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# The role of small mammals in the population dynamics of two native grassland forbs: *Lupinus sericeus* and *Lithospermum ruderale*

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THE ROLE OF SMALL MAMMALS IN THE POPULATION DYNAMICS OF  
TWO NATIVE GRASSLAND FORBS, *LUPINUS SERIECEUS* AND  
*LITHOSPERMUM RUDERALE*

By

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B.A., Lewis and Clark College, Portland, Oregon, 2000

Dissertation

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In Biology, Ecology

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## ABSTRACT

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The role of small mammals in the population dynamics of two native grassland forbs, *Lupinus sericeus* and *Lithospermum ruderale*

Chairperson: Dr. John Maron

Although post-dispersal seed predators are common and often reduce seed density, their influence on plant abundance remains unclear. We examined the impact of seed predation by small mammals, primarily deer mice (*Peromyscus maniculatus*), on seedling recruitment and plant establishment of two perennial grassland forbs: *Lupinus sericeus* (Fabaceae) and *Lithospermum ruderale* (Boraginaceae), using experimental seed addition and rodent exclusion treatments. For both species, small mammal exclusion increased the total number of seedlings that emerged, and these effects were still significant three years after seed addition, resulting in greater numbers of established plants inside exclosures than in control plots.

To shed light on how these relatively short-term rodent-driven reductions in seed abundance and recruitment might influence longer-term patterns of *L. ruderale* population growth, we combined experimental results with demographic data in stage-based population models. Model outputs revealed that rodent seed predation had a significant impact on *L. ruderale* population growth rate. These results demonstrate that rodent granivory can be a potent force limiting the abundance of a perennial forb.

In the third chapter, we examined the effects of multiple consumers on *L. sericeus* populations. We combined the experimental evidence of rodent-driven reduction in seedling recruitment in with the impacts of two other consumers, folivorous ground squirrels (*Spermophilus columbianus*), and herbivorous insects (Lepidopteran and Coleopteran larvae) on *L. sericeus* fecundity, with stage-based matrix models. We examined how these consumers, individually and in concert, influence the population growth of *L. sericeus* at three sites. Because consumers sequentially attack flowers, pre-dispersed seeds and then post-dispersed seeds, the opportunities for any given species to influence the population growth rate of *L. sericeus* is contingent on the impacts of the preceding consumer. We found that release from all consumers caused significant, and sometimes dramatic, increases in the population growth rate. These results suggest that despite high rates of asexual reproduction, consumers impose strong limits to the population growth and therefore the abundance of this long-lived forb.

The final chapter reflects outreach to the public school community, bringing scientific content and methods to an elementary school classroom in an inquiry demonstrating the importance of seed dispersal in plants.

## ACKNOWLEDGMENTS

It takes a village to raise a dissertation. That may not be quite how the saying goes, but it has been true in my graduate experience. I could not have finished, or even started, this dissertation without the academic mentorship and support of my advisor John Maron and the rest of my committee: Elizabeth Crone, Ray Callaway, Anna Sala, and Lila Fishman. My fellow Maron-Lab members provided advice (both academic and otherwise), stimulating conversation, and just plain fun. It might have been possible to get through grad school without Jenn, Jedediah, Lindsay, Matt, Cedar, Adam, Elliott, Jen, and Sarah, but I'm glad I didn't have to. From fond fondue-dinner memories, to the scars of lab-retreat games, I'm glad to have overlapped with all of these wonderful people.

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CHAPTER ONE

SMALL MAMMAL SEED PREDATION LIMITS THE RECRUITMENT AND  
ABUNDANCE OF TWO PERENNIAL GRASSLAND FORBS

## Abstract

Although post-dispersal seed predators are common and often reduce seed density, their influence on plant population abundance remains unclear. On the one hand, increasing evidence suggests that many plant populations are seed limited, implying that seed predators could reduce plant abundance. On the other hand, it is generally uncertain whether the magnitude of seed limitation imposed by granivores is strong enough to overcome density-dependent processes that could compensate for seed loss at later stages. We examined the impact of seed predation by small mammals, primarily deer mice (*Peromyscus maniculatus*), on seedling recruitment and subsequent plant establishment of two perennial grassland forbs: *Lupinus sericeus* (Fabaceae) and *Lithospermum ruderale* (Boraginaceae). The experiment combined graded densities of seed addition for each species with a small mammal exclusion treatment. Seedling recruitment and plant establishment were monitored in the experimental plots for up to three years. For both species, small mammal exclusion increased the total number of seedlings that emerged, and these effects were still significant three years after seed addition, resulting in greater numbers of established plants inside exclosures than in control plots. We also found evidence of seed limitation, with increasing density of seeds added leading to increased numbers of seedlings. Results from seed addition and small mammal exclusion experiments in later years also revealed significant impacts of small mammals on seedling emergence. These results suggest that granivores can have potentially important impacts in limiting forb abundance in grasslands communities.

## Introduction

Small mammal seed predators are common in many ecological systems, and due to their high metabolic rates they can consume large numbers of seeds relative to their mass or numbers (Reichman 1979, Brown and Munger 1985, Hulme 1993, 1998). Many studies on small mammal granivory have examined the details of seed predator behavior, quantifying how factors such as cover type, season, and seed characteristics (e.g. size, density, or nutrient concentration) influence seed loss. These studies have shown that rodents generally target larger, more nutrient-rich seeds (Mittelbach and Gross 1984, Brown and Munger 1985, Hoffman et al. 1995, Celis-Deiz et al. 2004), and that seed loss can be strongly influenced by habitat or vegetation cover (Mittelbach and Gross 1984, Hulme 1993, Manson and Stiles 1998, Maron and Kauffman 2006), seed density (Hulme 1993, Hulme 1994), and abundance of these rodents (Pearson and Callaway 2008). We know that large numbers of seeds can be removed by seed predators, and in some cases we can even make reasonable predictions about which plant species and communities are most likely to sustain heavy seed predation. Yet surprisingly little is known about the degree to which seed predation affects plant recruitment and longer term patterns of plant abundance.

Theory generally predicts that seed predation should have the greatest impact on plant numbers when populations are more strongly seed-limited as opposed to microsite limited (Harper 1977, Crawley 2000). When recruitment is seed limited, seed number and seedling numbers are directly correlated. Thus, any consumer-driven decrease in seed abundance translates directly to a decrease in recruitment. In contrast, when populations are microsite-limited, the relationship between seed availability and seedling

recruitment is decoupled. The magnitude of seedling recruitment is then governed by the availability of safe-sites for germination rather than the density of seeds (Harper 1977, Eriksson and Ehrlén 1992, Clark et al. 2007). Thus, when plant populations are safe-site limited, seed loss to consumers does not necessarily translate to reductions in subsequent seedling recruitment.

The few examples of post-dispersal seed predators affecting plant abundance come mostly from desert and dune systems, where there is relatively little established vegetation. Experimental studies have demonstrated that granivores can affect plant population abundance in coastal dune habitats (Kauffman and Maron 2006) and plant community structure in desert systems (Brown et al. 1979, Inouye et al. 1980, Davidson et al. 1984, Brown and Heske 1990). In a restoration context, experiments that have excluded rodents from planted prairie or wet-grassland sites have also shown impacts of granivores and herbivores on species composition (Edwards and Crawley 1999, Howe and Brown 2000, Howe and Brown 2001, Howe and Lane 2004, Howe et al. 2006). Yet in habitats with greater cover and within intact vegetation, small mammal granivores might have much less influence on plant abundance. For instance, Maron and Kauffman (2006) found differences in the impact of seed predation on seedling recruitment in adjacent dune and grassland habitats despite similar densities of small mammals. Reader (1993) showed that large-seeded species, those most vulnerable to predation, survived seed predation better when cover (live vegetation and litter) was present, but that cover was also a key factor inhibiting seedling emergence. These results suggest that the relative importance of seed predation and safe sites may shift in higher cover environments, but most long-term work has been done in arid habitats with relatively low

vegetative cover. We know much less about whether plant populations are limited by small mammal seed predation in communities with more established vegetation, where there may be greater competition for suitable germination sites, as well as less of a chance for small mammals encountering seeds.

Although there have now been a host of seed-addition experiments aimed at understanding the scope for changes in seed availability to alter plant abundance, experiments of this sort often have three major short-comings. First, in most of these studies, seed addition is done without manipulating consumer pressure (Turnbull et al. 2000, Clark et al. 2007). In this case, if seeds added to plots are subsequently (but “invisibly”) eaten by consumers, this can wipe out initial experimentally-imposed differences in seed density. As a result, one may find no relationship between seed density and seedling recruitment, and falsely conclude that a population is micro-site rather than seed limited, when in fact the reverse might be the case. Second, seed addition experiments rarely follow individuals past the season in which they emerge (Turnbull et al. 2000, Clark et al. 2007). Thus, these experiments often do not effectively measure negative density dependent survival that could compensate for seed loss. Finally, most seed addition experiments only add a single density of seeds to plots. In a recent meta-analysis of seed addition experiments Clark et al. (2007) found that only 26% of seed addition studies used more than one density of seeds. With only one seed density, usually compared to a zero-seed treatment, it is difficult to determine how variation in seed loss (imposed on variable seed production or availability) might translate into changes in seedling recruitment. While experiments and reviews examining evidence of seed limitation from a range of species in seed addition experiments have shown that seed

limitation might be more prevalent than generally thought (Eriksson and Ehrlén 1992, Turnbull et al. 2000), it has also been asserted that seed limitation is of relatively minor importance compared with other factors that would limit the establishment of seedlings (Clark et al. 2007, Poulsen et al. 2007).

Critical assessment of the impacts of seed predators on plant population dynamics requires examining several key factors. The first of these involves determining whether granivores limit seedling recruitment. For this to occur, a plant population must be seed-limited, so that reductions in seed abundance translate to lowered seedling recruitment. The second factor that must be determined is whether processes at later life stages, such as density-dependent mortality, compensate for initial differences in seedling abundance due to seed predation. Compensatory density-dependence acting on seedling survival could reduce or even eliminate any difference in seedling numbers that result from greater recruitment when seeds are protected from granivores. (Harper 1977, Howe and Brown 2001, Halpern and Underwood 2006). To date, most research on this topic has examined one but not both of these factors. For example, experiments have generally either explored seed limitation by seed addition without consumer manipulation, or examined post-dispersal seed predation without manipulating seed density. To gain a better understanding of the contexts in which seed predators will be most important, or to understand how seed limitation mediates the realized impact of seed loss in populations, it will be important to unite the two concepts and approaches in studies that can address both issues at once. This combined experimental approach has been rare, especially in natural systems, and it has been particularly rare for the fate of seedlings to be followed past emergence (but see Maron and Simms 1997, Edwards and Crawley 1999, Pearson

and Callaway 2008). This study examines both seed limitation and seed predation in a natural setting, to assess how post-dispersal seed predation affects plant abundance.

In this study we used a series of experiments crossing small mammal exclusion treatments with seed addition at a range of seed densities to address the following questions: 1) Is seedling recruitment for two species of heavy-seeded perennial forbs, *Lithospermum ruderale* and *Lupinus sericeus*, significantly depressed by post-dispersal seed predation from small mammals? 2) How seed-limited are these plant populations, and how does the degree of seed limitation change in the presence and absence of small mammal seed predators? 3) Do small mammal-driven changes in seedling recruitment persist, creating differences in the abundance of juvenile plants, or are any initial differences negated by subsequent density-dependent mortality?

### Methods

Study system: Experiments took place at seven sites in semi-arid grasslands in the Blackfoot Valley of western Montana. Sites were dispersed over approximately 50 km of river valley. The plant community in these grasslands is dominated by native perennial bunchgrasses (*Festuca idahoensis* and *Festuca scabrella*) and sagebrush (*Artemisia tridentata*) and contains a high diversity of native perennial forbs. Exotic species are present at these sites but generally occur at very low densities.

The focal plant species, *Lupinus sericeus* (Fabaceae) and *Lithospermum ruderale* (Boraginaceae) are both long-lived native perennial forbs. Aboveground growth begins in late April to early May and plants flower between May and early July. Both species are pollinated by a variety of generalist insects and set seed in July and August. These

species have relatively heavy seeds (mean seed weights  $\pm$  1 SD of mean: *Lupinus* =  $0.0210 \pm 0.004496$  g; *Lithospermum* =  $0.0211 \pm 0.005098$  g), which are dispersed locally around parent plants. Seeds of both species are commonly consumed by deer mice (Maron and Pearson unpublished data). Experiments using buried seeds in bags have revealed that *L. sericeus* seeds mostly germinate during their first spring (0-2% surviving beyond the first growing season) whereas most seeds of *Lithospermum* remain dormant in a seedbank for at least one year (>60% surviving in seed bags, and <3% germinating in seed addition plots in the first season, M. Bricker, unpublished data).

Although several small mammal species are present at sites (deer mice, *Peromyscus maniculatus*; montane voles, *Microtus montanus*; northern pocket gophers, *Thomomys talpoides*; Columbian ground squirrels, *Spermophilis columbianus*; and (rarely) yellow-pine chipmunks, *Tamias amoenus*; shrews, *Sorex*; and hares, *Sylvagus nutallii*), deer mice are the main post-dispersal seed predator. The other small mammal species are primarily herbivorous or florivorous, insectivorous, or in the case of *S. columbianus*, inactive when seeds are being dispersed from these plants. Neither *Lupinus* nor *Lithospermum* have eliasomes on their seeds and their seeds are not dispersed by ants. Very few seeds of either species were removed when left in trays in areas accessible to birds and insects, but not to small mammals (M. Bricker, unpublished data).

Small mammal exclosures were constructed in the spring of 2002 (at 3 sites) and during September 2004 (at 4 sites). At each site, we established one 10 m x 10 m control plot paired with one 10 x 10 m small mammal exclosure. Control and small mammal exclosure plots were separated by a minimum of 5 m, but were no farther apart than 20 m. Exclosures were constructed of 0.625 x 0.625 cm welded wire fencing buried to a

depth of 30-40 cm and extending 60 cm above ground. Fencing was topped with 20 cm of aluminum flashing to prevent small mammals from climbing over fences. Exclosures prevented most small mammal access, but we also set snap-traps inside exclosures to ensure they remained free from small mammals. Over the course of the 3-year study, we trapped a total of 21 mice in the 7 exclosures, half of which were trapped immediately after snow melt in early spring. These captures likely resulted from mice gaining access in winter via snow that had built up along the fences. The small mammal exclosures did not deter large grazing mammals present in the system; scat and tracks of elk and deer, as well as evidence of elk grazing, particularly in early spring, were clearly evident inside the small mammal exclosures as well as outside (M. Bricker, personal observation).

Seed addition experiments: In September 2004 we added 5 densities of seeds of each species to 0.5 x 0.5 m subplots within the seven 10 x 10 m small mammal exclosures and paired control plots. Within each plot there were 10 seed addition subplots (2 species x 5 seed densities), each spaced at least 0.5 m apart and at least 1 m from the perimeter of the plot. Seed addition subplots were placed randomly in experimental plots, which generally included established populations of *Lupinus* and *Lithospermum* (one of the seven sites did not have adult *Lupinus* present in the experimental plot, though there were naturally established populations nearby). If adult *Lupinus* or *Lithospermum* plants were present in the initially selected random location, the subplot was moved systematically along a transect within the plot until it fell on a 0.25 m<sup>2</sup> area without established adult plants. This prevented natural seed rain from falling into seed addition subplots. Each subplot received seeds of either *Lupinus* or *Lithospermum*, collected

locally in 2004. *Lupinus* were added at densities of 0, 25, 50, 100, and 200 seeds per 0.25 m<sup>2</sup>; *Lithospermum* were added at densities of 0, 50, 100, 200, and 300 seeds per 0.25 m<sup>2</sup>. These densities were chosen to span and extend past the natural range of seed densities produced by seed rain from large individual plants of each species (mean  $\pm$  SEM: *Lithospermum* 138.7  $\pm$  20.2; *Lupinus* 78.1  $\pm$  7.28). Seeds were scattered over the surface of undisturbed plots; no effort was made to bury seeds or force them into the soil surface.

From April through June of 2005 we censused subplots for seedlings approximately every 3 weeks, and thereafter monthly in July and August. Seedlings were counted when cotyledons had emerged from the seed coat. Cotyledons of both species are large and distinct from those of other species. The cotyledons persist for some time after drying up, making seedlings generally easy to distinguish from small returning plants. At each census we marked newly emerged seedlings and recorded the number of surviving and dead seedlings from previous censuses. In the spring and summer of 2006 and 2007 we continued to census new and surviving seedlings monthly, and tracked separately the survival of the cohorts that emerged in 2005, 2006, and 2007. The cumulative emergence (the total number of seedlings that emerged in the years 2005 to 2007) and the number of plants established at the end of the final growing season (plants that had emerged and were still alive in late July 2007) were analyzed with a split-plot ANOVA (PROC MIXED in SAS, vers. 9.1). Emergence and establishment were both log-transformed in these analyses. Small mammal exclusion treatment was a whole-plot factor, and seed density (treated as a discrete, categorical variable) was the sub-plot factor; site was used as blocking factor and species as a fixed factor. Taken together,

these analyses are conservative because: 1) seed density was used as a categorical rather than continuous variable due to the limited number of seed densities used, and 2) unlike many other seed addition studies, zero-seeds-added subplots were not used in analyzing small mammal and seed density impacts. We excluded zero-seeds-added subplots from the analyses because no or extremely few seedlings germinated from the resident soil seed bank. Thus, including these plots would have forced a positive relationship with seed density if any seeds germinated in seed addition plots. By excluding zero-seeds-added subplots, our results reflect the effects of seed predators on recruitment along a gradient of seed availability.

We repeated portions of these seed addition experiments in 2005 and 2006 in order to examine: 1) how seed limitation in the presence of small mammals varies across years, and 2) how seed predation and its impact on seedling recruitment vary across years. In 2005, we added seeds to a new set of 10 seed addition subplots (5 densities per species x 2 species) outside of small mammal exclosures. Inside the exclosures we added only one plot for each species, at a mid-range density of 100 seeds. This enabled us to compare predation pressure at one seed density across years, while at the same time determining the relationship between seed input and seedling output in the presence of small mammals across years. In 2006, we repeated only the 100-seed density, with one plot for each species, in the exclosure and control plots at each of the 7 sites. These were censused as described above for the summers of 2006 and 2007. *Lithospermum* plots set out in 2006 were also censused in the summer of 2008. To determine how seed density influenced recruitment outside of exclosures, we used PROC GLM (SAS vers. 9.1), with seed density (excluding zero-seed added plots), species and year as fixed factors, and log-

transformed cumulative emergence and cumulative establishment as response variables. For the 100-seed plots in and out of exclosures, we analyzed the results with a 3-way ANOVA (S-PLUS, version 7.0), with log of emergence in following year (for *Lupinus*) or 2 years after seed addition (for *Lithospermum*, due to the delay in emergence from seed dormancy) as response variable and year, species, and small mammal exclusion as fixed factors.

Because the seedlings germinated at a range of densities in seed addition plots, we were able to examine how variation in seedling and juvenile plant density affected survival. This enabled us to assess the extent to which density-dependent seedling mortality compensated for seed loss to predation. To do this, we used linear regression (PROC GLM, SAS vers 9.1) to examine the influence of seedling density (total number of seedlings emerged), small mammal treatment, and species, on mortality rates. Examining the impact of exclusion treatment on mortality rate allowed us to assess whether herbivorous small mammals, such as voles and ground squirrels, were contributing to any differences in plant abundance between exclosures and controls, and to separate the effects of granivory and herbivory. Mortality rate was calculated as a proportion for each plot by dividing the number of plants that died over the course of the experiment by the total number that had germinated. The mortality rate was arcsine-square root transformed for the regression analyses.

## Results

Effects of small mammal exclusion and seed density on seedling emergence and plant establishment: In the 2004 seed additions in and out of small mammal exclosures

at all seed densities, small mammal exclusion increased seedling emergence in both species, with cumulative emergence averaging 2.7 times higher inside of exclosures than in control plots (Fig. 1;  $F_{1,6.6} = 20.06$ ,  $P = 0.0033$ ). Three years after seed addition, the number of established plants still showed a significant impact of exclosure treatment (Fig. 1;  $F_{1,6.39} = 5.90$ ,  $P = 0.0488$ ). There was no significant difference between species in the rate of seedling emergence ( $F_{1,93.8} = 0.55$ ,  $P = 0.4617$ ) or establishment ( $F_{1,92.1} = 3.19$ ,  $P = 0.0774$ ). The small mammal exclosure by species interaction was not significant (emergence:  $F_{1,94.3} = 2.11$ ,  $P = 0.149$ ; establishment:  $F_{1,93.6} = 0.99$ ,  $P = 0.321$ ), nor was the exclosure by seed density interaction (emergence:  $F_{3,87.8} = 1.8$ ,  $P = 0.153$ ; establishment:  $F_{3,87.6} = 0.790$ ,  $P = 0.321$ ).

Indicative of seed limitation, the number of emerged seedlings increased with increasing seed densities (Fig. 1;  $F_{3,87.8} = 8.78$ ,  $P < 0.0001$ ), and these differences were still evident three years after the initial seed addition (Fig. 1;  $F_{3,87.6} = 8.23$ ,  $P < 0.0001$ ). Rates of emergence and establishment (plants per seed initially added) are reported in Appendix A.

Effects of seed density and year sown on seedling emergence outside of small mammal exclosures: As was the case for the 2004 seed addition experiment, in 2005 in the presence of deer mice, cumulative seedling emergence increased with increasing seed density in the two years following seed addition (Fig. 2;  $F_{3,102} = 3.32$ ,  $P = 0.0229$ ). However, the magnitude of seedling emergence varied depending on the years seeds were added (i.e. 2004 vs. 2005; Fig. 2;  $F_{1,102} = 8.16$ ,  $P = 0.0052$ ), and emergence differed between the two forb species ( $F_{1,102} = 8.44$ ,  $P = 0.0045$ ). There were no significant

species by year ( $F_{1,102} = 0.30$ ,  $P = 0.568$ ) or species by seed density ( $F_{3,102} = 0.05$ ,  $P = 0.986$ ) interactions.

Temporal variation in effects of seed predation on seedling emergence: The emergence of seedlings (in the year following seed addition for *Lupinus*, or the second year following seed addition in *Lithospermum*, due to the time lag in germination) in 100-seed plots in and out of small mammal exclosures showed a significant effect of exclosure treatment (Fig. 3;  $F_{1,74} = 7.481$ ,  $P = 0.0078$ ), and species ( $F_{1,74} = 20.389$ ,  $P < 0.0001$ ), but not of year seeds were added ( $F_{2,74} = 0.1710$ ,  $P = 0.843$ ). None of the interactions between species, year, and exclusion treatment were significant (species x year:  $F_{2,74} = 0.944$ ,  $P = 0.394$ ; species x exclusion:  $F_{1,74} = 1.585$ ,  $P = 0.212$ ; year x exclusion:  $F_{2,74} = 2.592$ ,  $P = 0.0816$ ).

Effects of density and small mammal exclosure treatment on plant mortality rate: Plant mortality was unaffected by the variation in plant density that resulted from adding more seeds to plots. Across the range of densities at which seedlings germinated in the experimental plots, there was no effect of seedling density on mortality rate ( $F_{46,21} = 1.32$ ,  $P = 0.25$ ). Mortality rate did not differ between small mammal exclosure and control plots, ( $F_{1,21} < 0.01$ ,  $P = 0.981$ ), or between species ( $F_{1,21} = 0.44$ ,  $P = 0.790$ ). The interaction between small mammal exclusion and seedling density was not significant ( $F_{10,21} = 1.43$ ,  $P = 0.135$ ). Figure 4 shows the change in the number of plants in the seed addition subplots, from the highest-density seed additions (200 seeds for *Lupinus*, 300 for *Lithospermum*). Mortality rates by rodent treatment and initial seed density are reported in Appendix A.

## Discussion

Protection from seed predation led to significant increases in seedling emergence and establishment for both *Lupinus sericeus* and *Lithoserpmum ruderale*, suggesting that post-dispersal seed predation by small mammals can substantially decrease the abundance of early life stages of these plants. Furthermore, gains in plant abundance from protecting seeds from deer mice were still evident and significant three years after seed addition, indicating the potential for lasting impacts of seed predation (Fig. 1). These results, along with other studies that have shown increases in seedling emergence with protection from small mammal seed predation (Edwards and Crawley 1999, Howe and Brown 2000, Maron and Kauffman 2006, Pearson and Callaway 2008) contrast with the expectation that seed predators consume a “doomed surplus” of seeds unlikely to germinate or establish (Hulme 1998, Crawley 2000). Unlike studies in which initial differences caused by rodent seed predation have faded with time due to density dependent mortality (Edwards and Crawley 1999, Howe and Brown 2001), we found no evidence of density dependent mortality rates over similar or longer time spans, even though seedlings occurred at extremely high densities in some of the plots (many high-density seed addition plots had over 50 seedlings per 0.25 m<sup>2</sup>). Clearly at some point these high densities will lead to a decrease in plant performance or survival. However, these plants are sparsely distributed in their natural populations in this area, suggesting that their populations could see significant increases in abundance due to release from rodent seed predation before density dependence would cause large declines in plant performance.

These experiments also showed higher numbers of seedlings in plots receiving higher seed densities (Figs. 1, 2). This positive relationship between seed input and seedling emergence was evident in both exclosure and control plots, though the number of seedlings was lower in the controls, where seeds had been exposed to small mammal predation. There was no interaction between seed treatment and small mammal treatment, indicating a consistent rate of return of seedlings per remaining seed within each small mammal treatment (protected or exposed). Similar to many studies reviewed in Clark et al (2007), we saw what was considered a relatively low effect size from seeds added, with an average of 0.2-0.3 seedlings per seed inside of small mammal exclosures and 0.05-0.2 seedling per seed outside of small mammal exclosures (Appendix A). However, this effect did lead to a 2 to 5-fold increase in seedlings between the lower and higher seed addition densities and an almost 3-fold increase in seedlings when plots were protected from seed predation. Recruitment of seedlings along demography transects through natural populations accessible to small mammals is quite low—well below the densities recorded in even the lowest-density seed addition subplots (M. Bricker, unpublished data). This suggests that in these areas, *Lupinus* and *Lithospermum* populations are limited by low seed availability due, in part, to seed predation by small mammals.

The length of this study allowed us to separate the effects of different guilds of small mammals on plant establishment. Because we followed plants from the 2004 cohort of seeds for three years, the small mammal exclusion treatments protected plants from small mammal herbivory as well as granivory. The frequency of censuses recording deaths of seedlings and young plants over the spring and summer made it possible to

examine whether mortality rates due to herbivory by small mammals (such as voles and ground squirrels), affected plant establishment. Mortality rates in and out of the exclosures did not differ for either species in this experiment, indicating that herbivory from small mammals was not a significant source of mortality among seedlings and young plants (Fig. 4). Although both granivorous and herbivorous small mammals have been shown to impact community composition and plant abundance (Edwards and Crawley 1999, Howe and Brown 2000, Howe and Brown 2001, Howe and Lane 2004, Howe et al. 2006, Kauffman and Maron 2006), in this study it appears that granivory, rather than herbivory, was the primary driver of the differences in plant abundance in and out of the small mammal exclosures.

Our results demonstrate several important considerations for seed addition studies. First, post-dispersal seed predators have the potential to lower the apparent evidence of seed limitation where they have access to added seeds. This supports the argument that seed addition experiments should explicitly consider or manipulate seed predation (Turnbull et al. 2000, Clark et al. 2007) particularly for plants with large or attractive seeds. If levels of seed limitation inferred from standard seed addition experiments were used to assess the potential for seed consumers to affect these populations, the low relationship between seed density and seedling emergence outside of the small mammal exclosures would lead to an underestimation of the degree of seed limitation and the capacity for seed predators to alter seedling abundance. The results inside of the exclosures, however, indicate that when protected from seed predators, these populations experienced strong seed limitation (Fig. 1). These results also highlight the importance of following seed addition experiments beyond seedling emergence. For the

*Lithospermum* seeds, for example, which were mostly dormant for the first year after seed additions, a standard interpretation might have been that these populations were strongly site limited, requiring particular, extremely rare, microsite conditions in order to germinate. Following these seed additions over multiple years showed that, though seedling emergence was delayed for a large proportion of the seeds, there was seed limitation in the population overall, as the number of emerging seedlings increased with increasing seed input

Visible and significant differences three years after seed additions show that the effects of small mammals and seed numbers are not fleeting differences quickly swamped out by density dependent processes or spatio-temporal variation (Fig. 1, lower panels). In fact, *Lupinus* plants added as seeds in 2004 have now begun to flower and set seed at some sites. Although most of the plants are still below the average size of adults in the surrounding populations, some have reached reproductive size, indicating that these initial differences can persist and affect overall plant abundance. The fact that both of these species occur at low to moderate densities in the areas surrounding the seed addition experiments (*Lithospermum* occurring in an average of 6.7 % of vegetation survey sub-plots, and *Lupinus* in an average 23% (Maron and Pearson unpublished data)) suggests that small mammal seed predation may be one factor limiting their abundance. This is supported, as well, by results from population projection analyses incorporating these experimental results into demographic matrix models, in which seed predation decreases the population growth rate for *Lithospermum* (M. Bricker, unpublished data).

Both *Lupinus* and *Lithospermum*, despite varied adult life histories, have very large and similarly sized seeds. Their uniform response to seed addition and rodent

exclusion supports the idea that large-seeded species will be particularly vulnerable to the effects of seed loss from small mammal granivory. Our results indicate that for large-seeded species, small mammal seed predation has strong potential to decrease adult plant abundance. This study adds to work in other systems that have shown small mammal seed predation to affect the abundance of plants in systems such as deserts, (Inouye et al. 1980, Davidson et al. 1984, Brown and Heske 1990), dunes (Maron and Kauffman 2006), and restoration plantings (Howe and Brown 2000, Howe and Brown 2001, Howe et al. 2002). Our results demonstrate that small mammal seed predation can lower plant abundance even in communities with denser cover, such as grasslands.

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Figure 1: Cumulative emergence (total number of seedlings emerged over three years) and establishment (number of individuals alive at end of 3<sup>rd</sup> growing season) three years after seed addition, in and out of experimental small mammal exclosures for *Lupinus* (left column) and *Lithospermum* (right column). Points show mean for the 7 experimental sites (error bars show  $\pm 1$  SEM).

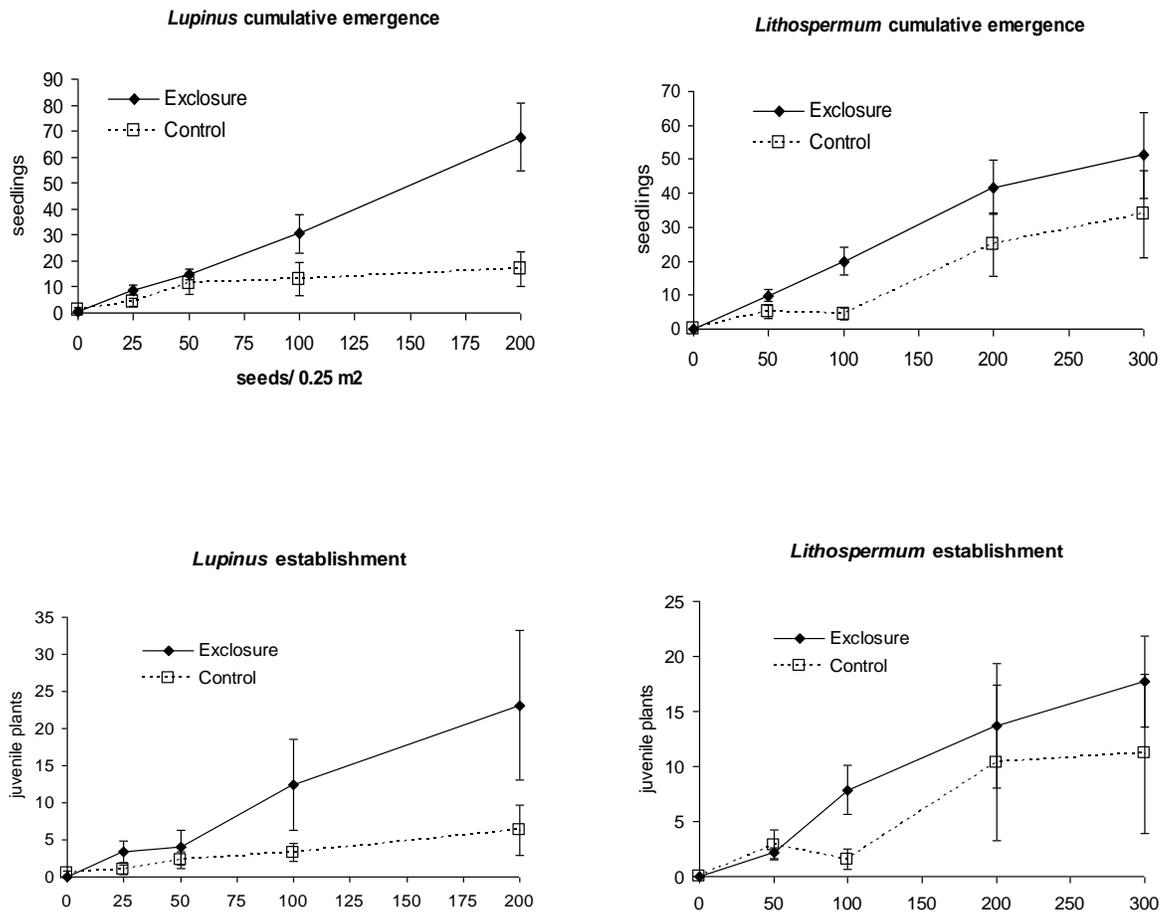


Figure 2: Mean ( $\pm$  SEM) of two-year cumulative emergence (total number of seedlings emerged over two seasons) for *Lupinus* and *Lithospermum*, for seeds added outside of exclosures in 2004 and 2005.

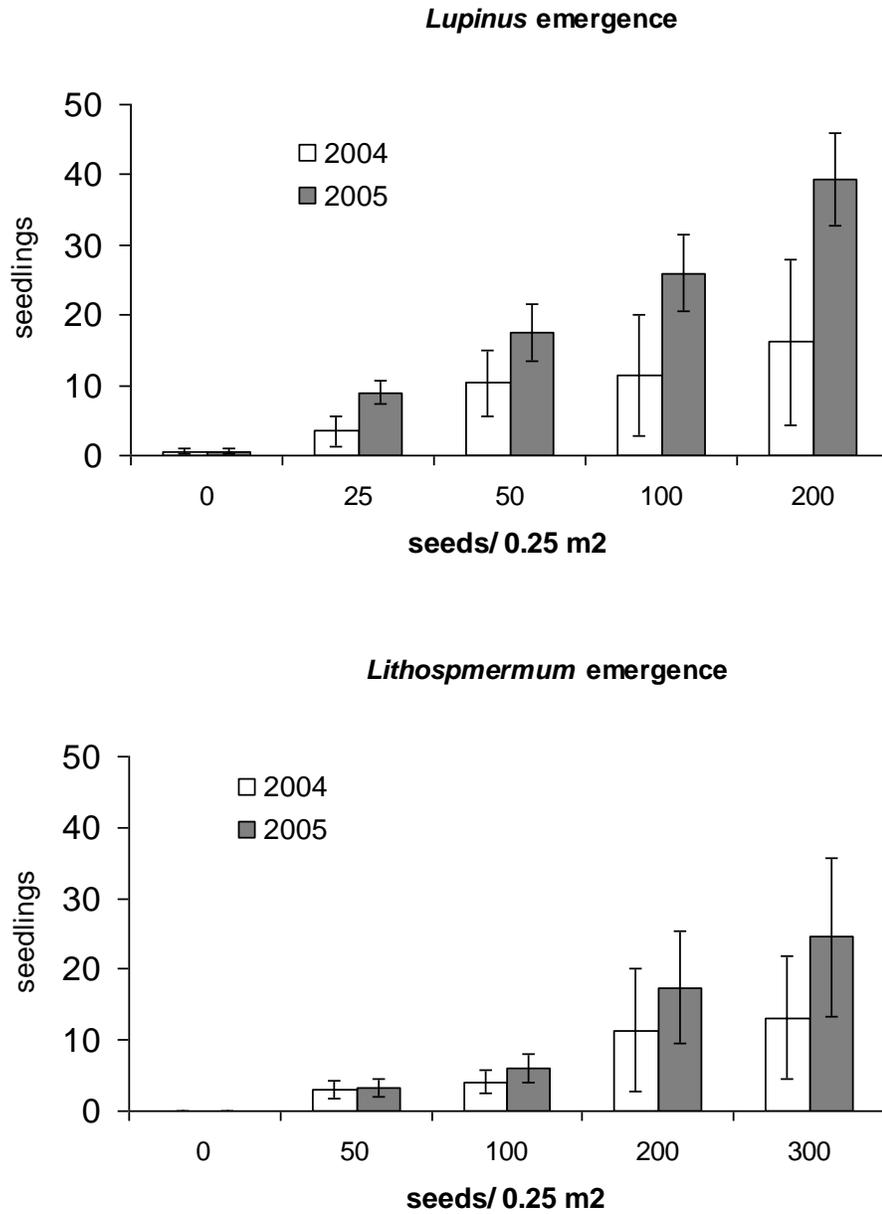


Figure 3: Mean ( $\pm$  SEM) number of seedlings emerged in the spring following seed addition (for *Lupinus*), or two years following seed addition (for *Lithospermum*). 2004 data as in Fig 1 for 100 seed plots.

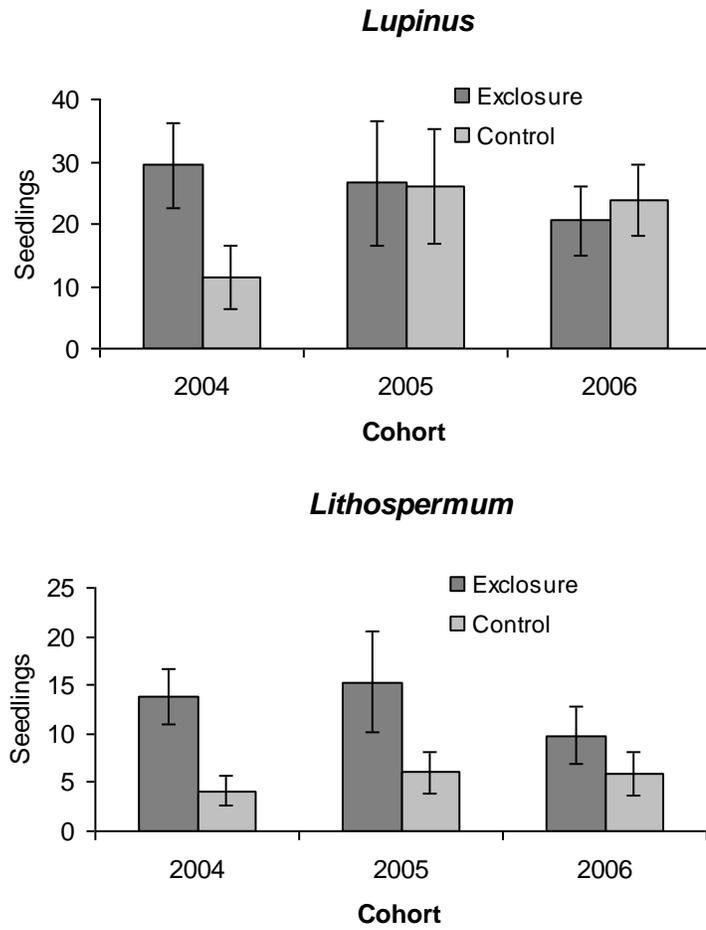
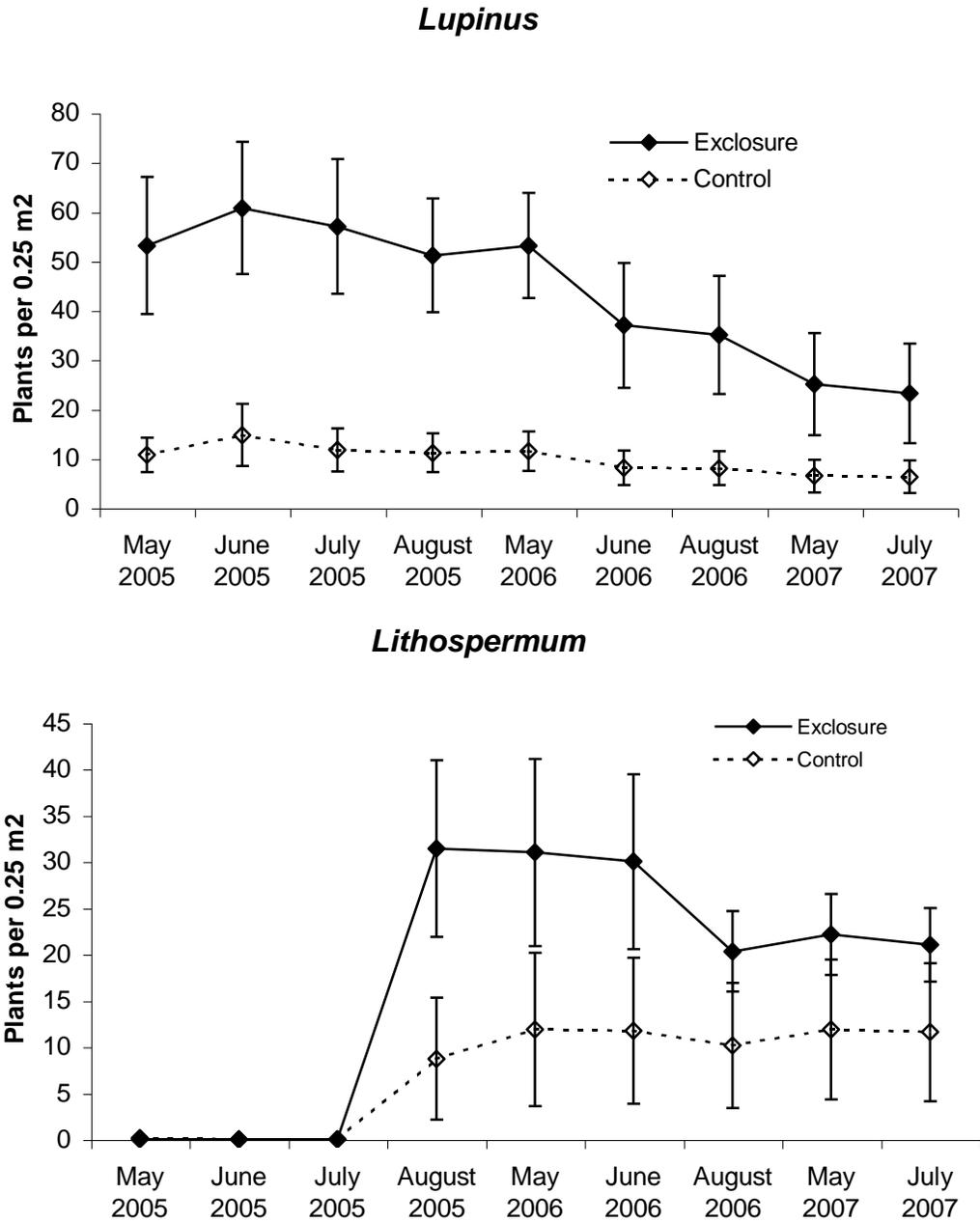


Figure 4: Mean (+ SEM) number of plants in seed addition plots at consecutive census points over the three years following seed addition. These graphs show the seed addition plots receiving the maximum number of seeds for each species—200 seeds per 0.25 m<sup>2</sup> subplot for *Lupinus* and 300 seeds for *Lithospermum*.



Appendix A: Rates of cumulative emergence, establishment, and mortality, for seed addition plots by seed density and small mammal exclusion treatment. Data are from the cohort of seeds added in 2004.

Table 1: Rate of emergence (number of seedlings emerged, per added seed), by seed addition density and small mammal exclusion treatment.

Emergence Rate

Species	Seed density	Exclosure		Control	
		Mean	SE	Mean	SE
<i>Lupinus</i>	25	0.354	0.078	0.160	0.065
<i>Lupinus</i>	50	0.300	0.040	0.226	0.084
<i>Lupinus</i>	100	0.304	0.073	0.129	0.063
<i>Lupinus</i>	200	0.339	0.065	0.084	0.033
<i>Lithospermum</i>	50	0.197	0.035	0.106	0.039
<i>Lithospermum</i>	100	0.200	0.041	0.046	0.017
<i>Lithospermum</i>	200	0.209	0.040	0.070	0.047
<i>Lithospermum</i>	300	0.170	0.042	0.062	0.043

Table 2: Rate of establishment (number of plants established at final census, per added seed), by seed addition density and small mammal exclusion treatment.

Establishment Rate

Species	Seed density	Exclosure		Control	
		Mean	SE	Mean	SE
<i>Lupinus</i>	25	0.137	0.058	0.040	0.028
<i>Lupinus</i>	50	0.080	0.047	0.046	0.022
<i>Lupinus</i>	100	0.124	0.062	0.033	0.013
<i>Lupinus</i>	200	0.116	0.050	0.031	0.017
<i>Lithospermum</i>	50	0.043	0.009	0.057	0.027
<i>Lithospermum</i>	100	0.079	0.022	0.016	0.010
<i>Lithospermum</i>	200	0.069	0.028	0.051	0.035
<i>Lithospermum</i>	300	0.059	0.014	0.037	0.024

Table 3: Rate of mortality in seed addition plots (number of plants that died, divided by the total number emerged in each plot), by seed addition density and small mammal exclusion treatment.

Mortality Rate		Exclosure		Control	
Species	Seed density	Mean	SE	Mean	SE
<i>Lupinus</i>	25	0.604	0.142	0.756	0.093
<i>Lupinus</i>	50	0.728	0.108	0.766	0.081
<i>Lupinus</i>	100	0.663	0.129	0.505	0.145
<i>Lupinus</i>	200	0.689	0.096	0.724	0.096
<i>Lithospermum</i>	50	0.692	0.088	0.469	0.185
<i>Lithospermum</i>	100	0.540	0.109	0.711	0.109
<i>Lithospermum</i>	200	0.686	0.091	0.537	0.179
<i>Lithospermum</i>	300	0.567	0.117	0.262	0.164

CHAPTER TWO

SMALL MAMMAL SEED PREDATION REDUCES POPULATION GROWTH IN A  
LONG-LIVED PERENNIAL FORB, *LITHOSPERMUM RUDERALE*

## Abstract

Loss of seeds to consumers is common in plant communities, but the degree to which these losses influence plant abundance or population growth is often unclear. This is particularly the case for post-dispersal seed predation by rodents, as most studies of rodent seed predation have simply quantified spatio-temporal variation in the magnitude of seed loss. In previous work, we showed that seed predation by deer mice (*Peromyscus maniculatus*) substantially reduced the seedling recruitment of *Lithospermum ruderale* (Boraginaceae), a long-lived perennial forb. To shed light on how relatively short-term rodent-driven reductions in seed abundance and recruitment might influence longer-term patterns of *Lithospermum* population growth, we combined experimental results with demographic data in stage-based population models. Model outputs revealed that rodent seed predation had a significant impact on *Lithospermum* population growth rate ( $\lambda$ ). With the removal of post-dispersal seed predation, projected population growth rates increased between 0.02 and 0.10, depending on site. Simulations varying the magnitude of seed predation pressure while holding other vital rates constant showed that seed predation caused significant declines in  $\lambda$  after 40% of seeds were consumed. Seed predation shifts the projected stable stage distribution of populations from one with a high proportion of young plants to one in which larger adult size classes dominate. Elasticities of vital also change, with germination and growth of seedlings and young plants becoming more important with the removal of seed predation. These results demonstrate that rodent granivory can be a potent force limiting the abundance of a perennial forb.

## Introduction

Plant consumers are major constituents of ecological communities and can have significant impacts on plant populations. The circumstances under which that potential is realized, however, remain unclear. We know from many individual-level studies on plants that consumers commonly depress plant size and fecundity, thus reducing the number of available seeds in plant populations (reviewed in: Crawley 1989, Louda et al. 1990, Huntly 1991, Marquis 1992, Crawley 1997). However, our understanding of how these reductions in the performance of individual plants influence long-term patterns of population growth and plant abundance remains much more limited (reviewed in: Gange 1990, Huntly 1991, Louda and Potvin 1995, Crawley 2000, Strauss et al. 2002, Maron and Crone 2006). It is still unclear how commonly reductions in seed abundance due to plant consumers influence plant abundance or dynamics.

Experimental studies quantifying how consumer-driven reductions in plant performance translate to changes in plant abundance are increasing, but are still limited in number (reviewed by Maron and Crone 2006). Most studies of consumer impacts on plant abundance have focused on short-lived plants with limited seed dormancy (Louda 1982a, b, Louda and Potvin 1995, Lennartsson et al. 1998, McEvoy and Coombs 1999, Maron et al. 2002, Rose et al. 2005, Shea et al. 2005). We still know relatively little about how common it is for consumers to limit the abundance or population growth of other types of plants. Long-lived perennial plants, plants with clonal reproduction, and those with long-lived seed banks, all represent common life-history types in ecosystems worldwide, but have received far less study of consumer impacts on their populations. There are several underlying reasons for this. For one, these traits can complicate the

experimental and demographic measurements and methods needed to quantify population impacts of consumers. In addition, plants with these life-histories are often assumed to be buffered at the population level from negative effects of consumers. This is because either: 1) the many reproductive events of long-lived perennials reduce the importance of seed loss in any one season or 2) seed banks “store” reproduction, reducing plant vulnerability to current seed loss. Empirical tests of these assumptions, however, remain rare. As such, our broader understanding of the importance of consumers in limiting plant abundance is still weak.

Not only has most research quantifying the impacts of consumers on plant populations tended to focus on plants with a particular suite of relatively simple life-histories, it has also focused mainly on the effects of sub-sets of the consumer assemblage, usually insects (Louda 1982b, 1983, Crawley 1989, Fagan and Bishop 2000, Maron et al. 2002) or ungulates (Galen 1990, Maschinski 2001, Frank et al. 2002, Knight 2004). Small mammal seed predators, though abundant in many communities, have been largely ignored in these population-level studies (but see Kauffman and Maron 2006, Maron and Kauffman 2006) despite the fact that they can consume large numbers of seeds (Mittelbach and Gross 1984, Brown and Munger 1985, Hulme 1998). Most studies of plant-rodent interactions have focused on understanding how seed predation is influenced by cover type, season, and seed characteristics (e.g. size, density, or nutrient concentration; (Mittelbach and Gross 1984, Hulme 1994, Hoffman et al. 1995, Maron and Simms 1997, Howe et al. 2002, Celis-Deiz et al. 2004)). How these sources of spatio-temporal variation in seed loss influence plant abundance is generally unknown (but see Kauffman and Maron 2006). Classic long-term rodent exclusion studies, mostly

in desert systems, have revealed that granivores can cause profound differences in plant community structure, as large-seeded annual species preferred by rodents increase with rodent exclusion (Brown et al. 1979, Inouye et al. 1980, Davidson et al. 1984, Brown and Heske 1990). While this work illustrates the importance of rodents in influencing community structure, the direct and indirect interaction pathways driving this result are not clear. For example, changes in abundance of particular species after rodent exclusion could be due small or moderate levels of seed predation (i.e., a relatively low proportion of seeds eaten) in a species where the seed stage or seed to seedling transition is extremely important to population growth. Conversely, the changes in composition could be due to extremely high levels of seed predation (i.e. very high proportions of seeds produced are eaten). In addition, rodent exclusion might shift competitive interactions among plants that alter community structure. Understanding which of these mechanisms underlie the observed changes could help us generalize such results and refine our predictions of when small mammal seed predation will be likely to significantly alter plant abundance.

There are several reasons why decreases in seed number due to consumers may not translate into changes in overall plant abundance. First, plant recruitment may be more limited by safe sites for germination than by seed availability. That is, the number of microsites favorable to germination or seedling survival may have more influence on the number of seedlings establishing than does the number of available seeds (Harper 1977, Eriksson and Ehrlén 1992, Crawley 2000). If populations are more strongly site limited than seed limited, seed reduction from consumers will have less power to reduce plant abundance. Second, even if a population is shown to be strongly seed-limited, if

seedling and young plant mortality is high, the short-term differences due to seeds lost to predation may be overshadowed later by other sources of mortality.

In a previous study we quantified how rodent seed predation by deer mice (*Peromyscus maniculatus*) affected the emergence of seedlings and the establishment of juvenile plants of a long-lived, large-seeded forb, *Lithospermum ruderale* (Boraginaceae). Through rodent exclusion and seed addition experiments, we found that cumulative seedling emergence was over 2.5 times higher in seed addition plots protected from rodent seed predators, compared to plots exposed to rodents (Bricker et al. *In press*). These reductions in seedling emergence remained significant up to two years after seedlings emerged, as there was no evidence of compensatory density dependence at these early life stages (Bricker et al. *In press*).

In this paper, we examine the extent to which changes in the number of seedlings and young plants that establish due to rodent seed predation influence the population growth of *L. ruderale*. This species has large seeds that make it vulnerable to seed predation and seed limitation, yet at the same time, possesses life history attributes such as long adult life-span and seed dormancy (albeit limited) that may buffer it from negative population-level impacts of seed predation. To infer population-level consequences of post-dispersal seed predation, we combined results of rodent exclusion and seed addition experiments with demographic monitoring and population modeling.

### Study System

Experiments and demographic monitoring took place in three study sites (Blackfoot, Bandy, and Kleinschmidt) dispersed over approximately 30 km of semi-arid grasslands in the Blackfoot Valley of western Montana. The plant community in these

grasslands is dominated by native perennial bunchgrasses (*Festuca idahoensis* and *Festuca scabrella*) and sagebrush (*Artimisia tridentata*) and contains a high diversity of native forbs. Exotic species are present at these sites but generally occur at very low densities.

The focal plant species, *Lithospermum ruderale* is a long-lived native perennial forb that is a common, but not dominant, member of the grassland plant community. It begins aboveground growth in late April to early May and flowers between May and early July. It grows as a cluster of one to many upright stems emerging from a common taproot. Flowers occur on short cymes born in the leaf axils or at the end of the stems. *Lithospermum* flowers are visited by a variety of generalist insect pollinators, including bumblebees, hawkmoths, solitary bees and flies (M. Bricker, personal observation). Plants sets seed in late July and August; relatively heavy seeds (mean  $\pm$  SD seed wt. =  $0.0211 \pm 0.005098$  g) fall from the plants as they mature in August and September. Seeds have a thick seed coat, lack eliasomes, and are not dispersed by ants.

Although several small mammal species are present at our study sites (deer mice, *Peromyscus maniculatus*; montane voles, *Microtus montanus*; northern pocket gophers, *Thomomys talpoides*; Columbian ground squirrels, *Spermophilis columbianus*; and (rarely) yellow-pine chipmunks, *Tamias amoenus*; shrews, *Sorex*; and hares, *Sylvagus nutallii*), deer mice are the main post-dispersal seed predator. The other small mammal species are primarily herbivorous, florivorous, insectivorous or, in the case of *S. columbianus*, inactive when seeds are being dispersed from these plants at the end of the summer. This study used 10 m x 10 m small mammal exclosures that were constructed in the spring of 2002. At each site, one 10 m x 10 m control plot was paired with one 10

x 10 m small mammal enclosure. A detailed description of the small mammal enclosures is given in Bricker et al (in press).

### Field Methods

Seed experiments: In order to estimate rates of seed predation and seedling germination, we carried out seed addition experiments using the small mammal enclosures described above. In 2004 and 2005, we added locally collected seeds to 0.25 m by 0.25 m sub-plots in 10 m x 10 m paired small mammal enclosure and control plots. In 2004 we added seeds at densities of 50, 100, 200, and 300 seeds per 0.25 m<sup>2</sup>, to subplots in and out of rodent enclosures at each site. In 2005 seeds were added at just one density; each site had one pair of seed addition sub-plots (one in enclosure and one in control) with 100 added seeds. At each site, we followed and recorded the emergence and survival of seedlings and young plants from both seed cohorts during the spring and summer of 2005, 2006, and 2007 (see Bricker et al. in press for details). These data were used to calculate rates of seedling emergence and seed predation.

To examine rates of seed survival in the soil seed bank, we performed seed burial experiments at these same sites. In the late summer of 2004 and 2005 we buried bags containing locally collected *Lithospermum* seeds at each site. Bags were 5 cm x 5 cm, made of 3 mm fiberglass mesh, and buried 1-2 cm deep in the soil. Each bag contained either 25 or 30 seeds. In August of 2005, 2006, and 2007, we excavated seeds buried the previous year and quantified how many of the original seeds remained intact. In 2005 and 2006, half of the seeds left intact were buried again to estimate survival to 2 years. Seeds missing or visibly damaged were considered removed from the seed bank through either germination or decay. These data, together with the germination data from seed

addition and rodent exclusion experiments, were used to estimate parameters related to seed survival in the soil seed bank, as detailed below.

Demographic monitoring: In the spring of 2005, we established permanently marked 0.5 m-wide belt transects through naturally occurring *Lithospermum* populations at each site, extending the transects until they included at least 120 adult (non-seedling) individuals (total transect lengths = 75 - 100 m). We marked and measured the size of all *Lithospermum* plants, including seedlings, that occurred on each transect. We monitored marked plants from spring 2005 through summer of 2007, which yielded three years of demographic data, and two transitions. Each year we measured the size of plants in several different ways: number of stems, height of tallest stem, average stem height, total stem height (the sum of the heights of all stems on an individual), and canopy area, (calculated by multiplying the length and width, measured parallel and perpendicular to the length of the demography transect, respectively). Size measures were taken in May (spring census) and August (summer census). During the spring census, we recorded whether each individual flowered or not, and marked any new seedlings. We recorded mortality of any marked plants in both spring and summer censuses. At the summer census we estimated fecundity by counting the number of seeds on each plant.

Selecting size metric and size class boundaries: Upon examining the data from the two censuses in each year, it was evident that many smaller plants and seedlings had senesced by the late-summer censuses and thus were not represented in that census. Therefore, the spring size measurements provided the most-complete data set, and were

used to classify plants by size. Seed counts from the late-summer censuses were used to calculate fecundity. We used logistic regression to determine which of the field measures of plant size best predicted survival and flowering probability (Morris and Doak 2002). Canopy area (ln transformed) provided the most explanatory power of survival and flowering for adult plants in models including size, site, year, and site x size interaction (for survival:  $r^2 = 0.1370$ ,  $P < 0.0001$ ; for flowering  $r^2 = 0.5385$ ,  $P < 0.001$ ), so this was used as the size metric for determining size classes.

Plants were divided into stages based on size for adults, and life stage. Seeds and seedlings represent distinct, time-bounded biological states, and are therefore treated as stage-classes. Seed classes (one and two year old seeds) are age-based, as is the seedling class. *Lithospermum* seedlings retain their cotyledons for much of the growing season, and were thus easy to distinguish from small plants. Plants that are older than seedlings (one year or more) are divided into size classes based on the measure of their canopy area.

Logistic regressions examining the relationship between size and survival showed stage (seedling or adult) and stage by size interactions to be significant. Within seedlings, there was no relationship between size and survivorship, so further regression analyses examining size and survival, flowering probability, and fecundity, excluded seedlings. We used logistic regression to determine size-class boundaries based on the relationship between plant area, survival, and probability of flowering (Morris and Doak 2002). We also used visual inspection of the graphical data to examine the minimum size for seed production and rates of fecundity versus size, to choose size class boundaries. Based on these patterns we divided adult (non-seedling) plants into three size classes

based on their canopy area: small ( $\leq 12 \text{ cm}^2$ ), medium ( $> 12 \text{ cm}^2$  to  $\leq 50 \text{ cm}^2$ ), and large ( $> 50 \text{ cm}^2$ ).

Parameter estimation: We estimated survival probability for the three adult size classes using the two-step process outlined in Morris and Doak (2002). That is, we first created a logistic regression of survival on canopy area (ln-transformed) using the whole dataset. When there were significant differences (based on Type III SS from logistic regression in PROC LOGISTIC, SAS) between sites, we generated separate regression equations for each site. We then used the fitted regression equation to calculate survival for each class based on the median size of individuals in that class at each site. We calculated seedling survival with counts from demographic data at each site. Data from the two transitions (i.e. the three years of data) were combined in these estimates.

We used the same general procedure to estimate the probability of flowering, creating a logistic regression relating whether an individual flowered and its canopy size. We used this fitted logistic regression equation to generate a probability of flowering for the medium and large size classes, based on the median size of individuals in that class. Small individuals were never observed to flower, so there is no term for flowering probability or fecundity for the small adult size class. Fecundity was calculated from the average number of seeds produced by a flowering plant in each size class.

The probability of surviving plants transitioning between classes was calculated directly from field counts. The proportion of surviving individuals in each size class transitioning to each of the other size classes (or staying in the same class) was calculated for each site. For the seedling stage, survival equals transition; all surviving seedlings move to the smallest adult size class at the next time step. No small adult to large adult

transition occurred at any site or year, so this transition was not included in the matrix analysis.

Seedling emergence rates and rates of dormancy in the soil seed bank were estimated using data from seed addition and buried seed-bag experiments. In these experiments, many seeds germinated in the second spring after they were produced, but few germinated in their first spring. This meant that rates of seedling emergence and seed predation could not be measured directly, because some unknown number of seeds initially added to the plots could die in the seed bank during the first year, making the size of the seed pool available to germinate in the second spring unknown. To circumvent this problem, we estimated seedling emergence using a mechanistic model of seedling emergence and survival. We generated maximum-likelihood estimates of: 1) the probability of a seedling emerging in year 1 (the first spring following the seed's production;  $P_{m1}$ ), 2) the probability of a seedling emerging in year 2 ( $P_{m2}$ ), 3) the probability of a seed dying in year 1 ( $P_{d1}$ ), 4) the probability of a seed dying in year 2 ( $P_{d2}$ ), 5) the probability of a seed being eaten by rodents in year 1 ( $P_{m1}$ ), and 6) the probability of a seed being eaten by rodents in year 2 ( $P_{m2}$ ) (Appendix A, Table 1). The sequence of seed fates was modeled such that seed predation occurred first, which is consistent with field observation suggesting that most seed predation occurs soon after seeds are released from the plants. Thereafter, seeds that are not eaten can germinate, die, or remain in the seed bank at each time step. The seed stages were age-based, and seeds were forced to progress through the age structure at each time step and did not live past three years old, which was consistent with the survival of seeds in the buried seed bag experiments.

Maximum likelihood estimates for the seed parameters were based on the observations (experimental outcomes), listed in Appendix A, Table 2. Within each set of data from seed burial and seed addition experiments at a given site and year, we constructed a joint probability function based on a binomial distribution, for the probability of each of the observed events. The general form of the binomial probability function is:

$$\text{Probability } (p) \text{ of } k \text{ events in } N \text{ trials} = p^k (1-p)^{N-k} \frac{N!}{k!(N-k)!}$$

Within a data set the final factorial term is a constant, so we dropped that term from the probability functions and wrote the probability of the observed number of events ( $k$ ) out of ( $N$ ) number of trials (e.g.,  $k$  = number of seeds that survive, out of  $N$  seeds buried in seed bags), as:

$$p^k (1-p)^{N-k}$$

This generated six joint likelihood functions within each data set (one for each observation). We used the solver function in Microsoft Excel (version 2003) to maximize the sum of the natural log of these likelihood functions, by changing the values of the six estimated parameters. The probability functions for each of the observations are given in Appendix A, Table 3. The maximum likelihood solutions created a set of estimated parameters that were most likely, given the data, for each set of observations, and thus avoided the problem of impossible combinations of rates that could occur if trying to calculate the parameters directly from each of the separate experiments. At each site we used data from 4 different seed addition plot pairs (the four different seed

densities, inside and outside of rodent exclosures) from 2004, and the data from the 100-seed addition plots in 2005.

We used likelihood ratio tests (Burnham and Anderson 1998) to test the significance of site and year by comparing models including site or year to those that did not, for each parameter. The likelihood ratio test compares relative support for two nested models using the formula:

$$2LL(\text{reduced model}) - (-2LL(\text{full model}))$$

to generate a test statistic that follows a chi-square distribution with degrees of freedom equal to the difference in the number of parameters between the two models. It thus penalizes a model that has extraneous parameters that do not significantly improve the fit of the model.

#### Model structure and simulations

We used the vital rates from demographic monitoring and our rodent exclusion experiment to construct stage-based matrix models with the general form of  $\mathbf{N}_{t+1} = \mathbf{A}\mathbf{N}_t$ , where  $\mathbf{N}$  is a vector of the number of individuals in each size class (and subscripted to denote an annual time step). The transition matrix  $\mathbf{A}$  is made up of matrix elements ( $a_{ij}$ ) representing the stage-specific transition rates calculated from vital rates (germination, survival, growth, fecundity, and seed predation (Appendix B). Figure 1 shows the life cycle diagram illustrating the stages and transitions comprising the matrix model.

Maximum likelihood estimates for seedlings emerging in year 2, and the probability of seeds dying in both years were significantly different between sites;

therefore we kept estimates of seed parameters separate by site. Year was a significant factor for the probability of seeds germinating or dying in both years. For adult vital rates, there were significant differences by site in estimates of survival and flowering probability; again, we calculated adult vital rates separately by site. We used these site-specific vital rates to create transition matrices for each of the three sites independently. The probability of germinating in the third spring after a seed is produced (i.e., from the “seed 2” class) was assumed to be equal to the probability of germinating in the second year ( $P_{g2}$ ). Models projecting population growth with rodent seed predation (“with mice”) included the probability of seeds being eaten ( $P_{m1}$ ,  $P_{m2}$ ); those projecting population growth in the absence of seed predation (“no mice”) did not (Appendix B).

With only two transitions, our ability to incorporate temporal variation into matrices was extremely limited; therefore, we averaged vital rate estimates between the years, for the matrices used to calculate sensitivity, elasticity, and stable age distribution. Within each site, we calculated a mean for each vital rate (combining the observations across multiple years, but keeping sites separate). These vital rates were combined into matrices used to calculate the elasticity of vital rates and the stable age distribution, with and without mice, at each site (Morris and Doak 2002). Table 2 shows the parameterized matrices resulting from the mean vital rate estimates.

To test the robustness of the model results to parameter uncertainty, and examine the significance of the change in  $\lambda$  due to removing rodent seed predation, we calculated growth rates as a bootstrap analysis based on re-sampling from the original datasets. For each vital rate, we resampled with replacement from the original data, and calculated that vital rate at each bootstrap iteration, from the re-sampled data (McPeck and Kalisz 1993).

For vital rates relating to seedling and adult survival, flowering, fecundity, and transitions between stages, the raw data for the bootstrapping came from the measurements of individual plants on demographic transects at each site. For seed-related vital rates (germination, survival in seed bank, and probability of being eaten by rodents), the data array for the bootstrapping was made up of the 5 maximum likelihood estimates for that site. We used these bootstrapped vital rates to calculate population growth rate ( $\lambda$ ) in the presence of small mammals. We calculated the mean of these 1,000 iterations, and 95% confidence intervals of  $\lambda$  by ordering the 1,000 estimates of  $\lambda$  and selecting the 25<sup>th</sup> and the 975<sup>th</sup> values as the lower and upper confidence limits, respectively.

This estimate of  $\lambda$  and its confidence intervals includes variance from all of the vital rates simultaneously. To estimate the difference (and confidence limits around that difference) in growth rate due specifically to small mammal seed predation ( $\Delta\lambda$ ), we created a bootstrapping routine where at each iteration, two matrices were built from the resampled vital rates. One matrix included seed predation while the other did not, but in all other vital rates, the two matrices were the same. At each iteration we calculated  $\lambda$  of both matrices and generated a metric of the change in growth rate ( $\Delta\lambda$ ) as:

$$\Delta\lambda = \lambda_{\text{no-mouse}} - \lambda_{\text{mouse}}$$

to reflect the increase in growth rate that would occur with the exclusion of rodent seed predation. As with the  $\lambda$  estimates, we calculated a mean and 95% confidence intervals for  $\Delta\lambda$  based on the 1,000 bootstrap iterations.

In order to examine how populations might respond to varying levels of seed predation, we calculated  $\Delta\lambda$  across a range of simulated predation intensities. These projections were done using the same bootstrapping methods described above, with the

exception of the mouse predation term ( $Pm_1$ ). In these simulations, we bootstrapped for the probability of seed predation using an array of ten numbers, with the proportion of 1's (seed eaten) and 0's (not eaten) varying to reflect a mean probability of being eaten between 0.1 and 1. We calculated a mean and 95% confidence interval for the value of  $\Delta\lambda$ , at each simulated rate of seed predation, for each site.

## Results

Likelihood ratio tests for the seed-related parameters revealed that the ability to parameterize the seed predation rates in years one and two separately was very low. Models that assumed that all seed predation occurred in year one (second year seed predation set to zero) performed significantly better in likelihood ratio tests ( $\chi^2 = 41.87$ ,  $P < 0.001$ ). This is consistent with field observations that most seeds are consumed in the first fall and winter after they are released from the plant. In our models, therefore, all seed predation occurs in the first year. Vital rates for both seed and adult parameters are reported in Table 1 for each site. Parameterized matrices built from these vital rates are reported in Table 2.

The average of the maximum likelihood estimates for seed predation ranged from 0.60 at Blackfoot, 0.89 at Kleinschmidt, to 0.99 at Bandy (Table 1). For Bandy, this seed predation rate estimate was consistent across all five combinations of observed patterns of germination and survival. Blackfoot and Kleinschmidt showed more variation in the sets of maximum likelihood estimates, with estimates ranging from 0 to 0.99 at Blackfoot, and 0.46 to 0.99 at Kleinschmidt.

*Lithospermum* populations exposed to ambient levels of post-dispersal seed predation by deer mice were relatively stable all three sites (Bandy  $\lambda = 0.966$ , 95% CI =

0.932 – 0.992; Kleinschmidt  $\lambda = 0.980$ , 95% CI = 0.950 – 1.01; Blackfoot  $\lambda = 1.08$ , 95% CI = 0.981 – 1.18; Fig. 2). When population growth was simulated in the absence of post-dispersal seed predation, population growth rate of *Lithospermum* increased significantly at all three sites ( $\Delta\lambda$  for Blackfoot = 0.0702, Bandy = 0.1169, Kleinschmidt = 0.0555; Fig. 3). Although populations at the three sites differed in their projected responses to seed predation (Fig. 3), the 95% confidence intervals around the estimate of the difference between populations with and without seed predation ( $\Delta\lambda$ ) did not overlap zero for any of the sites, indicating a significant impact of rodent seed predators on population growth rates across the sites.

Simulations varying the strength of seed predation showed that the difference in population growth rate due to seed predation ( $\Delta\lambda$ ) consistently increased with an increasing magnitude of seed predation. Interestingly, however, simulated seed predation that resulted in the death of between only 30-40% of available seeds was sufficient enough to reduce the growth rate of populations.

The stable stage distributions for the three sites shifted with the exclusion of seed predators (Fig. 6). In the absence of seed predation, the proportion of seeds and younger plants in the population became much higher than when seed predation was at natural levels. When seed predation was present, the largest stage classes dominated populations, whereas the seed and small plant stages were more dominant when seed predation was removed.

Elasticity analysis showed that regardless of seed predation, the vital rates with the largest elasticity value were the survival and stasis of individuals in the large-adult stage class (Fig. 5). The elasticity of these vital rates, though still quite high, was lower

in the presence of small mammal seed predation. With the exclusion of seed predators, the elasticity of reproductive vital rates (flowering probability and fecundity) increased, as did the importance of germination and seed survival (Fig. 5).

### Discussion

Small mammal seed predation caused a significant decline in projected population growth compared to what *Lithospermum* would experience without seed predation (Fig. 3). Thus, background levels of seed predation in these grassland communities is sufficient to lower the abundance of *Lithospermum* relative to what it could be in the absence of rodent seed consumers. A population modeling approach was especially useful in this case because *Lithospermum* has very slow rates of growth and a relatively long lifespan; based on our demography data, plants may live over 30 years. Therefore, empirically determining how these populations respond to rodent seed predators would be impractical in a standard experimental time frame.

For plants with a life-history strategy in which population growth relies directly on seed production each year, it follows that seed predation would have great potential to impact plant population growth. Our results, however, suggest that the potential for seed consumers to limit plant abundance is not restricted solely to plants where seed-related vital rates have high importance to population growth. Using demographic data for *Lithospermum*, we found low elasticity values for seeds, as has been commonly found for other long-lived perennial plants (Silvertown et al. 1993, Franco and Silvertown 2004), suggesting that there is little scope for consumer-driven changes in seed availability to alter plant abundance and population dynamics. Yet seed predation in our system was of

sufficient magnitude to reduce population growth of *Lithospermum* despite the low elasticities of the vital rates associated with the seed-to-seedling transition. Furthermore, the elasticity of different vital rates shifted depending on whether there was seed predation in the matrix or not. In the absence of seed predation, vital rates related to reproduction, germination, and growth of small plants increased relative to the importance of survival and stasis of older, larger plants. The fact that this biotic interaction shifted the elasticity values in the population suggests that we should be cautious in concluding that species interactions affecting low-elasticity vital rates will not affect population dynamics. Rather, it may also be important to also take into account the variation possible in those vital rates.

Seed predators are generally assumed to have greater impacts when populations are limited more by seeds than by microsites (Harper 1977). Systems that have represented most of the work on plant population responses to seed predation have been those where we might expect seed availability to be more limiting than microsites—generally, desert and dune systems, and planted prairie restorations, where seeds were added to initially bare ground (Edwards and Crawley 1999, Howe and Brown 2000, Howe and Brown 2001, Howe and Lane 2004, Howe et al. 2006). Greater cover of vegetation has been shown to inhibit seedling germination (Eriksson and Ehrlén 1992, Reader 1993), leading to the expectation that communities with denser vegetation will be less seed limited, and more site limited. This work complements what has been done in these other systems, showing that even in a higher cover environment, species may exhibit population-level responses to post-dispersal seed predation.

Our results also demonstrate the utility of incorporating experimental data on consumer impacts on a particular demographic transition in demographically-based stage-structured population models. For many species, particularly in areas with short growing season or harsh conditions, a slower life-history pattern is common, typified by long-lived adult stages, variable fecundity, and slow growth. These common life-history features can make direct observation of changes in abundance due to experimental manipulation of consumer pressure often unfeasible in an experimental time frame. Our work suggests that patterns of changing abundance of large-seeded plants observed in small mammal enclosure studies in other systems are not confined to the unique communities (primarily deserts) or life-histories (generally annual plants) that they studied. Even in this grassland community, with greater vegetative cover, and therefore less seed limitation, the impacts of small mammal seed predators are significant.

While our approach allowed us to forecast the long-term population-level consequences of rodent seed predation on *L. ruderalis*, there are several important caveats to bear in mind. First, we used deterministic population models, despite the fact that some vital rates differed between years. Having only three years of demographic data (two transitions) limited our ability to incorporate temporal variation in the matrix projections. As well, for models with fewer than five years of data, a deterministic model can be more accurate than a stochastic model based on limited data (Doak et al. 2005). Beyond these considerations, our primary goal was not to generate an extremely precise estimate for *L. ruderalis* population growth rate. Rather, we sought to determine how post-dispersal seed predation might change population growth. By bootstrapping from

re-sampled data from both years for all vital rates, we did incorporate temporal variation in vital rates into our estimates for how seed predation altered  $\lambda$  (i.e.  $\Delta\lambda$ ).

Second, we used an exponential population model that does not incorporate density-dependence in any form. Clearly, in a confined space, the density of individuals will, at some point, begin to cause decreases in the performance of individual plants, which can feed back to depress population growth. However, in previous work, we did test for negative density dependence and we did not find evidence for this. In seed plots where seedling density varied across a range of seed densities, we found no differences in the mortality rate of seedlings or young plants (Bricker et al, in press). Plant size at 2 years old was also not affected by density of plants in these plots (M. Bricker, unpublished data). We recognize that density-dependence could occur at other life stages. Yet in our system, plants were fairly sparsely distributed; thus there would need to be a dramatic increase in plant abundance due to release from rodent seed predation, before density dependence began to cause declines in plant performance. A central challenge for future work in this area is to determine how best to incorporate density dependence into population models that estimate consumer impacts on plant population growth/abundance (Halpern and Underwood 2006).

Finally, we recognize that some of the seed loss that influences recruitment in seed addition plots may occur because of dispersal as opposed to predation. That is, rodents that consume seeds may not always consume the seeds immediately, but may store them in surface-caches. Thus, there is always the possibility that not all of the seeds removed from our small-scale seed addition plots were actually eaten. However, there are several reasons why we think this unlikely to affect our results. First, deer mice often

break open the hard outer seed coat of *Lithospermum* seeds, eat the endosperm, and leave the seed coat. We often found empty seed coats in or near control (rodent access) seed addition plots, suggesting that seeds were being eaten near where they were discovered (M. Bricker, personal observation). Secondly, the demographic monitoring and searching of seed addition plots for seedlings required close scrutiny of the soil surface, and in 3 years, searching over 50 square meters at each site, we found only four instances of what appeared to be seedlings germinating in seed piles from a forgotten cache (M. Bricker, personal observation). Finally, other studies have shown that most of the seeds cached by rodents are ultimately consumed or die (Vander Wall 1998).

Historically, post-dispersal seed predators have often been assumed to have little impact on plant abundance, due in part to the assumption that any population has some surplus of seeds beyond what is needed to maintain the population. Furthermore, it has often been assumed that seed removal rates need to be severe in order for impacts to be felt at the population level. Harper (1977) encapsulated this idea by suggesting that a population could sustain tolerable levels of seed predation, wherein a certain number of seeds that were “doomed to die” from various other causes (as seeds or at later stages), could be eaten by consumers without substantially altering the numbers of adults in the population. In the *Lithospermum* populations we studied, however, the ambient levels of post-dispersal seed predation do not appear to fall within the range of “tolerable” seed predation. Moreover, based on our simulations, even reductions in seed availability of approximately 40% (well below what we estimated) would be sufficient to suppress population growth rates. This shows a similar pattern to work done with insect seed predators, in which Louda and Potvin (1995) showed, with a modified version of

Harper's original model, that there would be only a very minimal amount of seed predation (if any) that might be "tolerable" and that this was well below the levels observed in their system. In fact, the levels of seed predation that do not cause some reduction in plant density or population growth may generally be very small.

Figure 1. Life cycle diagram for *Lithospermum ruderale*, showing stages and transitions used in the matrix models.

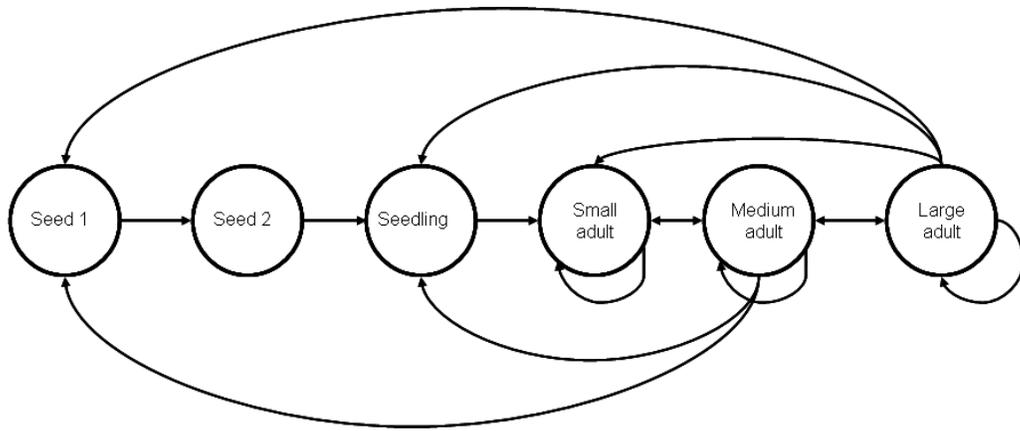


Figure 2. Population growth rate at each of the three sites, in the presence of small mammal seed predation.

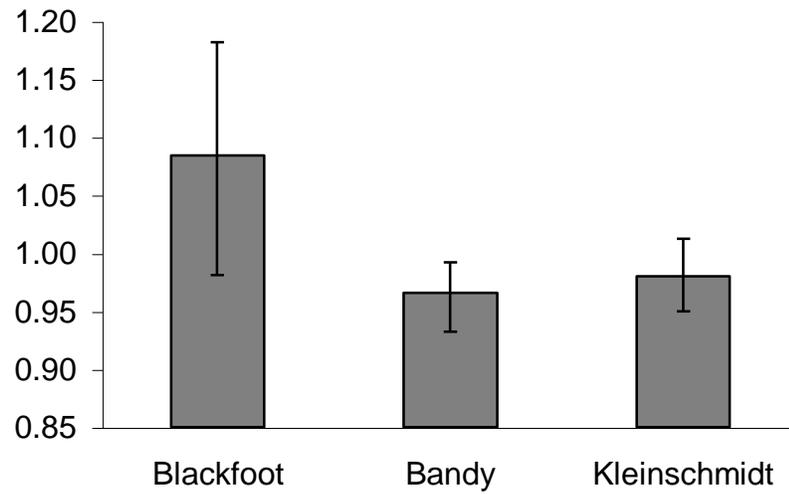


Figure 3. Difference in growth rate ( $\Delta\lambda$ ) due to release from seed predation by small mammals ( $\lambda$  without mice –  $\lambda$  with mice) at each of the three sites. Error bars show 95% confidence intervals generated by 1,000 bootstrap iterations.

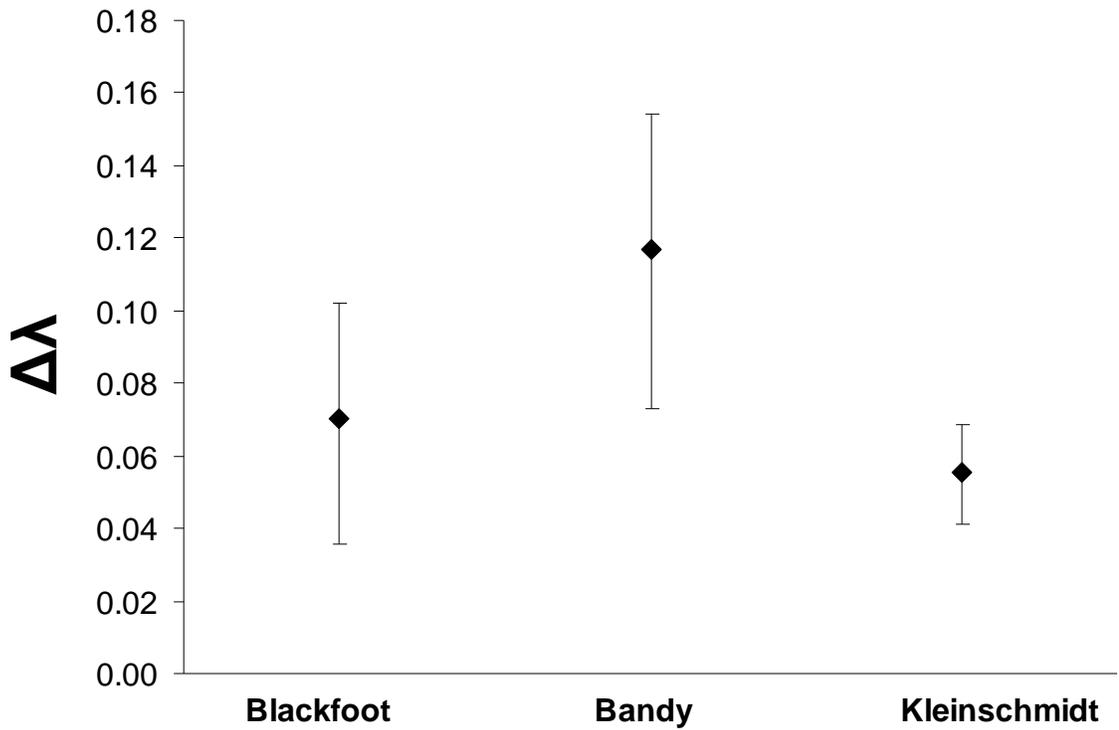


Figure 4. The difference in population growth rate calculated across a range of simulated seed predation intensities. Arrows indicate the natural level of seed predation estimated for each site.

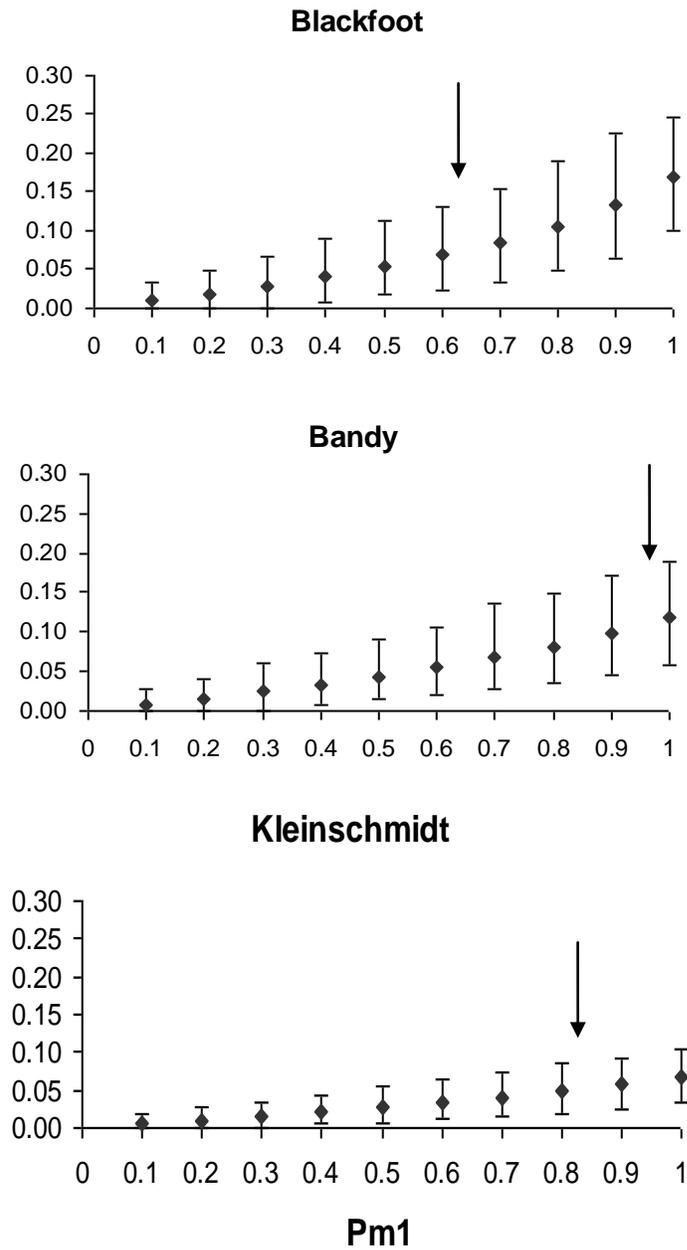


Figure 5. Elasticities of the vital rates underlying the matrix for each site.

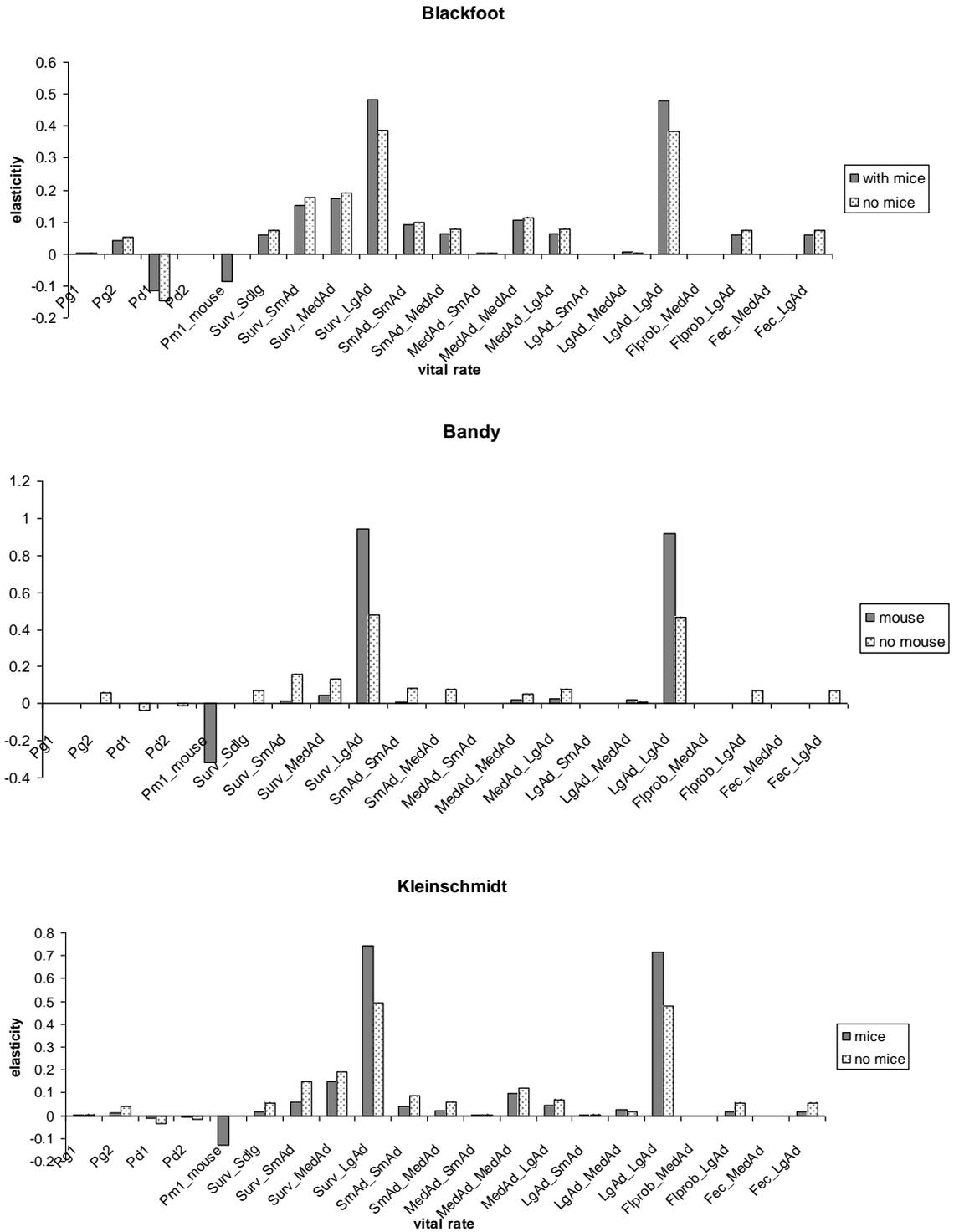


Figure 6. Stable age distributions projected from the matrix for each site, with and without rodent seed predation. The relative proportion of larger and older plants is dramatically lower when small mammal seed predation is prevented.

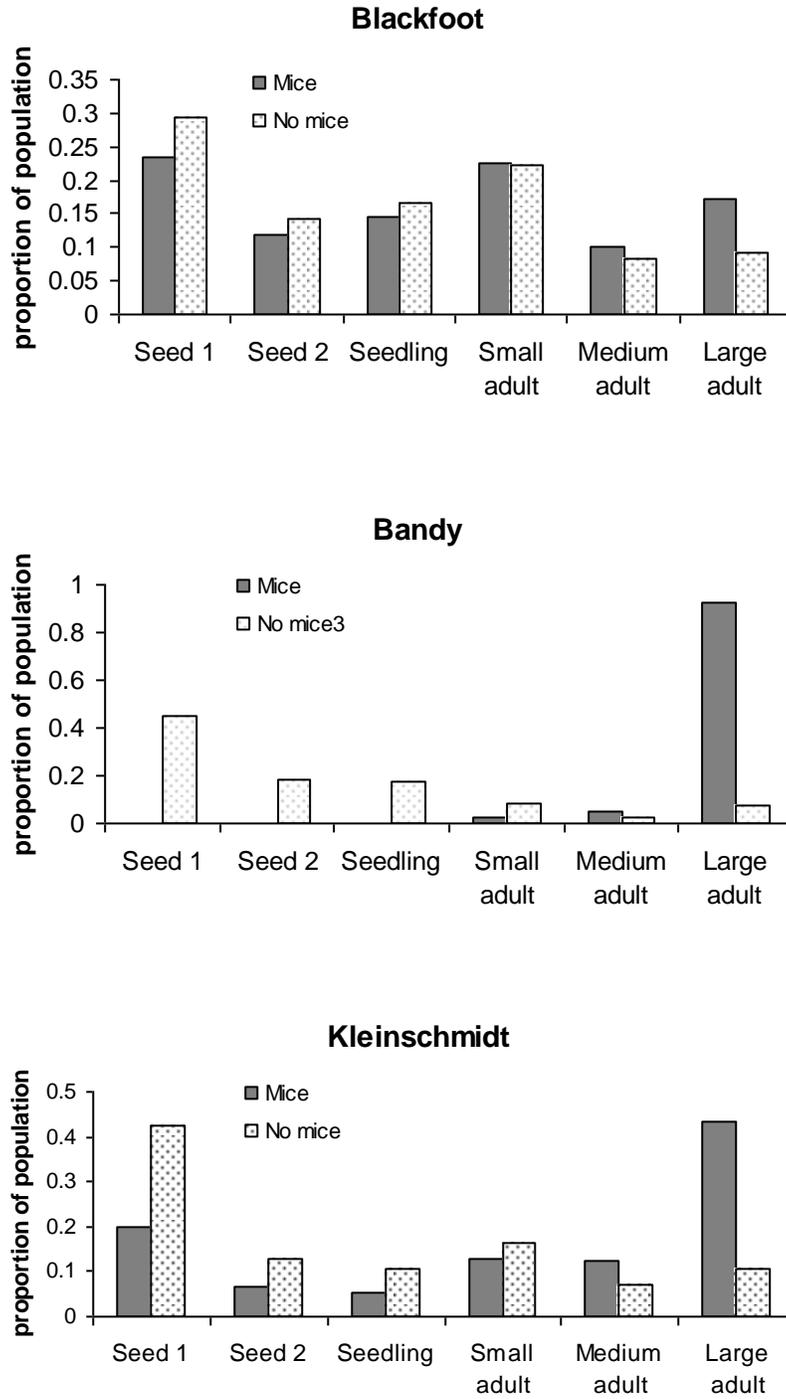


Table 1. Mean vital rates for each site.

<b>Vital rate symbol</b>	<b>Vital rate description</b>	<b>Blackfoot</b>	<b>Bandy</b>	<b>Kleinschmidt</b>
Pg1	probability of a seed germinating in first year	0.0078	0.0080	.00980
Pg2	probability of seed germinating in second year (applies only to seed 1 class)	0.4284	0.2955	0.1907
Pd1	probability of seed dying in seed bank in first year	0.6678	0.3524	0.3954
Pd2	probability of seed dying in seed bank in 2nd year	0.0118	0.2516	0.4880
Pm1	probability of seed being eaten by mice in year1	0.6000	.99999	0.8928
Pm2	probability of seed being eaten by mice in year 2	0	0	0
Surv_Sdlg	seedling survival	0.6634	0.2564	0.5915
Surv_SmAd	small adult survival	0.8300	0.7775	0.7765
Surv_MedAd	medium adult survival	0.9475	0.9455	0.9395
Surv_LgAd	large adult survival	0.9912	0.9855	0.9878
SmAd_SmAd	small adult stasis	0.7899	0.75	0.8254
SmAd_MedAd	transition: small adult to medium adult	0.2101	0.25	0.1746
SmAd_LgAd	transition: small adult to large adult	0	0	0
MedAd_SmAd	transition: medium adult to small adult	0.05405	0.05172	0.07792
MedAd_MedAd	medium adult stasis	0.7162	0.4655	0.7013
MedAd_LgAd	transition: medium adult to large adult	0.2297	0.4828	0.22078
LgAd_SmAd	transition: large adult to small adult	0	0.008264	0.007576
LgAd_MedAd	transition: large adult to medium adult	0.01941	0.02479	0.0530
LgAd_LgAd	large adult stasis	0.9806	0.9669	0.9394
Flprob_MedAd	medium adult flowering probability	0.02424	0.07843	0.06479
Flprob_LgAd	large adult flowering probability	0.9272	0.78471	0.8434
Fec_MedAd	medium adult fecundity (of flowering ind'ls)	1.000	2.375	0.25
Fec_LgAd	large adult fecundity (of flowering idl's)	12.52	12.68	8.310

Table 2: Parameterized matrices for each site built from vital rates presented in Table 1. For matrix elements that differ in the presence of seed predators, the value in the absence of seed predation is shown italicized and in parenthesis in the row below the with-predation values.

Blackfoot

	Seed 1	Seed 2	Seedling	Small adult	Med. adult	Large adult
Seed 1	0	0	0	0	0.0031 (0.0079)	1.5070 (3.7674)
Seed 2	0.5598	0	0	0	0	0
Seedling	0.4284	0.4284	0	0	0.0001 (0.0002)	0.0362 (0.0906)
Small adult	0	0	0.6634	0.6556	0.0512	0
Med. adult	0	0	0	0.1744	0.6786	0.0192
Large adult	0	0	0	0	0.2177	0.9720

Bandy:

	Seed 1	Seed 2	Seedling	Small adult	Med. adult	Large adult
Seed 1	0	0	0	0	0.000000001 (0.1191)	0.0001 (6.3643)
Seed 2	0.4529	0	0	0	0	0
Seedling	0.2955	0.2955	0	0	.0000000001 (0.0015)	.000000001 (0.076)
Small adult	0	0	0.2564	0.5832	0.0489	0.0081
Med. adult	0	0	0	0.1944	0.4402	0.0244
Large adult	0	0	0	0	0.4565	0.9530

Kleinschmidt:

	sd1	sd2	sdlg	smad	medad	lgad
sd1	0	0	0	0	0.0010 (0.0096)	0.4469 (4.1693)
sd2	0.3213	0	0	0	0	0
sdlg	0.1907	0.1907	0	0	0.00001 (0.0002)	0.0074 (0.0687)
smad	0	0	0.5915	0.6409	0.0732	0.0075
medad	0	0	0	0.1356	0.6589	0.0524
lgad	0	0	0	0	0.2074	0.9280

Appendix A.

Table 1. Observations used in maximum-likelihood functions to estimate seed-related vital rates.

<b>Observations:</b>	<b>Symbol</b>
Number of seeds added to seed addition plots	Ns
Number of seedlings in year 1 in rodent-excluded plots	Ks <sub>1</sub>
Number of seedlings in year 2 in rodent-excluded plots	Ks <sub>2</sub>
Number of seedlings in year 1 in rodent-accessible (control) plots	Kr <sub>1</sub>
Number of seedlings in year 2 in rodent-accessible (control) plots	Kr <sub>2</sub>
Number of seeds in bags, at start	Nb
Number of seeds in bags still alive in year 1	Kb <sub>1</sub>
Number of seeds from bags still alive in year 2	Kb <sub>2</sub>

Table 2. Parameters in maximum likelihood models used to estimate seed-related vital rates.

<b>Estimated parameters:</b>	<b>Symbol</b>
Probability of germinating in year 1	Pg <sub>1</sub>
Probability of germinating in year 2	Pg <sub>2</sub>
Probability of dying in year 1	Pd <sub>1</sub>
Probability of dying in year 2	Pd <sub>2</sub>
Probability of being eaten by mice in year 1	Pm <sub>1</sub>
Probability of being eaten by mice in year 2	Pm <sub>2</sub>

Table 3. Likelihood functions for maximum likelihood estimates of seed-related vital rates.

<b>Likelihood functions:</b>	
Likelihood for Ks <sub>1</sub>	= $Pg_1^{Ks_1} * (1 - Pg_1)^{(Ns - Ks_1)}$
Likelihood for Kb <sub>1</sub>	= $(1 - Pg_1 - Pd_1)^{Kb_1} * (Pg_1 + Pd_1)^{(Nb - Kb_1)}$
Likelihood for Ks <sub>2</sub>	= $(Pg_2^{Ks_2}) * (1 - Pg_2)^{(Ns * (1 - Pd_1 - Pg_1) - Ks_2)}$
Likelihood for Kb <sub>2</sub>	= $(1 - Pg_2 - Pd_2)^{Kb_2} * (Pg_2 + Pd_2)^{(Kb_1 - Kb_2)}$
Likelihood for Kr <sub>1</sub>	= $((1 - Pm_1) * (Pg_1))^{Kr_1} * (1 - ((1 - Pm_1) * (Pg_1)))^{(Ns - Kr_1)}$
Likelihood for Kr <sub>2</sub>	= $(1 - Pm_2) * Pg_2^{Kr_2} * (1 - (1 - Pm_2) * Pg_2)^{Ns * (1 - Pd_1 - Pg_1) - Kr_2}$

Appendix B: Matrix structure—shows the vital rates making up each matrix element.

With seed predation

	Sd1	Sd2	Seedling	Small Adult	Medium Adult	Large Adult
Sd1	0	0	0	0	$\text{FlrProb\_MedAd} * \text{Fec\_MedAd} * (1 - \text{Pg1} - \text{Pd1}) * (1 - \text{Pm1})$	$\text{FlrProb\_LgAd} * \text{Fec\_LgAd} * (1 - \text{Pg1} - \text{Pd1}) * (1 - \text{Pm1})$
Sd2	$(1 - \text{Pg2} - \text{Pd2}) * (1 - \text{Pm2})$	0	0	0	0	0
Seedling	$\text{Pg2} * (1 - \text{Pm2})$	$\text{Pg2} * (1 - \text{Pm2})$	0	0	$\text{FlrProb\_MedAd} * \text{Fec\_MedAd} * \text{Pg1} * (1 - \text{Pm1})$	$\text{FlrProb\_LgAd} * \text{Fec\_LgAd} * \text{Pg1} * (1 - \text{Pm1})$
Small Adult	0	0	Surv_Sdlg	Surv_SmAd * SmAd_SmAd	Surv_MedAd * MedAd_SmAd	Surv_LgAd * LgAd_SmAd
Medium Adult	0	0	0	Surv_SmAd * SmAd_MedAd	Surv_MedAd * MedAd_SmAd	Surv_LgAd * LgAd_MedAd
Large Adult	0	0	0	0	Surv_MedAd * MedAd_LgAd	Surv_LgAd * LgAd_LgAd

Without seed predation

	Sd1	Sd2	Seedling	Small Adult	Medium Adult	Large Adult
Sd1	0	0	0	0	$\text{FlrProb\_MedAd} * \text{Fec\_MedAd} * (1 - \text{Pg1} - \text{Pd1})$	$\text{FlrProb\_LgAd} * \text{Fec\_LgAd} * (1 - \text{Pg1} - \text{Pd1})$
Sd2	$(1 - \text{Pg2} - \text{Pd2})$	0	0	0	0	0
Seedling	Pg2	Pg2	0	0	$\text{FlrProb\_MedAd} * \text{Fec\_MedAd} * \text{Pg1}$	$\text{FlrProb\_LgAd} * \text{Fec\_LgAd} * \text{Pg1}$
Small Adult	0	0	Surv_Sdlg	$\text{Surv\_SmAd} * \text{SmAd\_SmAd}$	$\text{Surv\_MedAd} * \text{MedAd\_SmAd}$	$\text{Surv\_LgAd} * \text{LgAd\_SmAd}$
Medium Adult	0	0	0	$\text{Surv\_SmAd} * \text{SmAd\_MedAd}$	$\text{Surv\_MedAd} * \text{MedAd\_SmAd}$	$\text{Surv\_LgAd} * \text{LgAd\_MedAd}$
Large Adult	0	0	0	0	$\text{Surv\_MedAd} * \text{MedAd\_LgAd}$	$\text{Surv\_LgAd} * \text{LgAd\_LgAd}$

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## CHAPTER THREE

### NON-ADDITIVE CONSUMER IMPACTS ON THE POPULATION DYNAMICS OF *LUPINUS SERICEUS*, A CLONALLY REPRODUCING PERENNIAL FORB

## Abstract

Plants are damaged by many different consumers, some of which can substantially reduce individual plant performance. Groups of consumers may act additively, synergistically, or hierarchically, but most studies measure the impacts of a single consumer species. Thus we know little about the collective impacts of damage by suites of consumers or how such damage influences plant population dynamics and plant abundance. In previous work, we showed that post-dispersal seed predation by deer mice (*Peromyscus maniculatus*) significantly reduced the seedling recruitment of *Lupinus sericeus* (Fabaceae), a long-lived perennial forb capable of clonal reproduction through root-sprouting. Here we document the impacts of two other consumers: ground squirrels (*Spermophilus columbianus*) and herbivorous insects (Lepidopteran and Coleopteran larvae) on *L. sericeus* fecundity. We combine these experimental data into stage-based matrix models to examine how these consumers, individually and in concert, influence the population growth of *L. sericeus* at three sites. During the three years of our monitoring, sexual reproduction was virtually eliminated by consumers at two of the sites and dramatically reduced at a third. However, high rates of asexual reproduction enabled populations to persist in the face of this intense consumer pressure. Because consumers sequentially attack flowers, pre-dispersed seeds and then post-dispersed seeds, the opportunities for any given species to influence the population growth rate of *L. sericeus* are contingent on the impacts of the preceding consumer. Release from ground squirrels caused an average increase of 0.022 in  $\lambda$ ; eliminating ground squirrels and insects led to an average increase in  $\lambda$  of 0.034; together, the three types of consumers caused differences in population growth of 0.07 to 0.34. These results suggest that despite high

rates of asexual reproduction, which allows these populations to persist with minimal sexual reproduction, consumers still impose strong limits to the population growth and abundance of this long-lived forb.

## Introduction

Throughout their lives, plants are attacked by a variety of consumers that cause strong reductions in the performance of individual plants (reviewed in: Crawley 1989, Louda et al. 1990, Huntly 1991, Marquis 1992, Crawley 1997). The effects of these consumer-related declines in plant performance remain poorly studied. Many studies have quantified the individual and collective impacts of different consumers on plant performance (Strauss 1991, Gomez and Gonzales-Megias 2002, Scheidel et al. 2003, Amsberry and Maron 2006), and while a growing number of studies have examined how a single consumer species affects plant abundance (reviewed in Maron and Crone 2006), few have integrated the effects of multiple consumers on plant population dynamics (notable exceptions include Ehrlén 1995, 2002, Jongejans et al. 2006, Kauffman and Maron 2006). In addition, most studies of the effects of consumers on plant populations have generally focused on species more tractable to demographic monitoring—generally short-lived plants with minimal seed banks and distinct individuals. Thus, our ability to predict which consumers may exert the strongest control over plant populations or the most-intense selective pressures on plants is limited.

The life-history of a plant is predicted have a strong influence on the extent to which consumer damage translates to reductions in population growth and plant abundance (Silvertown et al. 1993, Franco and Silvertown 2004), but the ability to actually evaluate this pattern is hindered by the relatively small number of studies testing population responses (Maron and Crone 2006). Plants that reproduce asexually as well as via seeds may have a very different reaction to consumer pressure than those that do not, but studies on clonal plant demography have rarely included the impacts of consumers.

One of the few exceptions is Doak's (1992) study of *Epilobium latifolium*, which found that the frequency and intensity of herbivory by a single insect species could have substantial effects on the lifetime fitness (calculated via matrix models) of *E. latifolium*. Others have found, through long-term community monitoring with experimental herbivore exclusion, that periodic outbreaks of insects can alter the abundance of the clonally-reproducing *Solidago altissima* (Carson and Root 2000). These examples are the exception, however, as most plant-consumer studies focus on non-clonal plants. Despite their poor representation in the plant-consumer literature, clonally reproducing plants make up a significant portion of many communities, particularly at higher altitudes, and in areas with short growing seasons or harsh conditions.

Biotic interactions that alter plant abundance or fitness may have important consequences for the dynamics of populations or the selective pressures on plants' life-history and reproductive strategies as well as altering population dynamics. Populations and species of clonal plants often vary in the degree to which sexual and asexual reproduction drive population growth (Eriksson 1988, Mandujano et al. 2007). Consumers that reduce the amount of seed-based recruitment could create strong selective pressure on the allocation to different modes of reproduction, favoring plants that invest more in vegetative over sexual reproduction. While understanding the relative importance of sexual and asexual reproduction to population growth, or the factors affecting allocation patterns, have been a large focus of studies on clonal plants, these studies generally do not explicitly consider consumer impacts. Thus, examining the impacts of plant consumers on clonally reproducing plants is fundamentally important to our understanding of their ecology.

In a previous study, we found that post-dispersal seed predation by deer mice (*Peromyscus maniculatus*) caused strong reductions in the emergence of seedlings and establishment of young plants in the large-seeded perennial forb, *Lupinus sericeus* (Bricker et al, in press). *Lupinus sericeus* is a clonally reproducing native perennial in western Montana grasslands. Even though reductions in seed availability influence seedling recruitment and establishment for this species, overall plant abundance may be buffered from these impacts due to the production of clonal ramets. Here, via demographic modeling, we examine the individual and joint effects of three different types of consumers— herbivorous and flower-feeding ground squirrels (*Spermophilus columbianus*), leaf-feeding and pre-dispersal seed-feeding insects (Lepidoptern and Coleopteran larvae), and post-dispersal seed-eating deer mice (*Peromyscus maniculatus*)—on the population dynamics of *L. sericeus*.

### Field methods

Study system: *Lupinus sericeus* (Fabaceae) is a native perennial forb that is common, but not dominant, in the grasslands in our study area. *Lupinus sericeus* begins aboveground growth in late April to early May and flowers mostly between late May and early July. It produces relatively heavy seeds (mean seed weights  $\pm 1$  SD =  $0.0210 \pm 0.000771$  g), which are dispersed locally around the plants as pods open by explosive dehiscence. Plants grow in a rhizomatous-like pattern, with new ramets sprouting from underground horizontal roots that can be quite long. Excavations showed that ramets as far away as 20 cm can be connected via horizontal roots, while others much closer may be separate genets or connected ramets (M. Bricker, personal observation).

We performed experiments and demographic monitoring in three study sites (Blackfoot, Bandy, and Kleinschmidt) dispersed over approximately 30 km of semi-arid grasslands in the Blackfoot Valley of western Montana. The plant community in these grasslands is dominated by native perennial bunchgrasses (*Festuca idahoensis* and *Festuca scabrella*) and sagebrush (*Artemisia tridentata*) and contains a high diversity of native forbs. Exotic species are present at these sites but generally occur at very low densities. The small mammal community at our study sites include deer mice (*Peromyscus maniculatus*), montane voles (*Microtus montanus*), northern pocket gophers (*Thomomys talpoides*), Columbian ground squirrels (*Spermophilus columbianus*) and, rarely, yellow-pine chipmunks (*Tamias amoenus*), shrews (*Sorex*) and hares (*Sylvagus nutallii*). Two of these species feed on *L. sericeus*. Deer mice commonly consume dispersed *L. sericeus* seeds (Maron and Pearson, unpublished data), while ground squirrels (*S. columbianus*), the most abundant rodent species on most sites (Maron and Pearson, unpublished data) clip the growing stems and flowers of *L. sericeus*.

Consumer experiments: To examine the impact of ground squirrels on *L. sericeus* fecundity, we surveyed the number of pods produced per inflorescence on plants growing inside and outside of the rodent exclosures near the end of the flowering period in 2007. Censuses were conducted at the three demography sites, and at three additional sites where we had previously installed rodent exclosures of the same design. In each rodent exclosure and rodent exclosure control, we randomly placed four 1 m x 10 m belt transects across each 10 m x 10 m plot. We then counted the number of pods per raceme on all flowering *L. sericeus* that occurred in each belt. We pooled the data from all the

sites to calculate the mean number of pods per raceme on plants in the presence and absence of ground squirrels.

To determine the impacts of insect herbivores on *L. sericeus* seed production, in summer 2007 we performed an insect-exclusion experiment. At a single site (Bandy) we selected 74 flowering adult ramets near the demography transect and randomly assigned half of these to either an insecticide or control treatment. Plants in the insecticide treatment were sprayed to saturation weekly with a 0.0006 solution Acetamiprid (sold as Ortho<sup>®</sup>-Max<sup>™</sup> Flower, Fruit and Vegetable Insect Killer), a surface-application insecticide designed to kill and deter sucking and chewing insects. Control plants were sprayed weekly with the same amount water to control for water applied with insecticide. To minimize effects on pollinators, we sprayed plants early in the morning while temperatures will still cool so that the insecticide would dry before pollinators became active. Treatments were applied until plants set fruit and seeds were almost fully developed. Before pod dehiscence we collected pods from experimental plants and recorded the number of seeds per pod that were: 1) viable (i.e. endosperm filled with no signs of damage) or 2) visibly damaged by insects. The most common pre-dispersal seed predators were Coleoptera larvae that developed inside the pods chewing seeds from the outside, meaning that damaged seeds were easy to distinguish.

In order to estimate rates of post-dispersal seed predation by deer mice, and rates of seedling emergence, in 2004 and 2005, we added locally collected *L. sericeus* seeds to 0.5 by 0.5 m sub-plots in paired 10 m x 10 m rodent enclosure and paired equally sized control plots at each site (see Bricker et al. in press for details of how rodent enclosures were constructed). In 2004 we added 25, 50, 100, and 200 seeds to different subplots in

and out of rodent exclosures at each site. In 2005 100 seeds were added to an additional 0.5 x 0.5 m subplot in and outside of each rodent exclosure. At each site, we followed and recorded the emergence and survival of seedlings and young plants from both seed cohorts during the spring and summer of 2005, 2006, and 2007 (see Bricker et al. in press for details).

Demographic monitoring: At each of our three primary sites we established 1-meter belt transects within which we marked, measured, and mapped 400-500 *L. sericeus* ramets as well as any seedlings occurring on the transect. Total transect lengths at each site ranged from 25 to 40 meters. *L. sericeus* ramets can be connected underground over considerable distances. Shoots in close proximity within a “patch” can be connected underground, or can be independent genets. This pattern of cryptic belowground horizontal connections via root sprouting made it difficult to distinguish ramets from genets without extensive destructive excavations. In the absence of detailed knowledge about how plants were connected or the degree of physiological integration between ramets connected over different distances underground, we treated all shoots as individuals (ramets) and used demographic models to estimate the rate of population growth of this ramet population. This approach of modeling ramet population dynamics is commonly used when separating ramets from genets is problematic (Eriksson 1988, 1992, Berg 2002, Ellis et al. 2007).

We estimated ramet size using several metrics, including height, number of stems, number of leaves, and canopy area (calculated by multiplying the length and width, measured parallel and perpendicular to the length of the demography transect,

respectively). We measured size in an early-summer census in June each year. We continued to mark all new recruits (both seedlings and new vegetative ramets) and record the survival and size of all marked plants in June of 2006 and 2007, yielding three years of demographic data. In the spring census we also recorded whether a ramet had been visibly clipped by ground squirrels, and whether there was any evidence of infestation by leaf-rolling insects.

To estimate fecundity, we counted the number of inflorescences and pods on each marked plant during a late-summer census in late July or early August. Smaller, non-reproductive ramets had generally started to senesce at this point in the season, so the late summer census measured fecundity only, not plant size. Because pods open by explosive dehiscence, we could not count seeds directly on the plants in demography transects without altering the natural pattern of seed dispersal. We therefore used pods from plants adjacent to, but not included in, the demographic monitoring transects, to estimate the number of seeds per pod. We collected pods just before fruits were fully mature, then opened the pods and counted within each pod the number of good seeds.

To examine rates of seed survival in the soil seed bank, we performed seed burial experiments at each of our three study sites. In the late summer of 2004 and 2005 we buried bags containing 25 locally collected *L. sericeus* seeds at each site (6 bags per site in 2004, 12 in 2005). Bags were 5 cm x 5 cm, made of 3mm fiberglass mesh, and buried 1-2 cm deep in the soil. In August of 2005, and 2006, we excavated seeds buried the previous year and quantified how many of the original seeds remained intact. Seeds missing or visibly damaged were considered removed from the seed bank through either germination or decay. These data, together with the emergence data from seed addition

and rodent exclusion experiments, were used to estimate parameters related to seed survival.

### Modeling methods

Choosing stage classes: We examined the relationship between size and survival, and size and fecundity with logistic regression (Morris and Doak 2002). We found no significant relationships between size and survival, with the most highly supported model (including size as plant area, site, year, and size by site, size by year, and site by year interactions) explaining only 0.0154 % of the variation in survival of ramets. The probability of flowering showed a slightly stronger relationship with size, but size still explained very little of the variation in plant performance ( $r^2 = 0.202$ ). Visual inspection of graphical data relating size to various measures of fecundity (number of inflorescences or pods per plant) revealed no noticeable size patterns. Lacking a strong relationship between size and performance in our data, we chose to model the population dynamics with a stage-based matrix model in which plants were classified as seeds, seedlings, or ramets, and were not separated within those stages by size classes.

In order to examine whether ramets that were at least one year old performed differently from those that were newly emerged in a given season, we compared the performance of new and returning ramets in flowering probability and survival. We compared the rates of survival between new and old ramets for the year in which we had enough history to examine this (the 2006-2007 transition). Ramets that had been tagged in 2005 and were still alive in 2006 were considered “returning” ramets. Those that had been tagged in 2006 were “new” ramets. For both returning and new ramets, we counted the number alive and dead in the 2007 census. At each site, we tested for differences in

survival between new and old ramets using a 2 x 2 contingency table and chi-square test. We found significant differences in survival between new and old ramets at Kleinschmidt ( $\chi^2 = 3.88$ ,  $P = 0.049$ ), but not at Bandy or Blackfoot. For flowering probability, we were able to examine two years (2006 and 2007) for which the age of ramets was known. We found a significant difference in flowering probability between new and returning ramets at Bandy and Kleinschmidt in 2006 (Bandy  $\chi^2 = 20.08$ ,  $P < 0.0001$ , Kleinschmidt  $\chi^2 = 4.61$ ,  $P = 0.0318$ ). We therefore modeled ramets as two separate classes, depending on whether they had emerged that year or were returning from previous years. This generated a five-stage model consisting of one-year-old seeds, two-year old seeds, seedlings, new ramets, and returning ramets.

Estimating parameters: For each site, we estimated the survival of new and old ramets based on the counts from the 2006 to 2007 transition. We estimated the probability of a ramet flowering using counts from the 2006 and 2007 late-summer surveys at each site. The number of inflorescences per plant, and the number of pods per inflorescence, also came from the late-summer surveys in 2006 and 2007 and were calculated separately for new and returning ramets. The counts of seeds per pod came from site-specific counts from plants near the demographic transects in 2005. There were no significant differences in the number of seeds per pod between sites in that year; in 2006 and 2007 seed per pod counts were conducted at only two of the three sites, but these data were used in models for all three. To calculate the fecundity rates with release from insect and small mammal herbivores, we added the increase in number of pods per

inflorescence (for small mammal herbivores) or the number of seeds per pod (for insects) to the mean value for that vital rate at each site.

Very low seedling recruitment on the demographic transects meant that we had minimal data on the survival of naturally recruited seedlings. We therefore calculated seedling survival based on the individuals that recruited in seed addition plots (Bricker et al. in press) in and out of rodent exclosures. We found no differences in seedling mortality rates based on either density of seedlings in plots or whether or not seedlings occurred in or out of rodent exclosures (Bricker et al., in press). We pooled data from all seed addition plots within each site, including those added in both 2004 and 2005, and calculated seedling survival rate at each site from these totals. For the mean matrix, we averaged the survival rates calculated in the two different years.

We estimated the rate of new ramet production (clonal reproduction) based on the ratio of ramets in one year to ramets in the next, for each 1-meter segment of transect. That is, along the length of the transect at each site, we divided the transect into 1-m segments, counted the number of ramets (excluding seedlings) in one year, and the number of new ramets in the next year (as in Berg 2002). We averaged the rates from each of these 1-meter sections of transect at each site to obtain the values used in the mean matrix, pooling the rates calculated for the two available year-transitions (2005-2006, and 206-2007). We tested whether clipping by ground squirrels caused any increase in clonal reproduction using linear regression to examine the relationship between the proportion of ramets clipped, and the rate of clonal reproduction, in the 1-meter segments.

Seedling emergence rates and rates of seed dormancy in the soil seed bank were estimated using data from seed addition and buried seed-bag experiments. In these experiments rates of seedling emergence and seed predation could not be measured directly, because some unknown number of seeds initially added to the plots could die in the seed bank during the first year, making the size of the seed pool available to germinate in the second spring unknown. To circumvent this problem, we estimated seedling emergence using a mechanistic model of seedling emergence and seed survival. We generated maximum-likelihood estimates of: 1) the probability of a seedling emerging in year 1 (the first spring following the seed's production;  $P_{m1}$ ), 2) the probability of a seedling emerging in year 2 ( $P_{m2}$ ), 3) the probability of a seed dying in year 1 ( $P_{d1}$ ), 4) the probability of a seed dying in year 2 ( $P_{d2}$ ), 5) the probability of a seed being eaten by rodents in year 1 ( $P_{m1}$ ), and 6) the probability of a seed being eaten by rodents in year 2 ( $P_{m2}$ ) (Appendix A, Table 1). The sequence of seed fates was modeled such that seed predation occurred first, which is consistent with field observation suggesting that most seed predation occurs soon after seeds are released from the plants. Thereafter, seeds that were not eaten could germinate, die, or remain in the seed bank at each time step. The seed stages were age-based, with seeds forced to progress through the age structure at each time step and not living past three years old. This was consistent with the survival of seeds in the buried seed bag and seed addition experiments; the third year after seed addition, *L. sericeus* plots showed virtually no seedling recruitment, and most seeds in bags did not survive past their first year.

Maximum likelihood estimates for the seed parameters were based on the observations (experimental outcomes), listed in Appendix A, Table 2. Within each set of

data from seed burial and seed addition experiments at a given site and year, we constructed a joint probability function based on a binomial distribution for the probability of each of the observed events. The general form of the binomial probability function is:

$$\text{Probability } (p) \text{ of } k \text{ events in } N \text{ trials} = p^k (1-p)^{N-k} \frac{N!}{k!(N-k)!}$$

Within a data set the final factorial term is a constant, so we dropped that term from the probability functions and wrote the probability of the observed number of events ( $k$ ) out of ( $N$ ) number of trials (e.g.,  $k$  = number of seeds that survive, out of  $N$  seeds buried in seed bags), as:

$$p^k (1-p)^{N-k}$$

This generated six joint likelihood functions within each data set (one for each observation). We used the solver function in Microsoft Excel (version 2003) to maximize the sum of the natural log of these likelihood functions by changing the values of the six estimated parameters. The probability functions for each of the observations are given in Appendix A, Table 3. The maximum likelihood solutions created a set of estimated parameters that were most likely, given the data, for each set of observations, and thus avoided the problem of impossible combinations of rates that could occur if trying to calculate the parameters directly from each of the separate experiments. At each site we used data from 4 seed addition subplot pairs (the four different seed densities,

inside and outside of rodent exclosures) from 2004, and the data from the 100-seed addition plots in 2005.

Model structure and simulations: We used the vital rates from demographic monitoring and our insect and rodent exclusion experiments to construct stage-based matrix models with the general form of  $\mathbf{N}_{t+1} = \mathbf{A}\mathbf{N}_t$ , where  $\mathbf{N}$  is a vector of the number of individuals in each size class (and subscripted to denote an annual time step). The transition matrix  $\mathbf{A}$  is made up of matrix elements ( $a_{ij}$ ) representing the stage-specific transition rates calculated from vital rates (germination, survival, growth, fecundity, and seed predation). Figure 1 shows the life cycle diagram illustrating the stages and transitions making up the matrix model.

We used these site-specific vital rates to create transition matrices for each of the three sites independently. With only two transitions, our ability to incorporate temporal variation into matrices was extremely limited; therefore, we averaged vital rate estimates between the years, (combining the observations across multiple years, but keeping sites separate). These vital rates were combined into matrices used to calculate the elasticity of vital rates at each site (Morris and Doak 2002). Models projecting population growth with rodent seed predation included the probability of seeds being eaten ( $P_{m1}$ ); that projecting population growth in the absence of seed predation did not. Models projecting growth with release from insect or small mammal herbivory used the fecundity estimates in which the increase in fecundity measured in the experiments or surveys was added to the mean of the ambient fecundity value (in the presence of all consumers). Appendix B gives the model structure for each of these consumer scenarios.

To test the robustness of the model results to parameter uncertainty we calculated growth rates as a bootstrap analysis based on re-sampling from the original datasets. For each vital rate, we re-sampled with replacement from the original data, and calculated that vital rate at each bootstrap iteration from the re-sampled data (McPeck and Kalisz 1993). For vital rates relating to seedling and adult survival, flowering, fecundity, and transitions between stages, the raw data for the bootstrapping came from the measurements of individual plants on demographic transects at each site. Seedling survival was bootstrapped from the data on individuals in seed addition plots at each site. Bootstrap analyses of the clonal reproduction term re-sampled from a data array based on the rate of new clonal reproduction in each meter, pooling the values from both years at each site.

For the vital rates of seedling emergence, seed survival in the seed bank, and probability of a dispersed seed being eaten by mice, the data array for the bootstrapping was made up of the 5 maximum likelihood estimates for that site. For the vital rates affected by insect and ground squirrel herbivory (seeds per pod and pods per raceme, respectively) we bootstrapped by sampling from an array of 100 random numbers drawn from a Poisson distribution with a mean equal to the mean of the vital rate in the presence of the consumer for that site, plus the increase in pods per raceme or seeds per pod seen in the experiments or surveys quantifying the influence of that consumer.

We used these bootstrapped vital rates to calculate population growth rate ( $\lambda$ ) in the natural populations (i.e., in the presence of all types of consumers). We calculated the mean of these 1,000 iterations, and calculated the 95% confidence intervals of  $\lambda$  by ordering the 1,000 estimates of  $\lambda$  and selecting the 25<sup>th</sup> and the 975<sup>th</sup> values as the lower

and upper confidence limits, respectively. This estimate of  $\lambda$  and its confidence intervals includes variance from all of the vital rates simultaneously. To estimate the difference in growth rate ( $\Delta\lambda$ ), and the confidence limits around that difference due specifically release from consumer pressure, we created a bootstrapping routine where at each iteration, two matrices were built from the re-sampled vital rates. One of these reflected the ambient conditions, and the other eliminated one or more of the consumers. The two matrices were identical except for the vital rate(s) affected by the eliminated consumer(s). At each iteration we calculated  $\lambda$  of both matrices, and generated a metric of the change in growth rate ( $\Delta\lambda$ ) as:

$$\Delta\lambda = \lambda_{\text{consumer-removed}} - \lambda_{\text{ambient}}$$

to reflect the increase in growth rate that would occur with the exclusion of consumers. Specifically, we examined the effects of removing the following combinations of consumers, based on the order in which they influence plant fecundity and seed availability: 1) removing only ground squirrels, 2) removing ground squirrels and insects, 3) removing ground squirrels, insects, and mice, 4) removing mice only. As with the  $\lambda$  estimates, we calculated a mean and 95% confidence intervals for  $\Delta\lambda$  based on the 1,000 bootstrap iterations.

We also used the vital rates calculated for each site to examine the contributions of sexual reproduction to new individuals under different consumer scenarios. We calculated the number seedlings produced per ramet in four consumer scenarios (the presence of all consumers, with ground squirrels removed, ground squirrels and insects removed, and ground squirrels, insects, and mice removed) by calculating the fecundity and probability of seed germinating to become a seedling the next year, in each of these

scenarios. We examined the relative contribution of sexual and asexual reproduction to the new ramet class each year with either all or none of the consumers, by combining the terms for fecundity (with or without consumers), probability of seed predation, and the germination and survival probabilities of seedlings, compared to the vegetative reproduction term.

## Results

Consumer exclusion experiments: Plants protected from ground squirrel herbivory produced, on average, 0.866 more pods per raceme than did plants outside of rodent exclosures (Fig. 2;  $t_{4646} = 17.8$ ,  $P < 0.0001$ ). There was no significant relationship between the proportion of ramets clipped and the rate of new ramet production on the demography transects, even at the site with the highest rates of clipping (Blackfoot:  $F_{1, 36} = 1.148$ ,  $P = 0.48$ ). Clipping of vegetation by ground squirrels did not affect ramet survival at Kleinschmidt or Bandy ( $\chi^2 = 1.14$ ,  $P = 0.253$ ; Bandy  $P = 0.253$ ), but did lower the probability of survival at Blackfoot (survival probability for unclipped ramets = 0.600, clipped = 0.500;  $\chi^2 = 5.33$ ,  $P = 0.021$ ). Combined with the proportion of ramets that were clipped, this led to an increase in survival rate of 0.02 with the exclusion of ground squirrels, at Blackfoot.

Treating plants with insecticide reduced herbivory by leaf-rolling insects (Lepidopteran larvae). 43 % of control plants were attacked by these herbivores whereas none of the plants treated with insecticide were attacked; this rate of infestation in the control was similar to rates observed in demographic transects at all sites. This difference in herbivore pressure led to a significant difference between control and

insecticide-treated plants in the number of good (i.e., not visibly damaged by insect larvae) seeds produced per pod of 0.624 ( $F_{1,47} = 5.326$ ,  $P = 0.0254$ ; Fig. 3). However, insecticide treatment was not effective at reducing pre-dispersal seed predators whose larvae eat seeds from inside pods. We found no difference in the number of insect-damaged seeds per pod between control and insecticide-treated plants (Fig. 3). Plants from both treatments had an average of 0.146 insect-destroyed seeds per pod. Thus, our total estimate of seed destruction due to all forms of insect herbivory was 0.770 seeds per pod. The observed survival rates of plants with and without leaf-rolling insect activity on the demography transects were not significantly different ( $\chi^2 = 0.01$ ,  $P = 0.92$ ).

Previous experiments indicated that post dispersal seed predators (deer mice) reduced the rate of emergence of seedlings outside of rodent exclosures by an average of over 50% compared to what occurred inside rodent exclosures (Bricker et al, in press). When these differences in fecundity and seed predation are combined, they create marked differences in the number of seedlings emerging per plant (Fig. 5) at each site.

Vital rate estimates: Maximum likelihood estimates of seed survival and seedling emergence showed that most seeds either germinate or die in the first year after production (Table 1). Thus, although there are stages in the model for one and two year old seeds, plants almost never reach those stages, and there is effectively no seed dormancy. Based on differences in seedling emergence in and out of rodent exclosures we estimated with model-fitting that the probability of seeds being consumed by deer mice varied between the sites, with Bandy showing the lowest probability of a seed being eaten (0.122), followed by Blackfoot (0.340), and with the highest seed predation

occurring at Kleinschmidt (0.834). Other notable vital rate differences between sites included that the flowering probability of returning ramets at Kleinschmidt was almost double that of the other two sites and that Bandy was the only of the three sites in which any substantial number of pods per inflorescence were produced. At Blackfoot and Kleinschmidt therefore, sexual reproduction in the ambient consumer conditions is essentially zero. The ratio of new ramets to ramets in the previous year generated an estimate of clonal reproduction of 0.32-0.34 new ramets per old ramet, consistently across sites. The full set of estimated vital rates for all stages at each site is reported in Table 1.

Population projections and matrix analysis: Projections of growth rate for the three sites indicated fairly stable populations under ambient (i.e. all consumers present) conditions, with the 95% confidence intervals for  $\lambda$  at each site overlapping 1 (Fig. 4). The sequential removal of consumers by the order in which they impact seed abundance revealed that the increase in pods produced when ground squirrels were removed caused a small but significant  $\Delta\lambda$  across all sites; the removal of ground squirrels and insects together increased that difference, and the largest effects came with the removal of all three types of consumers (Fig. 6). Because earlier-acting consumers effectively eliminate seed production at two of the sites, the post-dispersal seed eating mice in isolation have no scope to affect population growth at Blackfoot or Kleinschmidt, and at Bandy the difference due to excluding mice in the presence of the other two types of consumers was non-significant ( $\Delta\lambda = 0.007$ , 95% CI = 0-0.026).

For the ambient populations, the survival of ramets and the clonal production of new ramets had the highest elasticity values (App. C). In ambient populations at the Blackfoot and Kleinschmidt sites, sexual reproduction is essentially zero, meaning these vital rates by necessity had elasticity values of zero in the presence of all consumers. When fecundity was elevated via release from the full suite of consumers, the vital rates related to sexual reproduction became much more important to population growth (App. C). The proportion of new ramets that are generated from sexual reproduction (i.e., surviving seedlings) vs. asexual reproduction (new ramets from roots sprouting) changes dramatically with the exclusion of consumers (Fig. 7). In the absence of consumers, sexual reproduction plays a much larger role in the generation of new individuals.

### Discussion

Taken together, our results indicate that three consumers (ground squirrels, insect herbivores, and deer mice) caused significant declines in the fecundity of *L. sericeus*. In the presence of the full suite of consumers, sexual reproduction at the three sites was effectively thwarted during the time period of this study. At two sites, there was no sexual reproduction whatsoever, and at a third site plants produced an average of only 0.3 seeds per ramet. We estimated that in the absence of these consumers, plants would produce 1.5-6 seeds per ramet (depending on site). Despite these consumer-induced declines in fecundity, *L. sericeus* populations at all our sites persist due to vigorous clonal growth (Fig. 4). Over the years in which we recorded demographic information, ramets produced an average of 0.33 new ramets per year. Yet while population persistence is clearly enhanced through clonal growth, the reductions in sexual reproduction that are

collectively imposed by all consumers limited the rate of population growth of this plant (Fig. 6).

The sequential nature of the types of damage these three consumers inflict on *L. sericeus* means that the ability of any particular consumer to affect population dynamics will depend not only on the intensity of pressure from that species, but also on that of the others. Because ground squirrels effectively eliminate the production of pods at two of the three sites, there is no scope for insects or mice to affect populations. It is only when the pressure from ground squirrel herbivory and florivory is lifted that we can examine the potential importance of the insects and post-dispersal seed predators. We found that the effects of these consumers were non-additive, and could be quite substantial (Fig. 6). This is particularly evident at the Kleinschmidt site, which shows the largest difference between ambient and no-consumer scenarios (Fig. 6). Here, high flowering probability for both new and returning ramets (Table 1) created large increases in fecundity with the removal of ground squirrels and insects, but due to high rates of seed predation, these effects could not be fully realized until seed predators were also removed.

Due in part to the importance of the other consumers, the impact of post-dispersal seed predation by deer mice on *L. sericeus* population growth was quite different than what we estimated for another large-seeded species in the same system, *Lithospermum ruderale* (Boraginaceae). Although deer mice similarly reduced seedling recruitment rates for the two species in seed addition experiments (0.26 seedlings per seed in rodent enclosures, and 0.11 seedlings per seed in control, Bricker et al. *In press.*), the impacts on *L. ruderale* population growth were considerably stronger than what we found for *L. sericeus*. For *L. sericeus*, deer mice alone were not enough to significantly alter the

growth rate of the ramet population, no matter how high the rates of seed predation were; *L. ruderalis* populations showed an increase in  $\lambda$  of 0.02 to 0.10 (depending on site), with the removal of post-dispersal seed predation by deer mice.

The high rates of clonal reproduction allow these populations to persist even in the absence of any seed-based recruitment. Like many other studies of clonally reproducing plants, we found that sexual reproduction was generally less important to population growth than clonal reproduction and plant survival under natural conditions (Eriksson 1988, Damman and Cain 1998, Wepler et al. 2006, Mandujano et al. 2007). Recruitment from seed into clonal plant populations has generally been considered to be rare, and of little importance to population dynamics except for in the establishment of new populations (Eriksson 1989 and references therein). Various studies have demonstrated, though, that in some clonal plants, sexual reproduction can be important to populations (Damman and Cain 1998, Berg 2002, Wepler et al. 2006). Our study provides some interesting perspective in that we found very little seedling recruitment, but this is due to an identifiable cause—reduction of seed production by consumers—which, if lifted, leads to a much higher importance of sexual reproduction. In the absence of consumers, sexual reproduction would constitute a much higher proportion of new ramet production than in the presence of consumers, at all sites (Fig. 7).

While our projection models allowed us to examine the population implications of multiple consumers on *L. sericeus*, we were not able to experimentally evaluate the factorial impacts of different combinations of consumers, because our experiments examined effects of consumers in isolation. Thus, our population projections do not fully take into account potential compensatory responses that may occur if only one consumer

is excluded but not others. We do not know the extent to which, for example, pre-dispersal seed predation by insects may compensate for a lack of flower-clipping by ground squirrels. Moreover, our experiments did not allow us to evaluate whether effects of one consumer might cause plants to change allocation patterns in ways that would then influence the outcome of another interaction.

Our estimates of the impacts of herbivorous insects are likely conservative, since our insecticide treatment was effective against only some of the insects that feed on *L. sericeus*. We often observed blister beetles (*Lytta spp.*, Meloidae) feeding on flowers and young pods, but insecticide was not effective at suppressing these herbivores. However, these omissions mean that functionally we have created conservative estimates of the impacts of these consumers.

One caveat to our findings is that our models did not include any estimates of density dependence. Failure to incorporate such density dependence into population models has been shown to lead to inaccurate predictions (Bierzychudek 1999, Halpern and Underwood 2006). We did test for effects of density on the survival and size of young plants in the rodent enclosure and seed addition experiments, and found no evidence of density-dependent mortality or reductions in growth rates in the first two years after germinating (Bricker et al. in press). Thus, it is unlikely that there is strong compensatory density-dependence at early life-stages that would alter our estimates of how consumers might influence plant population growth. Moreover, while density dependence will clearly influence the demography of plants in strongly increasing populations, the abundance at which *L. sericeus* is found in the surrounding populations suggest that there is significant room for them to increase with release from consumers

before such effects would be mitigated by negative density dependence, and that inter-specific competition from the rest of the plant community in these grasslands may be of greater importance than density-dependence within the *L. sericeus* populations.

A common complication in studies on the demography of clonally reproducing plants is that it is difficult to separate ramets from genets in the field. This generally necessitates an approach that uses demographic rates to forecast the population growth of ramets rather than genets (Eriksson 1988, Doak 1992, Eriksson 1992, Kaitniemi et al. 1999, Berg 2002, Ellis et al. 2007). If the demography and dynamics of ramets and genets are inherently different, this approach may be problematic. For some questions, understanding the genet dynamics specifically may be imperative. For example, modeling genet dynamics is preferable when examining the genetic structure of populations and how this might affect pollination, reproductive success, or selection on traits (Eriksson 1993, Eriksson and Bremer 1993, Damman and Cain 1998). In our study, however, we were most concerned with understanding how consumers affect the abundance of *L. sericeus* in this community, making ramet dynamics a reasonable estimate of how *L. sericeus* density might change with different consumer impacts.

In a plant with both sexual and asexual reproduction, consumers that reduce seeds may place selective pressure on the mode of reproduction favored, as well as having an effect on population growth. In these *L. sericeus* populations, the heavy attack from herbivores effectively eliminated or drastically reduced sexual reproduction in these populations during the three years of our study. This could cause strong selection favoring plants allocating more to clonal growth and vegetative reproduction as opposed to sexual reproduction. Plants with clonal reproduction can exhibit large variation in

their rates of clonal vs. sexual reproduction at both the species and population level (Damman and Cain 1998, Mandujano et al. 2007). In some species, patterns of allocation to sexual versus asexual means of reproduction are heritable (Ronsheim and Bever 2000), suggesting that the degree of clonality could respond to selection from consumers that affect one mode of reproduction over another. While we were not able to test for any response to selection or variation in clonality in our study, this presents interesting possibilities for examining how rates of clonal reproduction might vary with herbivore pressure.

Clonal reproduction in *L. sericeus* allows these populations to persist in the face of strong consumer pressure, even when consumers eliminate almost all sexual reproduction. The effect of each of these three guilds of consumers depends on the intensity of consumption from the other guilds, and their effects are non-additive. When one consumer is removed in isolation, the impact on population growth may be quite minimal, but if all consumer pressures are removed, the boost in sexual reproduction would allow these populations to increase dramatically, demonstrating that consumers are strongly limiting the abundance of *L. sericeus* in these grassland communities.

Table 1. Mean vital rates at each site. Survival rates in parentheses in the Blackfoot column reflect the survival rate of ramets in the absence of ground squirrels.

Vital rate	Blackfoot	Bandy	Kleinschmidt
Germination probability in 1st year	0.306	0.229	0.428
Germination probability in 2nd year	0.820	0.820	0.798
Probability of seed dying in 1st year	0.690	0.767	0.572
Probability of seed dying in 2nd year	0.180	0.180	0.200
Probability of seed being eaten by mice	0.340	0.122	0.834
Seedling survival	0.533	0.528	0.621
	0.566		
Survival new ramets	(0.586)	0.571	0.655
	0.620		
Survival returning ramets	(0.640)	0.579	0.552
Clonal reproduction	0.342	0.323	0.319
Flowering probability of new ramets	0.166	0.246	0.299
Flowering probability of returning ramets	0.146	0.155	0.288
# of inflorescences for new ramets	1.566	2.462	2.811
# of inflorescences for returning ramets	1.682	3.257	2.676
Pods per infl., new ramets	0.000	0.589	0.000
Pods per infl., returning ramets	0.000	0.865	0.005
Seeds per pod	1.294	1.609	1.500
Seeds per pod, without insect damage	2.064	2.379	2.270
Pods per infl., new ramets protected from herbivory	0.866	1.455	0.866
Pods per infl., returning ramets protected from herbivory	0.866	1.731	0.871

Figure 1. Life cycle diagram for *Lupinus sericeus*. Although there are stages for one and two year old seeds, the rates of germination and survival in the first year are such that plants almost never enter these stages.

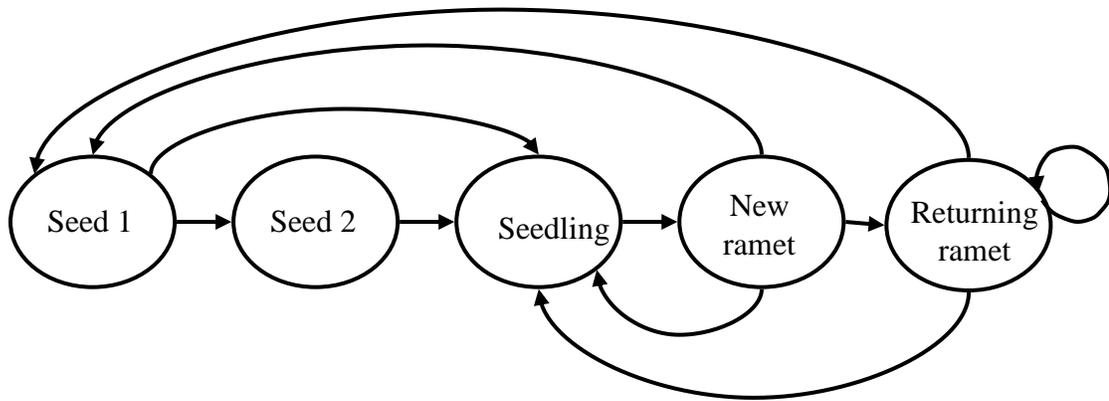


Figure 2. Mean number of pods per raceme on plants inside and outside of rodent exclosures, based on surveys from 2007. Error bars denote one standard error of the mean.

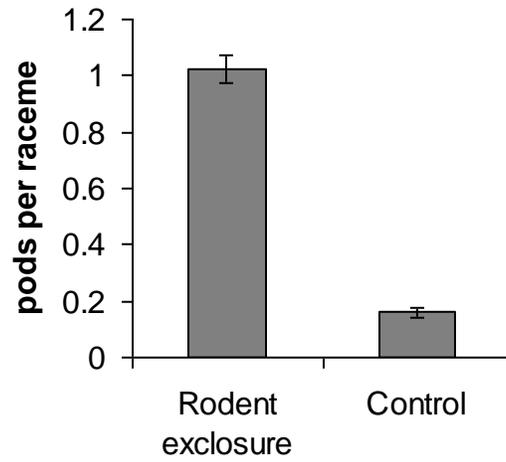


Figure3. The number of good and insect-damaged seeds on insecticide-treated or control plants.

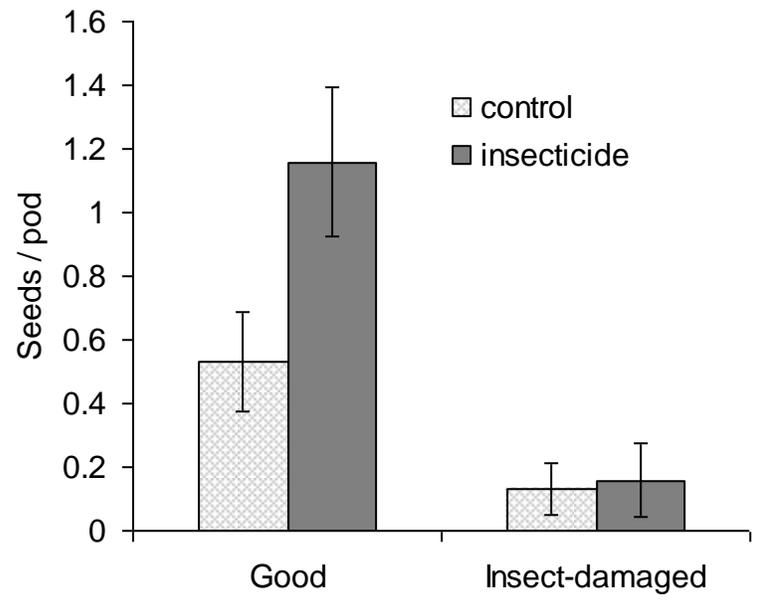


Figure 4. Population growth rates (error bars show 95% confidence intervals) for populations exposed to ambient levels of all seed consumers at each of the sites.

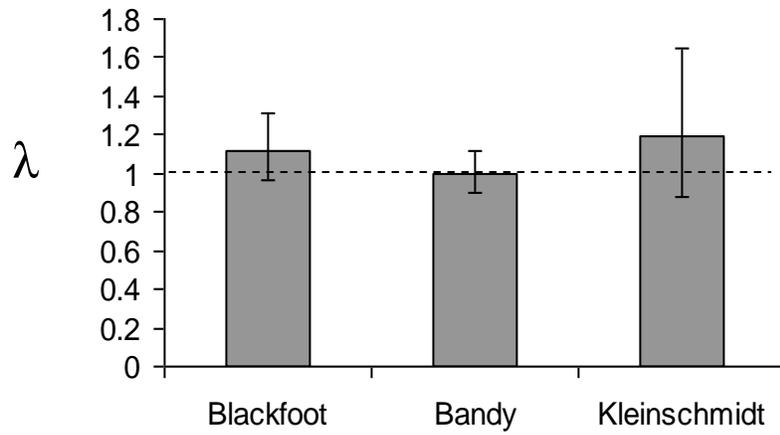


Figure 5. The number of seedlings produced per ramet, for a series of consumer combinations, in which consumers are eliminated by the order in which their effects are manifest. Note that under ambient conditions with all consumers, no seedlings are produced at Blackfoot or Kleinschmidt.

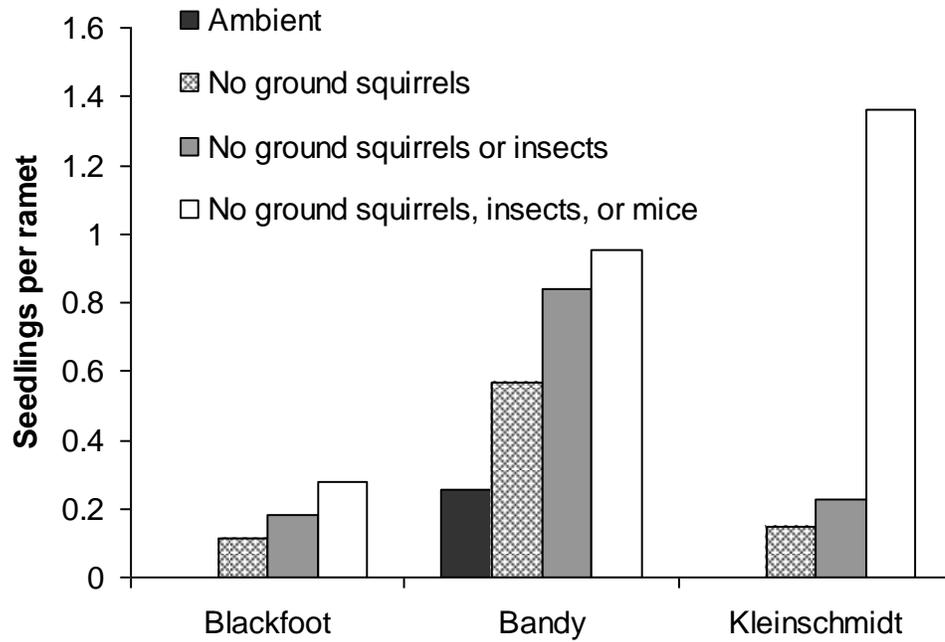


Figure 6. The difference in population growth rate due to specific combinations of consumers at each site. Solid diamonds represent the removal of ground squirrels only, open squares the removal of ground squirrels and insets, and X the removal of all consumers. Error bars show 95% confidence intervals of  $\Delta\lambda$ .

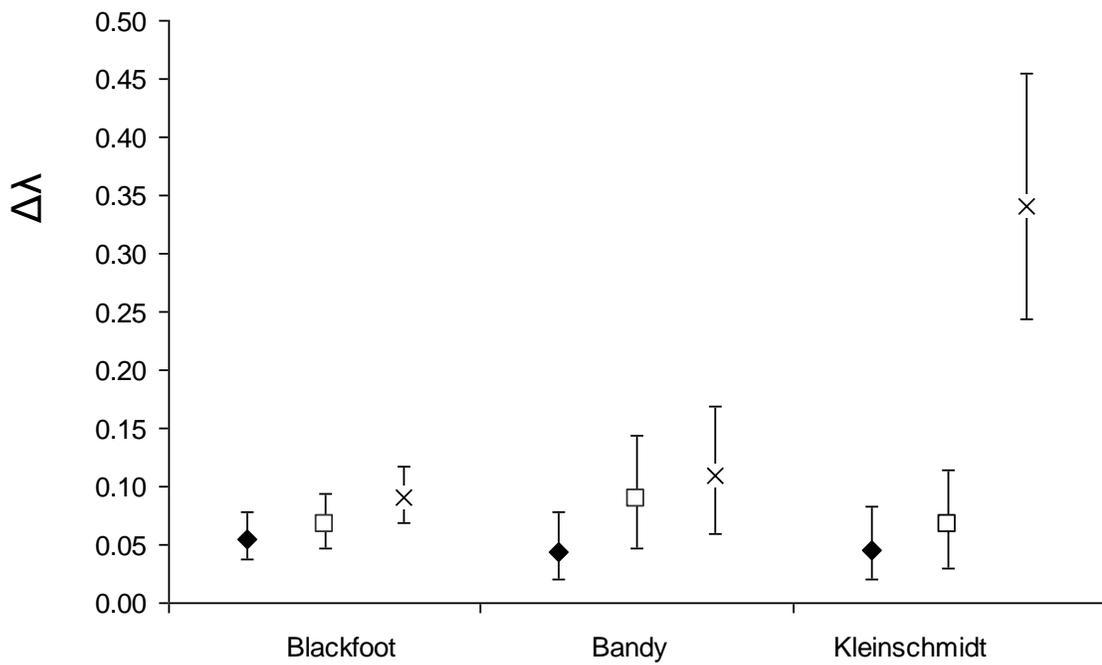
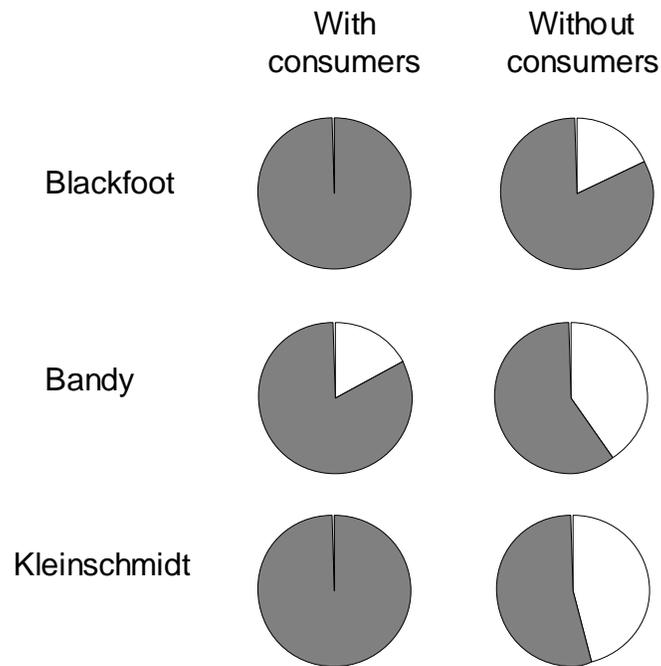


Figure 7. The proportion of new ramets each year that arise from asexual reproduction via root sprouting (gray) or sexual reproduction via surviving seedlings (white) with and without consumers at each site.



Appendix A.

Table 1. Observations used to estimate seed-related vital rates.

<b>Observations:</b>	<b>Symbol</b>
Number of seeds added to seed addition plots	Ns
Number of seedlings in year 1 in rodent-excluded plots	Ks <sub>1</sub>
Number of seedlings in year 2 in rodent-excluded plots	Ks <sub>2</sub>
Number of seedlings in year 1 in rodent-accessible (control) plots	Kr <sub>1</sub>
Number of seedlings in year 2 in rodent-accessible (control) plots	Kr <sub>2</sub>
Number of seeds in bags, at start	Nb
Number of seeds in bags still alive in year 1	Kb <sub>1</sub>
Number of seeds from bags still alive in year 2	Kb <sub>2</sub>

Table 2. Parameters in maximum likelihood models used to estimate seed-related vital rates.

<b>Estimated parameters:</b>	<b>Symbol</b>
Probability of germinating in year 1	Pg <sub>1</sub>
Probability of germinating in year 2	Pg <sub>2</sub>
Probability of dying in year 1	Pd <sub>1</sub>
Probability of dying in year 2	Pd <sub>2</sub>
Probability of being eaten by mice in year 1	Pm <sub>1</sub>
Probability of being eaten by mice in year 2	Pm <sub>2</sub>

Table 3. Likelihood functions for maximum likelihood estimates of seed-related vital rates.

**Likelihood functions:**

---

Likelihood for Ks1	=	$Pg_1^{Ks1} * (1 - Pg_1)^{(Ns - Ks1)}$
Likelihood for Kb1	=	$(1 - Pg_1 - Pd_1)^{Kb1} * (Pg_1 + Pd_1)^{(Nb - Kb1)}$
Likelihood for Ks2	=	$(Pg_2^{Ks2}) * (1 - Pg_2)^{(Ns * (1 - Pd_1 - Pg_1) - Ks2)}$
Likelihood for Kb2	=	$(1 - Pg_2 - Pd_2)^{Kb2} * (Pg_2 + Pd_2)^{(Kb1 - Kb2)}$
Likelihood for Kr1	=	$((1 - Pm_1) * (Pg_1))^{Kr1} * (1 - ((1 - Pm_1) * (Pg_1)))^{(Ns - Kr1)}$
Likelihood for Kr2	=	$(1 - Pm_2) * Pg_2^{Kr2} * (1 - (1 - Pm_2) * Pg_2)^{Ns * (1 - Pd_1 - Pg_1) - Kr2}$

## Appendix B.

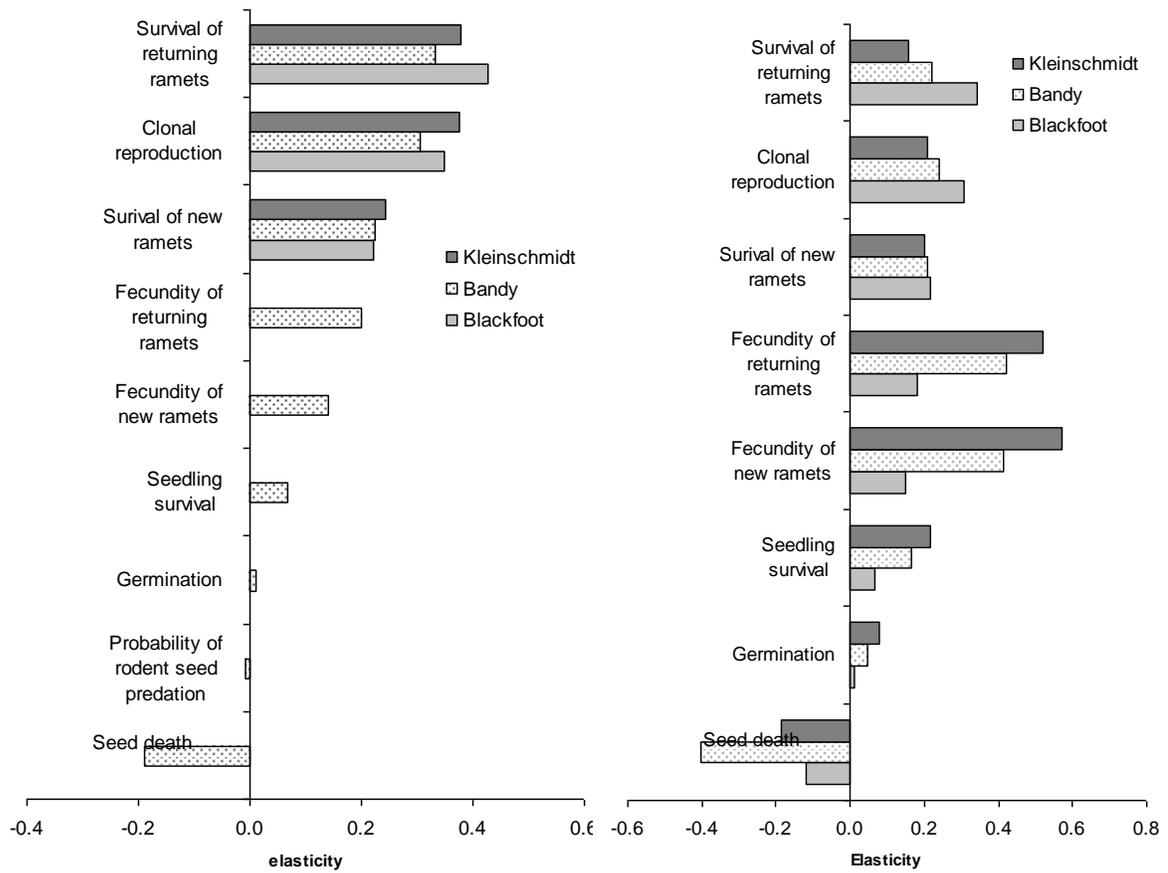
Table 1: Vital rates making up the matrix elements, and their abbreviations for the matrix form.

<u>Vital rate</u>	<u>Symbol</u>
Germination probability in 1st year	Pg <sub>1</sub>
Germination probability in 2nd year	Pg <sub>2</sub>
Probability of seed dying in 1st year	Pd <sub>1</sub>
Probability of seed dying in 2nd year	Pd <sub>2</sub>
Probability of seed being eaten by mice	Pm <sub>1</sub>
Seedling survival	ss
Survival new ramets	snr
Survival returning ramets	sor
Clonal reproduction	cr
Flowering probability of new ramets	f <sub>pnr</sub>
Flowering probability of returning ramets	f <sub>por</sub>
# of inflorescences for new ramets	inr
# of inflorescences for returning ramets	ior
Pods per infl., new ramets	pnr
Pods per infl., returning ramets	por
Seeds per pod	spp
Seeds per pod, without insect damage	sppNI
Pods per infl., new ramets protected from herbivory	pnrNGS
Pods per infl., returning ramets protected from herbivory	porNGS

Table 2. Matrices, composed of the vital rates, for each of the simulated consumer assembly scenarios. Stages are seed1=1, seed=2, seedling=3, new ramet=4, returning ramet=5.

Ambient					
	1	2	3	4	5
1	0	0	0	$f_{\text{pnr}} * i_{\text{nr}} * p_{\text{nr}} * s_{\text{pp}} * (1 - P_{\text{m1}}) * (1 - P_{\text{d1}} - P_{\text{g1}})$	$f_{\text{por}} * i_{\text{or}} * p_{\text{or}} * s_{\text{pp}} * (1 - P_{\text{m1}}) * (1 - P_{\text{d1}} - P_{\text{g1}})$
2	(1-Pd2-Pg2)	0	0	0	0
3	Pg2	Pg2	0	$f_{\text{pnr}} * i_{\text{nr}} * p_{\text{nr}} * s_{\text{pp}} * (1 - P_{\text{m1}}) * P_{\text{g1}}$	$f_{\text{por}} * i_{\text{or}} * p_{\text{or}} * s_{\text{pp}} * (1 - P_{\text{m1}}) * P_{\text{g1}}$
4	0	0	ss	cr	cr
5	0	0	0	snr	sor
No ground squirrels					
	1	2	3	4	5
1	0	0	0	$f_{\text{pnr}} * i_{\text{nr}} * p_{\text{nr}} * \text{NGS} * s_{\text{pp}} * (1 - P_{\text{m1}}) * (1 - P_{\text{d1}} - P_{\text{g1}})$	$f_{\text{por}} * i_{\text{or}} * p_{\text{or}} * \text{NGS} * s_{\text{pp}} * (1 - P_{\text{m1}}) * (1 - P_{\text{d1}} - P_{\text{g1}})$
2	(1-Pd2-Pg2)	0	0	0	0
3	Pg2	Pg2	0	$f_{\text{pnr}} * i_{\text{nr}} * p_{\text{nr}} * \text{NGS} * s_{\text{pp}} * (1 - P_{\text{m1}}) * P_{\text{g1}}$	$f_{\text{por}} * i_{\text{or}} * p_{\text{or}} * \text{NGS} * s_{\text{pp}} * (1 - P_{\text{m1}}) * P_{\text{g1}}$
4	0	0	ss	cr	cr
5	0	0	0	snr	sor
No ground squirrels or insects					
	1	2	3	4	5
1	0	0	0	$f_{\text{pnr}} * i_{\text{nr}} * p_{\text{nr}} * \text{NGS} * s_{\text{pp}} * \text{NI} * (1 - P_{\text{m1}}) * (1 - P_{\text{d1}} - P_{\text{g1}})$	$f_{\text{por}} * i_{\text{or}} * p_{\text{or}} * \text{NGS} * s_{\text{pp}} * \text{NI} * (1 - P_{\text{m1}}) * (1 - P_{\text{d1}} - P_{\text{g1}})$
2	(1-Pd2-Pg2)	0	0	0	0
3	Pg2	Pg2	0	$f_{\text{pnr}} * i_{\text{nr}} * p_{\text{nr}} * \text{NGS} * s_{\text{pp}} * \text{NI} * (1 - P_{\text{m1}}) * P_{\text{g1}}$	$f_{\text{por}} * i_{\text{or}} * p_{\text{or}} * \text{NGS} * s_{\text{pp}} * \text{NI} * (1 - P_{\text{m1}}) * P_{\text{g1}}$
4	0	0	ss	cr	cr
5	0	0	0	snr	sor
All consumers removed					
	1	2	3	4	5
1	0	0	0	$f_{\text{pnr}} * i_{\text{nr}} * p_{\text{nr}} * \text{NGS} * s_{\text{pp}} * \text{NI} * (1 - P_{\text{d1}} - P_{\text{g1}})$	$f_{\text{por}} * i_{\text{or}} * p_{\text{or}} * \text{NGS} * s_{\text{pp}} * \text{NI} * (1 - P_{\text{d1}} - P_{\text{g1}})$
2	(1-Pd2-Pg2)	0	0	0	0
3	Pg2	Pg2	0	$f_{\text{pnr}} * i_{\text{nr}} * p_{\text{nr}} * \text{NGS} * s_{\text{pp}} * \text{NI} * P_{\text{g1}}$	$f_{\text{por}} * i_{\text{or}} * p_{\text{or}} * \text{NGS} * s_{\text{pp}} * \text{NI} * P_{\text{g1}}$
4	0	0	ss	cr	cr
5	0	0	0	snr	sor

**Appendix C.** Elasticity values for vital rates at each site in the presence of all consumers (left panel) and the absence of all consumers (right panel). Fecundity values combine the added elasticities of the probability of flowering, the number of pods per raceme, and the number of seeds per pod.



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## CHAPTER FOUR

### PLANTS ON THE MOVE—TESTING WIND-DISPERSED SEEDS IN THE CLASSROOM

## Abstract

In this inquiry students consider how plants move, and experimentally test how well different types of seeds travel on the wind.

## Introduction

Many creative science experiences for young students expose them to the habits, patterns, and behaviors of animals, but leave out some of the interesting strategies that plants also have for accomplishing their life tasks. As a plant ecologist serving as a scientist in residence at an elementary school this year, I wanted to ensure that students learned some of the fascinating ecology and adaptations of plants. I was eager for them to learn more about plants than just the names of species and how to identify them using guides and keys. When it comes to directly interacting with, and doing experiments with organisms, plants have some distinct advantages over animals. Their diversity and accessibility allows students to use them in experiments, thus practicing important science inquiry skills.

This article describes an investigation I designed to help students appreciate the relationships between the form and function of plant structures, and lets them experimentally test a plant adaptation. In this lesson the students examine and compare different types of seeds and investigate which seeds travel farthest on the wind in a simple classroom experiment. This lesson has been used successfully with both fifth and sixth grade classes.

How do plants move from place to place?

To start students thinking about how seeds move and why this is important, I began the lesson with a general discussion of plant dispersal. I prompted the classes with open-ended questions like, “What are some things that make plants different from animals?” (plants, rooted in the ground, don’t move around from place to place) and “If plants don’t move, how do they get to new places, or places that used to be just bare dirt? How do you think new weeds get into your garden?” Students had some very creative responses, including “People move plants, like dig them up and put them in their yard” and “Sometimes parts of a plant break off, and it might wash away and put out roots in a new place,” and also mentioned that plants might move in a mudslide or flood. I encouraged all of these responses, but emphasized that for most plants, the seed stage is the time when most of a plant’s getting around happens. I then asked questions like, “What are some different ways that plants can get their seeds to new places?” and the class brainstormed about how seeds are moved by birds, mammals, wind, etc.

I brought in examples of various types of seeds and fruits and passed them around as the class came up with each of the different types of dispersal. Bird-dispersed seeds, included mountain ash berries and juniper berries. The familiar burrs that stick to dog hair and hikers’ socks represented seeds that get around on mammals. Wind-dispersed seeds included the “helicopter” fruits of maple trees as well as some of the seeds we used for the experiment (wild clematis, anemone, and yellow salsify).

Although it is admittedly a more rare form of seed dispersal, I find water-dispersed seeds to be particularly intriguing and often overlooked, so I brought in a whole fresh coconut to show the class, to get them thinking even more creatively about all the ways plants can move around. For the classes I was working with in Montana, this was

quite an exotic and interesting example! The fifth-grade students, in particular, were quite fascinated to think about something as large as a coconut being a seed, and asked all kinds of questions. “Do they float? Can we try floating it in the sink? Why don’t they break when they fall off of the tree? Can we eat it today?” One group in the second class wanted to test whether or not coconuts were wind-dispersed, so after the regular experiment we tried dropping it in front of the small desk fan and confirmed that it could not go very far, at least not on our light breeze. After several drops on the hard classroom floor it split open, much to the students’ excitement.

After discussing all these different ways that plants have of getting their seeds around, I gave students a chance to check out all the examples, then brought the group back together to talk about the specific experiment they would be doing in class to test wind-dispersed seeds. I also had the class brainstorm about why it might be important for plants to move their seeds around, again using open-ended questions such as, “What would happen if all the seeds just dropped straight under the plant that made them?” When we imagined as a class what that scenario would look like, the students immediately recognized that plants growing from the seeds would be very crowded, and might compete for light, water, and nutrients. They also suggested that moving might help the plant get to a better place to grow.

After this discussion I handed out several seeds of each of four different species to groups of students. They spent some time observing, drawing, and describing each of the types of seeds. Based on what they observed, they made predictions about which seeds would go the farthest on the wind, and recorded those predictions. Each group then tested their predictions by dropping seeds of each species in front of a fan and recording

how far they went. With the fifth graders students simply ranked the distance that one seed from each species traveled. The 6<sup>th</sup> grade class dropped multiple seeds of each species, measured the distance flown, and graphed an average distance for each species.

To learn more about how well students made the connection between seed form and function, I had students share their results and discuss their conclusions and thoughts on the experiment. We compared the distance traveled by seeds dropped by different groups, which caused students to note that there was a lot of variation, so we discussed what could have caused that variation. Student responses included “Maybe one of the fans was blowing faster than the other one, and some groups tested theirs on one and some on the other.” We were then able to examine whether that could have been a factor by classifying groups by which station they had used. We found that there were no consistent differences, so we ruled out the fans as a cause of the variation. They also suggested that “Maybe different people dropped the seeds a little bit differently, so they went farther or not as far” which led to revising the methods to ensure that all groups dropped their seeds from the same starting point in later classes. They also noted that “Some of the seeds were missing a bit of their fluff, so maybe some of them were different from others, even though they were the same kind.” This led to a discussion of why we use replication and compare averages, rather than making conclusions based on just one test.

To help evaluate how well students understood the concept of this experimental design, I reminded them of the different types of seed dispersal we had talked about earlier and asked students to describe how they would test how well seeds performed with that mode of dispersal. Bringing out the coconut again, I asked if they could design

an experiment that would test how well different types of seeds traveled on water, instead of on wind. The class suggested putting seeds in a tub of water to see how long they float, releasing them in the ocean or a lake and seeing where they went, and “racing” them down the river.

These discussions, and responses on student worksheets, indicated that this investigation was effective at addressing several of the National Science Standards (NRC 1996). Specifically, students made predictions and tested hypotheses; they practiced making accurate measurements, interpreted data, proposed alternative explanations for the patterns seen in their data, and critiqued the experimental design (all relating to content standard A for grades 5-8, Science as Inquiry). They also gained a better understanding of the diversity and adaptations of organisms (life sciences, content standard C, grades 5-8). My favorite illustration of their understanding of these adaptations comes from an anecdote from one of the fifth grade teachers who told me that on a field trip later in the month, a student pulled a burr off of his sock and held it up, exclaiming “Look, seed dispersal!”

### Testing wind-dispersed seeds in your classroom

Here are specific instructions on how you can try this investigation with students in your classroom.

#### Materials needed:

- 1 Small electric fan per testing station
- 1 Measuring tape and 1 ruler for each testing station.
- Datasheets for each group (see Figures 1 and 2).

- Seeds of 4 different plant species, with varying types of structures that may help with wind dispersal (Figure 3). Good choices may include dandelions, yellow salsify (also called goatsbeard, it looks like a giant dandelion and is fairly common in weedy fields), blanketflower, maple, elm, or cottonwood, and seeds of some grasses or wildflowers. Having a wide variety of structures will help, as will having one clearly non wind-dispersed seed for contrast (sunflower seeds or mustard seed are easily available from grocery stores if seed collecting is difficult).

#### Measuring and testing

Set up each testing station by placing a small electric fan on the floor, blowing at low speed. Stretch a meter tape out in front of the fan, with the zero end about 20 cm in front of the fan. Designate the zero end of the meter tape as the starting point from which to drop seeds, and have one student stand a ruler on end at the close end of the meter tape so that each seed is dropped from the same height.

Have each group of students bring their seeds to the testing station and drop one seed at a time of each species in front of the fan. As one student releases each seed, the other students in the group watch its flight and note where it lands along the measuring tape. They then record the distance each seed traveled on their datasheets (Figure 1). If time permits, have groups drop several seeds of each species, to increase the number of replicates across the class.

### Working with data

The approach to interpreting the data will depend on the age and math skills of the class. At the most basic, students can report the distance each seed traveled, record the distances on a chart on the board, and a teacher can help them average and make a graph. More advanced students can calculate the averages for their group and create their own bar graphs (Figure 2). Groups can also compare their individual results to an overall class average to discuss variability.

### Drawing conclusions

Have students rank the distance their seeds flew and display their bar graphs to the class. You can then use a class discussion, reflective writing, or science journaling to help students think about what these results mean. Start with basic questions such as “Which seeds went the farthest and the shortest distance?” and “How did your results compare to your predictions?” to help them make conclusions from their data. Then encourage them to consider the broader meaning of the evidence they collected and how it has influenced their thinking, with questions like “When you made your predictions, what did you think would make seeds travel well on the wind?” and “Do your results change what you think is most important for seeds to travel on wind?” Also help them to think about the design of the experiment by asking how they might do this experiment differently if they had it to do over again, or how they think it could be improved. Letting them explain or design an experiment to test a different type of dispersal will give them a chance to think about how they could apply similar methods to a different question.

### **Acknowledgements**

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Figure 1: Worksheet for predictions and experimental measurements.

Name \_\_\_\_\_

Your group has four different types of seeds. Take a minute to **observe** the seeds. Then, **describe** what each of the seeds looks like, and draw a picture of the seed:

Seed # 1: _____	Seed # 2: _____
Seed # 3: _____	Seed # 4: _____

We are going to test how far each of these different species of seeds travels by wind. But first, let's make some **predictions** about which of these seeds are adapted to travel by wind, and predict which will go the farthest.

Which seeds do you think move by wind? Why? \_\_\_\_\_

\_\_\_\_\_

Do any of these species look like they are not moved by wind? \_\_\_\_\_

Why not? \_\_\_\_\_

Write down your **prediction** of which seeds will go the farthest, by putting them in the order you expect, from longest to shortest distance flown:

\_\_\_\_\_

(longest) .....(shortest)

**The experiment:**

Now you will test your predictions. Drop each of the seeds one by one into the wind of the fan from the "Start" point. Record how far the seeds went.

Species	Distance		

Record how your seeds actually did. Which one went the farthest distance, and which one went the shortest?

\_\_\_\_\_

(longest) .....(shortest)

Figure 2: Worksheet for graphing and presenting flight distance data.

Make a bar graph using the average distances for your class. How far did each of the seed species travel, on average?

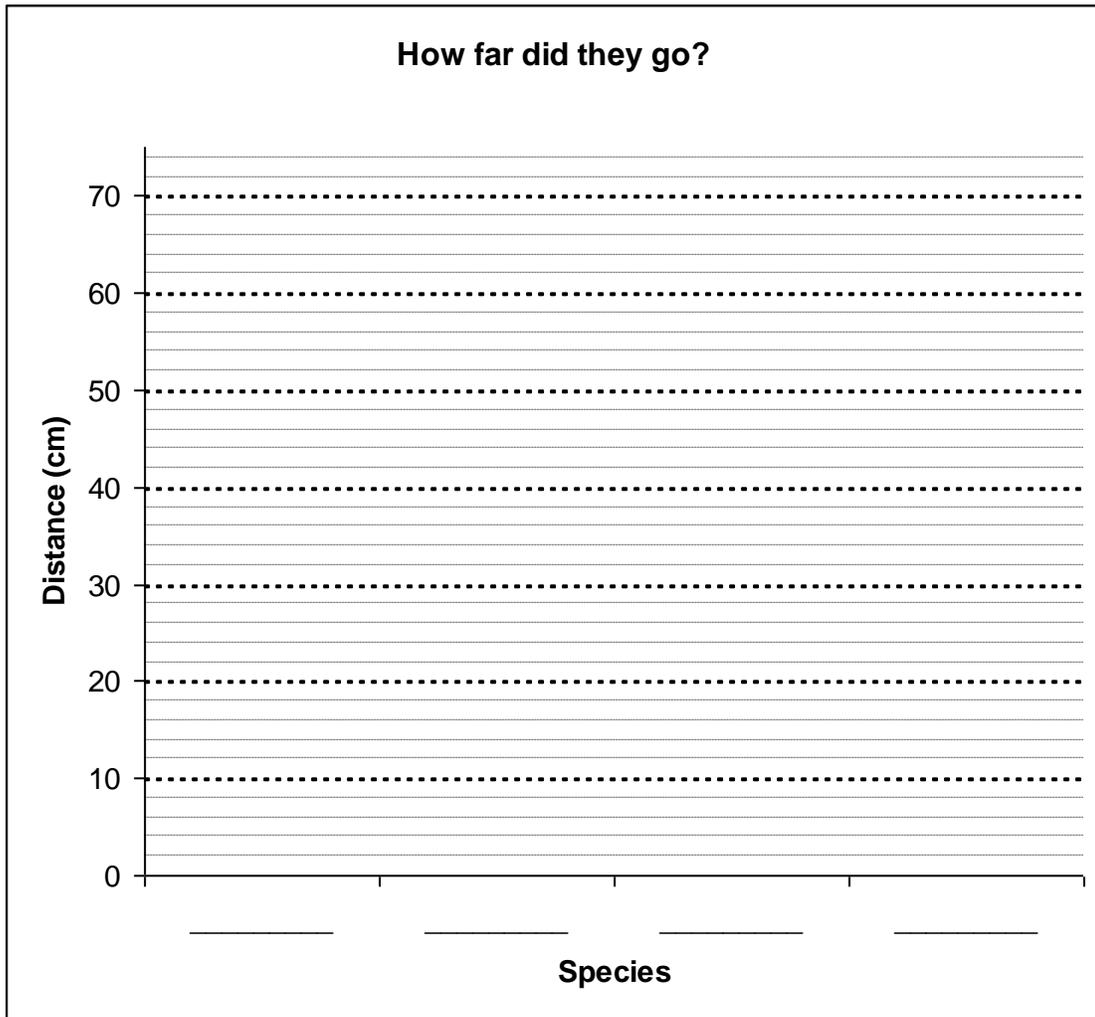
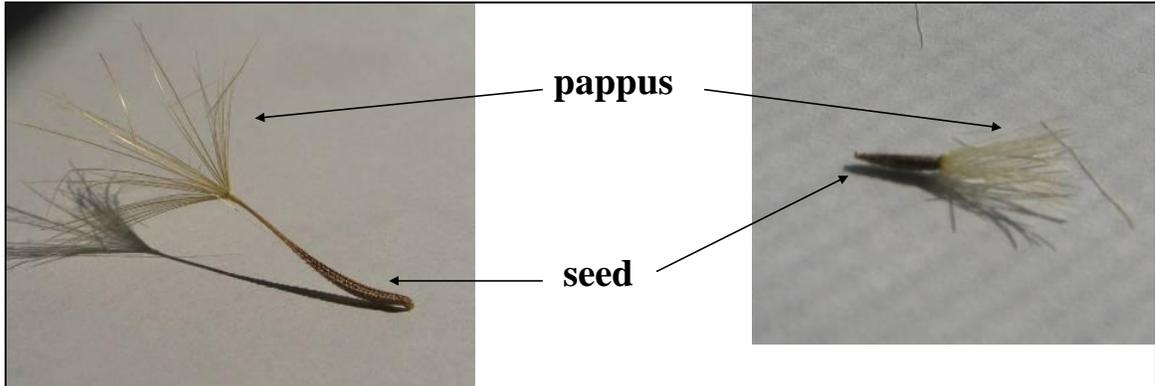


Figure 3: Many seeds have special features that help them travel on the wind.



A bristly or fluffy extension called a **pappus** is a common part of the fruit on seeds in the sunflower family, which can help with wind dispersal, or help seeds stick to animal fur.

A maple tree encloses its seeds inside a special type of fruit called a **samara**, that has two “wings” that help the seeds move on the wind. Each samara (or “helicopter!”) has two seeds inside.

