Effects of Height and Size Exclusion on Seed Preference Among Mammalian Granivores

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BIOS 35502: Practicum in Field Biology
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2010

ABSTRACT

The tree composition of a forest can be affected by many factors, one of which is seed predation by rodents. Granivores can preferentially prey upon or cache certain species of seeds, influencing the ability of that species to regenerate in a given forest. My research will analyze preference for seeds based on size group of mammals and scansorial capacity of granivores that are capable of climbing by placing feeders containing three species of seeds at ground and subcanopy heights with two different sized openings. Testing removals for black cherry (*Prunus serotina*), red maple (*Acer rubrum*), and sugar maple (*Acer saccharum*) seeds, I predicted that more seeds would be removed from ground feeders than from subcanopy feeders because of their accessibility, that more sugar maple seeds would be removed from large-opening feeders than from small-opening feeders because these larger seeds offer more energy reward, and that black cherry would be the most preferred seed because it is small and easy to transport. The analysis of data suggested that feeder height did not have an effect on total removal rate, that sugar maple seeds were more heavily foraged upon in large-opening feeders, and that both black cherry and red maple seeds were preferred over sugar maple seeds. These results suggest that granivores show a strong preference for certain seed species and that elevation will not necessarily deter a scansorial granivore from expending greater search effort to obtain seeds. This information supports the notion that the presence and varying prevalence of different species of granivores in a forest can affect forest regeneration.

INTRODUCTION

Seed predators can play a vital role in forest regeneration and tree recruitment. Although granivores can harm the survival of trees if they heavily consume the developing seeds, they can help the population if they disperse the seeds or cache them. A granivore can attribute future value to a seed, meaning that it values storing the seed for times of hardship. In this case the granivore would cache the seed, giving it the opportunity to germinate. If the granivore instead finds present value in the seed, it finds the immediate energy gain to be beneficial, eating the seed and eliminating any chance of it germinating. The method of caching can be either beneficial or detrimental to a seed. Seeds buried more deeply are less easily detected by potential predators, but the seeds must also be buried shallow enough to germinate (Vander Wall 1993). Seeds that are scatter hoarded may be more likely to survive than seeds that are larder hoarded because of decreased detection by predators (Janzen 1971). A granivore species may also differentiate among species they prefer to consume and among those they prefer to cache

(Pluncinski and Hunter 2001). In a study which altered accessibility to seeds based on granivore size, seed survival and seedling performance differed among the size classes of mammals (Paine and Beck 2007). Smaller mammals greatly reduced the abundance of seeds, while larger mammals did not greatly affect seedling recruitment. Small mammals may disproportionately prey on the seeds of common species, creating an advantage for rare tree species (Paine and Beck 2007). Seed predation on trees that are competitively superior as adults may increase the survival success of poorer competitors, leading to increased biodiversity and heterogeneity (Beckage and Clark 2005). Therefore, although seed predators can reduce the density of recruited seedlings, they may also increase the diversity (Paine and Beck 2007).

Different species within a size class of rodent may also have different preferences for seeds. It has been suggested that deer mice (*Peromyscus maniculatus)* prefer eastern white pine (*Pinus strobus*) seeds over balsam fir (*Abies balsamea*) (Martell 1970), whereas Southern red-backed voles (*Myodes gapperi)* prefer red spruce (*Picea rubens*) over white pine seeds (Abbott 1962). Since many rodent species occupy similar habitats, researchers need to study how different rodent species divide resources. If a species of granivore is overpopulated in an area, its predation impact on a tree species may be so great that it can possibly threaten that species' regeneration. A strong granivore preference for a seed species can hinder reproductive rates of tree species. This effect was observed in Ohio where less than 15 percent of a particular forest is composed of hickory and beech trees, but 50 percent of the diet of gray squirrels and fox squirrels consists of hickory and beech seeds (Janzen 1971).

I studied seed predation interactions in a northern hardwood-hemlock forest in order to determine how seed preference varies within the rodent seed predator guild, and how these preferences may affect forest regeneration patterns. Specifically, I investigated how seed preference varies according to which size of granivores were allowed to have access to various types of seeds. Feeders with differently sized openings were placed in the mammals' habitat to monitor removal rates under natural conditions. My hypothesis was that seed preference would vary among the different subgroups of mammals, so there would be a difference in the amount of each type of seed removed from the large-opening and small-opening feeders. I specifically hypothesized that a greater number of seeds would be removed from the ground feeders than from the subcanopy feeders since the ground feeders would be more easily accessible. Previous research has suggested that scansorial granivores are less likely to exert the effort needed to obtain seeds from a greater height when seeds are available on the ground (Flagel et al 2009; Chan unpublished data). I predicted that compared to small-opening feeders, the feeders with larger openings would have a greater amount of sugar maple (*Acer saccharum*) seeds removed from them since red squirrels (*Sciurus vulgaris*) and eastern chipmunks (*Tamias striatus)* have previously been shown to exhibit a preference for maple seeds (Plucinski and Hunter 2001) and would prefer the larger sugar maple seeds over the smaller red maple seeds because the larger seeds provide a greater energy gain. I also predicted that the feeders with small openings in the canopy will have a greater amount of black cherry (*Prunus serotina*) seeds removed since deer-mice have been shown to have a preference for this species (Whelan et al. 1991), and the small size of the seed makes it easier for them to handle. I hypothesize that mostly black cherry seeds will be removed from the small-opening feeders placed on the ground since these feeders will only allow access to deer mice, white-footed mice (*Peromyscus leucopus*), and Southern red-backed voles. I likewise hypothesize that mostly black cherry seeds will be removed from the small-opening feeders in the subcanopy resulting from heavy removals by deer mice.

METHODS

To determine the seed preference among granivores, twenty experimental feeders containing seeds were placed on the University of Notre Dame Environmental Research Center (UNDERC) property. Enclosures have not been shown to have a strong negative influence on the tendency of small mammals to remove seeds (Sullivan and Klenner 1993). The feeders, which were constructed for a previous research project (Chan unpublished data), were made of plexiglass and measured 50x15x15 cm. They had two different sized openings. Smaller circular openings measuring 2.5 centimeters in diameter were drilled into half of the plexiglass boxes and allowed small mammals, such as the white-footed mouse and deer mouse to enter, but were meant to exclude larger mammals such as chipmunks and squirrels (Pluncinski and Hunter 2001; Moore et al. 2007). However, it was observed that eastern chipmunks could gain access to the seeds through the small openings. The ends of half the feeders were left open to create larger openings measuring 15x15 cm and allowed larger mammals, such as the red squirrel (*Tamiasciurus hudsonicus*) to enter without excluding smaller rodents. Five feeders with larger openings and five with smaller openings were positioned at the subcanopy level at a minimum of 1.25 meters and a maximum of 3 meters (see methodology in Flagel et al 2009), while feeders on the ground were staked to prevent large mammals from moving them. Five feeders with larger openings, and five with smaller openings were positioned on the ground. The feeders at subcanopy level helped select for mammalian species that have an inclination to climb trees in order to forage for food, such as chipmunks, squirrels, and deer mice. Four different species of seed were initially placed in the feeders. The seeds used were black cherry, red maple, sugar maple, and white ash. White ash was eventually excluded from the study because of a supply shortage. The seeds were obtained from Sheffield's Seed Company and were microwaved for 45 seconds to kill the embryos (see Hsia and Francl 2007). The feeders were laced with pure vanilla extract as an attractant and spaced without bias at a minimum of 10 meters and a maximum of 24 meters apart in upland maple-fir patches within the northern hardwood-hemlock forest. Each ground feeder had a corresponding feeder placed above it in the subcanopy. Twenty seeds of each species were placed in the feeder and replaced every other day for 30 days between June and July. The amount and type of seeds removed were counted and removal rates of the seeds were analyzed to determine whether preference for certain species of seed was influenced by feeder height and accessibility to differently sized granivores. After data collection was complete, trail cameras were placed at the openings of one of each of the four treatments in an attempt to survey which animals were foraging upon the seeds. Cameras were not set up during the data collection of seed removals in order to avoid possible behavioral changes in response to camera flashes.

Statistical Analysis

The results of white ash seed predation were removed from the reported statistics because these seeds were not available throughout the entire course of the study. Data on black cherry, red maple, and sugar maple seeds were analyzed using methods explained by Lockwood (1998) and Manly (1993). Due to dependence among the seeds, the data needed to be converted into an independent response variable. The data were converted into proportions and values that could be analyzed by parametric tests, and ANOVAs were then run to determine significant differences. Data were first converted by dividing the number of seeds removed by the total seeds of each species placed in each feeder for each trial. These calculations gave a proportion value of seeds eaten. A control factor of one third the total seed density was then subtracted from the proportions to obtain adjusted proportion values that compensated for the dependency of each seed species being removed on the preference level for the other species of seeds and allowed the data to be analyzed by parametric tests.

The proportion values were added together to determine total seed removals per treatment on each day that data was collected. A two-way ANOVA was run on the total proportion removal values to analyze whether size of openings or height affected overall seed removal. Using the adjusted proportion values, two-way ANOVAS were used to determine how opening size and height affected each of the seed species. All p-values were corrected for by a Bonferroni test.

RESULTS

Analysis of Effects of Height and Opening-Size on Overall Removals

Height of feeders did not appear to affect tendency of seeds to be removed [$F_{2, 236}$ = 0.154, P =0.695], nor did the interaction between height and size [$F_{1, 236}$ = 0.003, P =0.913]. However, the size of the openings affected total removals rates [$F_{1, 236}$ = 27.913, P <0.001] (Table 1), with more seeds being removed from large-opening boxes than from small-opening boxes (Figure 1).

Analysis of Effects of Height and Opening-Size on Individual Seed Species

The removal of black cherry seeds was not affected by height [$F_{1, 236}$ = 3.830, P =0.052] or opening size [$F_{1, 236}$ = 2.462, P =0.118] (Table 2) when compared to a corrected p-value of 0.017. Similarly, the removal of red maple seeds was not affected by height [$F_{1, 236}$ =0 .541, P =0.474] or opening size [$F_{1, 236}$ = 0.360, P =0.449] (Table 3). The removal of sugar maple seeds was not affected by height [$F_{1, 236}$ = 0.000, P =0.989], but was affected by opening size [$F_{1, 236}$ = 4.974, P

<.001] (Table 4), with more sugar maple seeds being removed from large-opening rather than small-opening feeders (Figure 2).

Analysis of Seed Preference Across the Four Treatments

The means of the adjusted proportion values were analyzed to determine whether some seed species were more heavily preyed upon than others. Since three food choices were available, mean values of removals below 0.3333 indicate a lower preference for a seed species, while mean values of removals above 0.3333 indicate a strong preference for a seed species. It was concluded that black cherry seeds and red maple seeds were preferred over sugar maple seeds, since all mean numeric values for the removals of black cherry and red maple seeds are above 0.3333, and all mean numeric values for the removal of sugar maple seeds are below 0.3333 (Figure 3).

DISCUSSION

Effects of Height and Opening-Size on Overall Removals

The height of the feeders did not have the expected influence on overall removals. There was no significant difference in removal rates from ground and subcanopy boxes; therefore, my hypothesis that fewer seeds would be removed from higher feeders was not supported. These unexpected results may have occurred for several reasons. All feeders on the ground may have been almost completely depleted of seeds at some point before they were restocked. A granivore foraging at the research site may have found few seeds in the ground feeders, but many seeds in the subcanopy feeders. The energy expended climbing a tree to obtain sixty or less seeds was likely less than the energy needed to forage on the ground for more scarcely distributed seeds. Even if the ground feeders were not near depletion, a scansorial granivore may not have found it costly to climb a tree in order to obtain food. Feeders in the subcanopy could also allow granivores to forage without the risk of predation by larger mammals hunting on the forest ground. Since the feeders were mostly enclosed, they also protected the granivores from aerial attacks, such as those from owls. This combination of protection from both aerial and ground attacks may have made the subcanopy feeders favorable to some granivores. The ground feeders may be favorable as well because they protected granivores from aerial attacks, the seeds were easier to access, and some granivores, such as *Peromyscus leucopus*, are not inclined to climb trees to obtain food. More seeds were also removed from the larger-opening than smaller-opening feeders, likely because a greater number of granivores could access the seeds in the large-opening feeders.

Effects of Opening-Size on Sugar Maple Removals

My hypothesis that more sugar maple seeds would be removed from the large-opening feeders was supported. More sugar maple seeds were removed from feeders with larger sized openings than from feeders with smaller sized openings. These results may be explained by the fact that more mammals had access to the large-opening feeders, while the small-opening feeders limited access. A greater number and species of granivores foraging at the large-opening feeders could consume more seeds. However, several other factors could explain these results. According to the theory of optimal foraging, a more optimal food choice is often associated with a lower handling time (Pyke 1984). The small-opening feeders only allowed access to small granivores, and these granivores may have chosen black cherry and red maple seeds over sugar maple seeds because the sugar maple seeds are larger and potentially more difficult to handle. If a small granivore intended to cache a given seed, a sugar maple seed could be much more difficult to transport than the smaller black cherry seeds and the lighter red maple seeds. If a small mammal can more easily handle and transport the black cherry and red maple seeds, the sugar maple seeds would be less preferred in the small-opening feeders. The larger granivores foraging in the large-opening feeders would be more capable of handling the sugar maple seeds because the size of this seed would not have as much of a handling constraint on them. In addition, if smaller granivores had already removed most of the black cherry and red maple seeds, then mostly sugar maple seeds would be left for larger granivores to forage upon. The smaller-opening feeders mainly allowed access to *Peromyscus maniculatus, Peromyscus leucopus,* and at least some *Tamias striatus*, while the larger-opening feeders allowed access to these mammals as well as to squirrels. Squirrels, which tend to be scatter-hoarders (Steele et al 2008), prefer to cache seeds with a thicker coat (Siepielski and Benkman 2007). It would therefore be expected that many sugar maple seeds, as well as black cherry seeds, would be removed from the large-opening feeders, as was the case.

Preference Among the Three Seed Species

My hypothesis that black cherry seeds would be preferred in the small-opening feeders was partially supported. In all four of the feeder treatments, more black cherry and red maple seeds were removed than sugar maple seeds. However, there was no preference shown between black cherry and red maple seeds. Red maple seeds may have been preferred over sugar maple seeds because red maple seeds are produced in May and June while sugar maple seeds are produced in September and October. Research has shown that animals more heavily forage upon seeds that have more recently been produced (Price and Joyner 1997), such as those that are in season, a behavior described by the term search imaging. The granivores entering the feeders may have more heavily foraged upon red maple seeds because this seed is produced earlier in year and would therefore sooner be unavailable to the granivores. However, the sugar maple seeds would not be produced until the fall, so the granivores would not be inclined to search for these seeds in the spring and summer. On the other hand, black cherry seeds also are distributed in the fall during August and September, but the red maple seeds were not preferred over the black cherry seeds. Therefore, the effects of search imaging alone cannot fully explain these results. The characteristics of the seeds may also have a strong influence. In terms of optimal foraging, seeds which take less time to handle help increase the level of optimal foraging of an individual (Pyke 1984). The black cherry seeds have a thick coat, but their shape makes them easy to transport. I observed that rarely any black cherry seed shells were present in the feeders, suggesting that the black cherry seeds were removed from the feeders rather than eaten at the feeders. Visual observations as well as camera results also support this notion. Therefore, the feasibility of transporting the black cherry seeds probably had a greater affect on granivore preference than the ease of being broken open to be eaten. Out of the three seed species available to the granivores, the black cherry seeds could most easily be handled for transportation. The red and sugar maple seeds are both samara seeds, having wing-like structures that often have to be broken off before transportation. I personally observed chipmunks several times at the feeders, and they consistently gathered black cherry seeds first before gathering the red or sugar maple seeds. I also observed that the chipmunks could much more rapidly gather twenty black cherry seeds before gathering twenty of the other types of seeds. These results and observations suggest that the chipmunks could gain energy most quickly by gathering black cherry seeds. This factor is important for granivores that may have to quickly leave a patch site if a predation risk arises.

Effects on Forest Regeneration

Seed preference of granivores can greatly affect tree species composition. Seeds that are preferred by scatter-hoarding granivores may be more likely to develop into saplings. Seeds that are larder hoarded may experience greater competition and be less likely to survive. If a seed is preferred by a granivore and often consumed rather than cached, this species of plant may be put at a disadvantage as compared to other plants. Granivore preference as well as granivore caching behavior and location can have a great effect on tree survival. For instance, even though black cherry seeds are preferentially removed over sugar maple seeds, black cherry seeds are much less shade tolerant (Baker 1949). Therefore, unless a black cherry seed is cached in a dry sunny area or gap, a developing sugar maple may have a greater chance of surviving. Although sugar maple seeds were not preferred over black cherry and red maple seeds, the dominant composition of trees at the research site was made up of sugar maples. The sugar maple trees may survive better if the black cherry and red maple seeds are preferably consumed while the sugar maple seeds are preferably cached, or if the higher shade-tolerance of the sugar maple trees gives them an advantage. In addition, previous studies have suggested that larger seeds have a better chance of surviving as seedlings (Streng et al 1989).

Overall, many factors can affect forest ecosystems. My research strengthens the idea that species of granivores show strong preferences for particular species of seeds. Population fluctuations in granivores can then cause fluctuations in forest regeneration patterns. Studying seeds preference of granivores is essential to understanding forest ecosystems.

Several unintentional factors may have had an effect on the results of my study. At the start of the study, it was assumed that chipmunks would not be able to fit through 2.5cm diameter holes, as was supported in literature (Pluncinski and Hunter 2001). However, a chipmunk was observed multiple times entering the small-opening feeders. It also appeared that a single chipmunk had become acclimated to the research setup and often visited the feeders as soon as the seeds were restocked, usually removing all of the black cherry seeds. It is possible that chipmunks were the main granivores foraging at all four types of feeders and that these chipmunks removed the majority of the seeds, lowering the range of choices for other granivores to forage upon. In addition, the study was intended to involve four different types of seeds, including white ash. However, white ash seeds were in short supply since only a small amount could be obtained from the supplying seed company and were only used during the first ten days of the study. The availability of white ash seeds at the beginning of the study may have affected granivore preference for the other species of seeds. To compensate for this possibility all statistical tests were repeated on data collected while white ash seeds were available as well as on data collected when white ash seeds were no longer offered as a choice, and these tests revealed that the variability in presence of the white ash seeds did not affect the overall conclusions made from this study. In addition, the trail cameras showed the presence of eastern chipmunks and indiscernible species of mice. The night pictures yielded many indiscernible subjects because the flash reflected off the plexiglass feeders, and since the cameras are designed to record deer movement it is likely that they did not sense movement from many smaller sized granivores that may have passed by the cameras. A previous trail utilizing film cameras recorded various species of mice, suggesting effectiveness to sense smaller mammals varies by camera model.

Future studies could offer further insight into the effect of granivores on forest ecosystems. The eventual fate of a seed can affect its ability to develop into a sapling and then into an adult. A similar study to my research can be carried out using a tracking method on the seeds to determine where uneaten seeds are cached, at what depth, and in what environment. My study could also be modified by using a wider range of size openings to further determine which species of granivores are able to access the available seeds. A replication of my research could be implemented in the fall to determine whether season would have an effect on the results of the study and whether a search imaging effect is playing a role. If a search imaging effect is playing a role, it would be expected that more sugar maple seeds may be removed than red maple seeds in the fall. Laboratory studies of the handling times for various species of granivore and seeds could also be conducted. Proven survey methods, such as trapping, could also be included in future studies to help determine which granivores are most commonly entering the feeders.

ACKONWLEDGEMENTS

I would like to thank the Hank family for providing the funding necessary to conduct my research. I would also like to thank Dr. Belovsky and Dr. Cramer for use of the UNDERC property as a research site and for their guidance. I greatly appreciated the assistance of Heidi Mahon to analyze the data. I would like to thank Collin McCabe and Maggie Mangan for their help throughout the research course. Finally, I would like to thank my mentor, David Flagel, for his support and assistance in the designing of the study.

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TABLES

Table 1. **Analysis of variance results for effects of height and feeder opening size on total removal rates.** Feeder opening size, but not height, was found to affect total removal rates.

ANOVA				
Source	df	Mean Squares	F-Ratio	p-Value
Height	1	0.039	0.154	0.695
Size	1	7.021	27.913	**0.000**
Interaction of Height and Size	1	0.003	0.012	0.913
Error	236	0.252		

Table 2. **Analysis of variance results for effects of height and feeder opening size on removal of black cherry seeds.** Neither height not feeder opening size were found to significantly affect preference for black cherry seeds. A Bonferroni test was used to adjust for the p-values.

ANOVA-Black Cherry				
Source	df	Mean Squares	F-Ratio	p-Value
Height	1	0.128	3.830	0.052
Size	1	0.083	2.462	0.118
Interaction of Height and Size	1	0.010	0.299	0.585
Error	236	0.034		

Table 3. **Analysis of variance results for effects of height and feeder opening size on removal of red maple seeds.** Neither height nor feeder opening size were found to significantly affect preference for red maple seeds. A Bonferroni test was used to adjust for the p-values.

ANOVA-Red Maple				
Source	df	Mean Squares	F-Ratio	p-Value
Height	1	0.025	0.514	0.474
Size	1	0.018	0.360	0.549
Interaction of Height and Size	1	0.011	0.233	0.630
Error	236	0.049		

Table 4. **Analysis of variance results for effects of height and feeder opening size on removal of sugar maple seeds.** Height of feeders did not have a great effect on rates of removals of red maple seeds. The size of the feeder openings had a significant effect on the preferences for red maple seeds. A Bonferroni test was used to adjust for the p-values.

ANOVA-Sugar Maple				
Source	df	Mean Squares	F-Ratio	p-Value
Height	1	0.000	0.000	0.989
Size	1	4.974	84.107	**0.000**
Interaction of Height and Size	1	0.023	0.389	0.533
Error	236	0.059		

FIGURES

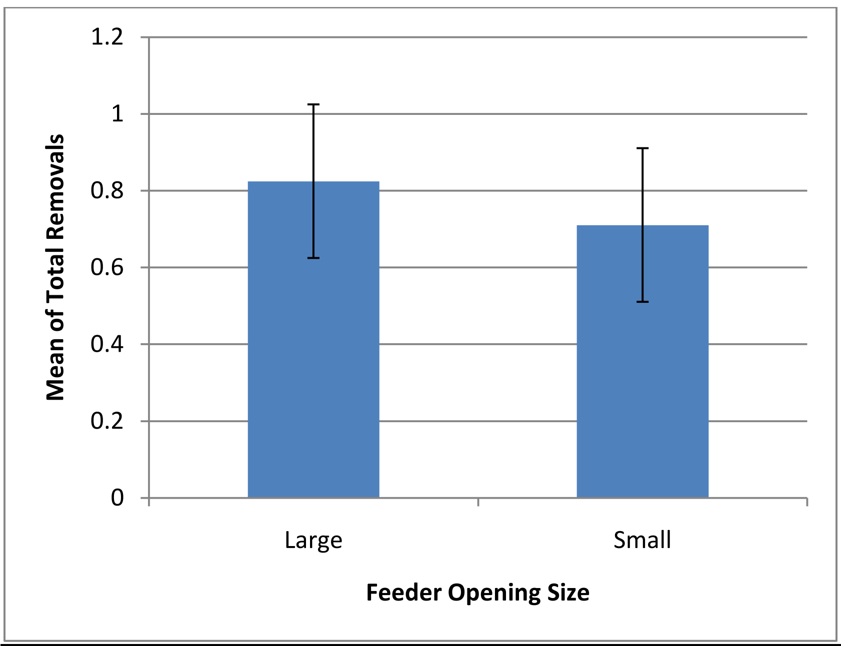

Figure 1. **Effect of feeder opening size on mean total removals.** Mean of proportions of seeds removed were analyzed. A mean proportion of 0.824 seeds were removed from large-opening feeders, while a mean proportion of 0.710 seeds were removed from small-opening feeders. Error bars denote one standard deviation and overlap because of the high variance in means, even though a significant difference was found between the treatments.

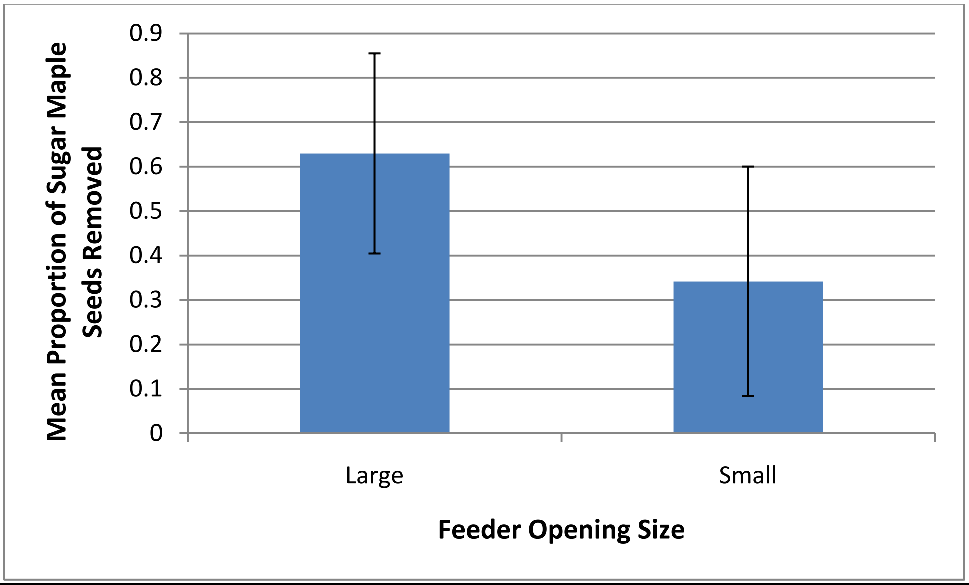

Figure 2. **Effect of feeder opening size on removals of sugar maple seeds.** Means were calculated using the adjusted proportion values. A mean adjusted proportion of 0.296 sugar maple seeds were removed from large-opening boxes, and a mean adjusted proportion of 0.008 seeds were removed from small-opening boxes. Error bars denote one standard deviation and overlap, although significant difference was found between the large and small opening feeders.

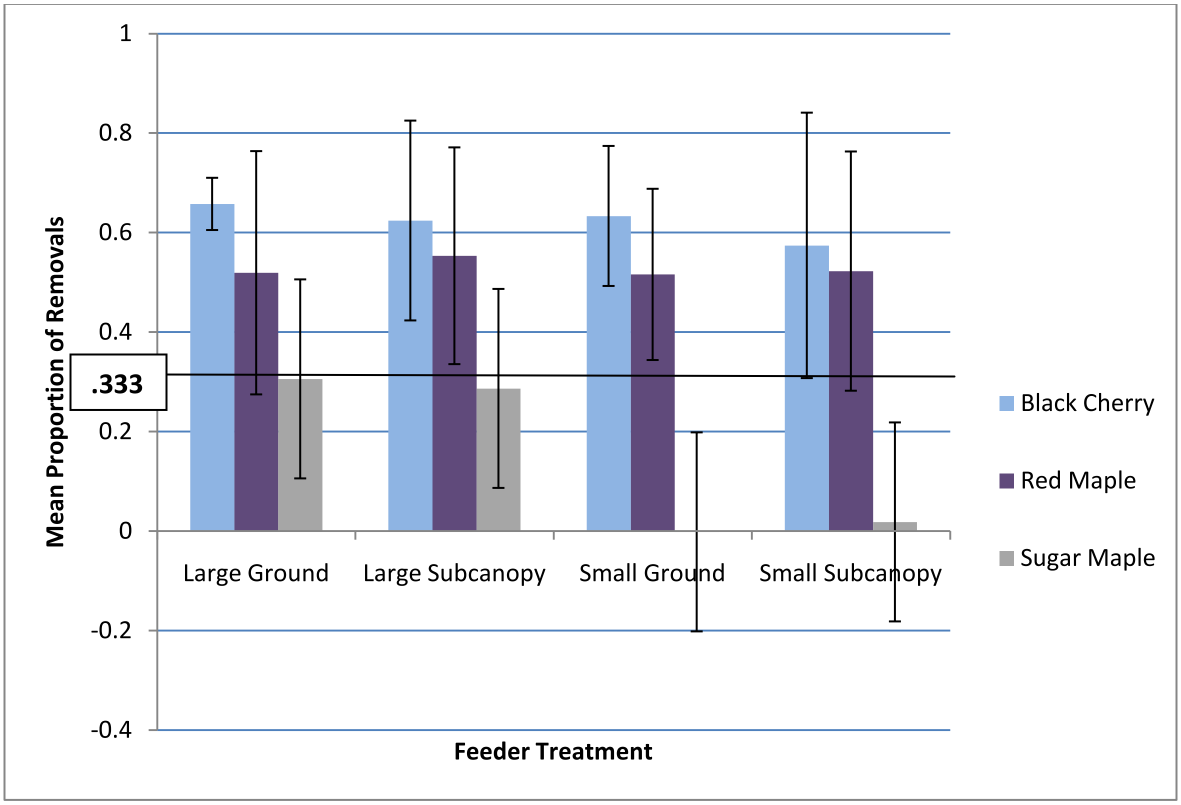

Figure 3. **Preference for species of seeds among four treatments.** Means were calculated using the adjusted proportion values, therefore some values are negative. Means above 0.333 indicate a strong preference, and means below 0.333 indicate low preference. A preference was shown for black cherry and red maple seeds over sugar maple seeds. Error bars denote one standard deviation.