Potential for shifting top-down pressure under climate change: seed preferences of northern *Tamias minimus* versus southerly *Tamias striatus*

BIOS 35502-01: Practicum in Field Biology

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2013

Abstract

As granivores, chipmunks have the ability to affect forest composition. Due to increasing global climactic temperatures, the ranges of chipmunk species are shifting north. In the northern Great Lakes forests, the least chipmunk (*Tamias minimus*) may be shifting north out of this region, and the eastern chipmunk (*Tamias striatus*) may be becoming more abundant. When there is an abundance of seeds, seed predators often prefer particular types of seeds over others. In this case, the preferred seed potentially loses the short-term apparent competition among the seed species. If *T. minimus* and *T. striatus* have different preferences, then the shift in species has the ability to alter apparent competition among reproducing trees in the Great Lakes forests. Using cafeteria-style feeding trials, I found that *T. minimus* highly prefer red maple (*Acer rubrum*) seeds. This contrasts with *T. striatus*, which was demonstrated in a previous study to prefer sugar maple (*Acer saccharum*) and beaked hazelnut (*Corylus cornuta*) seeds. This suggests that climate-induced shifts in granivores favor red maple and disfavor sugar maple and beaked hazelnut reproduction in the Great Lakes forests.

Introduction

Trees depend on dispersal and survival of their seeds in order to increase or sustain their populations. Seed dispersal is dependent upon both abiotic and biotic factors. In northern temperate forests, tree seeds are primarily dispersed by animals (Wang and Smith 2002). Animal species can either aid in the dispersal of seeds by caching them or make it more difficult for seeds to germinate through granivory. It has been well demonstrated that small rodents in particular (e.g. mice and chipmunks) can influence tree recruitment patterns in forests through such actions (Schnurr et al. 2004).

Seed predators influence tree recruitment patterns by creating apparent short-term competition within the seed bank that affects seed survival rates. Seeds do not directly compete with each other in this situation, but granivory instead results in indirect competition between seeds. If a granivore has a seed preference, the preferred seed will suffer higher rates of consumption while the less preferred seeds will have higher survival rates and therefore higher rates of germination (Veech 2001). In temperate forests, sciurids are one of the most abundant and largest seed predators and therefore, their seed predation may have a large effect on seed survival rates (Myers et al. 2009, personal observations). Thus, the chipmunks inhabiting the region may have the ability to affect forest composition in the Great Lakes area.

Climactic warming, meanwhile, may already be altering chipmunk distributions. Myers et al. (2009) has documented increases in several small rodent species of primarily southern distributions and decreases of northern species in the Great Lakes region. Least chipmunks (*Tamias minimus*) are a northern species with the southern limit of its range located in the Great Lakes forests. Eastern chipmunks (*Tamias striatus*) occupy both the Great Lakes and more southern areas in the central United States. Myers et al. (2009) found that in the Great Lakes forests *T. striatus* increased in abundance while the populations of *T. minimus* declined from 1981-2006. Throughout this 25 year study period, the average minimum daily temperature of the sites surveyed increased by 2.1°C. Myers recognizes that many factors contribute to the changing composition of small mammal species in the northern Great Lakes region, but hypothesizes that the increase in temperature is a significant contributing factor due to its consistency across the region and the large scale of the change.

In the presence of abundant resources, chipmunks often exhibit a preference for certain types of seeds (Chambers and MacMahon 1994). *T. striatus* in this region have been previously determined to prefer sugar maple (*Acer saccharum*) and beaked hazelnut (*Corylus cornuta*) seeds (S. Driscoll, unpublished). Using a similar study design, this experiment examined the seed preferences of *T. minimus*. If *T. striatus* and *T. minimus* have different foraging preferences for seeds, then the forest composition of the Great Lakes forests may be affected. Their differing seed preferences may in turn result in differing seed predation pressure, which could shift the apparent competition within the seed bank. Currently, the ecological significance of the shift in chipmunk species abundances is not known, but the sheer abundance of *Tamias* suggest such effects may be substantial (Myers et al. 2009).

One would hypothesize that *T. minimus* have different seed preferences than *T. striatus* because they occupy the same habitat in the Great Lakes forests. It would make sense that they would prefer to consume different seed species to decrease competition. More specifically, *T. minimus* may prefer red maple seeds because a similar trend occurs in other small mammals in this region. *Peromyscus maniculatus*, *Myodes gapperi*, *Zapus hudsonious*, and *Napaeozapus insignis*, all northern species, have been shown to display strong preferences for red maple seeds. On the other hand, *Peromyscus leucopus*, a southerly species, are more generalists and will consume red maple, sugar maple, and black cherry seeds (D.G. Flagel, unpublished data). Previous research has also shown that *T. striatus* prefer sugar maple and beaked hazelnut (S. Driscoll, unpublished data). If this trend extends to *Tamias*, then *T. minimus*, a northern species, should prefer red maple seeds.

Methods

This study was conducted at the University of Notre Dame Environmental Research Center (UNDERC), located on the border of the Upper Peninsula of Michigan near Land O'Lakes, Wisconsin. Eleven *T. minimus* were opportunistically trapped during the summer using

Tomahawk traps (Tomahawk Live Trap, Hazelhurst, WI) baited with apples and peanut butter. Once captured, the chipmunk was placed in a glass aquarium with a plywood cover. The bottom of the aquaria was covered in wooden bedding and a plastic container was present with polyfill bedding for nesting. A cloth covered sides of the aquarium so the chipmunk was not disturbed by other activities in the lab room during the trial and the open side of the aquarium was placed near a window to allow natural light to enter throughout the day. Striped sunflower seeds (*Helianthus annuus*) and water were available for consumption during a brief acclimation period.

Seed preferences were determined using cafeteria-style feeding trials, which have been used in previous studies to accurately represent the actual food habits of small mammals (Lobo et al. 2009, Page et al. 2001, Driscoll unpublished). At 2200h on the day of capture, the sunflower seeds were removed and a brief overnight starvation period began. Since *T. minimus* is diurnal, it should have been asleep for most of the starvation period (Verts and Carraway 2001). The starvation period ended at 0600h with the introduction of ten grams of each of five different kinds of seeds: sugar maple, beaked hazelnut, red maple, balsam fir (*Abies balsamea*), and pin cherry (*Prunus pensylvanica*), representing the most common seed-dependent woody species in the area (Curtis 1959, Flagel et al. *in prep*). The seeds were placed in an open container such that all were equally available to the chipmunk. At 1800h, twelve hours after the introduction of the seeds, the seeds were removed. The chipmunk was then released at the site of capture.

The seeds remaining, both in the food container and among the bedding, were separated by species and placed in a drying oven set on low for eight hours to remove any water mass gained from high humidity or urine during the trial. After drying, the final mass of each seed species was measured and was subtracted from the initial seed mass to determine the amount consumed. Selection ratios were calculated for each seed species by dividing the fraction consumed of each species by the total mass of seeds consumed (p_c) by the fraction of that species that was initially made available (p_a) (Page et al. 2001).

Selection ratio = p_c/p_a

p_c = (mass of species *i* consumed) / (total mass of all species consumed)

pa = (mass of species *i* introduced) / (total mass of all species introduced)

Selection ratios over one indicate that the seed species was preferred. Conversely, ratios less than one indicate that the seed was non-preferred. The forage ratios for each species in all eleven trials were analyzed using a Shapiro-Wilk, Kruskal-Wallis, and a Conover-Inman test in SYSTAT 13 (Cranes Software).

Results

Out of all eleven *T. minimus* used in trials, nine were male and two were female. The capture rate of *T. minimus* was not this skewed, but most females caught during this study were lactating and were therefore not used in a trial. An average of 12.95g of seeds out of a possible 50g were consumed during the trials.

The average selection ratio for each seed species among all eleven trials was calculated (Figure 1). A Shapiro-Wilk test indicated that the data were not normally distributed ($p<0.001$) so a Kruskal-Wallis test was run between selection ratios (test statistic= 25.61, df=4, $p<0.001$, Figure 1). A Conover-Inman post-hoc test was run and showed four significantly different pairs: red maple and balsam fir ($p<0.001$), red maple and beaked hazelnut ($p<0.001$), red maple and pin cherry ($p<0.001$), and red maple and sugar maple ($p<0001$). All other pairs of selection ratios between species were not significantly different.

Discussion

The selection ratio for red maple was significantly higher than that of all the other seeds in the trial, indicating that *T. minimus* strongly prefer red maple seeds, which confirms the hypothesis. There are a variety of possible explanations for this observed seed preference. Some factors known to influence seed preference include ease of handling and energy contained within the seed (Chambers and MacMahon 1994). Compared to other sciurids, *T. minimus* is fairly small. The mass of *T. minimus* in the Great Lakes forests range from 35-51g (Verts and Carraway 2001) whereas the mass of *T. striatus* range from 80-125g (Snyder 1982). For *T. minimus*, the energy expenditure and handling time needed to open the larger seeds (sugar maple and beaked hazelnut) may be too great, and thus they would avoid these seeds if others are available.

Another possible reason that *T. minimus* prefers red maple seeds could be due to the specific niche it is filling in the Great Lakes forests. The seed preferences of *T. minimus* are in contrast with those of *T. striatus,* which prefer sugar maple and beaked hazelnut and avoid red maple (S. Driscoll, unpublished). Both species of chipmunk currently inhabit the Great Lakes forests. Generally, chipmunks of different species have overlapping fundamental niches but non-overlapping realized niches (Heller 1971). In order to occupy the same region and still meet their energy needs, these two species of chipmunk may partition their resources in order to minimize interspecific competition. The larger *T. striatus* consumes the larger seeds that offer more energy but require more energy to open. It is possible that *T. minimus* reduces competition with *T. striatus* for seed resources by instead choosing to consume red maple seeds which require less handling time but offer less energy in return.

Because these two species of chipmunk occupy different realized niches, the shift in species composition in the Great Lakes forests may affect the short-term apparent competition among the seed bank. In the presence of abundant *T. minimus*, red maple seeds may lose the apparent competition and suffer higher rates of seed mortality. As *T. minimus* move northward due to increasing climate, they will likely become less abundant in the Great Lakes forests. Therefore, red maple will be released from granivory pressure and have a better ability to germinate. As well, if populations of *T. striatus* are increasing in the area, then their influence on the seed bank may be magnified. Since they prefer sugar maple and beaked hazelnut seeds, those species could lose the apparent competition within the seed bank more often. Combined, this climactic shift in chipmunk species composition will have a positive effect on red maple and a negative effect on sugar maple and beaked hazelnut. Although it is unclear how much of an effect chipmunk granivory has on forest composition, it can be hypothesized that forest composition will be pressured further to contain more red maple and less sugar maple and beaked hazelnut. This would be a top-down effect on forest composition due to increases in climactic temperature.

This top-down effect could also compound bottom-up effects on trees which are expected to shift under climate change. Climate change models (Iverson and Prasad 1998) predict that climate warming will have a bottom-up effect on forest composition by analyzing how climate influences growth conditions such as soil composition, nutrient availability, moisture, and atmospheric carbon dioxide. These models predict that sugar maple will be negatively affected by climate change in the Great Lakes forests as their optimal growing conditions move north. Based on my results, this predicted impact on sugar maple may be compounded by the top-down effect of increased seed predation also due to climate warming. Although the bottom-up effects of global warming are thought to negatively impact sugar maple, it has also been predicted that these same effects may positively impact red maple (Abrams 1998). Abrams found that the abiotic factors that result from an increase in climactic temperature correlate to an increase in red maple photosynthetic performance and biomass production. This bottom-up effect will also compound on the possible reduction of top-down seed predation pressure generated by shifting rodent populations, resulting in greater increases in red maple abundances in the Great Lakes forests than predicted solely by bottom-up models.

Further research on this subject could explore the reasons for the difference in seed preference between *T. minimus* and *T. striatus*. The handling time of each type of seed could be measured to determine if it is indeed easier to consume red maple seeds. The chemical breakdown of each seed species could also be explored to determine the energy gained from consumption of a seed as well as the specific nutrients each seed provides to the granivore. These factors could further shed light on why different species of chipmunks prefer different seeds.

This study on *T. minimus*, which found that they strongly prefer red maple seeds, is the first to examine their seed preferences. In conjunction with Driscoll's study on the seed preferences of *T. striatus* (unpublished 2012), it demonstrates that there are differences between the two *Tamias* species and if species populations shift due to climate change, seed predation pressure in the northern Great Lakes forests will also change. Most studies done on the impacts of climate change focus on bottom-up effects, but this pattern that has arisen in seed preferences between northern and southerly species of rodents suggest that climate change may also have top-down effects on forest composition. However, it is unclear how substantial this top-down impact will be. Ultimately, the next observational study should be conducted on the degree to which rodents impact forest composition of the Great Lakes forests compared to other consumers (i.e. white-tailed deer, *Odocoileus virginianus*) and abiotic factors.

Acknowledgements

I would like to thank the Bernard J. Hank Family Endowment for funding this project. I would also like to give thanks to David Flagel, Dr. Michael Cramer, and Dr. Gary Belovsky for all of their assistance and guidance. Many thanks to Riley Parrott and Cayla Bendel for their assistance in collecting data. Additional support has come from the UNDERC program and the University of Notre Dame which have provided the resources needed for this project.

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Figures

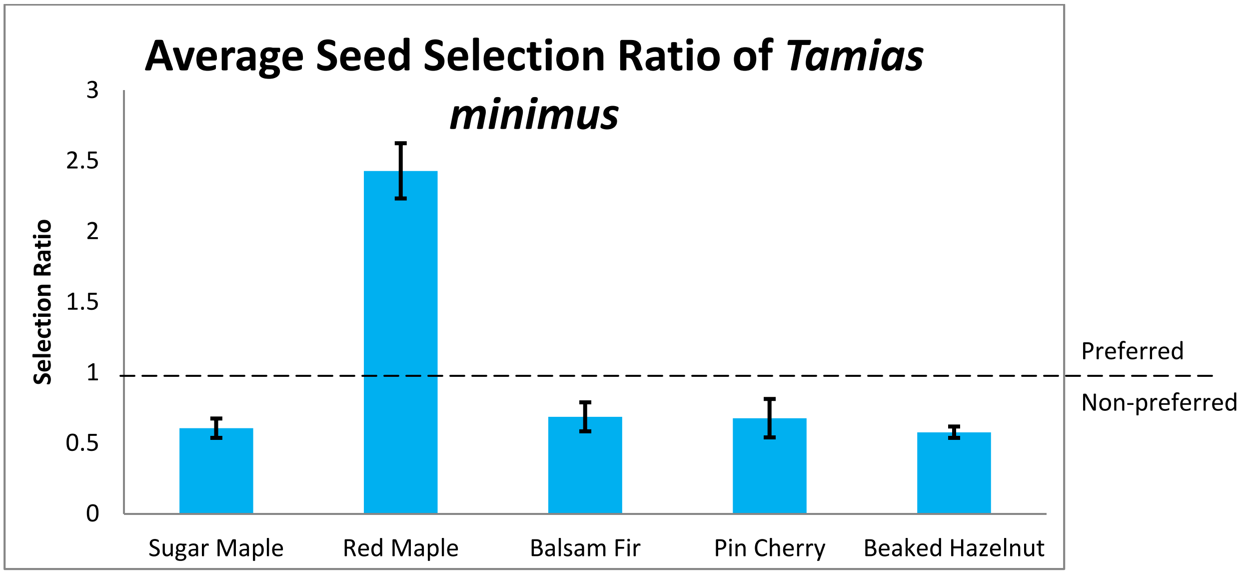

Figure 1. Average selection ratios of seed species for *T. minimus*. Selection ratios greater than 1 indicate a preference for that seed species; ratios less than one indicate an avoidance of that species. There is a significant difference between the selection ratio of red maple and the other seed species.