**Relative Seed Predation by *Peromyscus maniculatus* on Invasive and Native Species Pairs of Four Plant Genera found in Palouse Grass Prairies of Western Montana**

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**Abstract**

Many hypotheses have been made as to the mechanism behind the successful invasion of exotic species into non-native habitats, but the specific competitive advantages that invasive species possess relative to native species is not yet understood. The complex interaction between *Peromyscus maniculatus* and the seeds that they consume may have a significant effect on the successful invasion of exotic species. Four choice-based feeding trials were conducted in order to examine the relative seed preference of *P. maniculatus* for invasive species when presented with native species of the same genus. The four seed pairs studied were *Potentilla recta* vs. *Potentilla glandulosa*, *Lepidium perfoliatum* vs. *Lepidium virginicum*, *Agropyron cristatum* vs. *Agropyron spicatum*, and *Poa pratensis* vs. *Poa secunda*. No consistent preference for native or invasive seeds was found across the four genera, but *P. maniculatus* did prefer to consume certain genera as a group (p=0.003). *P. maniculatus* stored a greater mass of small seeds in their bedding than they did larger seeds ($R^2$=0.821, p=0.094). While *P. maniculatus* may reduce invasive species fecundity through consumption of its seeds or aid in an invader's spread through dispersal of its seeds, the mechanism behind relative seed preferences for invasive species requires additional investigation.

**Introduction**

Although thousands of plant species are introduced to non-native habitats each year, only a small percentage of these exotics become invasive species, fewer still become noxious (Carpenter and Cappuccino 2005, Parker and Gilbert 2007). Despite numerous studies regarding invasive species and their relationships with both native plants and native plant predators in the community they invade, scientists have yet to find the reason for some introduced plants' successful invasion into new ecological systems.

There are two main schools of thought regarding the predation of invasive species by native herbivores and the potential role of this interaction in either reducing the invasive species' fecundity or promoting the invaders survival in its new habitat (Johnson and Cushman 2007). In the "red-queen hypothesis," evidence of co-evolution between plants and their natural herbivorous enemies in their native habitat suggests that invasive plant species have not yet adapted defenses to protect themselves against native herbivores and therefore are susceptible to greater plant predation (Parker and Gilbert 2007). Contrastingly, the "enemy-release

hypothesis," predicts that invasive species experience less herbivory because their co-evolved natural enemies are not present in their new environment, giving them a competitive advantage over native species (Lake and Leishman 2004, Carpenter and Cappuccino 2005, Raghu et al. 2006, Parker and Gilbert 2007).

While many studies focus on the how herbivory alters the overall fitness of the plant and indirectly reduces its fecundity, other studies of invasive species have attributed invaders' success to large seed banks, rapid seedling emergence, and toxic seeds that are avoided by granivores, such as those of *Thlaspi arvense* and *Sinapis arvensis* (MacDougall and Wilson 2007). Despite the direct importance that seed characteristics have on the success of exotic plants in a non-native habitat, little is known about the complex relationship between native granivores and their seed predation of invasive species. Few studies have been conducted that examine the possible role that seed predators play in the successful invasion or invasion suppression of an exotic species.

*Peromyscus maniculatus* is a generalist granivore species that is found ubiquitously across North America (Kantak 1983). *Peromyscus* preferred seed choice is often based on the optimal foraging strategy, which is a method of selection which reflects a maximization of net energy gain by feeding on a particular food source (Lewis et. al. 2001). These granivores often choose to consume seeds on the basis of energy expended in obtaining the seed, such as ease with which they are husked or for which they are foraged (Kantak 1983), as well as the gross energy obtained, which is based on the seed's size and energy content (Lewis et al. 2001). These factors influence the willingness of *P. maniculatus* to consume invasive seeds that are available for consumption in their habitat.

While the consumption of seeds by *P. maniculatus* may have a detrimental effect on a plant's successful invasion into a region (MacDougall and Wilson 2007), *P. maniculatus's* preference for the seeds of certain invasive species may be beneficial in their dispersal. Although *P. maniculatus* directly consume some seeds for which they forage, approximately seventy percent of seeds that they handle are stored in shallow caches, usually with one or two seeds at each storage location (Vander Wall et. al. 2001). Unlike the seed storage mechanisms of other granivores, the shallow, small caches of *P. maniculatus* are better for the dispersal of cached seeds because smaller groups of seeds are better for seedling survival (Hollander and Vander Wall 2004). Seed caches further assist in seed dispersal by protecting seeds from other potential seed predators (Vander Wall et. al. 2005). Additionally, foraging *P. maniculatus* often accidently drop seeds as they are caching them, thus unintentionally dispersing them in their habitat.

This study examines the relative seed selection by *P. maniculatus* on four pairs of native and invasive species belonging to the same genus that are found in the Palouse prairie system. The seeds of each species in a seed pair are presented to *P. maniculatus* simultaneously in a choice-based feeding trial. Consistent with the "red queen hypothesis," I predict that *P. maniculatus* will prefer to consume seeds of the invasive species relative to the native species of each genus. Because of this seed preference, I further predict that *P. maniculatus* will attempt to store more of the invasive seeds in their bedding habitat, thus allowing invasive seeds to be dispersed locally to other locations.

**Methods**

*Mouse Capture and Acclimation*

Four experimental feeding trials were used to test whether the granivore, *Peromyscus maniculatus,* presented with a phylogenetically-related native and invasive plant species pair demonstrated choice.  All plant species and *P. maniculatus* were collected within the National Bison Range, Moiese, MT.  *P. maniculatus* were captured at one of three sites located on the National Bison Range.  Four days prior to experimentation, sixty-five collapsible Sherman traps were set in the evening between the hours of 1600 and 1900 MDT.  Each trap was baited with sweet feed, and approximately 0.1g of polyester material was provided as a means of insulation for captured animals.  Sweet feed was a dry grain mixture of corn, oats, and barley that was used as both a bait and feeding material during the acclimation period.  This food source was chosen due to its similarity in composition to the type of seeds that were presented in the feeding trial, as well as the fact that it provided the *P. maniculatus* with the necessary amount of protein required in their diet (>8%).  Traps were placed in areas where microhabitat conditions, such as patches of snowberry and thistle, which were found to be favorable for *P. maniculatus* capture during a pre-trial period, and a 1m flag was used to mark the location of each trap to allow for easy relocation.

The following morning between 0700 and 1000 MDT, all traps were checked for captures and then removed from the field.  All captured animals were identified and all non-target species were released.  Ten *P. maniculatus* were weighed in a mesh bag using an Avinet 500g spring scale, and then transported back to the lab for feeding trials.  Any additional *P. maniculatus* were released at the location of capture.

All *P. maniculatus* were acclimated to the same environmental and feeding conditions for three days prior to experimentation to reduce bias in feeding-trial preferences that may have occurred as a result of their diet in the wild. *P. maniculatus* were housed in clear plastic cages (30.5x16x11.5cm) and provided daily with moistened sweet feed ad. libitum, polyester bedding, and aspen chip bedding for absorption of waste materials. Each evening, including the day of capture, the animals were removed from their cages, the cage was wiped clean, and the mouse was provided with fresh bedding and food.

*Seed Collection*

The seeds of one invasive species and one native species belonging to the same genera were collected from various locations around the National Bison Range where the plants were found in abundance and during their natural seeding period. Two forb and two grass species were chosen on the basis of the presence of a native and invasive species of the same genera, as well as its abundance on the National Bison Range and the correspondence of its seeding period with the time of experimentation. When the target plants were located in the field, the seeds were removed from the rest of the plant by gently rolling the seed head between the fore finger and thumb and placing the seeds into a sealable plastic bag. If the seeds were not used immediately, they were kept frozen until the designated time of each trial to prevent seed molding and maintain moisture.

**Potentilla recta and Potentilla glandulosa.** Seeds were collected between 29 July 2007 and 31 July 2007. *P. glandulosa* seeds were found in close proximity to a backwater area of Mission Creek on the National Bison Range. Seed heads were collected if the seeds appeared

dry and dark brown in color. Seeds were removed from the head by gently squeezing the stem just below the seed head and running two fingers upward. Seeds were weighed into groups of 1.6g, sorted into bags, and stored frozen until use. *P. recta* seeds were found primarily in dry, lowland areas and collected if the seed pod was dry and light brown in color. To collect the seeds, the stem was broken just beneath the node of the first branches and the branched region containing all of the pods was tipped upside-down over a plastic bag. More seeds were removed by squeezing the pod between the forefinger and thumb so that it separated completely from the stem. Seeds were sorted from larger pieces of pod by sifting them through a wire mesh. Due to the fact that small pieces of debris were sifted through with the seeds and were unable to be removed by density gradients, the *P. maniculatus* were presented with a mixture of seeds and debris for *P. recta*. In order to determine the mass of seeds used in each trial, the proportion of the seeds' mass in the mixture was determined by measuring the mass of seeds and debris in a subsample. Using these calculations, approximately 3.8g of mixture (1.4g seeds) were measured into bags and frozen until use in the trial.

   *Lepidium perfoliatum* **and** *Lepidium virginicum*. Seeds were collected on 4 July 2007 in a dry, lowland area of the National Bison Range. The method for seed removal and collection was the same for both *L. perfoliatum* and *L. virginicum*. Plants were chosen for seed removal if they were completely dry and the pods were brittle with no remaining green color. To remove the seeds and pods from each branch of the plant, the branch was held over the bag and a forefinger and thumb were run from the bottom of the branch over each of the pods to the top of the branch. As pressure caused each pod to split into two pieces, the seeds were released from inside. Seeds were separated from the pod debris by sifting the seeds through a piece of wire

mesh.  Any additional pieces of pod were removed using forceps.  Seeds were separated into plastic bags, but were not frozen due to the close proximity of the trial date to the time of collection.

*Agropyron cristatum* **and** *Agropyron spicatum*.  *A. cristatum* seeds were collected on 25-26 July 2007 from a lowland site on the east side of the National Bison Range.  Seeds were collected from seed heads that were completely dry, indicated by a golden color seed head and easily removed seeds.  The seeds were removed directly from the seed head by applying pressure perpendicularly to the direction that the seeds were pointing and allowing them to drop into the bag below.  *A. spicatum* seeds were collected on 26 July 2007 at two locations: midland elevation site (1060 m) of an east-facing slope and a high elevation site (1370m) of an east-facing slope.  Seeds were harvested if the awns of the seeds were approximately perpendicular to the seed head.  Seeds were removed directly from the stalk by gently rolling the seed head in between a forefinger and thumb.  All *Agropyron* seeds were separated into groups with a mass of 1.3g and placed in the freezer.

*Poa pratensis* **and** *Poa secunda*. Seeds were collected on 6 July 2007.  *P. pratensis* were collected in two locations; one site was at a mid-elevation (approximately 1100 m), and one site was in a wetter lowland site (approximately 760 m).  *P. secunda* seeds were found entirely at a higher elevation site (approximately 1300 m).  For both species, the entire panicle was collected and retained in a bag until the seeds were separated.  Seeds were removed from the panicles by gently rolling the seed head in between the forefinger and thumb.  Groups of seeds weighing approximately 1.2g were placed into bags and stored at room temperature for 18 days until the trial date.

*Feeding Trial*

Each of the four feeding trials took place between 0700 and 1300 hours MDT, and each

lasted a total of four hours. Trials were conducted in the same type of plastic cages

(30.5x16x11.5cm) in which the *P. maniculatus* were housed. The seeds from the native and

invasive species were measured in Dixie cups that were cut to a height of 1.5 cm, and the seeds

were placed into the trial boxes for presentation to the *P. maniculatus* throughout the trial.

Another set of Dixie cups (also 1.5cm) were anchored to the bottom of the trial box, and the cups

containing the seeds were placed inside the anchored cups. Securing the cups reduced the

likelihood that the animal would tip over the cup and consequently, bias the results of the

experiment. Cups containing the native and invasive seeds were placed at one end of the

container, and the placement (left or right) of the native and invasive seeds was alternated so that

the seeds were not always on the same side of the container. A small amount of polyester

bedding was placed in the trial container to observe possible hoarding of seeds within the

bedding.

After the trial container was prepared, one of the ten mice that had undergone the three

day acclimation period was chosen for participation in the test. After retrieving the mouse from

its housing container in a mesh bag, the mouse was weighed using a 120g balance scale with 1

mg precision. Additionally, the sex of the mouse was noted and the length of the right foot was

measured from the tip of the longest toe to the first leg joint. For placement into the trial

container, the mouse was scruffed and lowered into the end of the container opposite of the

seeds. The trial box was secured with masking tape and placed to the side where it remained

undisturbed throughout the trial process. Six replicate trials were conducted, as well as two

control boxes in which seeds of both species were placed in a trial box without a mouse. Trial boxes were prepared and approximately 15 minutes preparation time was required for each replication box.

At the end of the four-hour trial period, the *P. maniculatus* were removed from the trial boxes and replaced into their housing cages. Debris such as chips of plastic, pieces of Dixie cup, and feces were removed from the cups with the remaining uneaten seeds before the mass of the seeds was determined. In order to look at potential differences in hoarding behavior between the native and invasive seed types, the intact seeds that were moved by the *P. maniculatus* from the original containers and left in the bedding or in other locations in the box were also sorted by seed type and their mass was determined. Several hours after the feeding trial, all *P. maniculatus* were released at the National Bison Range. *P. maniculatus* were newly collected for each of the feeding trials and no replicates were used. The *Lepidium* feeding trial was conducted 5 July 2007, the *Poa* feeding trial was conducted 25 July 2007, the *Agropyron* trial was conducted 28 July 2007, and the *Potentilla* trial was conducted 2 August 2007.

In addition to the measurements taken during the feeding trial, the average mass and average length of each seed was determined in order to note the characteristics of each seed. The lengths of twenty seeds were measured using a pair of calipers with a precision of 0.1mm. Five measurements were taken of the mass of 40 seeds, which were then used to calculate the average mass of each seed. Average seed measurements were used in order to examine the possible relationship between seed consumption and seed size in accordance with the optimal foraging theory.

*Analysis*

The examination of *P. maniculatus* utilization of seeds was determined by three response variables: mass of seeds removed from the cup, mass of seeds dispersed in the bedding, and mass of seeds consumed. The mass of seeds removed from the initially presented material was calculated by subtracting the mass remaining in the cup from the initial mass of seeds. The mass of each seed type dispersed in the bedding was calculated by identifying and separating dispersed seeds into species, and then seeds of each type were weighed. The consumption of seeds was calculated by subtracting the mass of seeds in the bedding from the mass of seeds removed from the cup. The change in mass experienced by the control was taken into consideration for all calculated response variables.

An ANOVA was conducted in order to examine two factors and their interaction effect for the amount of mass of seeds removed, the mass of seeds in the bedding, and the mass of seeds consumed for each species. The first factor was the genus type, looking at differences among *Lepidium*, *Poa*, *Agropyron*, and *Potentilla*. The second factor was whether the seed was native or invasive. Additionally, four pairwise t-tests were conducted in order to look more closely at the differences between invasive and native consumption within the same genus. A regression was also done to examine a possible relationship between the mass of the mouse and the number of seeds it consumed.

Three simple linear regressions were conducted for each of the three measured factors in order to look at possible relationships between the ratio of seed utilization of invasive to native, and their corresponding mass ratio. Seed mass ratio was the independent variable, and the ratio of seeds consumed or hoarded was defined as the dependent variable. An additional regression

was conducted in order to look at the relationship between the size of the mouse and the amount of mass it consumed. Mouse mass was plotted on the x-axis as the independent variable, and mass of seeds consumed was plotted on the y-axis as the dependent variable.

**Results**

In three of the feeding trials that were conducted, all six of the trial *P. maniculatus* successfully completed the trial without disturbance of their seeds. Only in the *Agropyron* was it necessary to remove one of the trials from the data set due to the fact that the mouse overturned the invasive trial cup.

ANOVA showed no overall trend in seed hoarding and consumption for each genus by *P. maniculatus* (Figure 1). A comparison of the total seed removal for each of the genera indicated that there was no significant difference among the four genera (p=0.704). Also, no significant difference was found among the genera in the total mass of seeds removed to the bedding (p=0.569). However, there was a statistically significant difference among the genera in the total number of seeds consumed (p=0.003). A Bonferoni post-hoc test indicated that there was significantly less mass of *Agropyron* seeds consumed than either *Lepidium* (p=0.070) or *Poa* (p=0.014). It also showed that there was significantly more mass of *Poa* seeds consumed than *Potentilla* seeds (p=0.020).

***Potentilla recta* and *Potentilla glandulosa***

*P. recta* seeds were crescent-shaped, dark brown in color, and had an average length of 1.071±0.08mm and an average mass of 0.15±0.003mg. The seeds for *P. glandulosa* were

noticeably larger with an average length of 3.272±0.71 mm and an average mass of 0.98±0.003mg.  Unlike the *P. recta*, the *P. glandulosa* seeds were irregularly shaped and covered in many stiff hairs that measured approximately one-fourth the length of the seed in size.

Because *P. recta* seeds were not fully separated from vegetative materials, several calculations were made in order to determine the mass of *P. recta* seeds removed from the cup and the amount consumed by the mouse.  Based on previous observations of mouse feeding behavior, the assumption was made that no debris presented with the *P. recta* seeds was consumed in the trial.  Thus, the mass of the debris that remained in the box was determined, and this value was subtracted from the initial calculated debris mass.  This difference then used to calculate the value of the seed mass remaining in the cup after the trial.  The mass of the cup was then used in combination with the bedding seed mass to determine the total seed mass consumed by the *P. maniculatus*.  Additionally, I assumed that the debris and seeds absorbed moisture at the same rate in the control. Therefore, the percent change in mass calculated in the control was used to convert the initial seed masses to values relative to the final.

There was no overall trend in the removal, consumption, and hoarding of *P. recta* or *P. glandulosa* seeds by *P. maniculatus* (Figure 2).  Total mass of seeds removed from the initial presented seed mass, did not differ significantly between the *P. recta* and *P. glandulosa* (p=0.439).  There is also no significant difference between the mass of each type of seed removed to the bedding (p=0.406) or consumed by the *P. maniculatus* (p=0.585).  Statistical t-tests may have limited inference as the six replicates used for removed, bedding and consumption for P. *recta*, and removed and bedding for *P. glandulosa* violated assumptions of normality.

### *Lepidium perfoliatum* and *Lepidium virginicum*

The seeds of *L. perfoliatum* and *L. virginicum* were very similar in size, but different in color and texture. *L. virinicum* seeds were red-orange in color and had an average length of 1.97±0.10mm and an average mass of 1.00±0.04mg. The seeds for *L. virginicum* averaged a length of 1.771±0.11mm and a mass of 1.08±0.11mg. Unlike the seeds of *L. perfoliatum*, those of *L. virginicum* were dark purple and had a hairier texture.

A greater mass of *L. perfoliatum* was utilized by the *P. maniculatus* (Figure 3). A significantly greater mass of seeds of *L. perfoliatum* was removed from the trial cup (p=0.0.016) and consumed by *P. maniculatus* (p=0.013). No statistically significant difference was found in the mass of seeds dispersed in the bedding (p=0.592). *L. perfoliatum* was consumed much more than it was moved to the bedding.

### *Agropyron cristatum* and *Agropyron spicatum*

Although the seeds of both *Agropyron* species had an awn as part of their morphology, the seed length measurements did not include the awn because it did not comprise a significant portion of the mass, nor was it part of the seed that was consumed by the mouse. The average length of *A. cristatum* was 4.69±0.50 mm with an average mass of 0.72±0.25mg. *A. spicatum* was more than twice as large, with an average length of 8.02±1.27mm and an average mass of 1.70±0.13mg. Both *Agropyron* seeds were a similar golden color and neither possessed hairs or bristles apart from a single awn.

No preference for either of the *Agropyron* species was demonstrated by *P. maniculatus* in the mass of seeds removed (p=0.509) and the mass of seeds dispersed in the bedding (p=0.738)

(Figure 4). However, *P. maniculatus* consumed significantly more *A. spicatum* than *A. cristatum* (p=0.072). Limited inference may be taken from this t-test because the data for native removed and bedding seed masses, and the data for the invasive bedding mass violated the assumptions of normality.

### *Poa pratensis* and *Poa secunda*

Seeds of the *Poa* genus were similar in shape, but variable in color, size and texture. *P. pratensis* was slightly darker in color than *P. secunda* and had tufts of fine hairs at the tip of each seed. The average length of *P. pratensis* was 2.97±0.52mm and mass was 0.36±0.09mg. *P. secunda* was longer on average, with a length of 4.01±0.43mm, but had a similar average mass of 0.35±0.16mg. *P. secunda's* seeds were slightly redder in color and lacked any hairs.

*P. maniculatus* showed a significant preference for the native *P. secunda* (Figure 5). A greater mass of seeds was removed from the *P. secunda* presented material than the *P. pratensis* (p=0.009). Although a greater proportion of this removed mass was attributed to seed consumption (p=0.011), a statistically greater mass of *P. secunda* seeds were also dispersed into the bedding material (p=0.014).

### Consumption Relative to Seed and *P. maniculatus* Size

Regression of the invasive to native ratio of total seeds removed did not show a significant relationship ($R^2$=0.402, p=0.366). Similarly, there was no relationship between the consumption ratio and seed size ratio ($R^2$=0.115, p=0.660). However, a relationship was found between the ratio of invasive to native seed mass in the bedding and the invasive to native seed

size ratio ($R^2$=0.821, p=0.094) (Figure 6), suggesting that the seeds stored and dispersed by *P. maniculatus* is increased as the size of the seed decreases.  Regression of the mass of seeds consumed vs. the mass of the *P. maniculatus* showed no significant relationship ($R^2$=0.003, p=0.729).  Even when these data are broken down to show consumption of seeds of individual plant species vs. mouse mass, no species showed an obvious relationship between these two factors.

## Discussion

*Peromyscus maniculatus* did not consistently show a preference for invasive or native species four all four genera tested.  Two of the feeding trials, *Lepidium* and *Agropyron*, demonstrated that *P. maniculatus* clearly preferred the invasive member of the species pair. Contrastingly, *P. maniculatus* in the *Poa* feeding trial clearly showed a preference for the native species relative to the invasive.  The inconsistent preference for the native or the invasive species of each genus suggests that *P. maniculatus* do not respond uniformly to the presence of invasive species' seeds in their habitat.

### *Potentilla recta* and *Potentilla glandulosa*

It is possible that no statistical significance was shown between *P. recta* and *P. glandulosa* because of the increased seed use for *P. recta* seeds.  If a method for successfully separating pod debris from the *P. recta* seeds were possible, direct measurements of seed mass could be taken and the error due to the presence of the pod debris may have been mitigated. Additionally, *P. recta* foliage has a high tannin content that makes it unpalatable to wildlife

(Dwire et. al 2006).  If tannins were present in the debris that accompanied the *P. recta* seeds, *P. maniculatus* may have been discouraged from choosing these seeds from the trial cup.  However, the findings of Dwire et. al (2006) contrast with field observations of *P. recta* plants during the seed collection period, indicating that although *P. recta* plants were abundant at the site of seed collection, many of the plants did not have seed pods because the florescence of the plant had been removed by herbivory, which was noted by the presence of clipped stems.  This suggests that the foliage of *P. recta* plants on the National Bison Range may be more palatable than other studies have concluded.

It is likely that the successful invasion of *P. recta* is neither positively nor negatively influenced by seed predation of *P. maniculatus* on its seeds.  *P. recta* is highly competitive in its non-native environment because the average *P. recta* plant produces over 6000 seeds each year, most of which have high viability and high germinability, and they saturate the seed bank (Dwire 2006).  Additionally, *P. recta* shows limited distribution of the seeds from the parent plant, suggesting that few of the seeds are transported by potential seed predators to cache locations. Despite these features that suggest high reproductive competitiveness for *P. recta*, it would be beneficial to repeat this feeding trial with direct mass measurements in order examine any significance that seed predation may have on distributing *P. recta* farther from the parent plant.

### *Lepidium perfoliatum* and *Lepidium virginicum*

Although there was no significant difference between the mass of seeds dispersed in the bedding, the apparent preference for *L. perfoliatum* could be beneficial for the successful dispersion of this invasive species.  In their caching activities, *P. maniculatus* store fewer seeds

in larder hoards, deeper caches in burrows, than they do in scatter hoards, caches with shallower burial (Hollander and Vander Wall 2004). Although scatter-hoarded seeds are generally buried 2-12mm beneath the surface, nearly 30% of cached seeds remain partially exposed (Vander Wall et. al 2001). Because of this unique caching strategy, *P. maniculatus* are ideal dispersers for species of the genus *Lepidium*, which require a high amount of light to germinate (Toole and Cathey 1961). Therefore, it is likely that *Lepidium* seeds not only benefit in their dispersal through the physical removal to another location, but *P. maniculatus* cache most of their seeds in a way that is beneficial to the germination of this plant. Additionally, Baskin and Baskin (2006) found *L. perfoliatum* seeds that survived in the seed bank for more than 40 years. Therefore, *L. perfoliatum* seeds that are cached at less ideal depths have a chance for germination in later growing seasons.

### *Agropyron cristatum* and *Agropyron spicatum*

Although there was no difference in the mass of seeds removed from the initial presented material or dispersed in the bedding, there was a greater consumption of *A. cristatum* seeds by *P. maniculatus* than seeds of *A. spicatum*. *A. spicatum* has been demonstrated to be an important food source of *P. maniculatus* in the Rocky Mountains (Pyke 1986), and therefore my observation may have different implications in a more natural setting. It is possible that *A. cristatum* is an even more valuable food source to *P. maniculatus* than *A. spicatum* and selected when given a choice between the two species. This result is even more significant when size of each seed is considered. Because *A. cristatum* is three times less massive than *A. spicatum*, the conversion of seed mass to seed number indicates that there is an even starker difference in the

number of *A. cristatum* seeds consumed to those of *A. spicatum*.  Since *P. maniculatus* are

known to transport only one seed at a time when they are dispersing seeds into individual caches

(Vander Wall 1997, Vander Wall et. al. 2001).  Therefore, if the mouse is expending more

energy transporting *A. cristatum* seeds individually, *A. cristatum* seeds may have a higher energy

content that would optimize the *P. maniculatus* expenditure.  Further investigation in the energy

content and nutritional value of *A. spicatum* seeds would help clarify this choice differential.

It is likely that consumption of *A. spicatum* seeds by *P. maniculatus* and other granivores

may affect its sustainability in a plant community.  Quinton et. al. (1982) found the seed

production of *A. spicatum* to be poor and variable, and thus would likely be affected more by

seed predation.  Additionally, like *P. recta*, it is likely that the successful invasion of *A. cristatum*

is dependent on other seed characteristics and not just the predation of its seeds by *P.*

*maniculatus*.  Dispersal related variables may not be as important to the successful invasion of *A.*

*cristatum* to an area as the biological pre-emption of native species (Bakker and Wilson 2004).

Other studies attribute the success of *A. cristatum* invasibility to their seed production and

overwhelming contributions to the seed bank (Marlette and Anderson 1986, Hansen and Wilson

2006).


***Poa pratensis* and *Poa secunda***

Even though a greater mass of *P. secunda* seeds were found in the bedding than *P.*

*pratensis*, the mass of *P. secunda* seeds consumed were four times greater than those dispersed

in the bedding.  This ratio of consumed to bedded seed mass is opposite of the ratios found in

prior studies.  Vander Wall et. al. (2001) found that *P. maniculatus* consumed only 29% of seeds,

while caching 71% of seeds.  Hollander and Vander Wall (2004) found similar results, with more than twice as many seeds being scatter-hoarded as consumed.  However, Ivan and Sihart (2000) demonstrated that rodents tended to cache non-preferred seeds while consuming more preferable ones.  It is possible that *P. secunda* is a more preferable food source for *P. maniculatus*, which would explain their decision to consume a greater proportion of the seeds.  This preference for *P. secunda*, particularly with respect to *P. pratensis*, may explain some of the success of the invasive *P. pratensis*.  Although some studies found that *P. maniculatus* were beneficial to the species whose seeds that they consume via the dispersal process, herbivory of native species' seeds and seedlings may also completely excluded native species from an area (MacDougall and Wilson 2007).  If this is the case for *P. secunda*, it may explain a selective advantage for *P. pratensis*.  In addition to less seed predation by *P. maniculatus*, *P. pratensis* seeds may have other adaptations that allow them to successfully invade the Palouse prairie habitat.  In their native habitat where soil moisture is greater, up to 35% of *P. pratensis* seeds may be removed from the seed bank due to fungal disease (Schafer and Kotanen 2003).  Because of the significantly reduced soil moisture of the Palouse prairie environment, the *P. pratensis* seeds may be free from this restraint in their reproduction.  Additionally, *P. pratensis* seeds that can remain viable in the seed bank for more than 40 years, thus giving them an advantage in the number of seeds available for germination during favorable conditions (Baskin and Baskin 2006).

**Conclusions**

The greatest total seed consumption occurred in the genera *Poa* and *Lepidium*, but each

of these genera had one species that was consumed in excess.  In the case of *Poa*, it was the

native species *P. secunda*, and in the genus *Lepidium*, it was the invasive *L. perfoliatum*.  Seeds

from the genus *Agropyron* were consumed the least of all the genera, which somewhat

contradicts observations in southern Wisconsin of *Agropyron* seed consumption by *P.*

*maniculatus* in which the majority of the *P. maniculatus* diet was comprised of *Agropyron*

species (Kantak 1983).  Investigation of relative consumption of various genera in the Palouse

prairie in contrast with a temperate woodland environment may give insight into the

susceptibility of one habitat to greater invasibility.  Additionally, the differences in preferences

for genera as a whole may have greater consequences in the effect of seed predation on the

invasiveness of a species within each genus.  If *P. maniculatus* consume or disperse more of one

species within a genus that makes up a greater portion of their diet, these granivores may exhibit

even greater selection pressure on the species in question.

In each trial, the mass of seeds consumed was defined as the difference between the mass

of seeds removed and the mass of seeds in the bedding.  In doing this calculation, the bedding

measurement was likely an overestimation of the actual bedding seed mass because the seeds in

the bedding were exposed to *P. maniculatus* urine, and therefore, they may have gained more

mass from moisture that was not accounted for in the control.  Thus, the consumption values are

probably an underestimation of the actual mass of seeds consumed.  The ratio of mass of seeds

consumed to mass of seeds dispersed and stored is inconsistent with other studies of *P.*

*maniculatus* caching, which found a greater percentage of the seeds cached than consumed by

the *P. maniculatus* (Vander Wall 1997, Vander Wall et. al. 2001). This may have been due in part to the set up of the trial, in which *P. maniculatus* were not able to bury the seeds that they decided to store. If the trial had been conducted in a larger system with a soft substrate, a greater percentage of the seeds may have been scatter hoarded by the test subjects.

Based on optimal foraging theory, we expect that *P. maniculatus* would store and consume seeds of greater mass. However, *P. maniculatus* has been shown to cache seeds of non-preferred species while consuming more preferable ones. It may be that smaller seeds are compatible with non-preferred seeds, and therefore the *P. maniculatus* choose to consume larger seeds and store smaller ones (Ivan and Sihart 2000). The amount of energy and nutritional requirements that an invasive seed contains is crucial in understanding the mechanism behind *P. maniculatus* preference and ultimately how the behavior of *P. maniculatus* with regard to seed type will affect the success of the species. The nutrition and energy content of the seeds in this study may have implications for the applicability of these results to the dynamics that occurs in the field. For example, all seeds that were used in this study were presented to the *P. maniculatus* without any obstructions, and there was little energy expenditure required to obtain them. However, in the field, where *P. maniculatus* have to forage for seeds and remove them from seed heads and pods, their seed preference may change based on the net energy required to obtain and consume seeds from a certain species.

Although this study provides insight into the relationship between *P. maniculatus* and invasive and native species pairs of four Palouse plant genera, the mechanism behind this relationship is still unclear. In order to understand the motivation for choosing one plant species over the other, further studies need to be conducted on the relative energy and nutrition of the

seeds of each species, the difficulty of foraging for each seed in the wild, and the relative abundance and seasonality of each species. *P. maniculatus* are known to prefer seeds that are more readily available in their environment (Kantak 1983). If this is true of the Palouse prairie system, there are two major implications that need to be studied. First, if invasive species become more abundant than native species of the same genus, will *P. maniculatus* feed more heavily on the invasive species and therefore curb its spread in the system or aid in its dispersal through caching? Secondly, does this imply that *P. maniculatus* will be able to adapt to an environment in which the percentage of invasive species are continually rising because they will alter their food preference to the species of the greatest abundance? Ultimately, the role of seed predation of invasive species not only provides information on the way in which these granivores are altering the composition of the plant community around them, but it also holds significant meaning for the way in which the consumers of the ecosystem adjust to their changing environment.

**Acknowledgements**

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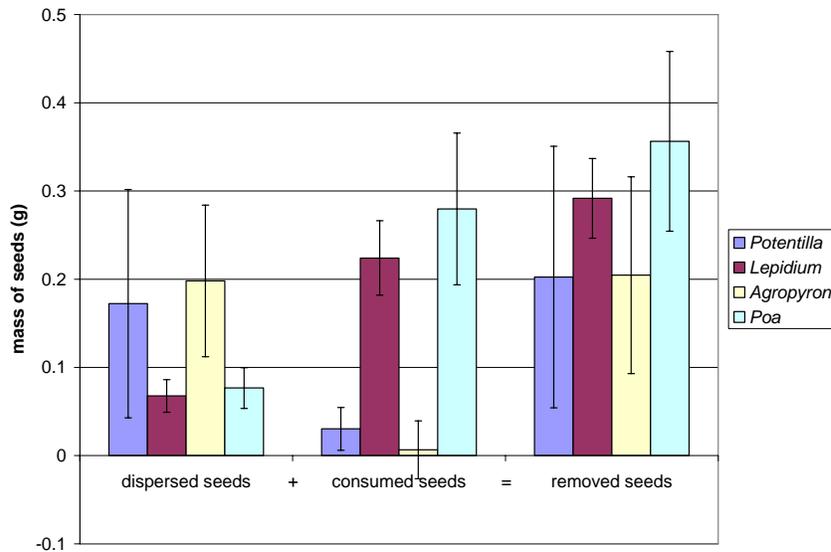
**Appendix**



Figure 1. Total seed mass utilized by *P. maniculatus* for four genera.  There were no significant differences among the genera for the total mass of seeds dispersed in the bedding (p=0.569) and the total mass of seeds removed (p=0.704).  The data did show a statistically significant difference in the total mass of seeds that were consumed (p=0.003).  A Bonferonni post-hoc test indicated that there was significantly more *Poa* seed mass consumed than *Agropyron* (p=0.014) and *Potentilla* (p=0.020), and more *Lepidium* seed mass was consumed than *Agropyron* (p=0.070).
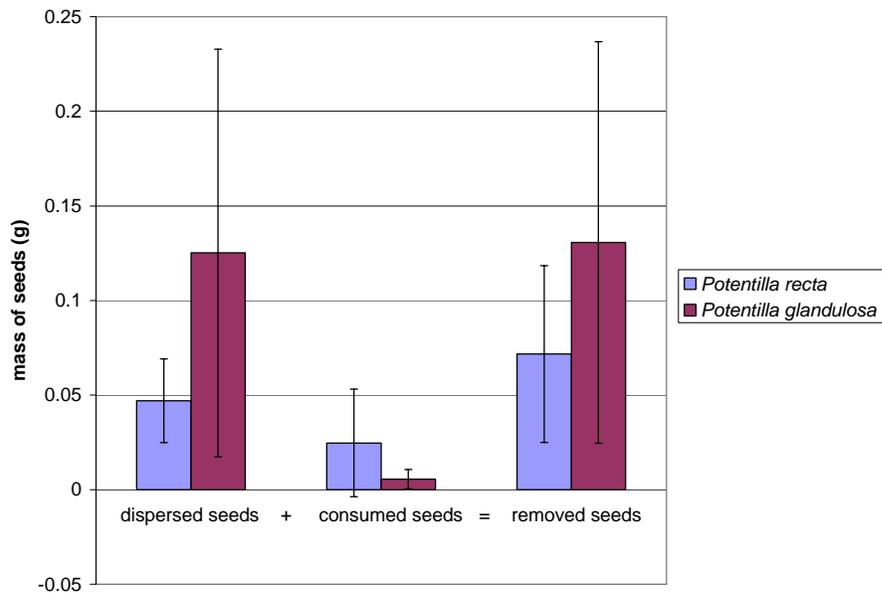
Figure 2.  In the feeding trial for the genus *Potentilla*, there was no significant difference in the mass of seeds dispersed by the *P. maniculatus* (p=0.439), the mass of seeds consumed (p=0.406), and the overall mass of seeds removed from the original mass (p=0.585).
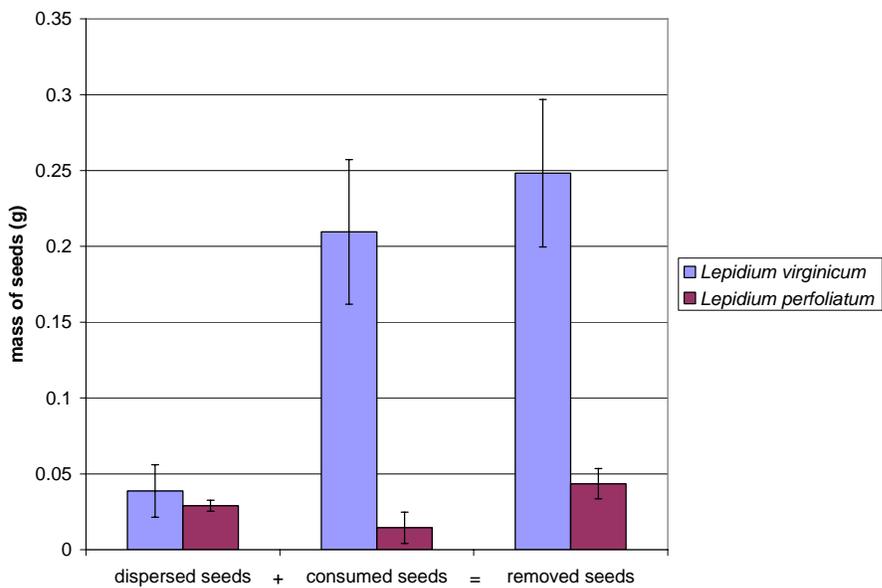


Figure 3. For the genus *Lepidium*, there was greater seed consumption and removal of *L. perfoliatum* over *L. glandulosa*.  Although there was no significant difference in the mass of seeds found in the bedding (p=0.592), there was a greater mass of *L. perfoliatum seeds* both removed from the initial mass (p=0.0013) and consumed (p=0.016).
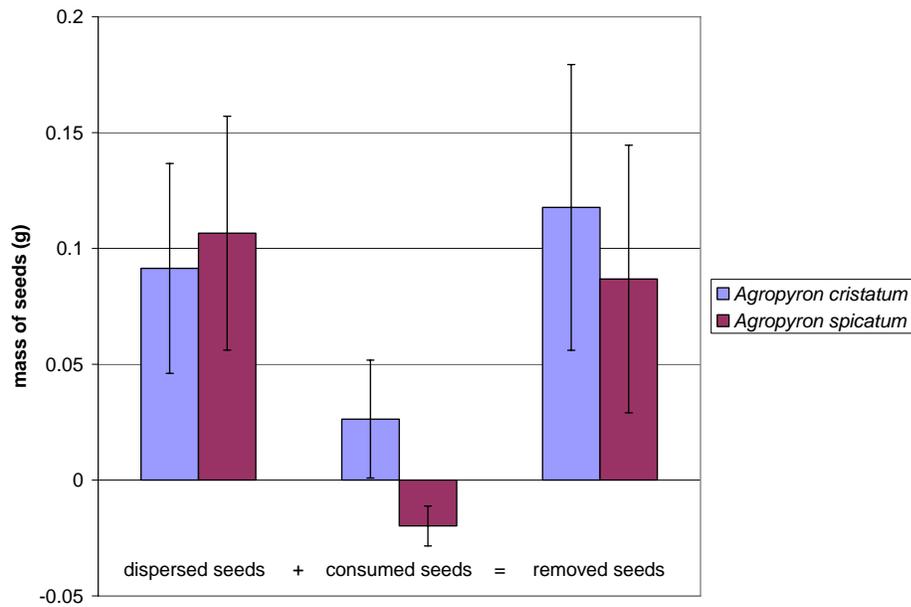
Figure 4. No clear trend was observed in seed preference of *A. cristatum* or *A. spicatum* across the response factors. There was no significant difference in the mass of seeds dispersed (p=0.509) and the mass of seeds removed (p=0.738). A greater mass of *A. cristatum* seeds were consumed than *A. spicatum* (p=0.072).
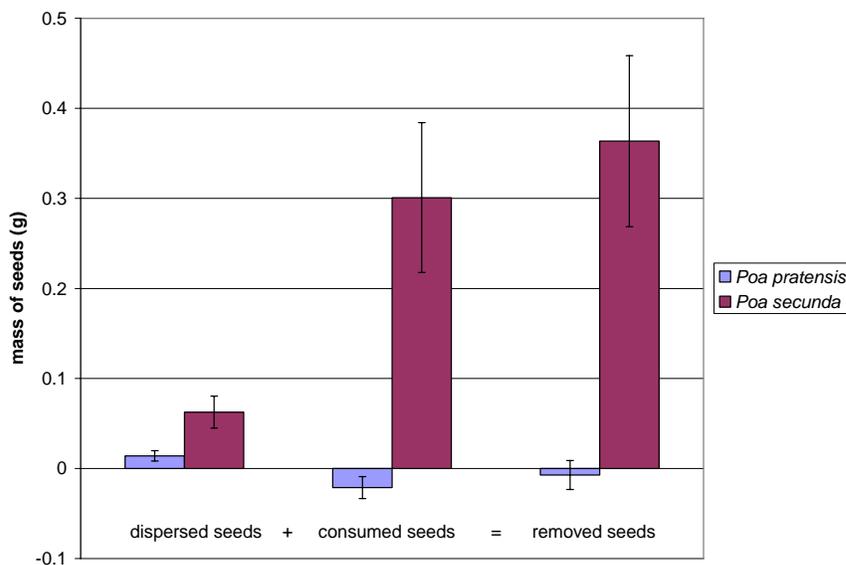


Figure 5. *P. maniculatus* removed significantly more mass of seeds from *P. secunda* (p=0.009). Of the removed amount, there was more seed mass in the bedding (p=0.014), as well as a greater seed mass consumed (p=0.011).
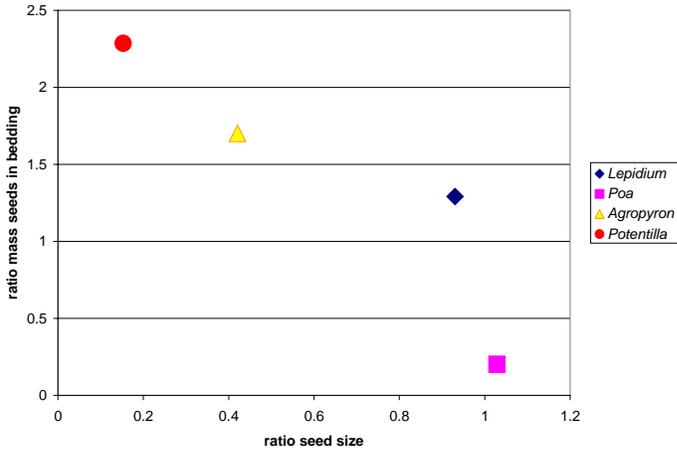
Figure 6. Relationship between amount and size of seeds dispersed. There was a negative relationship between the mass of seeds dispersed in the bedding and the size of the seed across each species of the four genera ($R^2$=0.821, p=0.094).
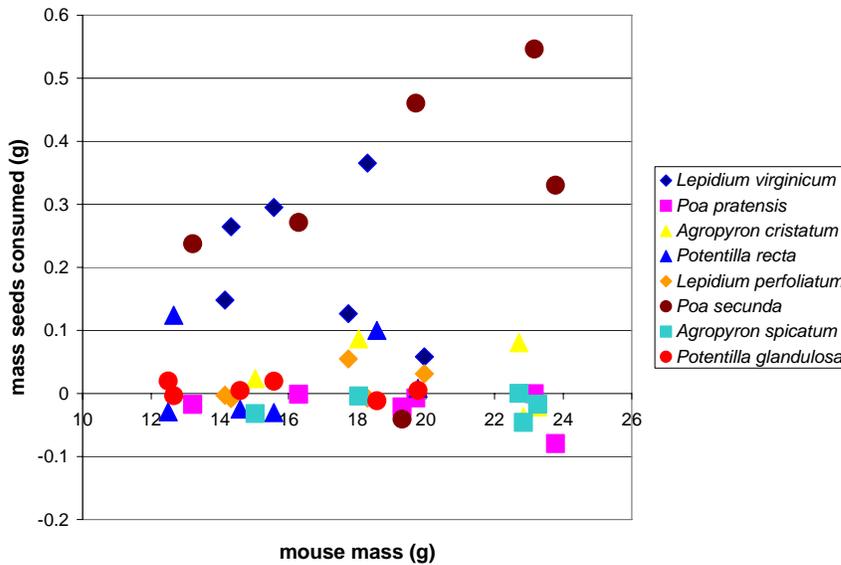


Figure 7. Relationship between mouse mass and mass of seeds consumed for each species. There was no overall relationship between the mass of seeds consumed by each *P. maniculatus* and its mass ($R^2$=0.003, p=0.729). No individual species showed a trend in consumption when *P. maniculatus* mass was considered.