

Peromyscus maniculatus seed selection as densities of seeds of native and invasive species from the Palouse prairie of western Montana are manipulated

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ABSTRACT

Granivorous rodent species are known to both remove viable seeds from the environment by predation and disperse seeds to new areas through caching. One such species, the Deer Mouse (*Peromyscus maniculatus*), is especially of interest in the Palouse Prairie because of its abundance in the area and its potential as a vector for seed dispersal, both of native and invasive seeds. Three pairs of plant seeds from the Palouse prairie, 1. Soft Brome (*Bromus hordeaceus*) and Cheatgrass (*Bromus tectorum*) 2. Bluebunch Wheatgrass (*Agropyron spicatum*) and Crested Wheatgrass (*Agropyron cristatum*), 3. Arrowleaf Balsamroot (*Balsamorhiza sagittata*) and Common Sunflower (*Helianthus annuus*), were selected to be presented to captured *P. maniculatus* in a choice-based, four hour, contained feeding trial. Three treatments, containing varying densities of seeds, were examined for each seed pair tested in this project. *Peromyscus maniculatus* was shown to change its preference of dispersal and consumption of seeds, based upon a preference index (e.g. an index analyzing both mass of seeds dispersed/consumed and original density of seeds available as a percentage, Figure 3). The average mass of each seed used in the study had no statistically significant relationship upon the mass of that seed being dispersed or consumed in feeding trials (Regression, $p > 0.05$ in all cases, Table 4) or upon the preference index of dispersal or consumption (Regression, $p > 0.05$ in most cases, Table 5). In general, *P. maniculatus* mass had little to no relationship with the total mass of seeds consumed or dispersed during feeding trials (Regression, $p > 0.05$ in all cases, Table 3). Furthermore, the total mass of seeds dispersed within the cages did not have a significant relationship with the total mass of seeds consumed during feeding trials (Regression, $p > 0.05$ in all cases, Table 7). The preference index of *P. maniculatus* with respect to both seed dispersal and seed consumption changed significantly between the pairs of seed species presented to *P. maniculatus* in all cases except *H. annuus* and *B. sagittata* with respect to dispersal, where *P. maniculatus* preferred to

disperse *B. sagittata* in only one treatment and never preferred to disperse *H. annus* (Kruskal-Wallis, $p < 0.05$, Figures 6, 7, 8, 10, 11, 12, and 14). *Peromyscus maniculatus* also dispersed seeds by mass predominantly proportionally to their abundance by mass at the start of the feeding trials except in the case of *B. sagittata* and *H. annus* when *P. maniculatus* dispersed neither seed by mass statistically significantly more than the other in any treatment (Kruskal-Wallis, $p < 0.05$, Figures 4, 8, and 12). No clear trend was found for *P. maniculatus* preferring native or invasive seed species within the pairs, supporting either the “Red Queen Hypothesis” or the “Enemy Release Hypothesis,” but the preference index in general was higher for seeds not in excess, showing that *P. maniculatus* may preferentially select to consume and disperse seeds in smaller density. *Peromyscus maniculatus* selection of low density seeds is especially of interest because of the small density of invasive seeds present when invasive plants expand their range to a new area. Understanding the mechanism of seed choice of *P. maniculatus* when foraging in the environment and the factors affecting its choice may be useful in predicting *P. maniculatus* effect in aiding or squelching invasions by novel plant species in the Palouse Prairie.

INTRODUCTION

Within the Palouse Prairie of western Montana, there are several important granivores that eliminate seeds by predation (Parker and Gilbert 2007; Westerman et. al. 2008; Bricker et. al. 2010) and aid in dispersing seeds through caching (Vander Wall et. al. 2001; Zwolak et. al. 2010). Among these granivores is the Deer Mouse (*Peromyscus maniculatus*), a small, terrestrial, nocturnal rodent often making shallow caches of seeds for which they preferentially forage in the wild (Vander Wall et. al. 2003). *Peromyscus maniculatus* is a significant vector for

seed dispersal within several environments (e.g. forests, grasslands, deserts) during all stages of succession (Siepielski et. al. 2008; Zwolak et. al. 2010; Pearson and Callaway 2008; Allen et. al. 2009). Understanding the behavior of *P. maniculatus* and other vectors during seed selection and dispersal is critical to anticipating the spread of invasive plants and implementing targeted management within an area of invasion (Shahid et. al. 2008; Allen et. al. 2009).

Currently, two hypotheses explain the mechanism behind the spread of invasive species: the “Red Queen Hypothesis” and the “Enemy Release Hypothesis” (Parker and Gilbert 2007; Jogesh et. al. 2008). The “Red Queen Hypothesis” states that native plants, having co-evolved with native predators, will have better suited anti-predator defenses and will therefore outcompete and limit the establishment of invasive species (Parker and Gilbert 2007). The “Enemy Release Hypothesis” states that invasive species in a new environment find themselves unchallenged by their own natural predators, and, being adapted to herbivory in ways that native predator species are not prepared to handle, will be more successful in discouraging herbivory than the native plant species (Jogesh et. al. 2008; Orians and Ward 2010; Cappuccino and Arnason 2006; Morrien et. al. 2010). Furthermore, invasive species, released from their natural predators in their indigenous environment, will be better suited for outcompeting native species of plants according to the “Enemy Release Hypothesis” (Jogesh et. al. 2008; Orians and Ward 2010; Cappuccino and Arnason 2006; Morrien et. al. 2010).

When *P. maniculatus* is presented with equal mass of two types of seeds, the factors associated with food selection are a relative nutritional content, the processing time required prior to consumption, and anti-predator defenses within each seed type, and these factors each contribute to an optimal foraging strategy, resulting in seed choice (MacArthur and Pianka 1966; Ebersole and Wilson 1980; Phelan and Baker 1992). Plants furthermore have adapted many

techniques to satiate *P. maniculatus* to increase the probability of their seeds surviving predation and harnessing this vector of seed dispersal (Vander Wall 2010). Satiating *P. maniculatus* is accomplished by making large nutritious seeds that can be cached, producing anti-predator defenses to discourage predation, and masting (Vander Wall 2010). Furthermore, the types of seeds output by plants and the quantity of seeds year to year also has a significant influence on the special distribution of caches by *P. maniculatus*, giving plants the ability to fine tune their seed output to maximize dispersal by seed dispersing animals (Moore et. al. 2007). While *P. maniculatus* moves a seed, the quantity of dispersed seeds in general also does not directly correspond to seed mortality rate (Moore and Swihart 2008).

If *P. maniculatus* preys selectively upon invasive seeds and does not disperse them, it may be inferred that those invasive seeds are better forage and were not well adapted to compete with the native predators (i.e. *P. maniculatus*), supporting the “Red Queen Hypothesis.” Conversely, if *P. maniculatus* preys selectively on native seeds and does not disperse them, it may be inferred that the invasive seeds, free from their natural predators, are better equipped than the native seeds to discourage predation, making the native seeds better forage for *P. maniculatus* and supporting the “Enemy Release Hypothesis.”

If *P. maniculatus* is presented with two types of seeds with differing abundance, I predict that *P. maniculatus* will forage selectively for the abundant seed, as was found in previous studies using other *Peromyscus* species (Phelan and Baker 1992; Ivan and Swihart 2000). This result will be especially if there is a disparity between the nutritional content, processing time, or anti-predator defenses between each pair of seeds (Phelan and Baker 1992; Ivan and Swihart 2000).

While *P. maniculatus* is an important vector for spreading seeds within an environment, the response of invasive species to a new environment is ultimately the deciding factor for the success or failure of an invasion (Xu et. al. 2010; Philips et. al. 2010; Ito and Saka 2009; Verhoeven et. al. 2009). Interestingly, the dynamic algorithm plants use to accomplish optimal allocation of energy to enhance these qualities initially changes vastly when a nonindigenous environment is encountered, due to new evolutionary pressures found at the perimeter of the range of these invading species (Harder and Johnson 2009). This allocation of energy generally favors a shift from anti-predator defenses to reproduction when a new environment is encountered by an invasive plant species (Xu et. al. 2010; Phillips et. al. 2010). After rapid adaptation, a period of lag follows where adaptations are less dramatic (Harder and Johnson 2009). Shifting energy allocation towards reproduction and growth and away from unnecessary chemical defenses often gives invasive species a much needed competitive edge relative to native species of plants in a new area (Xu et. al. 2010; Philips et. al. 2010; González et. al. 2010; Abhilasha and Joshi 2009).

Although invasive species are expanding their range when they enter a new area, little evidence has been found suggesting that development of chemical defenses by invasive species occurs between the beginning of invasion and throughout establishment under predation of the native predators in a new area, suggesting that biochemical defenses may assist in an invasion but are not the result of struggle between native herbivores and invasive species of plants (Lind and Parker 2010). In addition, invasive plants have been found to adopt a vigorous and aggressive stance toward spreading rapidly by increasing seed output in foreign areas by as much as order of magnitude, while allocating fewer resources toward chemical defenses as compared to native species in the area who must compete with highly adapted terrestrial herbivores

(Blossey and Notzold 1995; González et. al. 2010). Because of this increased reproductive edge, it is anticipated in this study that invasive species may indirectly harness *P. maniculatus* as a vector for spreading seeds rapidly when they increase seed output in a new environment, and may even use this increased reproductive behavior to hybridize with other individuals to decrease palatability to native granivores such as *P. maniculatus* (Grosholz 2010; Blossey and Notzold 1995). Because of hybridization, invasive species are not only capable of invading an area quickly but are also capable of creating hybrids which are able to better avoid predation than their parent invasives (Grosholz 2010). If *P. maniculatus* is found to select seeds based largely on abundance, it may also be possible that *P. maniculatus* is capable of highly impacting the spread of invasive species when their seeds are introduced into a new area in larger quantities relative to invasive species of plants in their core range (Blossey and Notzold 1995; González et. al. 2010).

The main questions to be addressed are:

1. Does *P. maniculatus* feed selectively based upon abundance when given two seed types related by genus or at least by tribe?
2. Does *P. maniculatus* disperse the most common seed by mass within the cage if given the choice between two types of seeds in differing abundances by mass?
3. What are the implications of the feeding preferences of *P. maniculatus* on seed dispersal and consumption of native and invasive plant species?
4. Does *P. maniculatus* weight have a significant effect on the mass of seeds spread or eaten by treatment?
5. Does the total mass of seeds moved have a significant effect on the total mass of seeds eaten by treatment?
6. Does the average mass of a seed have a significant relationship to *P. maniculatus* preference both with respect to dispersal and to consumption?

The purpose of this project is to examine the preference of *P. maniculatus* when presented with varying quantities of seeds, one species a native from the Palouse prairie of Montana and one invasive species of the same genus or tribe. In the control treatment, the

choice of *P. maniculatus* to disperse or consume each species of seed is made independently of variability in seed density because both species of seeds were presented in equal mass; however, in the excess density treatments, densities of seeds are uneven so that the seed choice of *P. maniculatus* was examined when relative abundance of seeds by mass was a factor. Because invasive species are known to output more seeds within a foreign environment regardless of chemical defense allocation (Parker et. al. 2007; Blossey and Notzold 1995), I am interested in understanding the role of seed abundance as a factor in food selection by *P. maniculatus*. If *P. maniculatus* are found to prefer seeds due to abundance rather than nutritional value and regardless of seed identity (i.e. native or invasive), the high output of invasive plants making seeds in a foreign area may strongly contribute to their spread by *P. maniculatus* and may also result in increased predation (Westerman et. al. 2008; Blossey and Notzold 1995).

I hypothesize that *P. maniculatus* will consume and spread seeds proportional to seed abundance, so that abundant seeds will be consumed and spread at a greater rate than rare seeds during feeding trials. This prediction does not particularly correlate with one or the other of the “Red Queen Hypothesis” or “Enemy Release Hypothesis” because *P. maniculatus* will feed preferentially on whichever seed type is most abundant, either native or invasive, being more easily found and of greater interest to foraging *P. maniculatus* than the uncommon seeds. I also hypothesize that average seed mass will be a significant factor in the foraging choice of *P. maniculatus* and that the size of each mouse will also affect the amount of seed consumption and dispersal throughout the feeding trials. Finally, I hypothesize that total mass of seed dispersed will not have a statistically significant positive relationship to total mass of seed consumed because of the behavior of *P. maniculatus* to both disperse seeds and cache (Vander Wall et. al. 2003).

Because the invasive seeds in a nonindigenous environment would be found at lower densities locally in their front of expansion into a nonindigenous area, prompting increased reproduction by invasive plants (Blossey and Notzold 1995), I furthermore predict that *P. maniculatus* will be a significant factor to consider when managing the spread of invasive species from one area to another early on in the invasion process. Understanding the mechanism of *P. maniculatus* seed choice while foraging will help clarify the role of *P. maniculatus* in the spread and recruitment of species.

METHODS

Trapping Peromyscus maniculatus

To obtain sufficient numbers of *P. maniculatus*, collapsible Sherman traps were baited and set in the evening (between 1800 and 2100 hours MST) and examined the following morning at sunrise (between 0600 and 0800 hours MST). A 1:1 mixture of oats and barley mixed with peanut butter was statistically proven to be preferred by *P. maniculatus* through a feeding trial involving four individuals (t-test, $t = 9.242$, $p = 0.0001 < 0.05$, Figure 2) over “Sweet Feed,” a mixture of corn, oats, and barley, which was used previously in studies involving capture of *P. maniculatus* in this area (Nowalk and Gerrish, UNDERC West, 2007). As *P. maniculatus* prefers the “Peanut Butter Bait,” this bait was used to bait the traps. Eighteen mice (i.e. 6 mice per treatment) were caught and used in the feeding trials per pair of seeds.

Peromyscus maniculatus were weighed using an Avinet (500 g) precision spring scale and sexed prior to initializing the acclimation period and feeding trials. During the minimum three day acclimation period, *P. maniculatus* were given equal daily amounts of the “Peanut Butter Bait” in each of two trays on either side of the cages and water near the center of the cage (Figure 1). Three sheets of phone book paper were provided as bedding during the acclimation

period. *Peromyscus maniculatus* were kept in clear plastic cages during the day, and cages were changed and cleaned at least every other day in the morning.

Data Collection/Feeding Trials

Prior to weighing out seeds for data collection, seeds were heated for 36 hours at 80⁰ C in a Constant Temperature Oven (Model DK-42) to remove excess moisture and ensure that the dry quantity of seed mass given to the mice was equal across replicates. The mass of seeds used were measured prior to these feeding trials using a balance (Model Scout-Pro accurate to 1 mg). During all three treatments, the mice were fed equal amounts of total food (i.e. total food = mass of seed 1 + mass of seed 2) while the mass of individual seed types were varied between the three treatments. The control treatment included equal masses of each seed type, set at 1.5 grams. In the native seed excess treatment, the native seed was at high density (2.5 grams) and the invasive seed was at low density (0.5 grams). In the invasive seed excess treatment, the native seeds were at low density (0.5 grams) and the invasive seeds were at high density (2.5 grams). Data collecting began at midnight and ended at 0400 hours MST before the sun rose to coincide with the natural foraging activity of *P. maniculatus*. Seeds were housed in metal receptacles placed at either end of the plastic cage and were secured using masking tape prior to the feeding trials to ensure that they did not spill and spread seeds outside the containers.

Consumption of seeds was determined using the mass of the seeds both within the metal receptacles and outside of these containers after junk components, such as feces, bedding, and shells, were removed. Furthermore, seeds found outside of the metal receptacles at the conclusion of feeding trials were collected and weighed separately than those found within the metal receptacles. Prior to weighing the seeds after feeding trials, the seeds were again heated in the oven for an additional 36 hours at 80⁰ C to avoid variance in seed mass due to moisture

absorption during feeding trials. Once the mass of seeds in the dish and seeds moved outside of the metal receptacles was known, the mass of seeds eaten by *P. maniculatus* during the four hour feeding trial was calculated by subtracting those masses from the total mass at the outset of the feeding trial.

After participating in a feeding trial, *P. maniculatus* was either released or, in minimal cases, re-acclimated for an additional three day period prior to participating in another feeding trial. *Peromyscus maniculatus* participating in more than one feeding trial were not presented with the same pair of the same treatment twice. Reusing *P. maniculatus* minimally and only presenting new seed pairs or new treatments to *P. maniculatus* being reused was meant to reduce bias in preference due to *P. maniculatus* participation in several similar feeding trials between the same pair of seeds.

Selecting Seed Pairs

Over the course of this project, the flora of Montana was scrutinized to select pairs of native and invasive species in the area that were related by genus or at least by tribe to be collected at the National Bison Range (Table 1). The only seed not collected on the National Bison Range was the Common Sunflower (*Helianthus annuus*) whose seeds were taken from a large bag of sunflower seeds already at the residence where this research was conducted, and, while this species is native to the area, it is significantly less abundant than Arrowleaf Balsamroot (*Balsamorhiza sagittata*) in this area and thus was paired with *B. sagittata* in the feeding trials. Pairing the seeds by taxonomic similarity was meant to reduce bias in food preference based upon seeds being significantly different in nutritional value from one another. These three pairs of seeds are the following: 1. *Bromus hordeaceus* and *Bromus tectorum*, 2.

Agropyron spicatum and *Agropyron cristatum*, and 3. *Balsamorhiza sagittata* and *Helianthus annuus*.

Statistical Analysis

Because of the smaller sample size of this study, the data was found to be predominantly non-normally distributed by Shapiro-Wilk normality test ($p < 0.05$). Nonparametric statistics such as the Kruskal-Wallis test were used to examine the difference in the mass of seeds dispersed and consumed during the feeding trials as well as the difference in consumption and dispersal preference indices between the three pairs of seeds. Linear regressions were used to examine the influence of *P. maniculatus* mass upon consumption quantities and mass of dispersed seeds within the plastic cages during feeding trials as well as the effect of average seed mass upon its own consumption and dispersal. The overall size of each seed species used in this project was calculated by measuring both the average mass using seven measurements of ten seeds of that type as well as average length of each of the seventy seeds along its long axis, and these parameters can be found in Table 1.

RESULTS

Soft Brome (*Bromus hordeaceus*) & Cheatgrass (*Bromus tectorum*)

P. maniculatus dispersed *B. tectorum* proportionally to its abundance between treatments (Kruskal-Wallis, KWTS = 12.813, $p = 0.002$); however, no statistically significant difference was found in the mass of *B. hordeaceus* seeds dispersed between treatments (Kruskal-Wallis, KWTS = 4.353, $p = 0.113$) shown in Figure 4. *Peromyscus maniculatus* also consumed *B. tectorum* proportionally to its abundance between treatments (Kruskal-Wallis, KWTS = 8.342, p

= 0.015), but no statistically significant difference was found in the mass of *B. hordeaceus* consumed by *P. maniculatus* between treatments (Kruskal-Wallis, KWTS = 4.300, p = 0.116) shown in Figure 5.

Peromyscus maniculatus preferred to disperse *B. tectorum* statistically significantly more than *B. hordeaceus* in the control treatment (Kruskal-Wallis, MWUTS = 35.000, p = 0.006) and in the excess *B. hordeaceus* treatment (Kruskal-Wallis, MWUTS = 36.000, p = 0.002), but *P. maniculatus* preferred to disperse *B. hordeaceus* statistically significantly more than *B. tectorum* in the excess *B. tectorum* treatment (Kruskal-Wallis, MWUTS = 0.000, p = 0.021) shown in Figure 6.

Peromyscus maniculatus preferred to consume *B. hordeaceus* statistically significantly more than *B. tectorum* in the excess *B. tectorum* treatment (Kruskal-Wallis, MWUTS = 0.000, p = 0.021) and in the excess *B. hordeaceus* treatment (Kruskal-Wallis, MWUTS = 3.970, p = 0.046), but *P. maniculatus* preferred to consume neither seed statistically significantly more than the other in the control treatment (Kruskal-Wallis, MWUTS = 25.000, p = 0.245) shown in Figure 7.

Peromyscus maniculatus mass had no statistically significant relationship to the total mass of *B. hordeaceus* and *B. tectorum* consumed or dispersed throughout the feeding trials (Table 6). *Peromyscus maniculatus* mass did have a statistically significant relationship with the mass of *B. hordeaceus* consumed in feeding trials (Regression, $R^2 = 0.355$, p = 0.015) and upon the preference index of consumption for *B. tectorum* (Regression, $R^2 = 0.473$, p = 0.003).

Crested Wheatgrass (*Agropyron cristatum*) & Bluebunch Wheatgrass (*Agropyron spicatum*)

Peromyscus maniculatus did spread *A. cristatum* (Kruskal-Wallis, KWTS = 11.962, $p = 0.003 < 0.05$) and *A. spicatum* (Kruskal-Wallis, KWTS = 14.363, $p = 0.001 < 0.05$) throughout the cages during feeding trials proportionally to each seed's density relative to total seed mass in the cages regardless of the density of the other seed, shown in Figure 8. Furthermore, a statistically significant difference was found in the amount of *A. cristatum* eaten (Kruskal-Wallis, KWTS = 11.112, $p = 0.004 < 0.05$) and *A. spicatum* eaten (Kruskal-Wallis, KWTS = 11.380, $p = 0.003 < 0.05$) between treatments regardless of the other seed in the cages, shown in Figure 9.

When examining the seed preference index of *P. maniculatus* for *A. cristatum* and *A. spicatum*, several interesting trends were observed. *Peromyscus maniculatus* statistically significantly preferred to disperse *A. cristatum* in the control treatment (Kruskal-Wallis, MWUTS = 5.000, $p = 0.037 < 0.05$) and *A. spicatum* in the excess *A. spicatum* treatment (Kruskal-Wallis, MWUTS = 36.000, $p = 0.004$), but preferred to disperse neither seed significantly more than the other by the preference index in the excess *A. cristatum* treatment (Kruskal-Wallis, MWUTS = 18.000, $p = 1.000$), shown in Figure 10.

With respect to the consumption preference index, a statistically significant difference was found in the preference index of *P. maniculatus* for *A. spicatum* in the excess *A. cristatum* treatment (Kruskal-Wallis, MWUTS = 32.000, $p = 0.019$), while no selectivity was found with the *P. maniculatus* preference index for either seed in the control treatment (Kruskal-Wallis, MWUTS = 27.000, $p = 0.150$) or in the excess *A. spicatum* treatment (Kruskal-Wallis, MWUTS = 10.000, $p = 0.200$), shown in Figure 11.

Peromyscus maniculatus mass was not found to be proportional to total mass of seed dispersed or consumed (Table 6).

Common Sunflower (*Helianthus annuus*) & Arrowleaf Balsamroot (*Balsamorhiza sagittata*)

Peromyscus maniculatus was not found to disperse either *H. annuus* (Kruskal-Wallis, KWTS = 4.121, $p = 0.127 > 0.05$) or *B. sagittata* (Kruskal-Wallis, KWTS = 3.355, $p = 0.187 > 0.05$) proportionally to their abundance, shown in Figure 12. In addition, *P. maniculatus* also did not consume either *H. annuus* (Kruskal-Wallis, KWTS = 3.118, $p = 0.210 > 0.05$) or *B. sagittata* (Kruskal-Wallis, KWTS = 3.665, $p = 0.160 > 0.05$) proportionally to abundance, shown in Figure 13.

A statistically significant difference was found in the dispersal preference index of *P. maniculatus* for *B. sagittata* in the excess *H. annuus* treatment (Kruskal-Wallis, MWUTS = 32.000, $p = 0.025$), while no statistically significant difference was found with *P. maniculatus* preference index for either seed in the control treatment (Kruskal-Wallis, MWUTS = 21.000, $p = 0.631$) or in the excess *B. sagittata* treatment (Kruskal-Wallis, MWUTS = 30.000, $p = 0.051$), shown in Figure 14.

The preference index of consumption for *P. maniculatus* was statistically significantly larger for *B. sagittata* than *H. annuus* in both the control treatment (Kruskal-Wallis, MWUTS = 33.000, $p = 0.016$) and the excess *H. annuus* treatment (Kruskal-Wallis, MWUTS = 36.000, $p = 0.004$). In the excess *B. sagittata* treatment, the preference index of *P. maniculatus* was statistically significantly larger for *H. annuus* than *B. sagittata* (Kruskal-Wallis, MWUTS = 4.000, $p = 0.025$) shown in Figure 15.

While *P. maniculatus* mass did not have a statistically significant effect on the total mass of seeds dispersed or consumed (Table 6), the mass of *P. maniculatus* did have a statistically significant effect on the mass of *H. annuus* consumed (Regression, $R^2 = 0.305$, $p = 0.017$).

Results Pertaining to All Seeds

The average mass of each seed used in the feeding trials did not have a statistically significant relationship with the average dispersal mass or consumption mass of that seed in all cases, shown in Table 4. In addition, the total mass of seeds dispersed during the feeding trials had no statistically significant relationship with the total mass of seeds consumed during feeding trials in all cases, shown in Table 6.

DISCUSSION

Soft Brome (*Bromus hordeaceus*) & Cheatgrass (*Bromus tectorum*)

Peromyscus maniculatus dispersed *B. tectorum* by mass proportionally to its abundance in feeding trials; however, *P. maniculatus* did not show the same effect on *B. hordeaceus*. Interestingly, the reverse effect in dispersal preference was found when examining the dispersal and consumption preference indices, where *P. maniculatus* had an increasing preference index for seeds in low mass abundance.

Increasing *B. tectorum* preference index for dispersal was found from the excess *B. tectorum* treatment, to the control treatment, and to the excess *B. hordeaceus* treatment. Conversely, increasing *B. hordeaceus* preference index for dispersal was found from the excess *B. hordeaceus* treatment, to the control treatment, to the excess *B. tectorum* treatment. This relationship indicates that *P. maniculatus* selectively prefers to spread seeds that are found in low abundance, which supports the hypothesis that *P. maniculatus* is a vector for invasive seed dispersal, particularly early on in an invasion where invasive seeds are not particularly abundant in the nonindigenous range.

The preference index for consumption indicated that *P. maniculatus* preferred to consume *B. hordeaceus* in both the excess *B. tectorum* treatment and in the excess *B. hordeaceus* treatment. This supports the “Enemy Release Hypothesis” in that *P. maniculatus* had a clear preference for the native seed, regardless of its density, within two of the treatments and did not prefer to consume *B. tectorum* in the control treatment. *Peromyscus maniculatus* also did not prefer *B. hordeaceus* in the control treatment, showing that this preference for *B. hordeaceus* found in two of the three treatments did not hold absolutely across the entirety of the experiments between *B. tectorum* and *B. hordeaceus*.

Crested Wheatgrass (*Agropyron cristatum*) & Bluebunch Wheatgrass (*Agropyron spicatum*)

Given the extreme effect of *P. maniculatus* on spreading seeds, regardless of their identity as native or invasive, proportionally to their abundance as reported in Figures 4 and 8, it is necessary that *P. maniculatus* be taken into serious consideration when managing the spread of invasive species into a new area. *Peromyscus maniculatus* must be considered because invasive plant species output as many as an order of magnitude more seeds in a nonindigenous environment (Blossey and Notzold 1995), and *P. maniculatus*, as a vector, will therefore both consume some seeds as well as disperse them throughout the new environment, potentially assisting with early invasions into new environments.

No absolute trend was found across all treatments for *P. maniculatus* preference index with respect to seed dispersal; however, the preference index of dispersal for *P. maniculatus* did change significantly from *A. cristatum* in the control treatment to *A. spicatum* in the excess *A. cristatum* treatment and excess *A. spicatum* treatment, showing that *P. maniculatus* can change its dispersal preferences based upon changing abundance of different forage available. By

selecting to preferentially disperse *A. spicatum* during the excess *A. cristatum* treatment, *P. maniculatus* also is shown as a possible vector of spreading rare seeds within the environment, particularly increasing the threat to the environment in the early stages of invasions when invasive seeds are found in low density.

Peromyscus maniculatus did not simply consume seeds based upon their relative abundance as originally hypothesized. The *P. maniculatus* preference index for consumption was significantly higher for *A. spicatum* in one of the three treatments, the excess *A. cristatum* treatment (Kruskal-Wallis, MWUTS = 0.001, $p = 0.004$), which supports the “Enemy Release Hypothesis” (Parker and Gilbert 2007). This result is likely because *P. maniculatus* is better adapted to eat native species such as *A. spicatum*, having evolved along with this native species, and is less familiar with newer invasive species in the area such as *A. cristatum*. In addition, this decreased predation on invasive species has implications for plant invasions because species such as *A. cristatum* are both released from their natural predators as well as less palatable to *P. maniculatus* or better adapted with anti-predator defenses against *P. maniculatus* predation, giving it a competitive edge on comparable native species such as *A. spicatum*.

Common Sunflower (*Helianthus annuus*) & Arrowleaf Balsamroot (*Balsamorhiza sagittata*)

In this seed pair, *P. maniculatus* was found to neither consume nor disperse either *H. annuus* or *B. sagittata* relative to their abundance between treatments; however, the preference index presented significantly different results.

The preference index for dispersal did identify *H. annuus* to be selectively spread throughout the cages by *P. maniculatus* during feeding trials (Kruskal-Wallis, MWUTS = 32.000, $p = 0.025$). This may be partially because of the large size of *H. annuus* relative to *B.*

sagittata (Table 1), as the literature has reported that large seeds are often cached because of their higher nutritional content (Vander Wall 2010). Furthermore, *H. annus* was found to be preferentially dispersed within the excess *B. sagittata* treatment where it was less abundant, supporting the hypothesis that *P. maniculatus* needs to be considered a factor in early invasions where invasive seeds are found at lower densities when expanding the core of their range.

The preference index for consumption was found to be significantly higher for *B. sagittata* in the control treatment (Kruskal-Wallis, MWUTS = 33.000, $p = 0.016$) and the excess *H. annus* treatment (Kruskal-Wallis, MWUTS = 36.000, $p = 0.004$), but this preference index was statistically significantly higher for *H. annus* in the excess *B. sagittata* treatment (Kruskal-Wallis, MWUTS = 4.000, $p = 0.025$). This relationship again illustrates that *P. maniculatus* readily can change its preference for seed consumption with changing densities of seeds available, and it also appears that *P. maniculatus* may prefer the less abundant seed when selecting forage in the wild. The preference of *P. maniculatus* to consume less abundant seed indicates that *P. maniculatus* may also be a factor in squelching early invasions by consuming invasive seeds that are not abundant in the nonindigenous regions of their range.

Discussion Pertaining to All Seeds

Interestingly, the mass of *P. maniculatus* participating in feeding trials seemed to have no effect on either the total mass of seeds spread throughout the cage (Regression, $p > 0.05$ in all cases) or the total mass of seeds consumed during the feeding trials (Regression, $p > 0.05$ in all cases) shown in Table 5. This is contrary to my hypothesis because it was originally expected that larger mice would require more sustenance than smaller mice, resulting in a directly proportional relationship between *P. maniculatus* mass and the total mass of seeds moved

throughout the cage and with the total mass of seeds eaten during the feeding trials. Given a larger sample size, this trend may be found as expected, but more study into the relationship between *P. maniculatus* weight and total mass of seeds eaten is required to make a more concrete conclusion.

Total mass of seeds moved also had no relationship with total mass of seeds eaten in all three treatments (Regression, $p > 0.05$ in all cases) shown in Table 6. This result has also been reported in the literature (Moore and Swihart 2008), that increased seed dispersal by rodents such as *P. maniculatus* does not always result in higher seed mortality.

FUTURE STUDIES

While this project has elucidated some of the details concerning seed selection by the Palouse prairie granivore, *P. maniculatus*, there are several future studies that would contribute significantly to our understanding of this vector of seed dispersal.

In addition to quantifying the mass of seeds spread throughout the feeding trials, variation in total mass seeds spread and eaten between seed pairs trials might be explained by different amounts of time spent foraging by *P. maniculatus* between replicates. Taking the mass of bedding torn up as a proxy for amount of time spent on activities other than foraging might help standardize between replicates and decrease deviation between replicates. Furthermore, the total amount of bedding torn up at the end of all feeding trials might also indicate the quality of forage each seed pair presents to *P. maniculatus*.

Though the sex of each mouse was determined and noted shortly after its capture, this study essentially ignored the difference in foraging between male and female *P. maniculatus*. Designing a study taking this parameter into effect might also help elucidate seed preference of

P. maniculatus between the sexes, which have furthermore been shown to partition the environment's resources and habitat space in the environment in the literature (Bowers and Smith 1979).

Another possible study examining caching behavior would use a cage of larger dimension, and the distance that seeds were removed from the tray during feeding trials could be recorded. The magnitude of spreading the seeds will allow us to better understand the rate at which *P. maniculatus* spreads seeds over a new space and may also provide information to the quality of the nutrition of each seed based upon the characteristics of spread of the seeds both in distance from the source and from one another (Moore et. al. 2007).

Peromyscus maniculatus is an important granivore and vector for seed dispersal in the Palouse prairie that should be considered when managing the spread of invasive species into new environments. Understanding both the preference of *P. maniculatus* for dispersing seeds and the affinity of *P. maniculatus* for consuming seeds is necessary to predict the effect of *P. maniculatus* in either squelching an invasion or assisting it in its early stages.

ACKNOWLEDGEMENTS

I would like to thank the entire UNDERC West class for their support during this project, specifically Sam Pecoraro and Garrett Coggon for help in setting up traps and Dave Chan for assisting me harvest seeds. I would also like to thank both of my terrific advisors, Page Klug and Gretchen Gerrish, for all their guidance in the execution of this project. Furthermore, I would like to thank Gary Belovsky and the Biology Department at the University of Notre Dame for the opportunity to conduct this research on the National Bison Range in Montana.

TABLES

Table 1: A Table detailing the three seed pairs selected in this project, including two pairs of grasses (pairs 1 and 2) and one pairs of forbs (pair 3). The two grass pairs are paired native and invasive species of the same genus, while the third pair consists of two native species found in the area of the same tribe (Helianthae).

Pair	Species	Native/Invasive	Dates Collected	Length(mm)/Weight(mg)
1	<i>Bromus hordeaceus</i> (Soft Brome)	Native	7-2-10	L = 9.080 ± 1.005 W = 2.829 ± 0.269
1	<i>Bromus tectorum</i> (Cheatgrass)	Invasive	6-23-10	L = 8.284 ± 0.418 W = 3.114 ± 0.313
2	<i>Agropyron spicatum</i> (Bluebunch Wheatgrass)	Native	6-24-10 6-26-10	L = 8.484 ± 1.012 W = 0.842 ± 0.486
2	<i>Agropyron cristatum</i> (Crested Wheatgrass)	Invasive	6-23-10 7-4-10	L = 10.094 ± 0.960 W = 2.742 ± 0.276
3	<i>Balsamorhiza sagittata</i> (Arrowleaf Balsamroot)	Native	6-25-10 6-26-10	L = 7.031 ± 0.658 W = 4.157 ± 0.704
3	<i>Helianthus annuus</i> (Common Sunflower)	Native	7-20-10	L = 10.791 ± 0.848 W = 70.629 ± 4.167

Table 2: Linear regressions between *P. maniculatus* mass and the mass of seed consumed/dispersed. Few relationships were found to be significant and fewer still followed the same general trend. In the equations presented, mouse weight is the independent variable (x) and the mass of seeds consumed or dispersed is the dependent variable (y).

Seed	C/D	Equation	R ²	p
<i>Bromus hordeaceus</i>	Consumed	$y = -0.025x + 0.733$	0.355	0.015
<i>Bromus hordeaceus</i>	Dispersed	$y = 0.003x + 0.400$	0.003	0.845
<i>Bromus tectorum</i>	Consumed	$y = 0.007x - 0.065$	0.102	0.228
<i>Bromus tectorum</i>	Dispersed	$y = 0.027x + 0.113$	0.052	0.860
<i>Agropyron cristatum</i>	Consumed	$y = -0.007x + 0.275$	0.019	0.586
<i>Agropyron cristatum</i>	Dispersed	$y = -0.036x + 1.496$	0.173	0.113
<i>Agropyron spicatum</i>	Consumed	$y = -0.010x + 0.397$	0.031	0.481
<i>Agropyron spicatum</i>	Dispersed	$y = -0.020x + 1.396$	0.012	0.660
<i>Balsamorhiza sagittata</i>	Consumed	$y = -0.006x + 0.576$	0.005	0.779
<i>Balsamorhiza sagittata</i>	Dispersed	$y = 0.018x - 0.099$	0.025	0.548
<i>Helianthus annuus</i>	Consumed	$y = 0.042x - 0.446$	0.305	0.017
<i>Helianthus annuus</i>	Dispersed	$y = 0.021x - 0.258$	0.158	0.103

Table 3: Linear regressions between mouse weight and preference index of seed consumed/dispersed. Few relationships were found to be significant. In the equations presented, mouse weight is the independent variable (x) and the preference index of seeds consumed/dispersed is the dependent variable (y).

Seed	C/D	Equation	R²	p
<i>Bromus hordeaceus</i>	Consumed	$y = -0.117x + 4.269$	0.068	0.330
<i>Bromus hordeaceus</i>	Dispersed	$y = 0.032x + 0.566$	0.014	0.668
<i>Bromus tectorum</i>	Consumed	$y = 0.131x - 1.924$	0.473	0.003
<i>Bromus tectorum</i>	Dispersed	$y = -0.103x + 3.945$	0.115	0.198
<i>Agropyron cristatum</i>	Consumed	$y = 0.131x - 1.754$	0.088	0.231
<i>Agropyron cristatum</i>	Dispersed	$y = 0.021x + 0.753$	0.014	0.637
<i>Agropyron spicatum</i>	Consumed	$y = -0.133x + 5.158$	0.050	0.374
<i>Agropyron spicatum</i>	Dispersed	$y = -0.014x + 1.904$	0.002	0.848
<i>Balsamorhiza sagittata</i>	Consumed	$y = -0.055x + 3.188$	0.012	0.664
<i>Balsamorhiza sagittata</i>	Dispersed	$y = -0.077x + 3.406$	0.031	0.0488
<i>Helianthus annuus</i>	Consumed	$y = -0.025x + 2.141$	0.002	0.858

<i>Helianthus annuus</i>	Dispersed	$y = 0.078x - 0.603$	0.069	0.294
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Table 4: Linear regressions between average seed masses (Table 1) and total mass consumed/dispersed by *P. maniculatus* by treatment. In the equations presented, the independent variable (x) is the average seed mass of each seed type and the total mass consumed/dispersed is the dependent variable (y). *H. annuus* was not included in these regressions because its mass was so much greater than other seeds used in this test and was found to skew the results of the regression significantly. However, removing this point had little effect on the significance of the regressions.

Treatment	C/D	Equation	R ²	p
Control	Consumed	$y = -0.077x + 0.457$	0.444	0.457
Control	Dispersed	$y = -0.210x + 1.210$	0.491	0.187
Excess Invasive Seed	Consumed	$y = 0.053x - 0.016$	0.420	0.237
Excess Invasive Seed	Dispersed	$y = 0.050x + 0.439$	0.014	0.852
Excess Native Seed	Consumed	$y = 0.128x - 0.150$	0.361	0.284
Excess Native Seed	Dispersed	$y = -0.426x + 1.806$	0.637	0.106

Table 5: Linear regressions between average seed masses (Table 1) and preference index of seed consumed/dispersed by *P. maniculatus* by treatment. In the equations presented, the independent variable (x) is the average seed mass of each type of seed, and the dependent variable (y) is the preference index of seeds consumed/dispersed. *H. annuus* was not included in these regressions because its mass was so much greater than other seeds used in this test, and was found to skew the results. However, removing this point had little effect on the significance of the regressions.

Treatment	C/D	Equation	R ²	p
Control	Consumed	$y = 0.101x + 0.835$	0.132	0.549
Control	Dispersed	$y = 0.049x + 0.874$	0.062	0.686

Excess Invasive Seed	Consumed	$y = -0.375x + 3.948$	0.030	0.780
Excess Invasive Seed	Dispersed	$y = 0.032x + 2.115$	0.001	0.967
Excess Native Seed	Consumed	$y = -0.093x + 1.281$	0.014	0.851
Excess Native Seed	Dispersed	$y = 0.201x + 0.974$	0.043	0.739

Table 6: Linear regressions between *P. maniculatus* weight and total mass of both seeds consumed/dispersed independently of treatment by seed pair. In the equations presented, the independent variable (x) is the weight of *P. maniculatus* used in the feeding trials and the dependent variable (y) is the total mass of both seeds consumed/dispersed in each seed pair.

Seed Pair	C/D	Equation	R ²	p
<i>B. hordeaceus</i> & <i>B. tectorum</i>	Consumed	$y = -0.019x + 0.688$	0.190	0.092
<i>B. hordeaceus</i> & <i>B. tectorum</i>	Dispersed	$y = 0.030x + 0.513$	0.068	0.330
<i>A. spicatum</i> & <i>A. cristatum</i>	Consumed	$y = -0.016x + 0.672$	0.027	0.518
<i>A. spicatum</i> & <i>A. cristatum</i>	Dispersed	$y = -0.056x + 2.892$	0.158	0.102
<i>B. sagittata</i> & <i>H. annus</i>	Consumed	$y = 0.036x + 0.130$	0.139	0.128
<i>B. sagittata</i> & <i>H. annus</i>	Dispersed	$y = 0.039x + -0.356$	0.100	0.200

Table 7: Linear regressions between the total mass of seed dispersed by *P. maniculatus* and the total mass of seed consumed by *P. maniculatus* regardless of treatment by seed pair. In the equations presented, the independent variable (x) is the total mass of seeds dispersed and the dependent variable (y) is the total mass of seeds consumed.

Seed Pair	Equation	R ²	p
<i>B. hordeaceus</i> & <i>B. tectorum</i>	$y = 0.009x + 0.310$	0.001	0.924
<i>A. spicatum</i> & <i>A. cristatum</i>	$y = 0.158x + 0.046$	0.049	0.379

B. sagittata & *H. annus*

$$y = -0.080x + 0.848$$

0.010

0.689

FIGURES

P. maniculatus Cage Floor Plan

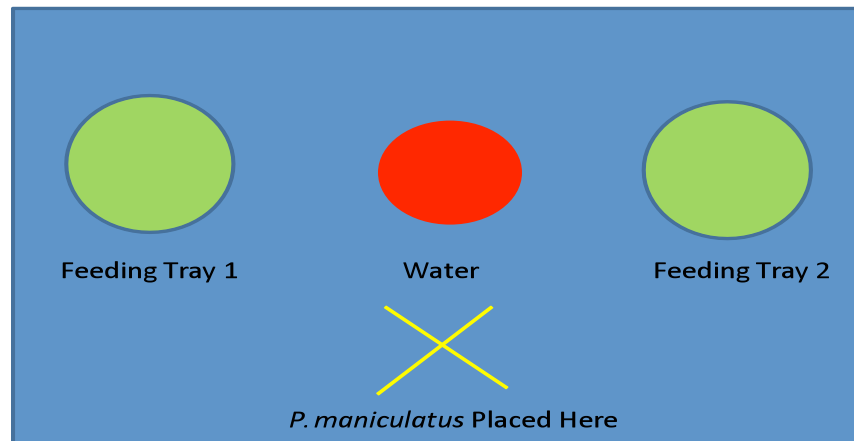


Figure 1: A diagram of the cages where *P. maniculatus* will be kept during acclimation period and participate in feeding trials. The placement of native and invasive seeds in feeding trays 1 and 2 will be alternated between trials to reduce bias. After the minimum three day acclimation, *Peromyscus maniculatus* will be removed from its acclimation cage at midnight and placed in the center of the feeding trial cages. *Peromyscus maniculatus* will be removed from the cage at 4am the following morning, and the mass of each type of seeds within each tray and outside of each tray will be calculated after heating in the oven for 36 hours. Dimensions of each cage are 30.5 x 16 x 11.5 cm. While water will be provided in the acclimation cage, no water will be in the feeding trial cages.

Mass Eaten (g)

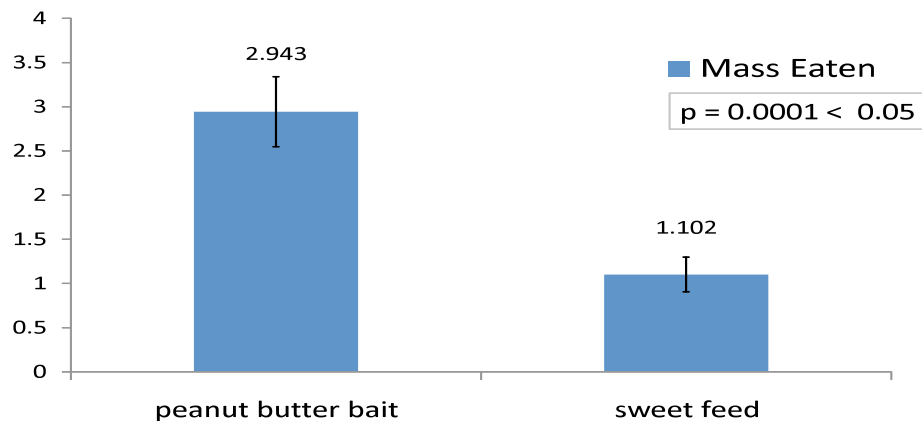


Figure 2: *Peromyscus maniculatus* consumption of the two types of bait examined in this project. Each mouse was provided with 10 g of each bait type and allowed to feed overnight (2200 hours to 0800 hours). A statistically significant difference (t-test, $t = 9.242$, $p = 0.0001$) was found in the preference of *P. maniculatus* for the peanut butter bait over sweet feed.

Preference Index Example Calculation

	Seed Type 1	Seed Type 2
Initially <i>P. maniculatus</i> is given	1.5 g. (50%)	1.5 g. (50%)
<i>P. maniculatus</i> consumes	0.5 g. (33%)	1.0 g. (67%)
<i>P. maniculatus</i> disperses	0.5 g. (62.5%)	0.3 g. (37.5%)
<hr/>		
Consumption Preference Index =	$33\% / 50\% = 0.66$	$67\% / 50\% = 1.44$
- <i>P. maniculatus</i> prefers to consume Seed Type 2 because the Consumption Preference Index is > 1		
Dispersal Preference Index =	$62.5\% / 50\% = 1.25$	$37.5\% / 50\% = 0.75$
- <i>P. maniculatus</i> prefers to disperse Seed Type 1 because the Dispersal Preference Index is > 1 .		

Figure 3: Sample calculations for the Consumption Preference Index and Dispersal Preference Index used to determine which seed is preferred by *P. maniculatus* in each of the feeding trial treatments.

Soft Brome (*Bromus hordeaceus*) & Cheatgrass (*Bromus tectorum*)

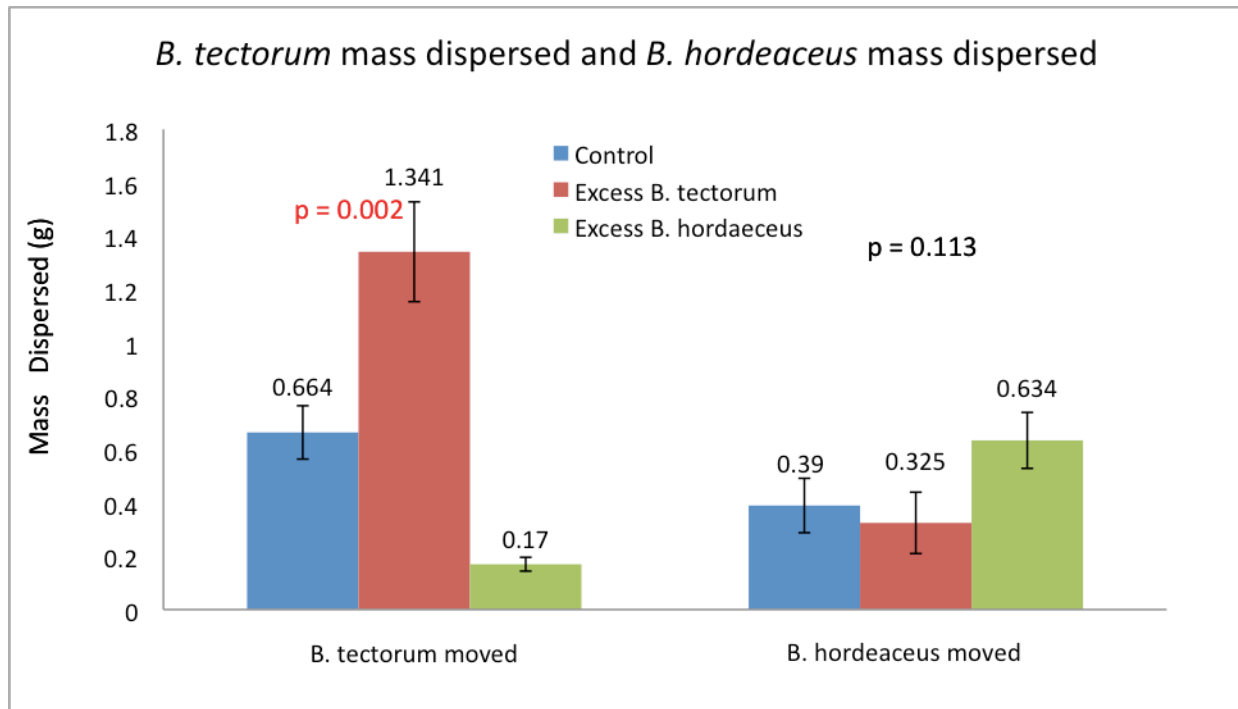


Figure 4: The relative masses of *B. tectorum* and *B. hordeaceus* moved by *P. maniculatus*. *B. tectorum* mass was dispersed proportionally to its abundance between treatments (Kruskal-Wallis, KWTS = 12.813, $p = 0.002$); however, no statistically significant difference was found in the mass of *B. hordeaceus* dispersed between treatments (Kruskal-Wallis, KWTS = 4.353, $p = 0.113$). The results of the Siegel-Tukey are also included; however, none of the treatments for *B. tectorum* dispersed are similar to one another ($p < 0.05$ in all cases).

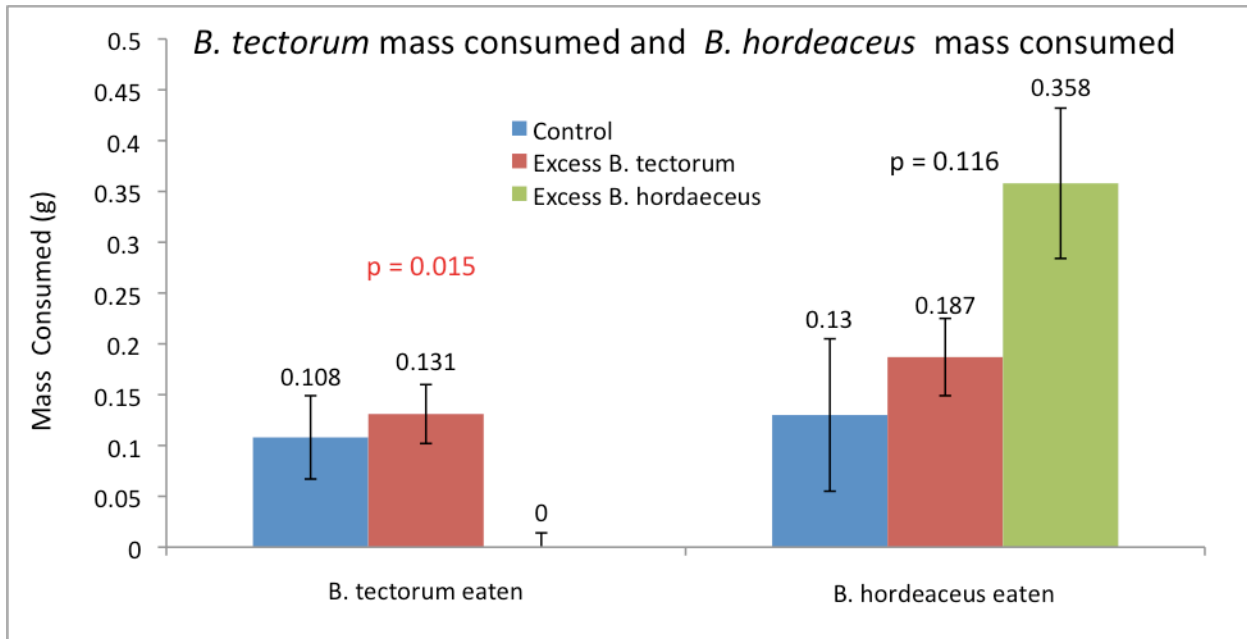


Figure 5: The relative masses of *B. tectorum* and *B. hordeaceus* consumed by *P. maniculatus*. *B. tectorum* mass was consumed proportionally to its abundance between treatments (Kruskal-Wallis, KWTS = 8.342, $p = 0.015$); however, no statistically significant difference was found in the mass of *B. hordeaceus* consumed between treatments (Kruskal-Wallis, KWTS = 4.300, $p = 0.116$).

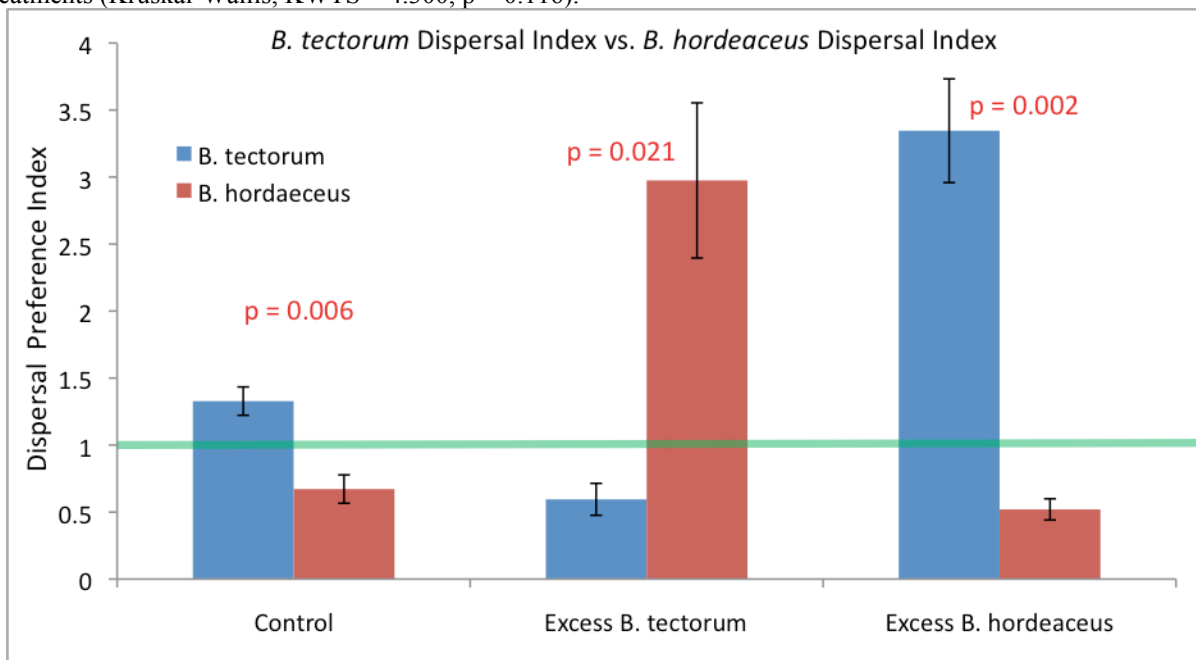


Figure 6: The dispersal preference index of *P. maniculatus* for *B. tectorum* and *B. hordeaceus*. *P. maniculatus* preferred to disperse *B. tectorum* statistically significantly more than *B. hordeaceus* in the control treatment (Kruskal-Wallis, MWUTS = 35.000, $p = 0.006$) and in the excess *B. hordeaceus* treatment (Kruskal-Wallis, MWUTS = 36.000, $p = 0.002$). *P. maniculatus* preferred to disperse *B. hordeaceus* statistically significantly more than *B. tectorum* in the excess *B. tectorum* treatment (Kruskal-Wallis, MWUTS = 0.000, $p = 0.021$). The green line is the cutoff for a significant preference index value.

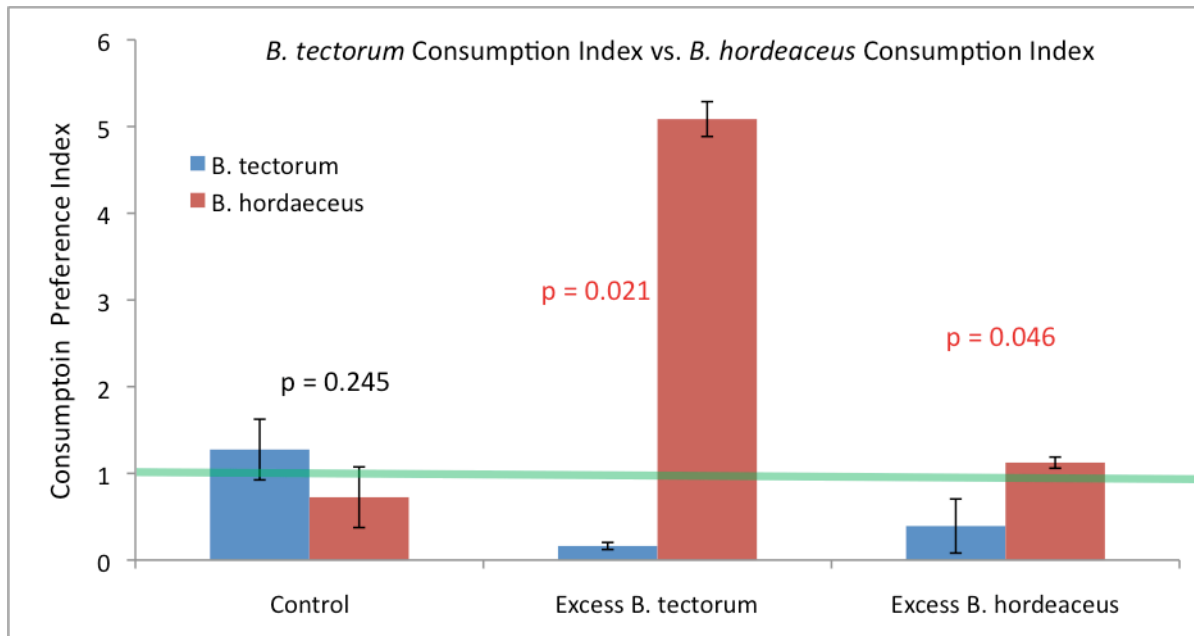


Figure 7: The consumption preference index of *P. maniculatus* for *B. tectorum* and *B. hordeaceus*. *P. maniculatus* preferred to consume *B. hordeaceus* statistically significantly more than *B. tectorum* in the excess *B. tectorum* treatment (Kruskal-Wallis, MWUTS = 0.000, $p = 0.021$) and in the excess *B. hordeaceus* treatment (Kruskal-Wallis, MWUTS = 3.970, $p = 0.046$). *P. maniculatus* preferred to consume neither seed statistically significantly more than the other in the control treatment (Kruskal-Wallis, MWUTS = 25.000, $p = 0.245$). The green line is the cutoff for a significant preference index value.

Crested Wheatgrass (*Agropyron cristatum*) & Bluebunch Wheatgrass (*Agropyron spicatum*)

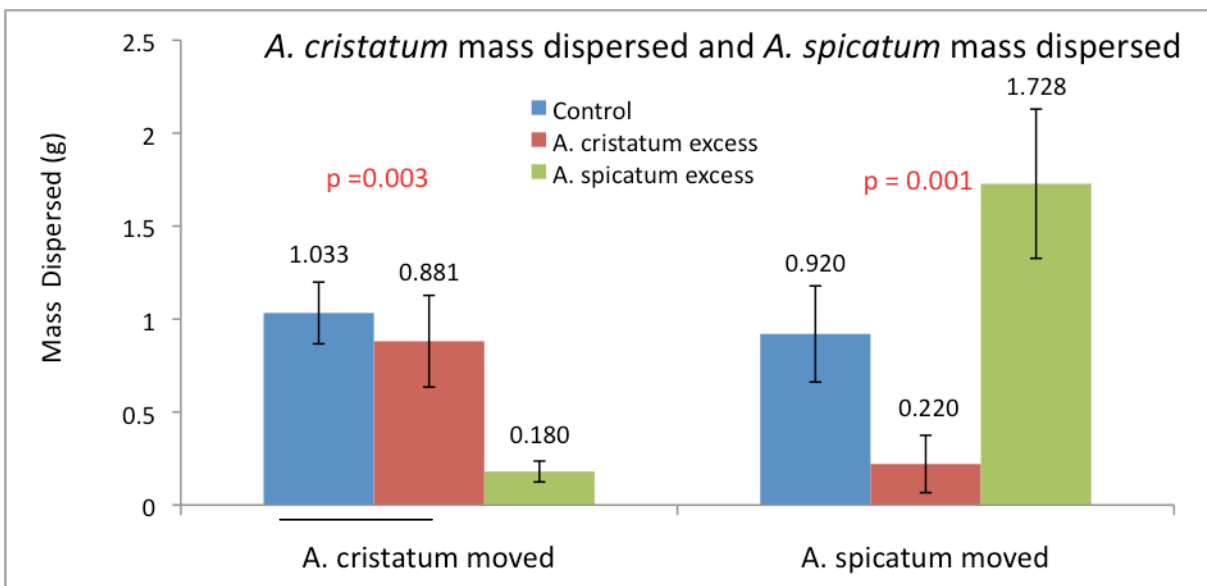


Figure 8: A bar graph showing that the amount of *A. spicatum* and *A. cristatum* moved throughout the cages for the three treatments. There was a statistically significant difference within treatments for both *A. spicatum* mass dispersed (Kruskal-Wallis, KWTS = 14.363, $p = 0.001 < 0.05$) and for *A. cristatum* mass dispersed (Kruskal-Wallis, KWTS = 11.962, $p = 0.003 < 0.05$). A Siegel-Tukey post hoc test was also run, and its results of similarity are signified by the horizontal bars.

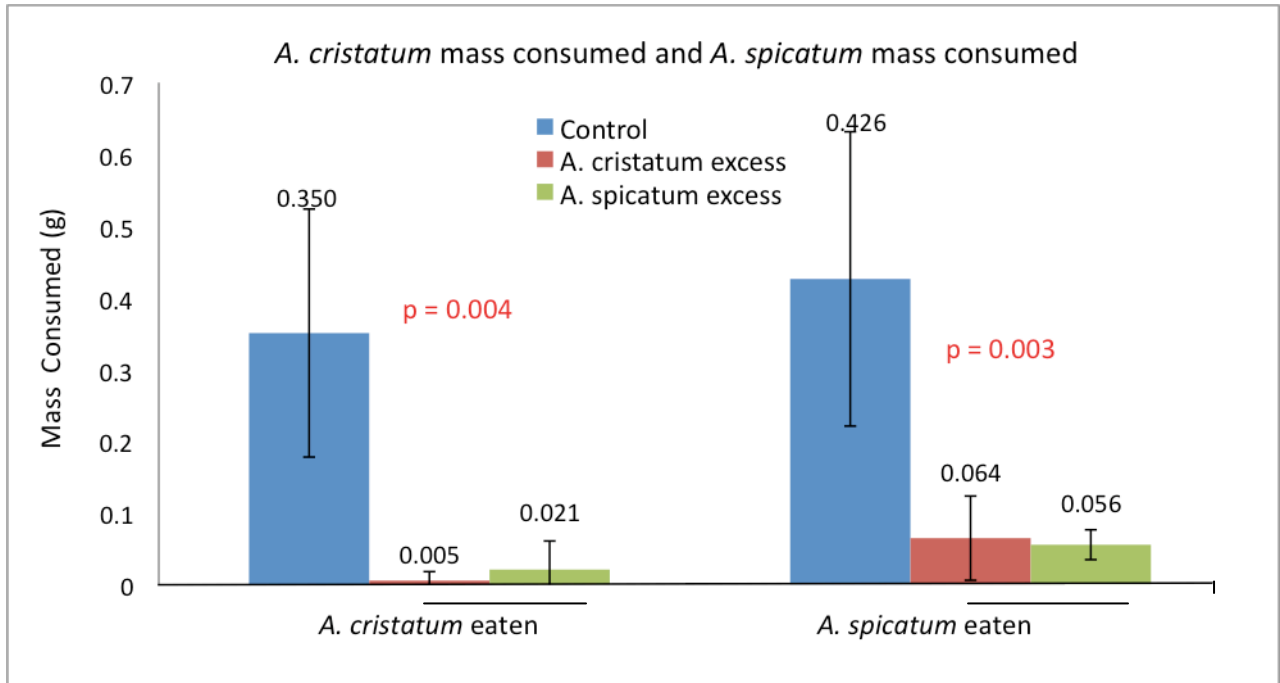


Figure 9: A bar graph showing the difference in seed mass consumed between treatments for *A. cristatum* and *A. spicatum*. A statistically significant difference was found between the amount of seeds consumed between treatments for *A. cristatum* (Kruskal-Wallis, KWTS = 11.112, $p = 0.004 < 0.05$) and *A. spicatum* (Kruskal-Wallis, KWTS = 11.380, $p = 0.003 < 0.05$). The results of the post hoc Siegel-Tukey analysis are also included, and its similarity results are signified by the horizontal bars.

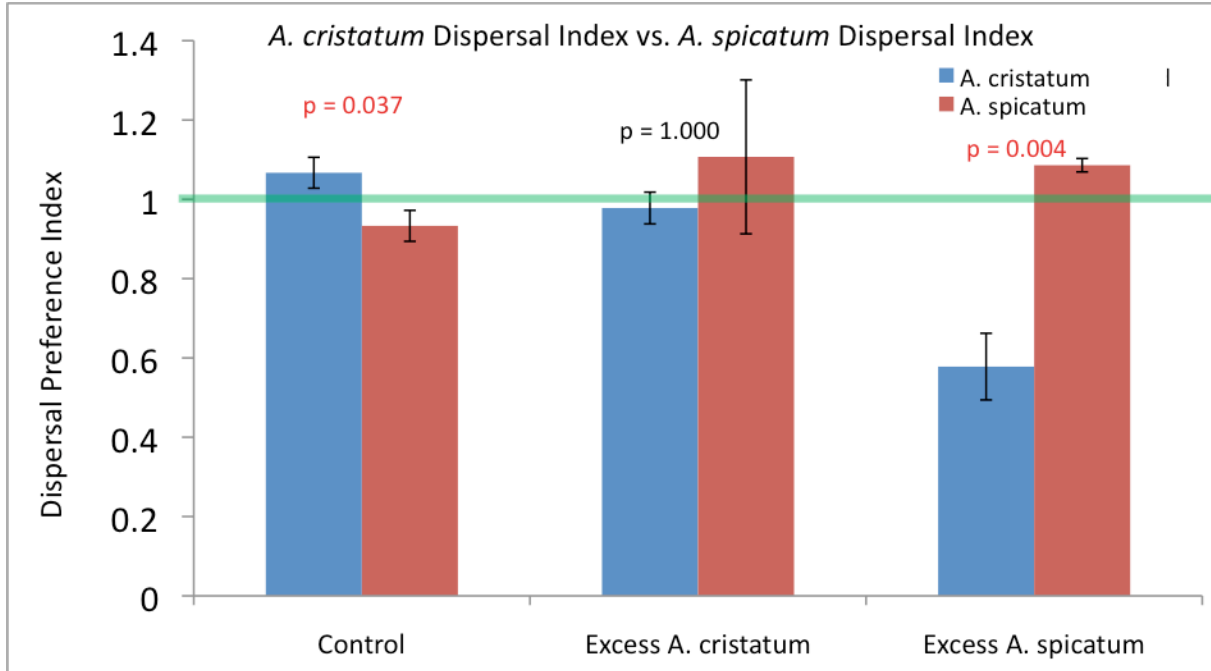


Figure 10: The preference index of *P. maniculatus* for dispersing *A. cristatum* and *A. spicatum* during feeding trials. *Peromyscus maniculatus* statistically significantly preferred to disperse *A. cristatum* in the control treatment (Kruskal-Wallis, MWUTS = 5.000, $p = 0.037 < 0.05$) and *A. spicatum* in the excess *A. spicatum* treatment (Kruskal-Wallis, MWUTS = 36.000, $p = 0.004$), but preferred dispersing neither seed by the preference index in the excess *A. cristatum* treatment (Kruskal-Wallis, MWUTS = 18.000, $p = 1.000$). The green line is the cutoff for a significant preference index value.

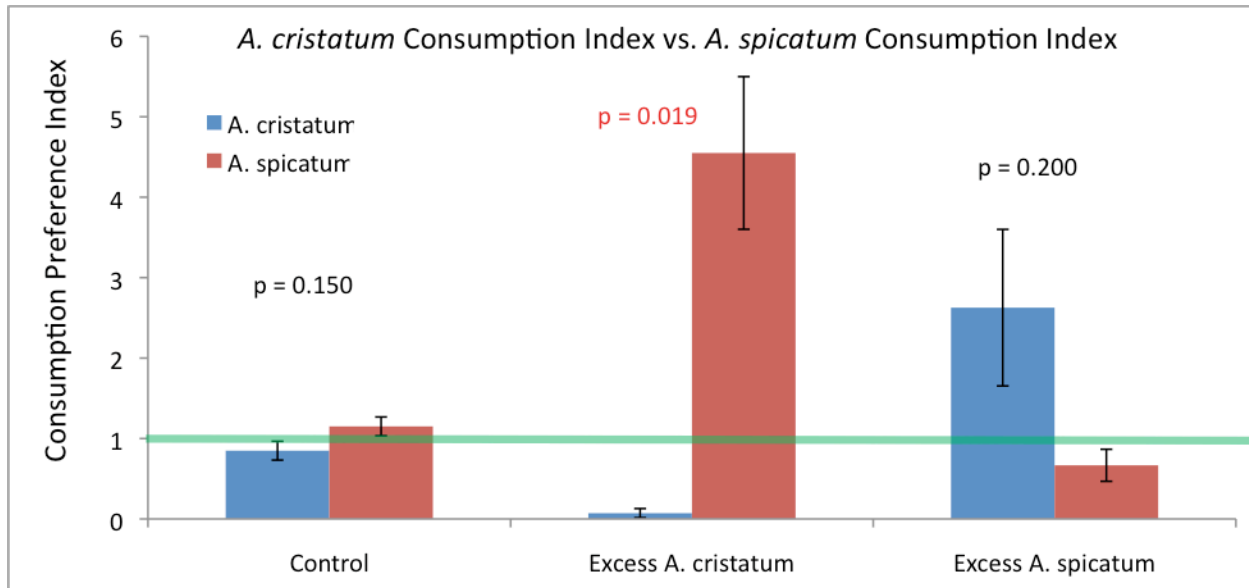


Figure 11: The preference index of consumption for *P. maniculatus* for *A. cristatum* and *A. spicatum*. A statistically significant difference was found in the preference index of *P. maniculatus* for *A. spicatum* in the excess *A. cristatum* treatment (Kruskal-Wallis, MWUTS = 32.000, $p = 0.019$), while no selectivity was found with *P. maniculatus* preference index for either seed in the control treatment (Kruskal-Wallis, MWUTS = 27.000, $p = 0.150$) or in the excess *A. spicatum* treatment (Kruskal-Wallis, MWUTS = 10.000, $p = 0.200$). The green line is the cutoff for a significant preference index value.

Common Sunflower (*Helianthus annuus*) & Arrowleaf Balsamroot (*Balsamorhiza sagittata*)

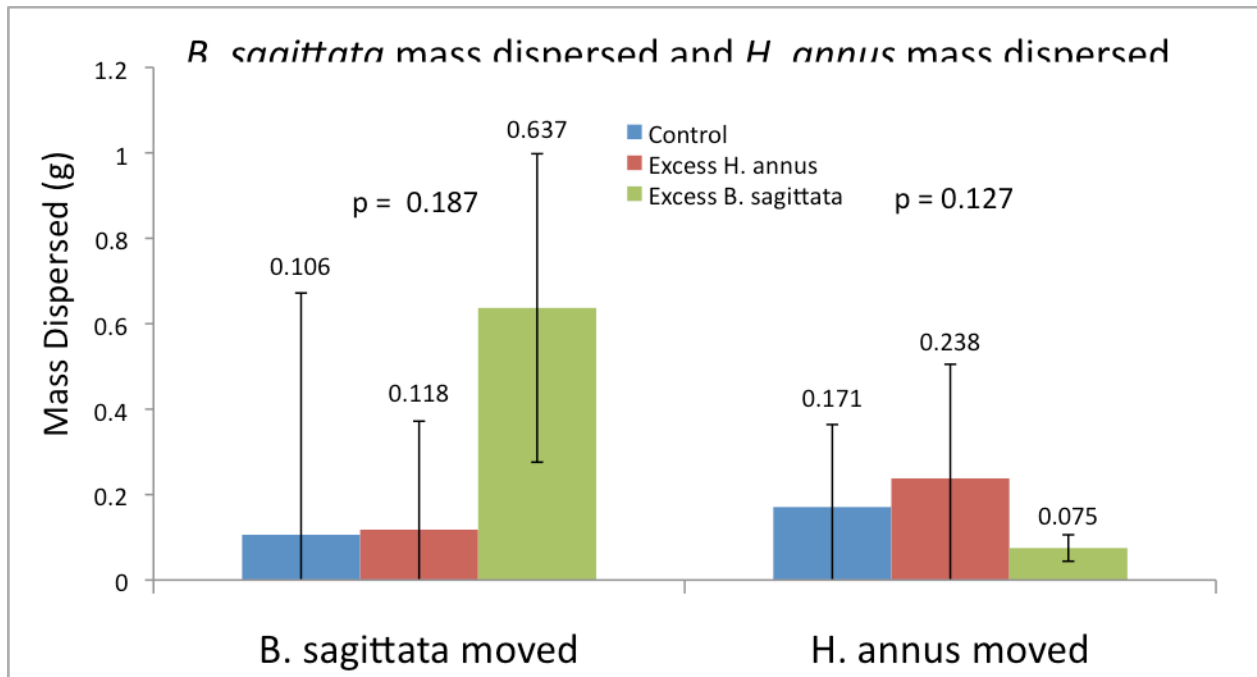


Figure 12: The relative masses of *B. sagittata* and *H. annuus* dispersed by *P. maniculatus* during feeding trials. No statistically significant difference was found in the amounts of *B. sagittata* (Kruskal-Wallis, KWTS = 3.355, $p = 0.187$) or *H. annuus* (Kruskal-Wallis, KWTS = 4.121, $p = 0.127$) between the treatments.

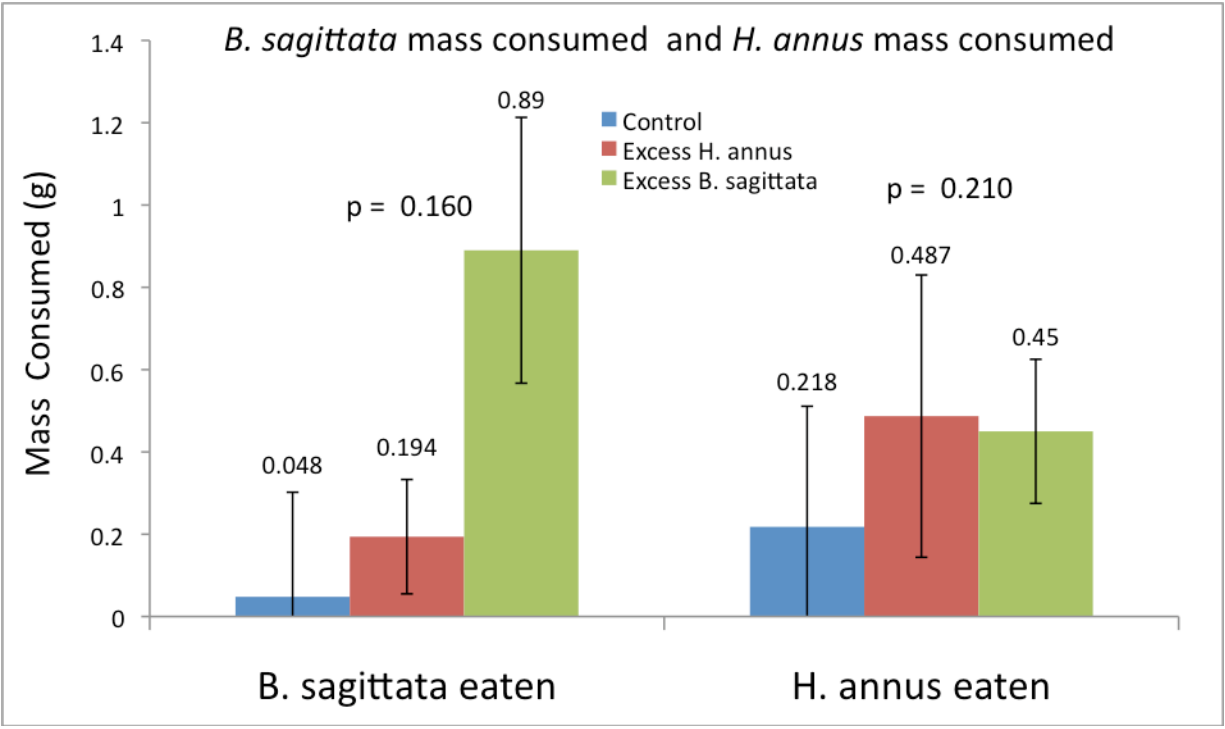


Figure 13: The relative masses of *B. sagittata* and *H. annus* dispersed by *P. maniculatus* during feeding trials. No statistically significant difference was found in the amounts of *B. sagittata* (Kruskal-Wallis, KWTS = 3.665, $p = 0.160$) or *H. annus* (Kruskal-Wallis, KWTS = 3.118, $p = 0.210$) consumed between the treatments.

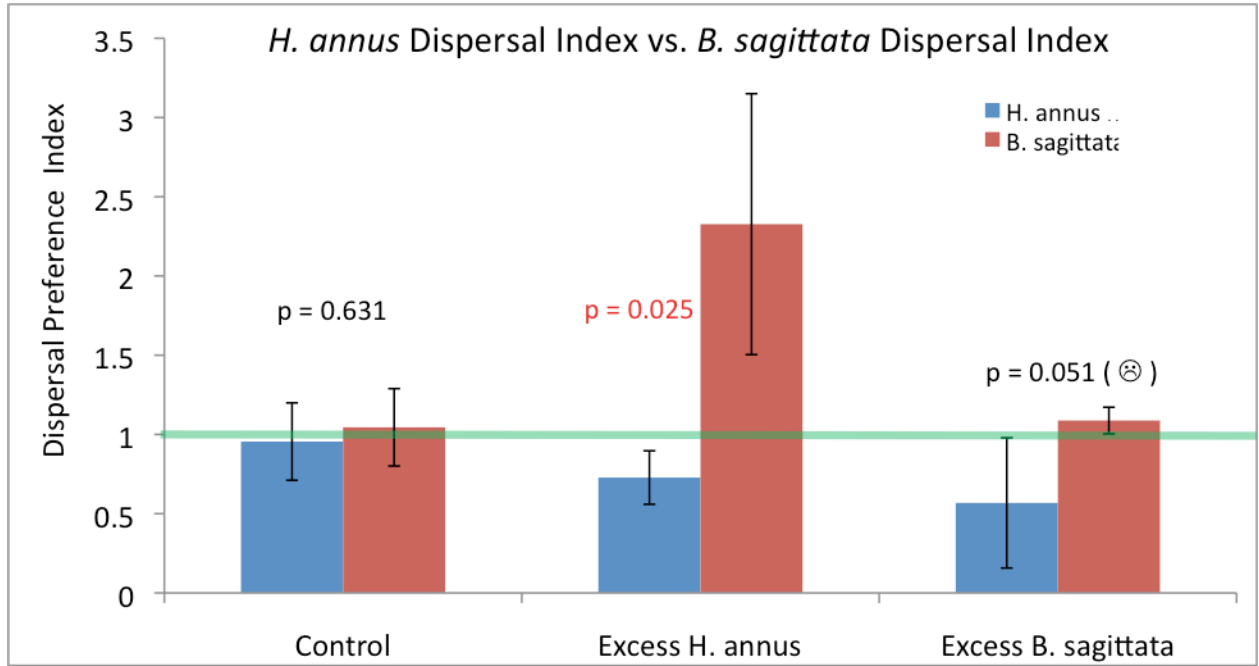


Figure 14: The preference index of dispersal for *P. maniculatus* of *H. annus* and *B. sagittata*. A statistically significant difference was found in the dispersal preference index of *P. maniculatus* for *B. sagittata* in the excess *H. annus* treatment (Kruskal-Wallis, MWUTS = 32.000, $p = 0.025$), while no selectivity was found with *P. maniculatus* preference index for either seed in the control treatment (Kruskal-Wallis, MWUTS = 21.000, $p = 0.631$) or in the excess *B. sagittata* treatment (Kruskal-Wallis, MWUTS = 30.000, $p = 0.051$). The green line is the cutoff for a significant preference index value.

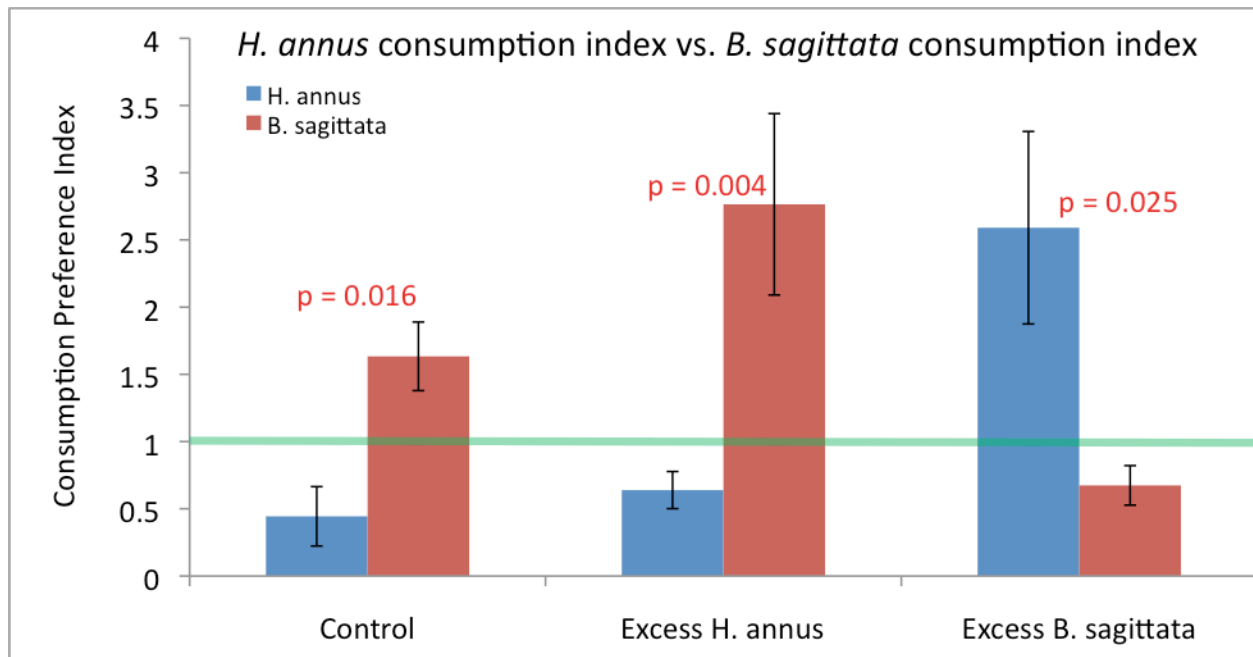


Figure 15: The consumption preference index comparison between *H. annus* and *B. sagittata* by *P. maniculatus*. The preference index of consumption for *P. maniculatus* was statistically significantly larger for *B. sagittata* than *H. annus* in both the control treatment (Kruskal-Wallis, MWUTS = 33.000, $p = 0.016$) and the excess *H. annus* treatment (Kruskal-Wallis, MWUTS = 36.000, $p = 0.004$). In the excess *B. sagittata* treatment, the preference index of *P. maniculatus* was statistically significantly larger for *H. annus* than *B. sagittata* (Kruskal-Wallis, MWUTS = 4.000, $p = 0.025$). The green line is the cutoff for a significant preference index value.

LITERATURE CITED

- Abhilasha, D. and Joshi, J. 2009. Enhanced fitness due to higher fecundity, increased defense against a specialist and tolerance towards a generalist herbivore in an invasive annual plant. *Journal of Plant Ecology*. 2(2): 77–86.
- Allen, Julia A.; Brown, Cynthia S.; Stohlgren, Thomas J. 2009. Non-native plant invasions of United States National Parks. *Biol Invasions*. 11:2195–2207.
- Blossey, Bernd and Notzold, Rolf. 1995. Evolution of Increased Competitive Ability in Invasive Nonindigenous Plants: A Hypothesis. *Journal of Ecology*. 83: 887-889.
- Bowers, Michael A. and Smith, Duane H. 1979. Differential Habitat Utilization by Sexes of the Deermouse, *Peromyscus Maniculatus*. *Ecology*. 60(5): 869-875
- Bricker, Mary; Pearson, Dean; Maron, John. 2010. Small-mammal seed predation limits the recruitment and abundance of two perennial grassland forbs. *Ecology*. 91(1): 85–92.
- Cappuccino, Naomi and Arnason, Thor J. 2006. Novel chemistry of invasive exotic plants. *Biol. Lett.* 2: 189–193.
- Ebersole, John P. and Wilson, Julian C. 1980. Optimal Foraging: The Responses of *Peromyscus leucopus* to Experimental Changes in Processing Time and Hunger. *Oecologia*. 46: 80-85.

- González, Angélica L.; Kominoski, John S.; Danger, Michael; Ishida, Seiji; Iwai, Noriko; Rubach, Anja. 2010. Can ecological stoichiometry help explain patterns of biological invasions? *Oikos*. 119: 779–790.
- Grosholz, E. 2010. Avoidance by grazers facilitates spread of an invasive hybrid plant. *Ecology Letters*. 13: 145–153.
- Harder, Lawrence D.; Johnson, Steven D. 2009. Darwin's beautiful contrivances: evolutionary and functional evidence for floral adaptation. *New Phytologist*. 183: 530–545
- Ito, Kiyoshi and Saka, Satoki. 2009. Optimal defense strategy against herbivory in plants: Conditions selecting for induced defense, constitutive defense, and no-defense. *Journal of Theoretical Biology*. 260: 453–459
- Ivan, Jacob S and Swihart, Robert K. 2000. Selection of Mast by Granivorous Rodents of the Central Hardwood Forest Region. *Journal of Mammalogy*. 81(2): 549-562.
- Jogesh, Tania; Carpenter, David; Cappuccino, Naomi. 2008. Herbivory on invasive exotic plants and their non-invasive relatives. *Biol Invasions*. 10:797–804.
- Lind, Eric M. and Parker, John D. 2010. Novel Weapons Testing: Are Invasive Plants More Chemically Defended than Native Plants? *PLoS ONE*. 5(5): 1-7.
- MacArthur, Robert H.; Pianka, Eric R. 1966. On Optimal Use of a Patchy Environment. *The American Naturalist*. 100(916): 603-609.
- Moore, Jeffrey E.; McEuen, Amy B.; Swihart, Robert K.; Contreras, Thomas A.; Steele, Michael A. 2007. Determinants of Seed Removal Distance by Scatter-Hoarding Rodents in Deciduous Forests. *Ecology*. 88(10): 2529-2540.
- Moore, J. E. and Swihart, R. K. 2008. Factors affecting the relationship between seed removal and seed mortality. *Can. J. Zool*. 86(5): 378–385.
- Morrien, Elly; Engelkes, Tim; Macel, Mirka; Meisner, Annelein; Van der Putten, Wim H. 2010. Climate change and invasion by intracontinental range-expanding exotic plants: the role of biotic interactions. *Annals of Botany*. 105: 843–848.
- Nowalk, Maura and Gerrish, Gretchen. 2007. Relative Seed Predation by *Peromyscus maniculatus* on Invasive and Native Species Pairs of Four Plant Genera found in Palouse Grass Prairies of Western Montana. BIOS 35503: Practicum in Environmental Field Biology.
- Orians, Colin M. and Ward, David. 2010. Evolution of Plant Defenses in Nonindigenous Environments. *Annu. Rev. Entomol*. 55:439–459.

- Parker, Ingrid M. and Gilbert, Gregory S. 2007. When there is no escape: The effects of natural enemies on native, invasive, and noninvasive plants. *Ecology*. 88(5): 1210–1224.
- Pearson, Dean E. and Callaway, Ragan M. 2008. Weed-Biocontrol Insects Reduce Native-Plant Recruitment Through Second-Order Apparent Competition. *Ecological Applications*. 18(6): 1489–1500.
- Phelan, John P. and Baker, Richard H. 1992. Optimal Foraging in *Peromyscus polionotus*: The Influence of Item-Size and Predation Risk. *Behaviour*. 121(1): 95-109.
- Phillips, Benjamin L.; Brown, Gregory P.; Shine, Richard. 2010. Life-history evolution in range-shifting populations. *Ecology*. 91(6): 1617–1627.
- Siepielski, Adam M. and Benkman, Craig W. 2008. A seed predator drives the evolution of a seed dispersal mutualism. *Proc. R. Soc. B*. 275: 1917–1925.
- Shahid, Amirah; Garneau, Danielle E.; Mccay, Timothy S. 2008. Selection of Seeds of Common Native and Non-native Plants by Granivorous Rodents in the Northeastern United States. *Am. Midl. Nat.* 162:207–212.
- Vander Wall, Stephen B. 2010. How plants manipulate the scatter-hoarding behavior of seed-dispersing animals. *Philosophical Transactions of the Royal Society B-Biological Sciences*. 365(1542): 989-997.
- Vander Wall, Stephen B.; Beck, Maurie J.; Briggs, Jennifer S.; Roth, Julie K.; Thayer, Ted C.; Hollander, Jennifer L.; Armstrong, Jennifer M. 2003. Interspecific Variation in the Olfactory Abilities of Granivorous Rodents. *Journal of Mammalogy*, 84(2):487–496.
- Vander Wall, S.B.; Thayer, T.C.; Hodge, J.S.; Beck, M.J.; Roth, J.K. 2001. Scatter-hoarding behavior of deer mice (*Peromyscus maniculatus*). *Western North American Naturalist* 61(1):109-113.
- Verhoeven, Koen J. F.; Biere, Arien; Harvey, Jeffrey A.; van der Putten, Wim H. 2009. Plant invaders and their novel natural enemies: who is naive? *Ecology Letters*. 12: 107–117.
- Westerman, Paula R.; Borza, Jaclyn K.; Andjelkovic, Jelena; Liebman, Matt; Danielson, Brent. 2008. Density-dependent predation of weed seeds in maize fields. *Journal of Applied Ecology*. 45: 1612–1620.
- Xu, Cheng-Yuan; Julien, Mic H.; Fatemi, Mohammad; Girod, Christophe; Van Klinken, Rieks D.; Gross, Caroline L.; Novak, Stephen J. 2010. Phenotypic divergence during the invasion of *Phyla canescens* in Australia and France: evidence for selection-driven evolution. *Ecology Letters*. 13: 32–44.

Zwolak, Rafal; Pearson, Dean E.; Ortega, Yvette K.; Crone, Elizabeth E. 2010. Fire and mice: Seed predation moderates fire's influence on conifer recruitment. *Ecology*. 91(4):1124–1131.