effects influence seed removal. Because the species effect was non-significant there was no evidence that these patterns differed among native species (Table 6.1A). In the individual species analyses native seed quantity also positively affected the harvest of all three native seed species, further supporting the lack of a species effect (Table 6.2, Fig. 6.1). In general, rodents tended to remove most of the available native seeds, but particularly harvested *P. spicata* over *L. cinereus* over *A. hymenoides*, as shown by the values associated with the isoclines.

In contrast to the positive intraspecific effect, the amount of native seed removed decreased slightly but significantly as the initial quantity of *B. tectorum* increased (see Table 6.1A), as shown by the shallow but positive slopes of the isoclines (Fig. 6.1). Therefore, *B. tectorum* provides a relatively weak but significant associational resistance to the native seeds (Fig. 6.1). In contrast to the overall analysis, however, native seed harvest was not significantly influenced by the amount of *B. tectorum* seed in the mixture for any of the three native species individually (Table 6.1A), further testament to the weakness of the effect.

Although no interactions were significant, the near significance of the *P. spicata* weight \times *B. tectorum* weight interaction (Table 6.2) is interesting. This interaction suggests that with an increasing amount of *P. spicata* seeds *B. tectorum* provides increasing associational resistance to the harvest of that native species, as shown by the increasing steepness of the isoclines as one moves up the y axis (Fig. 6.1).

Bromus tectorum seed harvest

Like the three native seed species considered in this research, harvest of *B. tectorum* seeds increased with intraspecific density in both the overall analysis (Table 6.1B) and in each of the individual analyses (Table 6.3, Fig. 6.2). Although highly significant, the intraspecific effects on *B. tectorum* harvest do not appear to be as strong as those acting on the native seeds (note that the values of the isoclines increase in value more slowly along the y-axis in Fig. 6.2 than in Fig. 6.1), likely indicating relatively lower preference of *B. tectorum* seed compared to the native seeds by the rodents.

Similarly, the amount of native seed initially available also had a significant positive effect on *B. tectorum* seed removal by rodents in both the overall (Table 6.1B) and the individual species (Table 6.3) analyses; this pattern is shown by the negative slopes of the isoclines in Fig. 6.2. Further, in the overall analysis the initial native seed weight \times species interaction was significant (Table 6.1), suggesting that although all native species positively affected *B. tectorum* harvest, they differed in the exact pattern of the effect (Fig. 6.2). The significant initial native seed weight \times initial *B. tectorum* seed weight interaction (Table 6.1) can be viewed as showing that the effect of *B. tectorum* on its own harvest depended on the initial quantity of native seeds, and the significant three-way interaction (Table 6.1) demonstrated that this relationship varied among the native seed species. This last point is clearly seen in the individual analyses where only *L. cinereus* had a interaction between initial native seed weight and initial *B. tectorum* weight, as revealed by the curvilinear nature of the isoclines for this species (Fig. 6.2). The curvature of these isoclines suggests that the effect of increasing native density is very strong at low native densities (steep isoclines slopes) but that with increasingly

greater native densities an equivalent increase in natives leads to less and less effect on *B. tectorum* harvest.

In general, more *B. tectorum* seed was removed when in combination with *L. cinereus* and *P. spicata*, and less when in combination with *A. hymenoides* (Fig. 6.2). More importantly, the consistent pattern of increased *B. tectorum* harvest when in mixture with native seeds is evidence for widespread and relatively strong associational effects of natives on *B. tectorum* seed harvest, as seen in the negative slopes of the isoclines in Fig. 6.2.

DISCUSSION

As expected, when more seed was available, more was taken by rodents. Although we evaluated seed weight rather than seed numbers, this reflects an effect of intraspecific density, which has been shown in other North American desert systems and in laboratory studies with related rodent species (Price and Heinz 1984, Bowers 1990, Veech 2001, Veech and Jenkins 2005). Because foraging behaviors of individual species were not evaluated, we contend that these intraspecific density effects are an inherent property operating at the community level of seed-eating rodents. We did not detect a lower threshold at which the rodents ceased foraging for any of the three native seed species. Therefore the sustained increase in harvest with increased availability of seeds is consistent with optimal foraging theory where the forager should maximize energy intake per time spent foraging (Charnov 1976). Granivorous animals of the eastern Great Basin live in an environment that is resource (i.e. seed) limited. These seeds come in annual pulses that can further intensify competition for seeds, which likely influences foraging

decisions in the face of potential risk of attack. Thus it would be expected to see sustained harvest when increasingly greater quantities of seeds are available; especially for the more preferred seed types like the native species used in this study (see Chapter 5).

Just as with the native species, more seeds of *B. tectorum* were removed when more seeds were initially available; however, rodents rarely completely depleted the *B. tectorum* seeds as they often did the native seeds. Moreover, results from another rodent removal experiment considering seven types of seeds (see Chapter 5) indicated that *B. tectorum* seeds are the least preferred seed type. Such low removal rates in field conditions are difficult to compare to laboratory experiments (Veech 2001) where risks differ and animals come from differing ecosystems where background seed resources vary, thus ultimately affecting seed preference in experimental settings. The relatively low removal of *B. tectorum* could simply be a function of the relatively high amounts of *B. tectorum* seeds available at our research area. Based on seed pool assays, the amount of cheatgrass naturally available for harvest was much greater than what was naturally available for any of the three targets used in this research (S. M. Ostoja, unpublished data).

It is also possible that *B. tectorum* seeds are less preferred due to their morphology and/or nutritional quality compared to the native seeds. For example, unlike the three native species used *B. tectorum* has long awns, which would make collection and placement within cheek pouches more difficult and potentially increase the predation risk associated with *B. tectorum* seed processing. This presumably increased time necessary for *B. tectorum* harvest may help explain the apparently low desirability of

cheatgrass. Considering preference in light of nutrition, Kelrick et al. (1986) reported that for nocturnal rodents, *B. tectorum* seed harvest ranked fourth out of six available seed types even though it had the second greatest percentage of soluble carbohydrates. Soluble carbohydrates are thought to be a good predictor of the relative desirability of seeds in sagebrush communities (see Kelrick and MacMahon 1985, Kelrick et al. 1986) because soluble carbohydrates are a water-efficient energy source and their relative percentage is a good measure of the available digestible energy available in a given food item.

Context dependence in terms of associational or indirect effects can vary in the strength of the interaction. Research results to date range from strong effects (Veech 2000) through intermediate effects (current report, Chapter 3) and weak effects (Chapter 5, Veech 2001) to non-existent effects (Hulme and Borelli 1999). In the present study, we have clearly shown that the type of seed patch influences seed harvest, and that there are both intraspecific and interspecific effects on harvesting. As noted, cheatgrass appears to be a low or marginally desirable species. However, it was removed in greater amounts when it occurred in patches with native species, even in low quantities. Veech and Jenkins (2005) reported that more *Oryzopsis hymenoides* (*Achnatherum hymenoides*) seed was harvested when mixed with a second species than when available alone, and suggested density-dependent effects as an explanation (because total seed density doubled). Their results potentially point to the importance of total seed density more so than to the seed identify in driving their observed patterns, although both factors are credited. Caccia et al. (2006) found that the removal of the less-preferred *Nothofagus dombeyi* seeds increased when they were present with *Austrocedrus chilensis* seeds,

similar to the results presented here; they also noted that the reciprocal indirect effect was not observed, pointing to the importance of seed identity in producing context-dependent effects of seed removal. We found that removal of *B. tectorum* seed was greater when present with any one of the three native seeds used in our research, and that the removal of *B. tectorum* was greater when there was more *B. tectorum* present. Thus, there were clear intraspecific and interspecific effects on the harvest of these relatively undesirable seeds. However, although all native species affected *B. tectorum* seed harvest qualitatively the same; they all differed in the exact pattern of the effect (see Fig. 6.2). Again, the identity of the neighbor, not merely the quantity of the neighbor present, is important in terms of the fate of associated seeds.

Theoretically, such context-dependent seed removal could result in context-dependent seed survival, seed dispersal, and recruitment. Because we, as have others, found that the makeup of seed mixtures or seed neighborhoods to affect harvest rates by rodents we would like to note the potential effects on plant population dynamics. If seed harvest depends on several factors including patch density, mixture of patch, as well as microhabitat and dynamics of the predator population then so would seedling germination. Therefore the seed patch makeup could influence both the size and structure of a plant community. We note that *B. tectorum* did not affect the harvest of all three native seeds in the same way; each varied in terms of identity and overall density influences and the same is true for how each native species influenced how *B. tectorum* was harvested. Therefore the resultant patterns for plant populations is a shifting template in both time and space of which could change given variations in the local seed neighborhood, amount of seeds and as shown here seed identity.

These results have potentially important implications for sites chosen for restoration as well as for the conservation and management of sites where *B. tectorum* presently is or potentially will become an important species. The results of this study (and see Chapter 3 and 5) suggest that native seeds will be harvested preferentially over cheatgrass when the two occur in field conditions, reducing the establishment of natives in weed-dominated communities to the extent that harvesting is predation. Moreover, such selective seed preferences potentially facilitate the persistence of cheatgrass. Although the presence of native seeds increases cheatgrass harvest, it is probably insignificant given the incredibly high densities of cheatgrass seeds in such systems (Humphrey and Schupp 2001).

However, the concept of associational effects in general has more far reaching implications for restoration. It is common practice to restore disturbed landscapes by applying large quantities of seed hoping to revegetate a site with desirable perennial plants that are suitable for wildlife habitat, livestock forage, erosion control, water infiltration, and more. Because these sites very often have granivorous rodents present (Chapter 4), the potential for seed to be lost via predation to these animals is a real concern. With our increased understanding of the importance of seed mixture contexts to seed harvesting, the consideration of which species to put in seed mixtures and the relative amounts of each should become an increasingly important aspect of seed material selection. If selected seed mixes could be developed that fulfill traditional goals (e.g. rapid establishment, competitive ability) while reducing the rodent harvesting of desirable species restoration could become easier.

REFERENCES

- Bach, C. E. 1980. Effects of plant density and diversity on the population dynamics of a specialist herbivore, the striped cucumber beetle, *Acalymma vittata* (Fab.). *Ecology* **61**:1515-1530.
- Bowers, M. A. 1990. Exploitation of seed aggregates by Merriam's kangaroo rat: harvesting rates and predatory risk. *Ecology* **71**:2334-2344.
- Brown, J. H. 1973. Species diversity of seed-eating rodents in sand dune habitats. *Ecology* **54**:775-787.
- Brown, J. H., and E. J. Heske. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* **250**:1705-1707.
- Brown, J. H., D. W. Davidson, and O. J. Reichman. 1979. An experimental study of competition between seed-eating desert rodents and ants. *American Zoologist* **19**: 1129-1143.
- Brown, J. H., D. W. Davidson, J. C. Munger, and R. S. Inouye. 1986. Experimental community ecology: the desert granivore system. Pages 41-61 in J. Diamond and T. J. Case, editors. *Community ecology*. Harper and Row, New York, USA.
- Brown, J. S. 1999. Vigilance, patch use and habitat selection: Foraging under predation risk. *Evolutionary Ecology Research* **1**:49-71.
- Caccia, F. D., E. J. Chaneton, and T. Kitzberger. 2006. Trophic and non-trophic pathways mediate apparent competition through post-dispersal seed predation in a Patagonian mixed forest. *Oikos* **113**:469-480.
- Callaway, R. M., D. Kikodze, M. Chiboshvili, and L. Khetsuriani. 2005. Unpalatable plants protect neighbors from grazing and increase plant community diversity. *Ecology* **86**:1856-1862.
- Chambers, J. E., and J. A. MacMahon. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. *Annual Review of Ecology and Systematics* **25**:263-292.
- Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* **9**:129-136.
- Hay, M. E. 1986. Associational plant defenses and the maintenance of plant diversity: turning competitors into accomplices. *American Naturalist* **128**:617-641.

- Hay, M. E., and P. J. Fuller. 1981. Seed escape from heteromyid rodents: the importance of microhabitat and seed preference. *Ecology* **62**:1395-1399.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* **12**:197-229.
- Holt, R. D., and B. P. Kotler. 1987. Short-term apparent competition. *American Naturalist* **130**:412-430.
- Howe, H. F., and J. S. Brown. 2001. The ghost of granivory past. *Ecology Letters* **4**:371-378.
- Hulme, P. E. 1994. Post-dispersal seed predation in grasslands: its magnitude and sources of variation. *Journal of Ecology* **82**:645-652.
- Hulme, P. E., and T. Borelli. 1999. Variability in post-dispersal seed predation in deciduous woodland: relative importance of location, seed species, burial and density. *Plant Ecology* **145**:149-156.
- Humphrey, L.D., and E.W. Schupp. 2001. Seedbanks of *Bromus tectorum*-dominated communities in the Great Basin. *Western North American Naturalist* **61**: 85–92.
- Janzen, D. H. 1971. Seed predation by animals. *Annual Review of Ecology and Systematics* **2**:465-492.
- Jorgensen, E.E., S. Demarais, and S. Neff. 1995. Rodent use of microhabitat patches in desert arroyos. *American Midland Naturalist* **134**:193-199.
- Kelrick, M.I., and J.A. MacMahon. 1985. Nutritional and physical attributes of seed and some common sagebrush steppe plants: some implications for ecological theory and management. *Journal of Range Management* **38**:65-69.
- Kelrick, M.I., J.A. MacMahon, R.R. Parmenter, and D.V. Sisson. 1986. Native seed preferences of shrub-steppe rodents, birds and ants: the relationship of seed attributes and seed use. *Oecologia* **68**:327-337.
- Longland, W.S. 1994. Effects of artificial canopies and illumination on seed patch selection and heteromyid rodents. *American Midland Naturalist* **132**:82-90.
- Longland, W. S., S. H. Jenkins, S. B. Vander Wall, J. A. Veech, and S. Pyare. 2001. Seedling recruitment in *Oryzopsis hymenoides*: are desert granivores mutualists or predators? *Ecology* **82**:3131-3148.
- Longland, W. S., and M. V. Price. 1991. Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? *Ecology* **72**:2261-2273.

- McMurray, M. H., S. H. Jenkins, and W. S. Longland. 1997. Effects of seed density on germination and establishment of a native and an introduced grass species dispersed by granivorous rodents. *American Midland Naturalist* **138**:322-330.
- Nelson, J. F., and R. M. Chew. 1977. Factors affecting seed reserves in the soil of a Mojave Desert ecosystem, Rock Valley, Nye County, Nevada. *American Midland Naturalist* **97**:300-320.
- Price, M. V. 1979. The role of microhabitat in structuring desert rodent communities. *Ecology* **59**:910-921.
- Price, M. V., and K. M. Heinz. 1984. Effects of body size, seed density, and soil characteristics on rates of seed harvest by heteromyid rodents. *Oecologia* **61**:420-425.
- Price, M. V., and R. H. Podolsky. 1989. Mechanisms of seed harvest by Heteromyid rodents - soil texture effects on harvest rate and seed size selection. *Oecologia* **81**:267-273.
- Price, M. V., and S. H. Jenkins 1986. Rodents as seed consumers and dispersers. Pages 191-235 in D. R. Murray, editor. *Seed dispersal*. Academic Press, Sydney, Australia.
- Price, M. V., and N. M. Waser. 1985. Microhabitat use by heteromyid rodents: effects of artificial seed patches. *Ecology* **66**:211-219.
- Rausher, M. D. 1981. The effect of native vegetation on the susceptibility of *Aristolochia reticulata* (Aristolochiaceae) to herbivore attack. *Ecology* **62**:1187-1195.
- Schupp, E. W., and M. Fuentes. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* **2**:267-275.
- Schupp, E. W. 2007. Suitable sites for dispersal are context dependent. Pages 445-46 in A. J. Dennis, E. W. Schupp, R. J. Green, and D. A. Westcott, editors. *Seed dispersal: theory and its application in a changing world*. CAB International, Wallingford, UK.
- Tahvanainen, J. O., and R. B. Root 1972. The influence of vegetation diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia* **10**:321-346
- Theimer, T.C. 2005. Rodent scatter-hoarders as conditional mutualists. Pages 283-296 in: P.-M. Forget, J. E. Lambert, P. E. Hulme, and S. B. Vander Wall, editors. *Seed Fate: predation, secondary dispersal, and seedling establishment*. CAB International, Wallingford, UK.

- Vander Wall, S. B. 1998. Foraging success of granivorous rodents: effects of variation in seed and soil water on olfaction. *Ecology* **79**:233-241.
- Veech, J. A. 2000. Predator-mediated interactions among the seeds of desert plants. *Oecologia* **124**:402-407.
- Veech, J. A. 2001. The foraging behavior of granivorous rodents and short-term apparent competition among seeds. *Behavioral Ecology* **12**:467-474.
- Veech, J. A., and S. H. Jenkins. 2005. Comparing the effects of granivorous rodents on persistence of Indian ricegrass (*Oryzopsis hymenoides*) seeds in mixed and monospecific seed patches. *Western North American Naturalist* **65**:321-328.
- West, N.E. 1968. Rodent-influenced establishment of ponderosa pine and bitterbrush seedlings in central Oregon. *Ecology* **49**:1009-1011.

Table 6.1 MIXED procedure regression results for weight of native seeds harvested (A) and the weight of *B. tectorum* seed harvested (B) as a function of varying *B. tectorum* and native seed amounts combining the data from all three species of natives.

A. Native seed harvested			
Effect	df	F	P
Species	2,43	0.19	0.829
Initial native seed weight	1,43	626.14	<0.001
Initial native seed weight × species	2,43	0.02	0.983
Initial <i>B. tectorum</i> seed weight	1,43	6.29	0.016
Initial <i>B. tectorum</i> seed weight × species	2,43	0.04	0.965
Initial native seed weight × initial <i>B. tectorum</i> seed weight	1,1209	0.10	0.754
Initial native seed weight × initial <i>B. tectorum</i> seed weight × species	2,1209	1.90	0.149
B. <i>Bromus tectorum</i> seed harvested			
Effect	DF	F	P
Species	2,43	1.99	0.149
Initial native seed weight	1,44	63.86	<0.001
Initial native seed weight × species	2,44	4.85	0.013
Initial <i>B. tectorum</i> seed weight	1, 42	107.62	<0.001
Initial <i>B. tectorum</i> seed weight × species	2, 42	0.56	0.577
Initial native seed weight × initial <i>B. tectorum</i> seed weight	1,1195	9.75	0.002
Initial native seed weight × initial <i>B. tectorum</i> seed weight × species	2,1195	3.17	0.043

Table 6.2. Results from the MIXED procedure for the weight of native seed harvested by species as a function of the quantity of *B. tectorum* seed and of native seed in the mixture.

Effect	df	F	P
<i>Achnatherum hymenoides</i> seed harvest			
<i>A. hymenoides</i> seed weight	1,15	273.48	<0.001
<i>B. tectorum</i> seed weight	1,15	2.56	0.129
<i>A. hymenoides</i> seed weight \times <i>B. tectorum</i> seed weight	1,415	0.10	0.755
<i>Leymus cinereus</i> seed harvest			
<i>L. cinereus</i> seed weight	1,14	164.67	<0.001
<i>B. tectorum</i> seed weight	1,14	2.16	0.164
<i>L. cinereus</i> seed weight \times <i>B. tectorum</i> seed weight	1,399	0.67	0.413
<i>Pseudoroegneria spicata</i> seed harvest			
<i>P. spicata</i> seed weight	1,13	215.66	<0.001
<i>B. tectorum</i> seed weight	1,13	1.79	0.203
<i>P. spicata</i> seed weight \times <i>B. tectorum</i> seed weight	1,396	3.61	0.058

Table 6.3. Results from the MIXED procedure of *B. tectorum* seed harvested by species as a function of each of the quantity of *B. tectorum* and of the native seed in the mixture.

Effect	df	F	P
<i>Bromus tectorum</i> seed harvest when present with <i>Achnatherum hymenoides</i>			
<i>A. hymenoides</i> seed weight	1,15	15.87	<0.001
<i>B. tectorum</i> seed weight	1,15	36.48	<0.001
<i>B. tectorum</i> seed weight \times <i>A. hymenoides</i> seed weight	1,409	0.12	0.734
<i>Bromus tectorum</i> seed harvest when present with <i>Leymus cinereus</i>			
<i>L. cinereus</i> seed weight	1,14	41.50	<0.001
<i>B. tectorum</i> seed weight	1,13	34.26	<0.001
<i>B. tectorum</i> seed weight \times <i>L. cinereus</i> seed weight	1,393	12.61	0.004
<i>Bromus tectorum</i> seed harvest when present with <i>Pseudoroegneria spicata</i>			
<i>P. spicata</i> seed weight	1,14	9.72	0.007
<i>B. tectorum</i> seed weight	1,13	37.87	<0.001
<i>B. tectorum</i> seed weight \times <i>P. spicata</i> seed weight	1,392	2.25	0.134

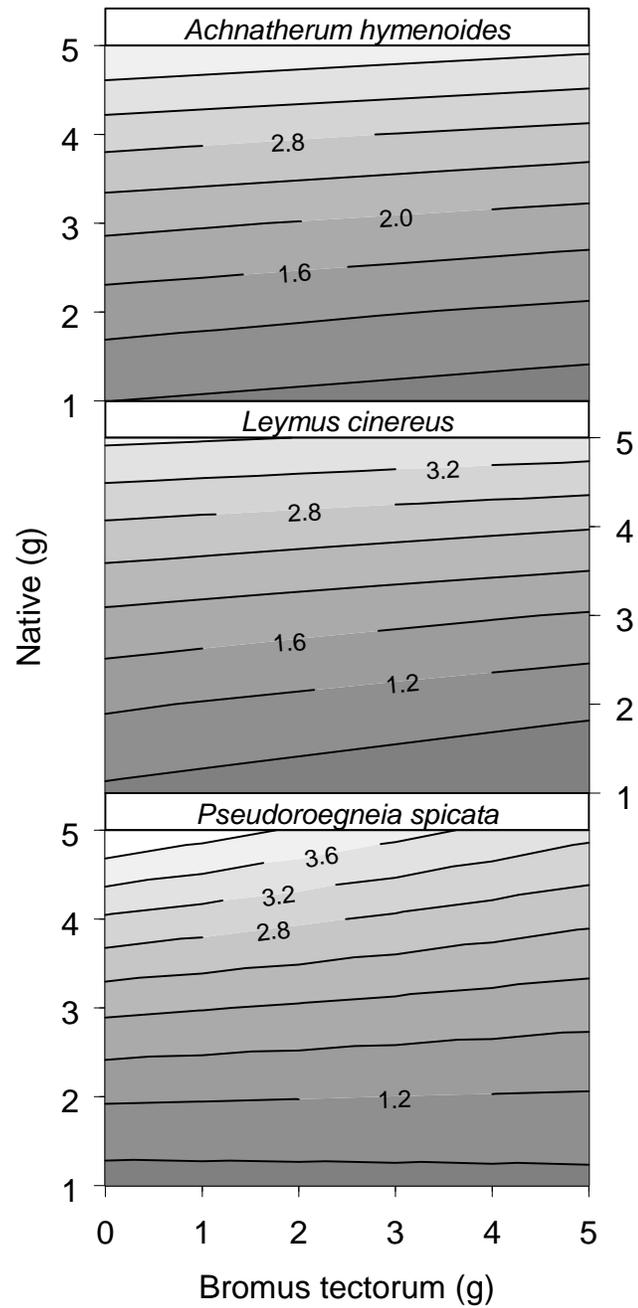


Figure 6.1. Native seed removal for each of the three native seed species as a function of varying native/*B. tectorum* seed densities. Each individual isocline indicates all density combinations of the two species that yield a constant level of seed harvest for a given native seed species (y-axis).

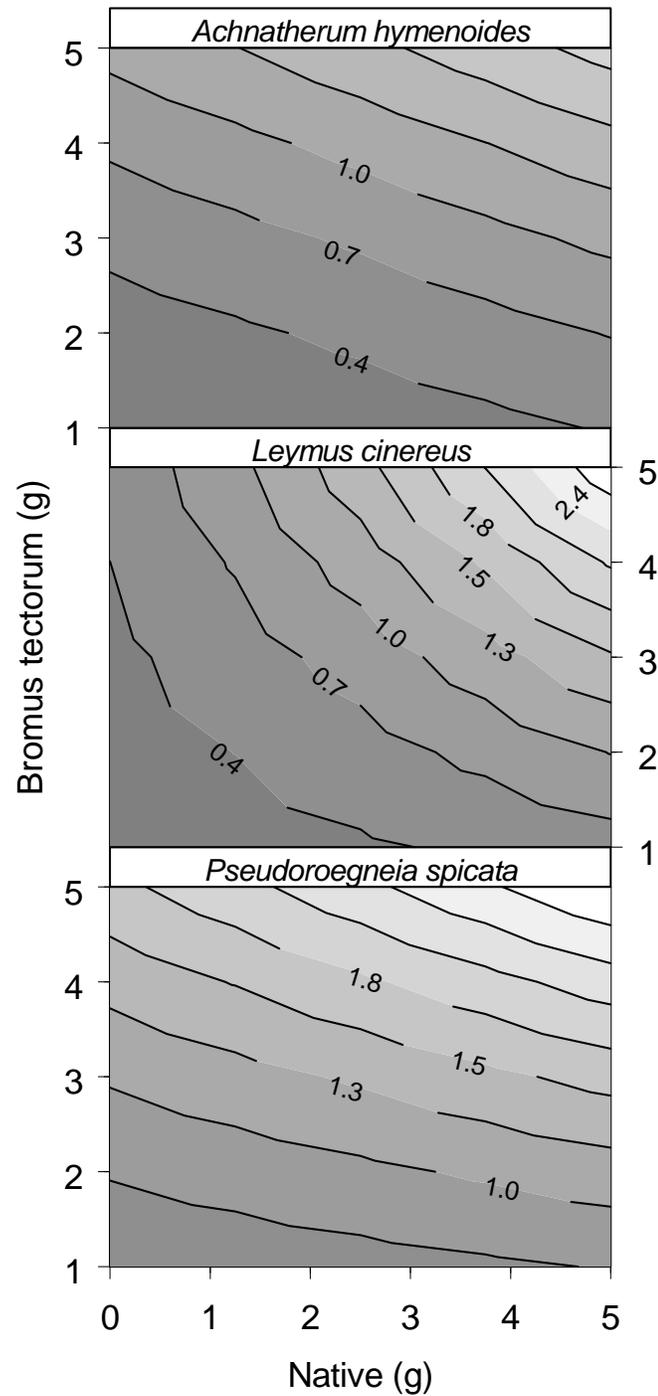


Figure 6.2. *Bromus tectorum* seed removal when present with each of the three native seed species as a function of varying *B. tectorum*/native seed densities. Each individual isocline indicates all density combinations of that two species mixture which yields a constant level of seed harvest for *B. tectorum* (y-axis).

CHAPTER 7

GRANIVORY IN THE CONTEXT OF RESTORATION: ECOLOGICAL
FOUNDATIONS AND MANAGEMENT APPLICATIONS⁷**I. Abstract**

Through selective seed predation and seed dispersal granivorous animals can have important and in some cases keystone effects on plants and their activities are key processes affecting plant population dynamics and community structure in North American deserts. Currently, regions home to these organisms have been altered by the invasion of exotic species that alter physical and biological dynamics (i.e. shortened fire return interval, soil structural/biological changes, shifting inter-specific competitive interactions, etc.) in ways that appear to promote their persistence. As such, the restoration of western semi-arid and arid lands has been applied extensively in hopes of redirecting disturbed and invaded landscapes toward a trajectory deemed desirable for wildlife, agricultural, recreational, and many other values. Given that restoration often involves the application of large quantities of seed, it is important to carefully consider the potential impacts of granivores on the process of restoration. Within an ecological context, we present information and ideas, some revisited and some novel, that are relevant to granivory in the context of ecological restoration. Additionally, we suggest specific ecologically-based strategies that if employed might be useful for minimizing negative impacts to the granivore community of restoration activities and minimize the negative effects these animals on the success of ecological restoration of western semi-

⁷ Coauthored by Steven M. Ostoja and Eugene W. Schupp

arid and arid rangelands of North America. Because this is a topic that has rarely been considered in detail, many of these ideas have only limited support at this point.

II. Introduction

A. HISTORICAL PERSPECTIVE

Because nearly all semi-arid and arid rangelands in western North America are occupied by rodents and seed harvesting ants (Brown et al., 1979, 1986; Longland, 1993), the feeding and associated activities of these animals have remained a concern for management and restoration on western rangelands for the better part of the last century (Smith & Aldous, 1947; Spencer, 1954; Majer, 1989). For the most part, these organisms have been considered as pests or at least as seemingly undesirable components of the range from the perspective of range scientists. These animals have even been labeled “animal weeds” (Osborn & Allan, 1949; Tevis, 1953; Halazon & Herrick, 1956). This negative viewpoint stems from the direct destruction of seeds and seeded plants (*i.e.*, granivory) by many rodents and ants. Not all of these organisms have been considered pests; many species are rare, do not graze plants used by livestock or big game, or do not interfere with seeding projects. For example, insectivorous species such as *Onychomys* spp. (grasshopper mice), unlike most other rodent species, have historically been considered beneficial as consumers of insect pests (Hansen & Vaughan, 1965).

Nonetheless, many species of rodents, especially mice (*Peromyscus* spp., *Perognathus* spp.) and kangaroo rats (*Dipodomys* spp.), can cause extensive seed destruction and can heavily even browse emerging seedlings (Reynolds, 1950, 1958). In fact, Vallentine (1989) suggests that rodents are responsible for more bitterbrush (*Purshia*

tridentata) seeding failures than any other single factor and Clements and Young (1996) reported that *Dipodomys ordii* (Ord's kangaroo rat) was for a major predator of *P. tridentata* seedlings. Similarly, *D. merriami* (Merriam kangaroo rat) found and removed large quantities of sown seeds from depths as great as 1 inch (2.54 cm) and North American deer mice (*P. maniculatus*) were primarily responsible for consuming 98% of grass seed broadcast in one study (Nelson et al., 1970). In addition, harvester ants (*Pogonomyrmex* spp.) have been reported to destroy between 15-20% of the vegetation of some ranges in New Mexico (Race, 1966). Bohart and Knowlton (1953) noted that because harvester ants harvest seeds at great distances from their mounds (< 30m), the likelihood of their impact on perennial grass reseedings and on natural recovery of disturbances was great. It is not surprising, therefore, that actions have frequently been taken to minimize the impacts of rodents and ants.

Early measures to deal with these "animal weeds" were based on lethal population control to halt or prevent further serious damage to range and pasture lands. The principal methods of control included poisoning, trapping, shooting, and exclusion (Storer & Jameson 1965). In the middle part of the last century, Strychnine (LD₅₀ 30) was widely used as an aboveground toxicant in rodenticide baits. Others suggested that treating seeds with a repellent (e.g. coated seed) might help prevent seed losses (Reynolds, 1958). Poisoning was also directed at insects as well; for example, harvester ant control could be accomplished with a carbaryl bait or spray (Vallentine, 1989). The pesticidal bait hydramethylnon was also promoted for use on harvester ants (Vallentine, 1989). Today, these measures of reducing the negative impact of these animals on semi-arid and arid landscapes do not appear to be in widespread use, although it is difficult to

evaluate to what degree practices like these are still used because most are illegal, socially un-acceptable, or environmentally inappropriate. In the following sections we provide an overview of measures that are ecologically based and that can hopefully help minimize the negative impacts of these animals and that should not have system wide deleterious affects.

B. AN ECOLOGICAL CONTEXT AND RATIONALE

As a subdiscipline of ecology, restoration ecology is one that, under ideal conditions, integrates theory and application (Jordon et al., 1987). It has been suggested that restoration success could be improved by considering such efforts within a framework that is process oriented, attempts autogenic repair, and considers landscape interactions (MacMahon, 1987; Whisenant, 1999), all while implementing structural components (e.g., plant materials, etc.) as a means toward system-wide functional repair. Research that explores the effects of animals on plant establishment fits well within this framework of restoration ecology because directing plant community development requires an understanding of how ecological processes and interactions can be integrated with management application (Majer, 1989; Whisenant, 1999; Howe & Brown, 2001). Land managers and ecologists will need technology integrated with appropriate resources, as well as a sound understanding of landscape- and ecosystem-level interactions to find success in semi-arid and arid land (arid land hereafter) ecological restoration (Kelrick and MacMahon, 1985; Jordan et al., 1987; Milton et al., 1994; Archer and Pyke, 1991; MacMahon, 1997).

Perhaps one of the most important yet largely overlooked ecological processes that may affect restoration success is “seed eating” or granivory (Wilson et al., 1990; Howe & Brown, 2001). Granivory may be especially important in arid lands in the western USA (Parmenter et al., 1984; Brown & Heske, 1990) because nowhere else has such a diversity of granivores (Davidson et al., 1980; Kelt et al., 1996). In addition, these granivores can comprise a significant component of the faunal biomass and can exert substantial impacts on ecosystems via selective seed dispersal and seed predation (Davidson, 1977a; Crist & MacMahon, 1992, 1994; Vander Wall, 1992, 1994; Heske et al., 1993, 1994; Polis & Strong, 1996; Kelt & Brown, 1999). We contend that arid-land restoration on western rangelands should include a consideration of the potential positive as well as negative impacts of granivores, and ultimately on their management as well. The goal should be to minimize the negative effects of granivory on reseeding success while acknowledging that in at least some cases the seed dispersal behaviors of granivores might aid in restoration where traditional methods are limited in feasibility.

Restoration of arid lands is at minimum a two-step process. Site or seed bed treatments are often used to reduce the standing biomass and/or seed reserves of undesirable species because seeding directly into weedy stands is not often successful. Site treatments commonly used include mechanical (e.g., disking, harrowing, mowing, or chaining), fire, and/or chemical treatments (i.e., herbicide applications). Once the site is prepared, the application of restoration seeds occurs. Rangeland drills are the most common and successful method of seed application on degraded landscapes (Young & McKenzie, 1982; Vallentine, 1989; Monsen et al., 2004). This process involves seeds dropped into furrows created by disk wheels at a specified depth which is dependent upon

seeding mix, edaphic properties, regional precipitation, and other factors, all of which interrelate to biological and physical features specific to each site. Alternatively, aerially broadcasting seed and then working the seeds into the soil with a harrow or chain are also widely used. At remote sites, sites in wilderness areas with restrictions, or sites with challenging topography seeds may be aerially broadcast without working them into the soil mechanically.

The impact of ant and rodent granivores can vary depending on the seeding method (i.e. drill or surface broadcast) and on the granivores in question. Because ants cannot locate and dig for buried seeds (Davidson, 1977b; MacMahon et al., 2000), they should have little impact on the success of drilled seed, if the drilling is properly done. In contrast, rodents can detect seeds buried in the soil (Vander Wall, 1990; 2003, Vander Wall et al., 2001) can detect buried seeds by smell and searching and thus potentially can remove large amounts of drilled seeds. The selective consumption of restoration seeds can have profound impacts on immediate restoration success and, by increasing the resource base, on granivore communities. Deer mice (*Peromyscus maniculatus*), a ubiquitous rodent species in North America, can consume an amount of seed equal to 30%-40% of their body weight, and remove seed equal to 174% of their body weight when preferred seed types are available (Everett et al., 1978). Such an event post seeding would result in significant seed loss and consequently severely impact restoration success.

To manage the granivore-seed interaction in ways that maximize restoration success, it is important to consider how site treatments, methods of seeding, and resource supplementation via seeding might both adversely and positively affect granivore

communities. Within an ecological context, we present information to consider these animals when they are present and a potential concern within the general framework of restoration in western arid-lands predominantly as granivores but graminivory will also be treated but to a lesser extent. In so doing, we extend specific ecologically-based strategies that if employed could both minimize negative impacts to granivore communities and minimize the negative effects these animals may have on the process of ecological restoration.

III. Considerations of Granivory and Restoration – Ecological Context

A. SEED ESCAPE MECHANISMS

A theoretical foundation of seed escape was given originally by Janzen (1971) and Connell (1971) in their respective landmark papers (Janzen-Connell hereafter). Simply put, this model helps explain a possible evolved pathway allowing seeds to persist and ultimately survive in the face of seed predators (Clark & Clark, 1984). As the term implies, the seed is “escaping” peril. Applications of seed escape in a restoration setting were to our knowledge first offered by Archer and Pyke (1991) and are herein extended with specific examples for direct application. Elements of the original Janzen-Connell idea can be understood in temporal and spatial seed escape scenarios, each of which then establishes the template for the appropriate management options. Therefore, specific applications of variations of these ideas are offered that, if successful, can minimize seed losses to predation and/or secondary dispersal when such are un-desirable. In addition to these, we consider predator satiation as a form of seed escape.

B. SPATIAL SEED ESCAPE

In the context of Janzen-Connell, seed escape in space occurs when the seed is dispersed away from the parent plants. Such dispersal is thought to reduce seed mortality by reducing predation by distance-dependent predators concentrating their foraging near the seed sources and by density-dependent predators concentrating their foraging in higher density seed patches, which are generally assumed to be closer to parents. Note, however, that even very far from parents, high densities of seeds can result in very high levels of mortality (Schupp et al., 2002). Similarly, escape in space can occur if seeds are dispersed into habitats that are less suitable to seed predators (Schupp, 1993), such as when the natural matrix vegetation provides required cover for granivores while the more exposed restoration site does not. Based on these ideas, then, more seeds should escape harvesting by rodents when: 1) the seeded area is larger and thus has more area far from edges, 2) the seeded area has reduced edge to interior ratio (e.g., round rather than elongated) and thus has reduced access across edges and has more of the core far from edges, 3) seed density is much less in the restoration site than in the surrounding natural matrix, and 4) the seeded restoration site is much less suitable for the seed predators than is the natural matrix vegetation. Note that these arguments depend on the natural matrix vegetation rather than the restoration site being the major source of granivores, which in at least some cases is true (Chapter 4, Longland, 1993).

Given this, there are potential applications of the concepts of seed escape in space to restoration reseedings, though they have been little explored. The first two points relate to project design. If possible, restoration applied to larger and squarer sites might be more desirable from the perspective of reducing seed harvesting. However, in many if not most

cases the size and shape of the restoration site is not under the control of the restorationist but is determined by the disturbance that created the need for restoration. Point three is a potential problem in that seeding increases the density of seeds in the restoration site, in many cases probably to levels higher than in the surrounding natural matrix. Seeding at greatly reduced densities might in some cases reduce losses to granivores (but see section D below), but would likely fail to establish sufficiently densely to stabilize the site and exclude weeds. However, it might be feasible to aerial seed a buffer zone of surrounding natural matrix with sacrifice seeds (see below) to reduce the foraging of granivores out into the restoration site. Point four might be most important to consider in the context of planning the restoration project; for example, if you know that the granivore community is greatly reduced in the restoration site relative to the natural matrix then seed loss will be expected to be less of a problem and the strategies presented above will be more likely to succeed than if the granivore community is only slightly reduced. However, there might be management strategies for reducing the suitability of the restoration site to granivores even further, such as installing owl perches in the restoration site, especially near the perimeter, or promoting predators in some other manner (see below).

C. TEMPORAL SEED ESCAPE

To apply ideas about seed escape in time to restoration we need to distinguish long-term (e.g. multiple years) versus short-term escape mechanisms (e.g. multiple occurrences within a single year). A long-term seed escape framework would suggest that seeding be done in years of low seed predator population sizes. Conceptually, this technique could be used by applying seeds when seed predator populations were

declining or naturally low, such as seeding following a sustained drought or other stochastic event that negatively impacts the granivore community. This technique dictates that the restorationist has knowledge of the granivore community and how natural disturbances (e.g. fire, drought) might negatively affect the animal population and thus provide a window for safer seeding. An obvious concern is that conditions adversely affecting the granivore population(s) can also be unsuitable for the success of sown seeds (e.g. drought periods). Conversely, increased rainfall suitable for re-seeding is reported to positively affect native rodent and ant communities (Brown and Ernest 2002). Precipitation in desert communities is the primary factor determining plant productivity, hence seed production and ultimately granivore population growth; however, relationships are complex and vary among habitat types (Ernest et al., 2000; Brown & Ernest, 2002). Nonetheless, increased rainfall following a drought might provide a narrow window for seeding when precipitation is suitable for plant establishment and granivore communities have not yet fully recovered.

A common disturbance within the Great Basin desert and other arid systems where *Bromus tectorum* (cheatgrass) and other non-native annual grasses dominate are recurrent fires (Pellant, 1989; Brooks et al., 2004). However, we know very little about how rodent and/or ant communities respond to such disturbance events. There is some indication of increased activity of some species of *Dipodomys* rodents on recently burned sites in western Nevada, USA (S. Ostoja unpubl.), at least in the short-term. Whether such shifts in rodent community assemblages persist long-term are not known, though. In at least one study, there was little difference in rodent populations between burned and unburned plots, although the proportion of bipedal to quadrupedal heteromyids did differ

(Fitzgerald et al., 2001). If bipedal and quadrupedal heteromyids interact with seeds differently (e.g. proportion cached as opposed to consumed immediately) such community structure changes could be important for seeding success. Understanding the responses of the granivores to fire or similar disturbances could help restorationists better predict and plan for the types of seed-granivore interactions that will occur with reseeded.

A short-term seed escape framework might be based on rodent foraging activity as a function of moon phase and seasonality (Price et al., 1984; Lockard & Owings, 1974). Rodent activity (i.e. foraging) is frequently reduced directly before and during full moon periods (Kaufman & Kaufman, 1982; Clarke, 1983). During these “brighter” periods of the lunar cycle rodents themselves are more prone to predation and therefore reduce their susceptibility by minimizing the amount of time spent foraging (Bowers, 1988). Seeding just before full moon could minimize at least initial seed losses and may be most effective if done in concert with another strategy (e.g. sacrifice seed application – discussed below). Such an approach might also be especially useful with aerial seeding since even a relatively short window of reduced granivore activity should allow at least a few more seeds to move into the soil by physical means (Chambers, 2000) and thus be less obvious to granivores.

When seeding a site that has a high proportion of rodents in the family Heteromyidae and/or Sciuridae, temporal considerations become more complicated. These animals place seeds both in “scatter-hoards” or “caches,” small groups of shallowly buried seeds in scattered caches throughout the home range, and in “larder-hoards,” one to a few hoards of many seeds generally at least relatively deep in the

burrow system (Vander Wall, 1990). It is scatter hoards that are most likely to survive to produce plant recruitment while larder hoards are generally equivalent to death.

Heteromyids appear to spend more time scatter-hoarding in early and mid season, then shift to larder-hoarding later in the season in preparation for winter (Murray, 2003). In a laboratory setting *Dipodomys merriami* (Merriam's kangaroo rat) scatter-hoarded during trials conducted at 25° C but nearly exclusively larder-hoarded in a 5° C environment (Murray, 2003). Many other seed caching rodents have the same behavior (Vander Wall, 1990).

Thus, harvested seeds from fall seedings are likely not to be cached, but rather placed in a larder where they are unlikely to germinate or at least establish. In contrast, harvested seeds from seedings earlier in the season could be re-seeded by the rodent via seed caching behavior. There are numerous reports of the successful germination and establishment that occur when caches are not recovered by the cacher or pilfered by another animal (Longland et al., 2001). In a large-scale restoration effort in western Nevada, USA, seeded species harvested and subsequently cached by either *Dipodomys* spp. or *Perognathus parvus* successfully established and ultimately contributed to restoration success (S. Ostoja, E. Schupp, and W. Longland, unpubl.). However, for at least two native restoration seed species (*Achnatherum hymenoides* and *Pseudoroegneria spicata*) experimentally simulated drilled seeds were significantly more likely to germinate and establish seedlings than were the same number of seeds that were seeded (i.e. cached) by a single *D. ordii* (Ord's kangaroo rat) individual in field conditions at an experimental range in Utah, USA (S. Ostoja & E. Schupp, unpubl.). This preliminary result suggests that at least for the species involved, the harvesting and subsequent

caching of drilled seed could have an overall negative effect on the success of some reseeded undertakings, even though establishment results. However, the effect would not be as negative as it is when the rodents involved are more pure seed predators.

Like rodents, seed eating ants change their foraging behavior seasonally (MacMahon et al., 2000). In many regions of the west harvester ant (*Pogonomyrmex* and related genera) foraging decreases in autumn due to cooler temperatures. It is reported that in the genus *Pogonomyrmex*, warm desert species forage between March and November whereas higher elevation species forage from April to October (MacMahon et al., 2000). Therefore, in contrast to expectations for rodents, fall seedings should suffer less seed predation by ants than spring or summer seedings. Since mounds of *Pogonomyrmex* spp. can reach densities of 10-40/hectare in disturbed habitats and can cover >10% of the land area (Mull & MacMahon, 1996, 1997; MacMahon et al., 2000), minimizing their impact can be extremely important. However, because of ant foraging behavior these considerations are really only relevant for broadcast seeding.

Lastly, some granivore species, such as the rodents *Dipodomys* spp. and *Tamias* spp., can be active all year and therefore may influence restoration more significantly, or at least differently, than species that are only active seasonally, such as *Perognathus* spp. rodents and seed harvesting ants (Hansen, 1978; Price & Jenkins, 1986; Polis, 1991; Mares, 1993; Longland, 1994). Differences among granivore species in overall seed harvesting behavior and in the fate of harvested seeds suggests that an understanding of the species composition and knowledge of their behavior is critical for predicting the impacts of granivores on restoration success (Janzen, 1969; Mares & Williams, 1977; Lawhon & Hafner, 1981; Kelrick et al., 1986).

D. MAST SEEDING AND PREDATOR SATIATION

Mast seeding is an evolved strategy of many plant species which effectively reduces seed predation via the production of an overabundance of seeds, generally on a supra-annual basis (Kelly & Sork, 2002). This can operate as years of synchronized mast fruit production at the population level or even synchronized fruit production by multiple species in the community (Liebhold et al., 2004). In either case, years of abundant seed production can satiate the granivore community and result in high seed survival (Li & Zhang, 2003). Additionally, in years of abundant seed production some rodents alter their foraging behavior and cache a higher percent of the seeds they handle (Li & Zhang, 2003), potentially switching from being nearly exclusively seed predators in years with few seeds to reasonably effective seed dispersers in years of abundant seeds.

From a management perspective, if the consumer population sizes are known the amount of seed likely to be lost can be calculated from an energetic or perhaps some other approach. At a minimum, this would allow land managers to estimate how much seed to apply to have sufficient numbers surviving to establishment without having so many seeds that intense competition occurs during seedling establishment or that the granivore populations build excessively high. Moreover, this model of predator satiation can also be used when the land manager provides another type of seed in addition to the target seed (a form of sacrifice seeding – see below). As more is learned about the interactions between granivores and seeds it might be possible to modify seeding strategies in order to also maximize caching behavior of appropriate rodent species.

IV. Granivory and Restoration Considerations – Management Application

A. SEED DISCOVERY CUES

The manners in which granivores assess their environment to effectively extract resources from it are critically important for understanding the interaction between granivory and restoration as well as for devising strategies that minimize the impact of granivory (Davidson, 1993). This section considers mechanisms granivores use to find seeds, which forms the ecological basis for outlining concepts and models to consider with the goal of management to reduce the potential negative impact of granivory and associated activities of these organisms.

Seed harvesting ants are single-load, central place foragers who selectively remove seeds from many plant species (Crist & MacMahon, 1991a, 1991b, 1992; MacMahon et al., 2000). Seed selectivity is reported to depend upon many attributes of the seeds, including among others abundance, nutritional quality, morphology and size (Crist & MacMahon 1991a, 1992). Moreover, seeds infected with certain pathogens (i.e. endophytic and/or saprophytic fungi) have been reported to be selectively rejected by ant workers (Knoch et al., 1993). For example, endophyte-infected *Festuca arundinacea* (fescue) seeds were harvested less frequently than non-infected seeds by two populations of *Pogonomyrmex rugosus*, but not by a population of *P. occidentalis*; moreover, infected seeds that were harvested were mostly placed into refuse piles (Knoch et al., 1993).

Because harvester ants are central place foragers they are thought to deplete seed resources more near their central nest and along trails radiating from the nest (Hobbs, 1985; Mull & MacMahon, 1996). Moreover, ants do not dig for seed buried in the soil

and thus are only able to remove seeds that are available on the soil surface and that they have physically contacted (Mull and MacMahon, 1997; MacMahon et al., 2000). Once an ant comes in contact with a seed it chemically evaluates the seed and determines if it is viable and/or deemed worthy of transport back to the colony (Hölldobler & Wilson, 1990; Mayer et al., 2005). It is thought that only some small fraction of seed collected and returned to the nest by foragers is successfully dispersed (MacMahon et al., 2000). Consequently, then, the bulk of collected seed is thought to be effectively removed from the seed pool because it is consumed or buried deep in underground chambers (Hölldobler & Wilson, 1990).

In contrast to ants, rodents are able to locate seeds using olfaction and tactile cues as well as by random searching. In addition, many rodent species can also differentiate between edible and non-edible seeds using olfaction and tactical cues, which may allow for the preferential selection of viable seeds (Vander Wall, 1993, 2003). Olfaction appears to have an especially important role in the ability of rodents to locate and acquire seed resources, and a keen sense of olfaction might be an evolutionary adaptation of organisms living in arid environments (Vander Wall et al., 2003). Because substrate moisture is known to greatly influence rodent ability to detect buried seeds by olfaction, there should be a greater selective pressure placed on olfactory abilities of desert rodents living in xeric environments (see Vander Wall, 1993; Vander Wall et al., 2003). Moreover, nocturnal rodents can rely less on visual cues for detecting seeds than can diurnal rodents and thus should be expected to have an especially keen sense of smell (Vander Wall et al., 2003).

The odors coming from seeds are important in the pilfering by rodents of caches made by other rodents as well as by birds (Vander Wall, 1990), and moist soil increases the ability of most rodents to locate buried seeds (Vander Wall, 1993, 1998; Vander Wall et al., 2003). Research suggests that organic molecules are released from seeds as they imbibe water in the moist soil (Duke et al., 1983; Simon & Mills, 1983), and rodents use these odors as cues that resources are buried below. As one example, Vander Wall (1995) reported that *Peromyscus maniculatus* (deer mouse), *Perognathus parvus* (Great Basin pocket mouse), and *Tamias amoenus* (yellow pine chipmunk,) found nearly all *Purshia tridentata* (antelope bitterbrush), *Oryzopsis (Achnatherum) hymenoides* (Indian ricegrass), and *Pinus contorta* (lodgepole pine) seeds (>99%) buried in a moist substrate, but less than 15% of the seeds buried in a dry substrate. However, there is a large degree of interspecific variability when it comes to the rodent's ability to find buried resources in general and in the effect of moisture on this ability (see Vander Wall et al., 2003). For example, *Perognathus parvus* (Great Basin pocket mouse) in the study above found more than 80% of the seeds buried in the dry substrate, which may be suggestive of an enhanced olfactory ability compared to the other species (Vander Wall, 1995).

Overall, these ideas of seed discovery may have important management implications when re-seeding. Increasingly, seeds coated with beneficial fungi are used in restoration. Although no research exists comparing coated versus non-coated seed in terms of seed selectivity, one would expect ants to reject these types of restoration seeds (Knoch et al., 1993; Crist & Friese, 1993). Rodents, however, might differentially select these fungus coated seeds (Rebar & Reichman, 1983; Reichman & Rebar, 1985; Reichman et al., 1986). For example, it has been shown that *D. spectabilis* preferentially

selected slightly moldy seeds to non moldy and highly moldy seeds (Reichman & Rebar 1985).

Considering the keen sense of rodent olfaction, the handling of seeds during harvesting and preparation for seeding can increase detection and harvesting by rodents (Wenny, 2002). Thus, reducing direct human skin contact with seeds might reduce seed harvesting. It might also be possible to treat seeds in ways that would mask odors that rodents use to locate buried seeds. The use of predator cues such as fox or coyote urine scent might not only mask the odor of seeds, but might also discourage rodent foraging and ultimately reduce seed losses (see below). However, there is little evidence that natural predator cues alone deter rodent activity (Brinkerhoff et al., 2005; Orrock & Danielson, 2004; Orrock et al., 2004). Alternatively, activated carbon has been shown to sequester organic compounds in soil environments (Kulmatiski & Beard, 2006), and thus might reduce the amount of volatile organic seed compounds reaching the surface and diminish rodents' ability to use olfaction as means of seed detection and removal. Research addressing these interactions with desert granivore species, as well as other ways to mask seed odors would be valuable.

B. SACRIFICE SEEDING

It might be possible to improve the success of restoration by discouraging recovery of seeds that have been drill or broadcast seeded by also adding more desirable seeds. This concept is referred to as sacrifice seeding, diversionary food, decoy seeding, and dummy seeding (Archer & Pyke, 1991; Longland & Bateman, 1998; Sullivan, 1979; Sullivan & Sullivan, 1982, 2004). Certain commercial seeds such as millet are highly

preferred by desert granivores (Price, 1983; Longland, 1994; Chapter, 5). For rodents this concept would rely on them caching both seeds, however selectively consuming the less costly decoy seed as the sacrifice seed to reduce predation of less preferred target seeds. Therefore, it should be possible to reduce rodent and ant predation on seeded restoration species by supplying a sufficient amount of a preferred commercial seed as a sacrifice that would be preferentially consumed, allowing restoration seeds to escape predation (Longland & Bateman, 1998). For example, Longland and Bateman (1998) found that *Panicum miliaceum* was highly preferred to *Atriplex canescens*, and therefore suggested its potential use as a decoy seed when saltbush (*Atriplex* spp.) is seeded in restoration.

The application of this model is founded on the ecological idea of indirect effects, in this case mediated by consumers (Atsatt & O'Dowd, 1976; Holt, 1977; Holt & Kotler, 1987; Veech 2000, 2001; Theimer, 2005; Miller et al., 2007). Because granivores are selective in seed choice, they can induce indirect interactions among the available seeds in two major ways. First, seed predators can induce apparent competition (Veech, 2000, 2001; Caccia et al., 2006), also referred to as associational susceptibility (Chapter 1). This type of indirect interaction occurs when an increase in the quantity of the seed of one species leads to a decrease in the abundance (i.e. increased seed harvest) of another species. Second, seed predators can also induce apparent mutualism (Calloway et al., 2005), also referred to as associational resistance (Wahl & Hay, 1995; Chapter 1). This occurs when an increase in the quantity of seed of one species leads to an increase in the abundance (i.e. reduced seed harvest) of another species (Holt, 1977; Miller et al., 2007).

Sacrifice seeding represents this second type of indirect interaction, where the addition of the sacrifice seed leads to increased seed survival of the restoration species.

Sacrifice seeding might simply reduce initial harvesting of restoration seeds by ant and rodent granivores; that is, the granivores would selectively harvest the sacrifice seeds leaving more of the restorations seeds untouched. Alternatively, sacrifice seeding could operate in more complex ways. For example, it could be used to minimize recovery and consumption of restoration seed caches that had already been made by rodents, or to increase the scatter-hoarding rate of restoration seeds and reduce their subsequent relocation and removal. The timing of application of both restoration seed species and sacrifice seeds should be considered in the context of the type of restoration effort and the nature and diversity of the granivores. Longland and Bateman (1998) suggested that the ideal time to present sacrifice seeds would be sometime after the restoration seeding has occurred because rodents would then preferentially select and consume the decoy, becoming temporally satiated and thus consume fewer restoration seed caches that had already been made. In contrast, Sullivan and Sullivan (1982) simultaneously applied sunflower seeds as sacrifice to reduce predation on pine seeds. They applied a ratio of two sunflower seeds to one pine seed which resulted in 50-82% survival of pine seed after 3 weeks and 42-72% after 6 weeks, compared with 12-15% and 8-10% survival, respectively, in the absence of sunflower (also see Sullivan, 1979).

Seed material selection for sacrifice seeds should ideally consider a metabolic understanding of seed selectivity (i.e. interactions between macronutrients and metabolically recovered water, see Chapter 1; Frank, 1988), as well as the means of seed discovery and/or rejection (e.g. seeds infected with endophytic fungi, etc.). In addition, a

careful evaluation of selectivity in terms of seed mixtures is important. Limited research suggests varying seed mixtures (combinations of species) can alter removal rates and/or types of seed removed, which is a very important consideration in reseeded (Chapter 6), especially when considering sacrifice seeding – a “sacrifice seed” that led to increased consumption of desirable seeds (i.e. associational mutualism) would be a failure.

C. SEARCH IMAGE DISTRACTION

Rodents and ants are thought to develop search images for particularly abundant seeds in the environment (Brown et al., 1979; Hölldobler & Wilson, 1990; MacMahon et al., 2000). The use of color dyed seeds might reduce seed predator removal rates due to the lack of a search image for uniquely colored seeds. However, we do not have any evidence that suggests the application of this technique would work. If it works at all, this is most likely to help with rodent seed predation because ants are not visual foragers. In addition, rodents might quickly learn to identify new seed colors as suitable food items. Lastly, research using fluorescent pigments to track seeds in the field, report that the powder did not deter heteromyid rodents from using experimental seeds (Longland & Clements, 1995)

D. TOP – DOWN MANIPULATION

It has been suggested (Hall et al., 1981; MacMahon, 1987; Archer & Pyke, 1991) that providing artificial perches or nesting structures for predatory birds or approach refugia for mammalian predators might help reduce seed predator populations or at least alter their behavior to the extent that they harvest fewer seeds. Several species of birds of prey

used artificial perches in a northern California alfalfa fields, including *Tyto alba* (Barn owls), *Buteo jamaicensis* (red-tailed hawks), and *Falco sparverius* (American kestrel) (Hall et al., 1981). When the perches were set up in a wildlife reserve in the Central Valley of northern California additional species used the perches for hunting and feeding, including *Asio flammens* (short-eared owls) and *Speotyto cunicularia* (burrowing owls). Artificial perches around the perimeter of irrigated soybean crops increased the number of diurnal raptors visiting and hunting over these crops and this increase reduced both the rate of mouse population increase and the maximum mouse population density (Kay et al., 1994). However, there is no data to date that we are aware of on whether this technique significantly reduces rodent seed and/or seedling predation, thus allowing for increased restoration success.

E. RODENT MEDIATED AUTOGENIC REPAIR

It is possible that in certain circumstances it could be beneficial to augment the “attractiveness” of the repair site (e.g. providing artificial nest boxes and resource supplementation) to animals that disperse propagules of desirable species. When dealing with large areas or when it is not either physically or economically prudent to conduct extensive reseeded activities, other mechanisms to “reseed” an area could prove promising. One such mechanism would rely on the scatter-hoarding behaviors of rodents to potentially aid in seed dispersal and seedling establishment and to ultimately increase plant diversity in areas where diversity was reduced due to disturbance (e.g. fires, overgrazing) and subsequent exotic invasions (e.g. cheatgrass, knapweed) (West, 1968; McAdoo et al., 1983; Archer & Pyke, 1991; Vander Wall, 1992; McMurry et al., 1997).

Such an approach might be especially useful in situations where the desire is to augment diversity in the understory of a degraded shrubland. In this framework, recruitment could be enhanced by rodent seed caching if the probability of seed germination and seedling establishment were increased relative to seeds that were not dispersed using such techniques (Archer & Pyke, 1991; Longland et al., 2001). In line with this idea, Longland et al. (2001) reported that seedling establishment for a native perennial grass was >90% more likely to occur when the seeds were previously handled by a single granivorous rodent than if those seeds were handled by either birds or ants or went unhandled. On the other hand, it has been suggested that seed caching by rodents is not likely to enhance opportunities for colonization and may not move seeds far enough from the primary seed source to escape distance responsive seed predators (Hulme, 1994; Hulme & Borelli, 1999). In addition burial of several seeds within a cache can increase intra-specific competition among seedling and attract density-dependent granivores. Nonetheless, the potential of rodent caching for augmenting species abundance and diversity in shrub understories is sufficient to warrant further research, especially into techniques designed to increase caching rates and reduce cache recovery rates.

V. Synthesis

In the better part of five decades, we have come from viewing granivores as nothing more than rangeland pests to seeing them more complexly as integral components of rangelands that have important effects on many landscapes throughout the arid west, some negative and some positive. A more thorough understanding of granivore effects on desirable restoration species as well as on undesirable weeds will

greatly aid in the ecological restoration of arid rangelands. Efforts to realize the greatest level of success in restoration while reducing negative impacts to the granivore communities should initially consider detailed investigation of the population and community dynamics of the granivorous animals specific to the site of restoration. With that base line information, one can better assess species-specific seed preferences, rates of direct consumption, rates of removal, dispersal distances, cache sizes, and seed caching rates by these granivores animals. Moreover, research that explores ecologically-based strategies to reduce the negative impacts of granivores on restoration efforts is strongly encouraged. Careful consideration of both the effect of restoration activities on granivores as well as the effect of granivores on the success of restoration will ultimately allow resource managers and ecologists to make more informed choices and improve the success of restoration in western landscapes.

VI. Concluding Remarks

The invasion of *B. tectorum* initiated an extraordinary amount of research on both the impact of *B. tectorum* on invaded communities and on the restoration of cheatgrass-dominated landscapes. At the current rate of invasion and subsequent conversion of many community types by cheatgrass we may be witnesses to one of the greatest ecologically and economically significant invasions in the United States to date. Needless to say this situation is dire, and it is complicated further by changing fire regimes that allow for the sustained persistence and the further spread of cheatgrass. Despite extensive research on cheatgrass, little attention has focused on the potentially key role of granivores in the restoration of these systems.

Our research is directly related to the dynamic (cheatgrass invasion/restoration) outlined above in two important and inter-related ways. First, because highly degraded landscapes are the focus of ecological restoration activities where seed application is a common strategy, it is important to assess the major granivore communities in intact sagebrush communities and in nearby communities that had undergone conversion from sagebrush to cheatgrass domination. Second, it was critical to begin developing an understanding of patterns of seed harvest by these granivores using a variety of experimental frameworks. These sets of studies are not only of basic ecological interests, but are also important for developing management strategies for restoration of these degraded lands.

Research focused on the importance of ant and rodent granivores in arid- and semi-arid systems dates back to before the middle of the last century. However, the impact on ant and rodent communities of cheatgrass invasion and subsequent conversion of these systems is not well studied. Our evaluation of rodent and ant communities showed interesting and very different responses of these two major groups of granivores to cheatgrass conversion. In chapter 2, we reported on significant increases in total ant abundances in cheatgrass communities compared to the sagebrush-dominated communities. While the common groups showed increased numbers, however, the uncommon species/functional groups appeared to be mostly negatively impacted by cheatgrass. In contrast, as has been shown in other similar systems, rodents are overwhelmingly negatively impacted by the conversion to cheatgrass domination (Chapter 4). Only 5 of 9 rodent species captured in sagebrush site were found to occur in the cheatgrass sites, with great reductions in abundances.

The second focus of research was on seed removal by these groups with special attention to the possible occurrence of associational effects among seed mixtures as mediated by these seed removers. We found that ant seed removal to be complex and to vary according to the scale of the patch; thus, ant seed removal was highly context-dependent (Chapter 3). Removal of seeds by ants was simultaneously dependent on the background vegetation (large-scale among patch), foraging distance from the nest mound (small-scale among patch), and the seed mixture context (within patch). In particular, we were able to show the occurrence of associational effects, specifically associational resistance of native seeds when present with cheatgrass seeds in the mixture (within-patch). The results from the first rodent seed removal experiment (Chapter 5) used a novel statistical technique in the ecological sciences to show that rodents have marked preferences for some seeds over others and that more seeds in general were removed in sagebrush compared to cheatgrass-dominated sites. In chapter 6, we demonstrated that the amount of total seed initially present and the particular seed mixture both contributed to varying patterns of seed removal. In that chapter we were able to show the occurrence of associational susceptibility of *B. tectorum* seeds in the presence of native seeds in mixture. Although the reciprocal effect may occur, we did not find strong evidence in support of it.

Lastly, the general review provided in chapter 1 highlights factors that contribute to seed removal, and the current chapter (Chapter 7) outlined ecologically-based techniques that could minimize the negative consequences of granivores in the process of ecological restoration. These reviews provide the framework for the current research as well as provide valuable syntheses to guide future research.

VII. Literature Cited

- Archer, S. & D. A. Pyke.** 1991. Plant-animal interactions affecting plant establishment and persistence on revegetated rangeland. *J. Range Manage.* 44: 558-565.
- Atsatt, P. R. & D. J. O' Dowd.** 1976. Plant defense guilds. *Science* 193: 24-29.
- Bohart, G. E. & G. F. Knowlton.** 1953. Notes of food habits of the western harvester ant. *Proc. Entomology Soc.* 53: 151-153.
- Bowers, M. A.** 1988. Seed removal experiments on desert rodents: the microhabitat by moonlight effect. *J. Mammal.* 69: 201-204.
- Brinkerhoff, R. J., N. M. Haddad & J. L. Orrock.** 2005. Corridors and olfactory predator cues affect small mammal behavior. *Journal of Mammalogy* 86: 662-669.
- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant & D. A. Pyke.** 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54: 677-688.
- Brown, J. H., D. W. Davidson, J. C. Munger & R. S. Inouye.** 1986. Experimental community ecology: The desert granivore system. Pp 41-61 *in* Diamond J. Case T.J. (eds.), *Community Ecology*. Harper and Row, New York, USA.
- Brown, J. H., D. W. Davidson & O. J. Reichman.** 1979. An experimental study of competition between seed-eating desert rodents and ants. *Am. Zoo.* 19: 1129-1143.
- Brown, J. H., O. J. Reichman & D. W. Davidson.** 1979. Granivory in desert ecosystems. *Ann. Rev. Ecol. Syst.* 10: 201-227.
- Brown, J. H., & M. K. Ernest.** 2002. Rain and rodents: Complex dynamics of desert consumers. *BioScience* 53: 979-997.
- Brown, J. H. & E. J. Heske.** 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250: 1705-1707.
- Caccia, F. D., E. J. Chaneton & T. Kitzberger.** 2006. Trophic and non-trophic pathways mediate apparent competition through post-dispersal seed predation in a Patagonian mixed forest. *Oikos* 113: 469-480.

- Callaway, R. M., D. Kikodze, M. Chiboshvili & L. Khetsuriani.** 2005. Unpalatable plants protect neighbors from grazing and increase plant community diversity. *Ecology* 86: 1856-1862.
- Chambers, J. C.** 2000. Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: Implications for restoration. *Ecol. Appl.* 10: 1400-1413.
- Clark, D. A. & D. B. Clark.** 1984. Spacing dynamics of a tropical rain forest tree: Evaluation of the Jansen-Connell model. *Am. Nat.* 124: 769-788.
- Clarke, J. A.** 1983. Moonlight's influence on predator prey interactions between short-eared owls (*Asio flammeus*) and deer mice (*Peromyscus maniculatus*). *Beh. Ecol. Sociobio.* 13: 205-209.
- Clements, C. D., & J. A. Young.** 1996. Influence of rodent predation on antelope bitterbrush seedlings. *J. Range Manage.* 49: 31-34.
- Connell, J. H.** 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pp. 298-312. *in* den Boer, P. J. and Gradwell, G. R. (eds.), *Dynamics of populations*. Centre for Agriculture Publishing and Documentation, Wageningen.
- Crist, T. O. & J. A. Macmahon.** 1991a. Foraging patterns of *Pogonomyrmex occidentalis* (Hymenoptera, Formicidae) in a shrub-steppe ecosystem - the roles of temperature, trunk trails, and seed resources. *Environ. Entomol.* 20: 265-275.
- Crist, T. O. & J. A. Macmahon.** 1991b. Individual foraging components of harvester ants - Movement patterns and seed patch fidelity. *Insectes Soc.* 38: 379-396.
- Crist, T. O. & J. A. MacMahon.** 1992. Harvester ant foraging and shrub-steppe seeds: Interactions of seed resources and seed use. *Ecology* 73: 1768-1779.
- Crist, T. O. & C. F. Friese.** 1993. The impact of fungi on soil seeds: Implications for plants and granivores in a semiarid shrub-steppe. *Ecology* 74: 2231-2239.
- Crist, T. O. & J. A. MacMahon.** 1994. Harvester ant foraging and shrub-steppe seeds: Interactions of seed resources and seed use. *Ecology* 73: 1768-1779.
- Davidson, D. W.** 1977a. Species diversity and community organization in desert seed-eating ants. *Ecology* 58: 711-724.
- Davidson, D. W.** 1977b. Foraging ecology and community organization in desert seed-eating ants. *Ecology* 58: 725-737.
- Davidson, D. W.** 1993. The effects of herbivory and granivory on terrestrial plant succession. *Oikos* 68: 23-35.

- Davidson, D. W., J. H. Brown & R. S. Inouye.** 1980. Competition and the structure of granivore communities. *Bioscience* 30: 233-238.
- Duke, S. H., G. Kakefuda & T. M. Harvey.** 1983. Differential leakage of intracellular substances from imbibing soybean seeds. *Plant Physiol.* 72: 919-924.
- Ernest, S. K. M., J. H. Brown & R. R. Parmenter.** 2000. Rodents, plants and precipitation: Spatial and temporal dynamics of consumers and resources. *Oikos* 88: 470-482.
- Everett, R. L., R. O. Meeuwig & R. Stevens.** 1978. Deer mouse preferences for seed of commonly planted species, indigenous weed seed and sacrifice foods. *J. Range Manage.* 31:70-73.
- Fitzgerald, C. S., P. R. Krausman & A. L. Morrison.** 2001. Short-term impacts of prescribed fire on a rodent community in desert grasslands. *Southwest. Nat.* 46: 332-337.
- Frank, C. L.** 1988. Diet selection by a heteromyid rodent: Role of net metabolic water production. *Ecology* 69: 1943-1951.
- Halazon, G. & E. H. Herrick.** 1956. Controlling damage caused by animals. *Kansas Agricultural Experiment Station Circulation* 328. 25 pages.
- Hall, T. R., W. E. Howard, & R. E. Marsh.** 1981. Raptor use of article perches. *Wild. Soc. Bull.* 9: 296-298.
- Hansen, R. M. & T. A. Vaughan.** 1965. Plains pocket gopher studies. *Colorado Agricultural Experiment Station Project Report* Number 164. 2 pages.
- Hansen, S. R.** 1978. Resource utilization and coexistence of three species of *Pogonomyrmex* ants in an upper Sonoran grassland community. *Oecologia* 35: 109-117.
- Heske, E. J., J. H. Brown & Q. Guo.** 1993. Effects of kangaroo rat exclusion on vegetation structure and plant species diversity in the Chihuahuan Desert. *Oecologia* 95: 520-524.
- Heske, E. J., J. H. Brown & S. Mistry.** 1994. Long-term experimental study of a Chihuahuan Desert rodent community: 13 years of competition. *Ecology* 75: 438-445.
- Hobbs, R. J.** 1985. Harvester ant foraging and plant species distribution in annual grassland. *Oecologia* 67: 519-523.

- Hölldobler, B. & E. O. Wilson.** 1990. The ants. Belknap Press of Harvard University Press.
- Holt, R. D.** 1977. Predation, apparent competition, and the structure of prey communities. *Theo. Pop. Biol.* 12: 197-229.
- Holt, R. D., & B. P. Kotler.** 1987. Short-term apparent competition. *Am. Nat.* 130: 412-430.
- Howe, H. F. & J. S. Brown.** 2001. The ghost of granivory past. *Ecol. Lett.* 4: 371-378.
- Hulme, P. E.** 1994. Post dispersal seed predation in grassland - Its magnitude and sources of variation. *J.Ecol.* 82: 645-652.
- Hulme, P. E. & T. Borelli.** 1999. Variability in post-dispersal seed predation in deciduous woodland: relative importance of location, seed species, burial and density. *Plant Ecol.* 145: 149-156.
- Janzen, D. H.** 1969. Seed-eaters versus seed size, number, toxicity and dispersal. *Evolution* 23: 1-27.
- Janzen, D. H.** 1971. Seed predation by animals. *Ann. Rev. Ecol. Syst.* 2: 465-492.
- Jordon, W. R. III, M. E. Gilpin & J. D. Aber.** 1987. Restoration ecology: ecological restoration as a technique for basic research. Pp. 3-23 *in*: Jordon, W. R. III., M. E. Gilpin, J. D. Aber (eds.), *Restoration ecology: a synthetic approach to ecological research*. Cambridge University Press, UK.
- Kaufman, D. W. & G. A. Kaufman.** 1982. Effect of moonlight on activity and microhabitat use by Ord's kangaroo rat (*Dipodomys ordii*). *J. Mammal.* 63: 309-312.
- Kay, B. J., L. E. Twigg, T. J. Korn & H. I. Nicol.** 1994. The use of artificial perches to increase predation on house mice (*Mus domesticus*) by raptors. *Wild. Research* 21: 95-105.
- Kelly, D. & V. L. Sork.** 2002. Mast seeding in perennial plants: Why, how, where? *Ann. Rev. Ecol. Syst.* 33: 427-447.
- Kelrick, M. I. & J. A. MacMahon.** 1985. Nutritional and physical attributes of seed and some common sagebrush steppe plants: some implications for ecological theory and management. *J. Range Manage.* 38: 65-69.
- Kelrick, M. I., J. A. MacMahon, R. R. Parmenter & D. V. Sisson.** 1986. Native seed preferences of shrub-steppe rodents, birds and ants: the relationship of seed attributes and seed use. *Oecologia* 68: 327-337.

- Kelt, D. A., J. H. Brown, E. J. Heske, P. A. Marquet, S. R. Morton, J. R. Reid, K. A. Rogovin & G. Shenbrot.** 1996. Community structure of desert small mammals: Comparisons across four continents. *Ecology* 77: 746-761.
- Kelt, D. A. & J. H. Brown.** 1999. Community structure and assembly rules: confronting conceptual and statistical issues with data on desert rodents. Pp 75-107 *in*: E. Weiher and P. Keddy (eds.), *Ecological assembly rules: Perspectives, advances, retreats*. Cambridge University Press, Cambridge, UK.
- Knoch, T. R., S. H. Faeth & D. L. Arnott.** 1993. Endophytic fungi alter foraging and dispersal by desert seed-harvesting ants. *Oecologia* 95: 470-473.
- Lawhon, D. K. & M. S. Hafner.** 1981. Tactile discriminatory ability and foraging strategies in kangaroo rats and pocket mice (Rodentia: Heteromyidae). *Oecologia* 50: 303-309.
- Li, H.-J. & Z.-B. Zhang.** 2003. Effects of rodents on acorn dispersal and survival of the Liandong oak (*Quercus liaotungensis* Koidz.). *For. Ecol. Manage.* 176: 387-396.
- Liebhold, A., V. Sork, M. Peltonen, O. N. Bjørnstad, R. Westfall, J. Elkinton & M. H. J. Knops.** 2004. Within-population spatial synchrony in mast seeding of North American oaks. *Oikos* 104: 156-164.
- Lockard, R. B. & D. H. Owings.** 1974. Seasonal variation in moonlight avoidance by bannertail kangaroo rats. *J. Mammal.* 55: 189-193.
- Longland, W. S.** 1993. Desert rodents in disturbed shrub communities and their effects on plant recruitment. Pages: 209-215 *In* B. Roundy, D. MacArthur, J. Haley, and D. Mann (eds.), *Proceedings: wildland shrub and arid land restoration symposium*, Las Vegas NV.
- Longland, W. S.** 1994. Seed use by desert granivores. Pp 233-237 *in* B. S. Monsen and S. G. Kitchen, (eds). *Symposium on ecology, management, and restoration of intermountain annual rangelands*. USDA Forest Service, Boise, Idaho.
- Longland, W. S. & S. L. Bateman.** 1998. Implications of desert rodent seed preferences for range remediation. *J. Range Manage.* 51: 679-684.
- Longland, W. S., & C. Clements.** 1995. Use of fluorescent pigments in studies of seed caching by rodents. *J. Mammal.* 76: 1260-1266.
- Longland, W. S., S. H. Jenkins, S. B. Vander Wall, J. A. Veech & S. Pyare.** 2001. Seedling recruitment in *Oryzopsis hymenoides*: are desert granivores mutualists or predators? *Ecology* 82: 3131-3148.

- MacMahon, J. A.** 1987. Disturbed lands and ecological theory: An essay about a mutualistic association, Pp. 221-237. *in* W. R. Jordon III, M. E. Gilpin, and J. D. Aber (eds.), Restoration ecology: A synthetic approach to ecological research. Cambridge University Press, New York, USA.
- MacMahon, J. A.** 1997. Ecological restoration. Pp. 479-511 *in* G.K. Meffe and C.R. Carroll (eds.), Principles of conservation biology, second edition. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.
- MacMahon, J. A., J. F. Mull & T. O. Crist.** 2000. Harvester ants (*Pogonomyrmex* spp.): Their community and ecosystem influences. *Ann. Rev. Ecol. Syst.* 31: 265-291.
- Majer, J. D.** 1989. Fauna studies and land reclamation technology – a review of the history and need for such studies. Pp. 5-33 *in* J.D. Majer (ed.), Animals in primary succession. The role of fauna in reclaimed lands. Cambridge University Press, New York, New York, USA.
- Mares, M. A.** 1993. Heteromyids and their ecological counterparts: a pandesertic view of rodent ecology and evolution. Pp. 652-714 *in* H. H. Genoways and J. H. Brown (eds.), Biology of the heteromyidae. American Society of Mammalogists, Special Publication No. 10.
- Mares, M. A. & D. F. Williams.** 1977. Experimental support for food particle size resource allocation in heteromyid rodents. *Ecology* 58: 1186-1190.
- Mayer, V., S. Olzant & R. C. Fisher.** 2005. Myrmecochorus seed dispersal in temperate regions. Pages 175-204. *in* P.-M. Forget, J.E. Lambert, P. E. Hulme and S. B. Vander Wall (eds.), Seed Fate. CAB International.
- McAdoo, J. K., C. C. Evans, B. A. Roundy, J. A. Young & R. A. Evans.** 1983. Influence of Heteromyid rodents on *Oryzopsis hymenoides* germination. *J. Range Manage.* 36: 61-64.
- Miller, A. M., C. McArthur & P. J. Smethurst.** 2007. Effects of within-patch characteristics on the vulnerability of a plant to herbivore. *Oikos* 116: 41-52.
- Milton, S. J., W. R. J. Dean, M. A. du Plessis & W. R. Siegfried.** 1994. A conceptual model of arid rangeland degradation. *BioScience* 44: 70-76.
- Monsen, S. B., R. Stevens & N. L. Shaw** compilers. 2004. Restoring western ranges and wildlands. Gen. Tech. Rep. RMRS-GTR-136, 3 volumes. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. Pages 1–294 (Vol I), Pages 295–698 (Vol II), Pages 699–884 (Vol III).

- Mull, J. F. & J. A. MacMahon.** 1996. Factors determining the spatial variability of seed densities in a shrub-steppe ecosystem: The role of harvester ants. *J. Arid Environ.* 32: 181-192.
- Mull, J. F. & J. A. MacMahon.** 1997. Spatial variation in rates of seed removal by harvester ants (*Pogonomyrmex occidentalis*) in a shrub-steppe ecosystem. *Am. Mid. Nat.* 138: 1-13.
- Murry, A. L.** 2003. Competitive environment and temperature affect food-hoarding behavior of Merriam's kangaroo rats (*Dipodomys merriami*). M.S. thesis, University of Nevada, Reno, 66 pages.
- Nelson, J. R., A. M. Wilson & C. I. Goebel.** 1970. Factors influencing broadcast seeding in bunchgrass range. *J. Range Manage.* 23: 163-170
- Orrock, J. L., & B. J. Danielson.** 2004. Rodents balancing a variety of risks: invasive fire ants and indirect and direct indicators of predation risk. *Oecologia* 140: 662-667.
- Orrock, J. L., B. J. Danielson & J. Brinkerhoff.** 2004. Rodent foraging is affected by indirect, but not by direct, cues of predation risk. *Beh. Ecology* 15: 433-437.
- Osborn, B. & P. F. Allan.** 1949. Vegetation of an abandoned prairie dog town in tall grass prairie. *Ecology* 30: 322-332.
- Parmenter, R. R., J. A. MacMahon & S. B. Vander Wall.** 1984. The measurement of granivory by desert rodents, birds and ants: a comparison of an energetics approach and a seed-dish technique. *J. Arid Environ.* 7: 75-92.
- Pellant, M.** 1989. The cheatgrass-wildfire cycle --are there any solutions? Pp. 11-18 *in* E. D. McArthur, E. M. Romney, S. D. Smith, and P. T. Tureller, editors. Symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology management. USDA Forest Service, Las Vegas, NV.
- Polis, G. A. & D. R. Strong.** 1996. Food web complexity and community dynamics. *Am. Nat.* 147: 813-846.
- Polis, G. A.** 1991. Food webs in desert communities: complexity via diversity and omnivory. Pp. 383-437 *in* Polis, G. (ed.), *The ecology of desert communities*. University of Arizona Press, Tucson, USA.
- Price, M. V.** 1983. Laboratory studies of seed size and seed species selection by heteromyid rodents. *Oecologia* 60: 259-263.
- Price, M. V., N. M. Waser & T. A. Bass.** 1984. Effect of moonlight on microhabitat use by desert rodents. *J. Mammal.* 65: 353-356.

- Price, M. V., & S. H. Jenkins.** 1986. Rodents as seed consumers and dispersers. Pp. 191-235 *in* D. R. Murray, (ed.), Seed dispersal. Academic Press, Sydney, Australia.
- Race S. R.** 1966. Control of western harvester ants on the rangeland. New Mexico Agricultural experiment Station Bulletin Number 502. 21 pages.
- Rebar, C. & O. J. Reichman.** 1983. Ingestion of moldy seeds by heteromyid rodents. *J. Mammal.* 64: 713-715.
- Reichman, O. J. & C. Rebar.** 1985. Seed preferences by desert rodents based on levels of moldiness. *Animal Beh.* 33: 726-729.
- Reichman, O. J., A. Fattaey & K. Fattaey.** 1986. Management of sterile and moldy seeds by a desert rodent. *Animal Beh.* 34: 221-225.
- Reynolds, H. G.** 1950. Relation of Merriam's kangaroo rats to range vegetation in southern Arizona. *Ecology* 31: 456-463.
- Reynolds, H. G.** 1958. The ecology of the Merriam kangaroo rat (*Dipodomys merriami* Mearns) on the grazing lands of southern Arizona. *Ecol. Mono.* 28: 111-127.
- Schupp, E. W.** 1993. Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio* 107/108: 15–29.
- Schupp, E. W., T. Milleron & S. E. Russo.** 2002. Dissemination limitation and the origin and maintenance of species-rich tropical forests. Pp. *in*: D. J. Levey, W. R. Silva, and M. Galetti, (eds.), Seed dispersal and frugivory: Ecology, evolution and conservation. CABI Publishing, Wallingford, Oxfordshire, UK.
- Simon, E. W. & L. K. Mills.** 1983. Imbibition, leakage and membranes. Pp. 9-27 *in* C. Nozzolillo, P.J. Lea and F.A. Loewus, (eds.), Mobilization of reserves in germination. Plenum Press, New York, USA.
- Smith, F. & E. Aldous.** 1947. The influence of mammals and birds in retarding artificial and natural reseeding of coniferous forests in the United States. *J. Forestry* 45: 361-369.
- Spencer, D. A.** 1954. Rodents and direct seeding. *J. Forestry* 52: 824-826.
- Storer, T. L. & E. W. Jameson Jr.** 1965. Control of rodents on California farms. California Agricultural Experiment Station Circulation 535. 50 p.
- Sullivan, T. P.** 1979. The use of alternative foods to reduce conifer seed predation by the deer mouse, (*Peromyscus maniculatus*). *J. Appl. Ecol.* 16: 475-495.

- Sullivan, T. P. & D. S. Sullivan.** 1982. The use of alternative foods to reduce lodgepole pine seed predation by small mammals. *J. Appl. Ecol.* 19: 33-45.
- Sullivan, T. P. & D. S. Sullivan.** 2004. Influence of a granivorous diversionary food on population dynamics of montane voles (*Microtus montanus*), deer mice (*Peromyscus maniculatus*), and western harvest mice (*Reithrodontomys megalotis*). *Crop Prot.* 23: 191-200.
- Tevis, L., Jr.** 1953. Effects of vertebrate animals on seed crops of sugar pine. *J. Wildl. Manag.* 17: 121-131.
- Theimer, T. C.** 2005. Rodent scatter-hoarders as conditional mutualists. Pp. *in* 283-296 *Seed Fate*, P.-M. Forget, J. E. Lambert, P. E. Hulme and S. B. Vander Wall, (eds.), CABI.
- Vallentine, J. F.** 1989. Range developments and improvements. Third edition, Academic Press, San Diego, California, USA. 524 pages.
- Vander Wall, S. B.** 1990. Food hoarding in animals. University of Chicago Press, Chicago.
- Vander Wall, S. B.** 1992. Establishment of Jeffrey pine seedlings from animal caches. *West. J. Appl. For.* 7: 14-20.
- Vander Wall, S. B.** 1993. A model of caching depth: implications for scatter hoarders and plant dispersal. *Am. Nat.* 141: 217-232.
- Vander Wall, S. B.** 1994. Seed fate pathways of antelope bitterbrush: dispersal by seed-caching yellow pine chipmunks. *Ecology* 17: 1911-1926.
- Vander Wall, S. B.** 1995. Influence of Substrate Water on the Ability of Rodents to Find Buried Seeds. *J. Mammal.* 76: 851-856.
- Vander Wall, S. B.** 1998. Foraging success of granivorous rodents: Effects of variation in seed and soil water on olfaction. *Ecology* 79:2 33-241.
- Vander Wall, S. B.** 2003. How rodents smell buried seeds: a model based on the behavior of pesticides in soil. *J. Mammal.* 84:1089-1099.
- Vander Wall, S. B., M. J. Beck, J. S. Briggs, J. K. Roth, T. C. Thayer, J. L. Hollander & J. M. Armstrong.** 2003. Interspecific variation in the olfactory abilities of granivorous rodents. *J. Mammal.* 84: 487-496.

- Vander Wall, S. B., T. C. Thayer, J. S. Hodge, M. J. Beck & J. K. Roth.** 2001. Scatter-hoarding behavior of deer mice (*Peromyscus maniculatus*). *West. N. Am. Nat.* 61: 109-113.
- Veech, J. A.** 2000. Predator-mediated interactions among the seeds of desert plants. *Oecologia* 124: 402-407.
- Veech, J. A.** 2001. The foraging behavior of granivorous rodents and short-term apparent competition among seeds. *Behavioral Ecology* 12: 467-474.
- Wahl, M., & M. E. Hay.** 1995. Associational resistance and shared doom: effects of epibiosis on herbivory. *Oecologia* 102: 329-340.
- Wenny, D. G.** 2002. Effects of human handling of seeds on seed removal by rodents. *Am. Mid. Nat.* 147: 404-408.
- West, N. E.** 1968. Rodent-influenced establishment of ponderosa pine and bitterbrush seedlings in central Oregon. *Ecology* 49: 1009-1011.
- Whisenant, S. K.** 1999. *Repairing damaged wildlands: A process-oriented, landscape-scale approach.* Cambridge University Press.
- Wilson, M. F., B. L. Rice & M. Westoby.** 1990. Seed dispersal spectra: A comparison of temperate plant communities. *J. Veg. Sci.* 1: 547-562.
- Young, J. A. & D. McKenzie.** 1982. Rangeland drill. *Rangelands* 4: 108-113.

APPENDICES

April 28, 2008

To Whom It May Concern:

This letter is to acknowledge our co-authorship of material presented in Chapter 2 of Steven Ostoja's dissertation titled "Granivores and restoration: Implications of invasion and considerations of context-dependent seed removal." I am a co-author with Steven and Eugene W. Schupp (Steven's Major professor), on the publication entitled "Ant assemblages in intact sagebrush and converted cheatgrass-dominated habitats in Rush Valley Tooele County, Utah, USA" which has been submitted to the journal *Western North American Naturalist*. As per the instructions of the USU manual on graduate students theses and dissertations, I (we) grant permission for this material to be published in Steven's dissertation.

Kelly Sivy

April 28, 2008

To Whom It May Concern:

This letter is to acknowledge our co-authorship of material presented in Chapter 5 of Steven Ostoja's dissertation titled "Granivores and restoration: Implications of invasion and considerations of context-dependent seed removal." I am a co-author with Steven and Eugene W. Schupp (Steven's Major professor), on the publication entitled "Rodent harvesting from seed mixtures and beta-distributed regression as an alternative ecological analysis" which has been submitted to the journal Ecology. As per the instructions of the USU manual on graduate students theses and dissertations, I (we) grant permission for this material to be published in Steven's dissertation.

Susan Durham

March 20, 2008

To Whom It May Concern:

This letter is to acknowledge our co-authorship of material presented in Chapter 6 of Steven Ostoja's dissertation titled "Granivores and restoration: Implications of invasion and considerations of context-dependent seed removal." I am a co-author with Steven and Eugene W. Schupp (Steven's Major professor), on the publication entitled "Inter- and Intra-specific seed densities affect seed preferences by granivorous rodent". As per the instructions of the USU manual on graduate students theses and dissertations, I (we) grant permission for this material to be published in Steven's dissertation.

Susan Durham

CURRICULUM VITAE

Steven Muir Ostoja

Ecologist, United States Geologic Survey, Western Ecological Research Center,
Yosemite Field Station, 610 Sierra Street, Bishop, CA 93514

Education

Ph.D. Ecology, Conservation Biology specialization, Utah State University, 2008

M.S. Biological Sciences, California Polytechnic State University, 2002

B.S. Ecology and Systematic Biology, California Polytechnic State University, 1996

Experience

Ecologist, USGS-BRD, Western Ecological Research Center, 2007- Present

Graduate Teaching Assistant, Utah State University, 2003-2007

Instructor, Utah State University, 2006-2007

Teacher, Sacramento City Unified School District, 2000-2002

Biologist, Sycamore Environmental Consultants Inc., 2000

Restoration Fellow, The Nature Conservancy, Santa Cruz Island preserve, 1998-1999

Teaching Associate, California Polytechnic State University, 1996-1998

Publications

Ostoja, S. M. and E. W. Schupp. *In prep.* Rodent assemblages in Great Basin sagebrush communities and converted *Bromus tectorum* habitat types.

Ostoja, S. M. E. W. Schupp and, K. J. Sivy. *In prep.* Ant assemblages in Great Basin sagebrush and converted cheatgrass monocultures habitat in Rush Valley, Tooele County, Utah.

Newbold, T. A. S., S. M. Ostoja, and J. P. Rieder *In prep.* Effect of cheatgrass on locomotor ability of rodents and lizards.

Murray, A.L., W. S. Longland, S. M. Ostoja, and E. W. Schupp. *In review.* The affect of prescription fire on the recapture success of two species of *Dipodomys* in Western NV.

Ostoja, S. M., E. W. Schupp, W. S. Longland, and J. A. MacMahon. *In prep.* Considerations of ant and rodent granivory and arid-land and desert restoration.

Ostoja, S. M., E. W. Schupp and S. Durham. *In prep.* Total seed densities and relative proportions affect seed preferences by granivorous rodents.

Ostoja, S. M., S. Durham and E. W. Schupp. *In prep.* Evidence for associational interactions among seed mixtures? Beta-distributed regression produces alternative conclusions.

Ostoja, S. M., and E. W. Schupp *In prep.* Associational resistance and the importance of among- and within-patch characteristics on seed selectively.

Sivy, K. J., S. M. Ostoja, and E. W. Schupp. *In prep.* Tales from a sandbox: Predator cues and foraging behavior of two Heteromyids.

Ostoja, S. M. 2002. Structure of *Pinus muricata* (Bishop Pine) forests on Santa Cruz Island, California. Cal Poly State University, M.S. Thesis, 96 pages.

Ostoja, S. M. and R. C. Klinger. 1999. The relationship of bishop pinecone morphology to serotiny on Santa Cruz Island, California. Proceedings of the 5th Symposium on the Biology of the California Islands.

Technical Reports

- Ostoja, S. M., E. W. Schupp, D. Pyke, P. Doescher, M. Brunson, and M. Pellant. *In prep.* Ecology, management and restoration of cheatgrass invaded Wyoming big sagebrush communities in the intermountain west.
- Ostoja, S. M. and R. Black. 2006. Naval air command unmanned aerial vehicle (NAVAIR UAV) launch and recovery pad sensitive biological resources site investigation U.S. Army Dugway Proving Ground, Utah. HDR Engineering Inc.

Conference and Symposium Presentations

- Ostoja, S. M. Ecological and management implications of post fire seed banks in the Mojave Desert. Desert tortoise council, Las Vegas NV 2008, Oral Presentation
- Ostoja, S. M. Direct and indirect effects of fire on rodents and ants: Examples from the Great Basin. American Society of Fire Ecology, Tucson AZ 2008, Oral Presentation – Invited.
- Ostoja, S. M. Implications and applications of granivores and sagebrush desert restoration. U. C. White Mountain research station symposium. Bishop CA 2008, Oral Presentation – Invited
- Ostoja, S. M. and E. W. Schupp. Man versus kangaroo rat: A comparison of two traditional seeding methods to seeding by *Dipodops ordii*. Ecological Society of America annual meeting, San Jose CA. 2007 – Oral Presentation
- Sivy, K. J., S. M. Ostoja, and E. W. Schupp. Direct and indirect cues of predation effect foraging behavior of two heteromyid rodent species. Ecological Society of America annual meeting, San Jose CA. 2007 – Poster Presentation
- Ostoja, S. M. and E. W. Schupp. Small Mammal Granivory and Restoration: Implications of seed predation and seed dispersal. Society for Range Management annual meetings Reno NV. 2007 – Oral Presentation
- Ostoja, S. M. and E. W. Schupp. Total seed densities and relative proportion affect seed preferences by granivorous rodents. Ecological Society of America annual meeting, Memphis TN. 2006 – Oral Presentation
- Rieder, J. P., S. M. Ostoja, and T. A. S. Newbold. Effect of cheatgrass on locomotor ability of rodents and lizards: That stuff is dense! Ecological Society of America annual meeting, Memphis TN. 2006 – Oral Presentation
- Ostoja, S. M. and E. W. Schupp. Evidence for indirect effect in seed removal by granivorous rodents in the Great Basin of Utah. Ecological Society of America annual meeting Montréal B.C. 2005 – Poster.
- Ostoja, S. M. and E. W. Schupp. Evidence for indirect effects in seed removal rates mediated by seed harvesting ants and rodents in two vegetation types in the Great Basin of Utah. Society for Range Management annual meetings Fort Worth TX 2005 – Poster.
- Ostoja, S. M. Variations and limitations of diversity and species composition in bishop pine forests on Santa Cruz Island CA. Ecological Society of America meetings Portland OR 2004 - Poster.

- Klinger, R.C. and S. M. Ostoja. Thirty years of research: The California Channel Islands. Fifth California Islands symposium. March 1999 – Oral Presentation.
- Ostoja, S. M. and R. C. Klinger. The relationship of bishop pinecone morphology to serotiny of Santa Cruz Island. Fifth California Islands symposium. April 1999 – Oral Presentation.
- Ostoja, S. M. Morphology and variation in bishop pinecones on Santa Cruz Island. California Botanical Society graduate student meetings California Polytechnic State University. February 1999 – Oral Presentation.
- Ostoja, S. M. Ecology of Bishop pine forests on Santa Cruz Island. California Botanical Society graduate student meeting. University of California. February 1998 – Oral Presentation.

Research Grants

- USU Ecology Center Research Support Award, 2005-06, \$2,000.00
- USU Ecology Center Research Support Award, 2004-05, \$3,500.00
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Awards

- USU School of Graduate Studies, Outstanding Dissertation Fellowship, 2006-07, \$5,000.00
- Stokes-Leopold Memorial Scholar Award, College of Natural Resources 2006-07
- USU Ecology Center Dissertation Stipend, 2006-07, \$12,500.00
- Society for Range Management, 1st place Ph.D. poster, Ft. Worth, TX, 2005
- Presidents List, Utah State University, 2003
- California Botanical Society; 1st place for completed research, U.C., Berkeley, 1999
- Deans List, Cal Poly State University, 1997

Technical Classes and Training

- Design and Analysis of Mark-resight Studies - Utah State University, 2006
- Wilderness First Responder – National outdoor leadership school, 2002
- Project learning tree – Environmental issues: Municipal solid waste training, 2001
- Project learning tree – Environmental education curriculum training, 2000
- Arthur Carhart national wilderness training – Wilderness curriculum, 1998
- Project wild – Environment education curriculum training, 1998
- Wildlands Studies– Colorado Plateau field study program. San Francisco, 1995

Professional Associations

- California Botanic Society
- Ecological Society of America
- Society for Range Management
- American Society of Mammalogists

Leadership Appointments and Committees

- Chair, Graduate Student Council, USU College of Natural Resources, 2006-07

Senator, Graduate Student Senate, USU College of Natural Resources, 2004-05 & 2005-06

Department representative, Graduate Student Council, USU College of Natural Resources, 2004-05 & 2005-06

Ecology Center Graduate Student Seminar Committee, USU, 2003-04 and 2004-05

Manuscript and Book Chapter Reviews

American Midland Naturalist

Biotropica

Journal of Arid Environments

Western North American Naturalist

Ecology text book chapters, Population Ecology and Community Ecology