Preferential foraging behavior of forest deer mice (Peromyscus maniculatus gracilis) on native and non-native Picea seeds

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Abstract

Exotic plant invasions can lead to serious biodiversity and economic losses, with negative effects on many ecosystems. The factors leading to invasive plant success have been well documented and studied, but little is known about the impact of granivory on invasive plants. *Peromyscus maniculatus* is the most widely distributed *Peromyscus* species, and has been suggested to cause substantial loss of tree seed crops through seed predation. In this experiment, I study the preferential feeding behavior of deer mice on the seeds of the non-native, non-invasive blue spruce (*Picea pungens*) and the native white spruce (*Picea glauca*) in the Upper Peninsula of Michigan. Mice were captured and allowed to feed freely on equal amounts of both seeds, and were revealed to significantly prefer the larger non-native *P. pungens* seeds to *P. glauca*. Though factors that contribute to invasive plant success are highly complicated and non-exclusive and further experimentation is necessary to understand the complex aspects of the optimal foraging theory when applied to granivory, preference for *P. pungens* seeds by the widespread deer mice may suggest that seed predators play an important role in invasive plant establishment and improve our understanding of invasive flora as well as suggesting mitigative action.

Introduction

Exotic plant invasions have become ubiquitous across the United States, even in what were once the most pristine ecological environments (Richardson et al. 2000). The success of invasive species of flora can lead to serious biodiversity and economic losses, with negative and far reaching bottom-up effects on many ecosystems. Management and prevention of species invasion is vital to mitigating these negative effects. (U.S. National Arboretum 1999). Predation on plants by various consumers may strongly influence the establishment of non-native flora. Many previous studies of the effects of consumers on invasive plant biology have focused on foliovores (Daehlher 2003), but have not taken granivores into account.

Focusing on the foraging preference of the widespread granivorous rodent, *Peromyscus maniculatus gracilis,* on the seeds of one non-native (*Picea pungens*) and one native (*Picea glauca*) spruce may illuminate the impact granivores play in invasive plant success. *P.*

maniculatus are the most widely distributed *Peromyscus* species (Håkon et al. 2012; Haas and Heske 2005), and are generalist feeders that are capable of causing substantial loss of tree seed crops through seed predation (Hooven 1973). As a result, understanding the seed preferences of *P. maniculatus* may help us further understand the establishment of invasive species and suggest management opportunities. Shahid et al. (2009) suggest that granivorous rodents preferentially feed on native species when given the choice between seeds of native and non-native plants. Selection of native seeds over invasive seeds by rodents, especially those as widespread as *P. maniculatus*, may therefore magnify the success of invasives in outcompeting native plants. (Shahid et al. 2009).

The blue spruce (*Picea pungens*) is a member of the pine family (*Pinaceae*) native to many areas of the Western United States as well as Pennsylvania in the east, and has been introduced without attribution as invasive to some states of the Eastern U.S. as well as southern areas of Canada (U.S. National Arboretum 2012a). Blue spruce establish by way of seed production in cones every 2 to 3 years, thriving in exposed mineral soil in close proximity to seeding trees (Alexander 1974). Trees thrive in climates that are generally cool and humid, with most annual precipitation occurring in the summer, and an average July mean temperature between 13.9° and 15.0° C and January mean temperature between 3.9° and 6.1° C (Bates 1924). Blue spruce is used commercially and is important for decorative purposes; many variations are cultivated as ornamental Christmas trees (Bongarten and Hanover 1985). Blue spruce has been introduced to the Upper Peninsula (UP) of Michigan and is found throughout the state at commercial nurseries (Bongarten and Hanover 1985; Igoe and Peterson 1995) with one non-native tree identified on the University of Notre Dame Environmental Research Center (UNDERC) property where this experiment was conducted.

White spruce is native to much of the Northern U.S. and Canada (U.S. National Arboretum 2012b). It is known to grow under highly variable conditions, including extreme climates and soils (Elliot 1979). White spruce is a monoecious member of the pine family (*Pinaceae*) and reproduces by cones every 2-6 years (Elliot 1979; Waldron 1965; Zasada 1980). White spruce is an important economic resource, used for timber and wood fiber (Nelson 1977). It is native to the UP of Michigan, and well established where this study was conducted (Ritchie and MacDonald 1986; U.S. Arboretum 2012b).

Previous studies suggest that *P. maniculatus* avoid consuming seeds of non-native, invasive plant species (Pearson et al. 2011) that are largely successful in dominating ecosystems. However, blue spruce is not currently considered to be an invasive species, nor does it have a documented history of rapid takeover and success in areas where it is not native but present, as plants labeled “invasive” do (U.S. Arboretum 1999; U.S. Arboretum 2012a). For this study, “non-native” plants are those which are simply found living outside of what has been established as their native range, and “invasive” plants are those non-native species whose introduction, success, and range expansion cause harm to biodiversity and the introduced plants’ respective ecosystem (Binggeli 1996; Parker and Gilbert 2007). At UNDERC, the one blue spruce on property shows no signs of “invasive” characteristics, though the average climate of UNDERC property weather patterns (estimated as similar to that of Marquette, WI) corresponds to the ideal blue spruce habitat in both average annual temperature and precipitation patterns (National Oceanic and Atmospheric Association 2012). Blue spruce has been introduced ornamentally and at nurseries throughout the Upper Peninsula, but has not been documented as invasive in the northern United States (Bongarten and Hanover 1985; Igoe and Peterson 1995; U.S. Arboretum 2012a).

Aside from observed establishment success of the plant, another important factor was predicted to play a role in *P. maniculatus* seed feeding preferences. Optimal foraging theory would support a prediction that deer mice would feed on larger, more energetically efficient seeds when given a choice between seeds of different sizes (MacArthur and Pianca 1966). Previous studies have provided overwhelming support that a number of species feed preferentially on larger prey. Among others, swallows and bluegill sunfish have been strongly suggested to select their food items based on size in order to optimize energy returns in regards to handling time and food acquisition by consistently choosing the largest food items (Turner 1982; Werner and Hall 1974). However, *P. maniculatus* foraging on other species of seeds (*Acer*) did not show a preference for the larger species (Cramer, unpublished mss.). Other studies specific to granivores suggest that many pine trees have evolved to produce large seeds because they are most attractive to seed predators which cache food (Vander Wall 2003).

Given this information combined with the lack of invasive success by blue spruce in the area of study, I hypothesized that deer mice would preferentially feed on the seeds of the non-native *P. pungens* over those of native *P. glauca* when given free choice between equal amounts of both seed types. Preference towards *P. pungens* seeds by laboratory mice may suggest one reason why blue spruce has not been successful in propagating in the Upper Peninsula region, and lead to a greater understanding of the factors that influence plant invasions.

Materials and Methods

Study area - All experiments were conducted on the University of Notre Dame Environmental Research Center (UNDERC) property, which comprises approximately 3035 hectares on the border between Wisconsin and the Upper Peninsula of Michigan (46° 13' N, 89° 32' W). All mice were captured from two randomly located trapping grids, [Storage (46° 13' 36.957" N, 89° 32' 25.745" W) and Bono (46° 13' 6.753" N, 89° 30' 52.538" W)] within second-growth forests that were dominated by sugar maples. Three incidental mice captures were also used for seed trials.

Experimental Procedure — Trapping: All mice used in the experiment were *P. maniculatus gracilis* individuals obtained by live-trapping from the UNDERC site in May, June, and July 2012. Trapping grids contained 25 traps in a 5 x 5 configuration with 15 m spacing between each trap. Test-mice were live-trapped using Sherman traps (7.62 x 8.89 x 22.86 cm; H. B. Sherman Traps, Inc., Tallahassee FL) baited with rolled oats, black oil sunflower seeds, and peanut butter. Upon initial capture, all animals were identified as *P. maniculatus gracilis* (based on ear length; Kurta 1995), sexed, weighed, measured and individually marked with ear tags (monel 1; National Band and Tag Co., Newport, KY). Subjects were housed in individual cages with sand as bedding, and provided polyfill nesting material and food and water ad libitum. Lactating or pregnant females were not used for any trials.

Experimental Procedure – Seed Preference Trials: Five hours prior to testing, all food was removed from cages. For each trial, subjects were provided with 5 grams each of *Picea glauca* and *Picea pungens* seeds, separated into two feeding petri-dishes and placed in the cage. Seeds were obtained from a professional seed company (Sheffield's Seed Co., Inc., Locke NY), and were weighed to the nearest 0.01 g. The following morning, the dishes were removed and all sand thoroughly sifted for uneaten seeds. Seeds were separated by species (based on length) and separated from hulls before all intact uneaten seeds were weighed to the nearest 0.01 g. Amount of seeds consumed was obtained by subtracting the weight of the uneaten seeds from the initial weight placed in each cage. Selectivity was estimated for each seed type using forage ratios: p_c/p_a, where p_c is the proportion of consumed seeds that were type i and p_a is the proportion of all available seeds that were type i (Page et al. 2001). Data were analyzed using a paired t-test to account for statistical dependence, and SYSTAT v.13 was used for all statistical tests.

Experimental Procedure – Seed Size: Seed size between species was determined to be significantly different in order to verify experimental results. 50 seeds of each species were measured, and results were analyzed statistically using a two variable t-test in SYSTAT v.13.

Results

Twenty-five feeding trials were run before data was analyzed. There was a significant difference between the selectivity of deer mice foraging on *P. pungens* and *P. glauca* seeds. *P. pungens* seeds were selectively consumed over *P. glauca* seeds (mean $\pm$ SE; *P. pungens*, 1.39 $\pm$ 0.13; *P. glauca*, 0.66 $\pm$ 0.13, t_{24}= -3.114, p = 0.005; Figure 1).

There was a significant difference between the length of *P. pungens* and *P. glauca* seeds (mean $\pm$ SE; *P. glauca*, 2.27 $\pm$ 0.35; *P. pungens*, 4.10 $\pm$ 0.33; t_{98}= -27.047, p < .001; Figure 2).

Discussion

The experimental results support the hypothesis - that deer mice preferentially feed on *P. pungens* seeds over *P. glauca* seeds. Preference towards *P. pungens* may indicate that granivores play an important role in the establishment of blue spruce in non-native areas and point towards granivory as an important component of the success or failure of non-native plant propagation, and the clear preference towards blue spruce seeds by native deer mice may suggest one reason that blue spruce has not successfully established or become invasive in the Upper Peninsula region or on UNDERC property, where temperature, precipitation, and soil conditions seem to be otherwise supportive of the species (Bongarten and Hanover 1985; Igoe and Peterson 1995; National Oceanic and Atmospheric Association 2012; U.S. Arboretum 2012a). Past studies have strongly suggested that deer mice feed on the seeds of native species over strongly invasive plants (Pearson et al. 2011; Shahid et al. 2009), and field experiments by Pearson et al. (2011) support that deer mice preferentially feed on the seeds of native plants even when those of invasives are larger and seem more energetically efficient. My experimental findings may suggest that preferential predation on blue spruce seeds by deer mice may be one factor in the non-native *P. pungens*'s inability to successfully establish and become invasive in the UP of Michigan.

The family *Pinaceae*, to which both blue and white spruce belong, has been documented as having the most proportionally invasive species of the plant kingdom (Rejmánek and Richardson 2004). Rejmánek and Richardson (2004) propose that the life history traits which allow for successful conifer invasion are: small seed mass (< 50 mg), short juvenile period (< 10 year), and short intervals between large seed crops. My experimental results suggesting preference towards large seeds by *P. maniculatus* may be one important reason small seed mass leads to successful conifer propagation.

However, it is immensely difficult to define exactly what factors lead to successful species invasion. Complicated and interacting abiotic and biotic factors play a role in the success of invasive plant species (Lanbrinos 2002; Richardson 2000). Many factors have been suggested in attempts to understand what contributes to invasive plant success. Plant residence time, genetic make-up, local ecosystem community structure, mutualisms, resource use, and reproduction and dispersal strategies are a few of the factors that have been extensively studied and implicated in the conception of a prosperous invasive species (Rejmánek et al. 2005; Richardson et al. 2000; Stohlgren et al. 1999). These factors are highly complicated and integrative (Rejmánek et al. 2005; Richardson et al. 2000) and were not taken into account in my experiment.

Furthermore, an unnatural element was added to experimentation by the manner in which both types of *Picea* seeds were presented to trial mice. In their natural state, *P. maniculatus* would find spruce seeds encased in cones, greatly impacting their handling time and foraging costs (Vander Wall 1994). Previous studies have suggested that the rodents responsible for the greatest seed removal from pine cones cache seeds for winter months (Vander Wall 1994 and 2003). Seed dispersion patterns are also suggested to play an important role in granivore selectivity (Kerley and Erasmus 1991), and were ignored in our experimental protocol. Further experimentation involving the foraging behavior of deer mice when presented with full cones of both *P. pungens* and *P. glauca*, as well as differences in mice predation habits on individual seeds and cones would help improve understanding of *P. maniculatus* granivory, add an important element of real-world application, and validate my experimental results.

Further issues regarding optimal foraging theory and plant establishment success impede my ability to say with much assurance that preferential feeding by granivorous *P. maniculatus* on *P. pungens* seeds is the main inhibitor to blue spruce success in the Upper Peninsula region. Further experimentation is also necessary to establish the caloric and energetic value of consumed seeds and individual mouse handling times, which may play a large role in mouse feeding preferences alongside seed size (Kerley and Erasmus 1991; MacArthur and Pianka 1966; Turner 1982; Werner and Hall 1974).

In a world that is increasingly affected by exotic plant invasions, it is immensely important for scientists to understand the factors that lead to invasive flora success so as to suggest mitigative action that can save ecosystem biodiversity for intrinsic and economic purposes (U.S. National Arboretum 1999). Though the factors influencing success are both complicated and abundant (Rejmánek et al. 2005, Richardson et al. 2000), one factor that will contribute to our understanding in this area is the study of the foraging preferences of granivores. In my experiment, *P. maniculatus*, one of the most widespread granivores in North America (Håkon et al. 2012), fed preferentially on non-native and non-invasive *P. pungens* seeds when presented with seeds of native and non-native spruce, supporting my hypothesis and, combined with findings from similar studies, allowing me to plausibly assert that the feeding preferences of mammalian granivores may be one factor influencing the success of invasive plant species. Further experimentation is needed to illuminate the complicated relationships between seed predation, plant invasivity, and ecological community structure.

Figures

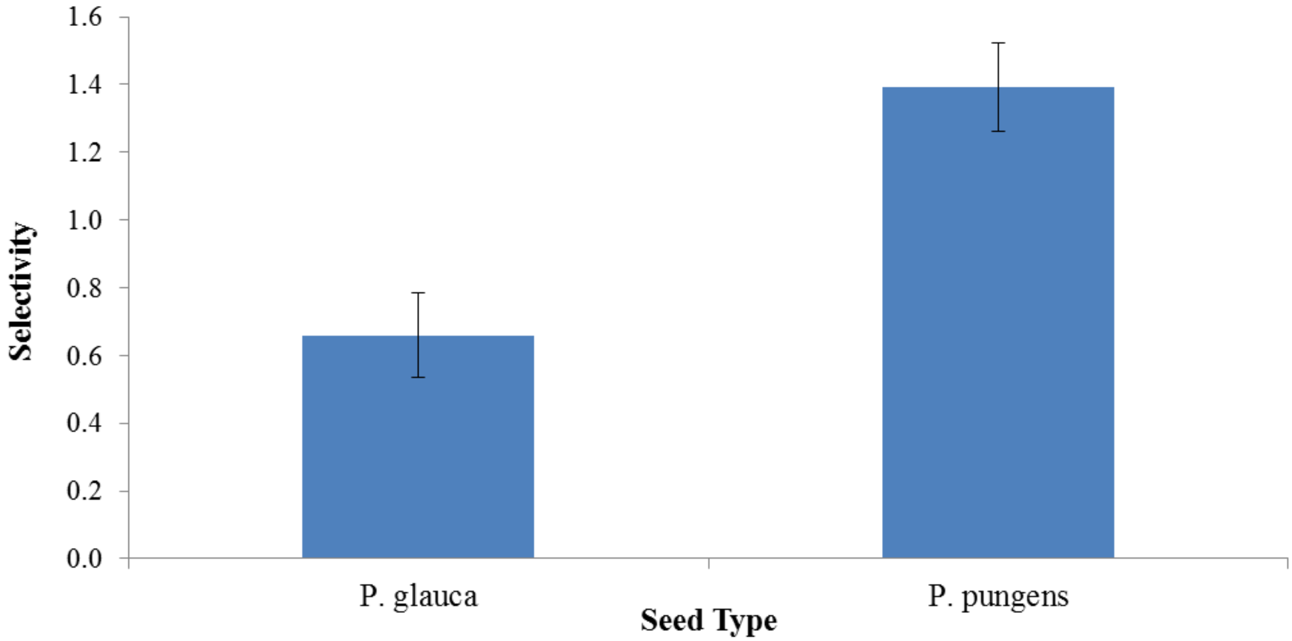

Figure 1: Selectivity Index of *P. maniculatus* individuals on *P. glauca* and *P. pungens* seed types. A paired t-test comparing foraging selectivity of deer mice on *P. glauca* and *P. pungens* seed types reveals that there is a significant difference between foraging selectivities, yielding values: t_{24}= -3.114 and p = 0.005.

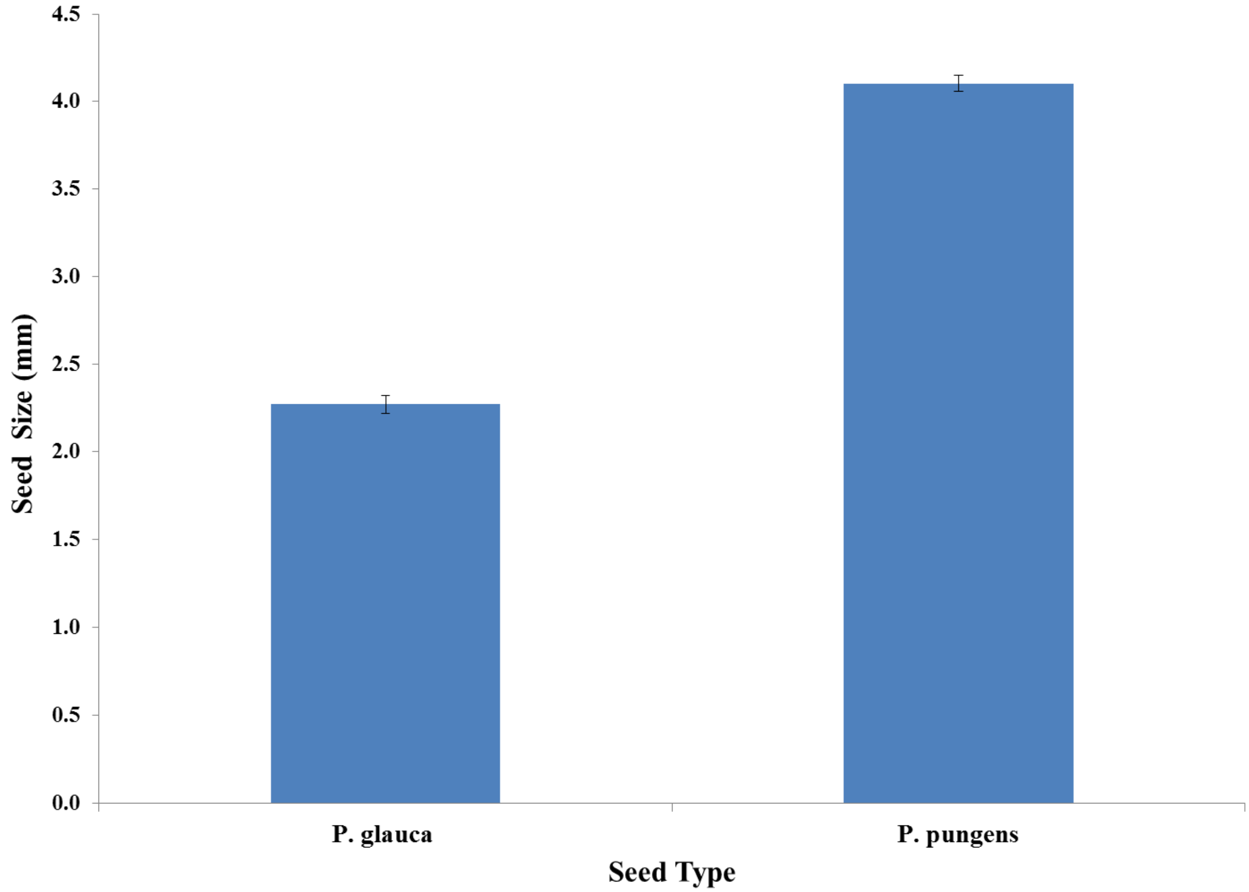

Figure 2: Differences in *P. glauca* and *P. pungens* seed size (length, mm). Results of a two-sample t-test reveal a significant difference between the size in length of *P. glauca* and *P. pungens* seeds, yielding values: t_{98}= -27.047 and $p < .001$.

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References cited

Bates C. 1924. Forest types in the central Rocky Mountains as affected by climate and soils. U.S. Department of Agriculture, Bulletin 1233: 152.

Binggeli P. 1996. A taxonomic, biogeographical and ecological overview of invasive woody plants. *Journal of Vegetation Science,* 7: 121-124.

Bongarten B. and Hanover J. 1985. Provenance variation in blue spruce (Picea pungens) at eight locations in the northern United States and Canada. *Silvae Genetica*, 35, 2-3: 67-74.

Daehler C. 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annual Review of Ecology, Evolution and Systematics*, 34:183—211.

Elliott D. C. 1979. The stability of the northern Canadian tree limit: - current regenerative capacity. Thesis (Ph.D.), University of Colorado, Department of Geography, Boulder: 192.

Haas J. and Heske E. 2005. Experimental study of the effects of mammalian acorn predators on red oak acorn survival and germination. *Journal of Mammalogy*, 86, 5:1015-1021.

Håkon M, Stout J, Doonan T and Parkinson C. 2012. Investigating niche and lineage diversification in widely distributed taxa: phylogeography and ecological niche modeling of the *Peromyscus maniculatus* species group. *Ecography*, 35: 54–64.

Hooven E. 1973. Effects of vegetational changes on small forest mammals. Oregon State University, School of Forestry: 75-97.

Igoe M and Peterson N. 1995. A phomopsis canker association with branch dieback of Colorado blue spruce in Michigan. *Plant Diseases*, 79: 202-205.

Kerley G and Erasmus T. 1991. What do mice select for in seeds? *Oecologia*, 86, 2 :261-267.

Kurta A. 1995. Mammals of the Great Lakes region, revised edition. University of Michigan Press, Ann Arbor, Michigan, USA.

Lanbrinos J G. 2002. The variable invasive success of Cortaderia species in a complex landscape. *Ecology*, 83: 518–529.

MacArthur R H and Pianka E. 1966. On optimal use of a patchy environment. *The American Naturalist*, 100, 916: 603-609.

National Oceanic and Atmospheric Administration, United States Department of Commerce. 2012. National weather service forecast office, Wausau, WI. Available: http://www.nws.noaa.gov/climate/index.php?wfo=grb (July 17, 2012).

Nelson R K. 1977. Forest resources in the culture and economy of native Alaskans. *In Proceedings, Symposium on North American Forest Lands at Latitudes North of 60 Degrees*, September 19-22: 207-225.

Page L K, Swihart R K, and Kazacos K R. 2001. Seed preferences and foraging by granivores at raccoon latrines in the transmission dynamics of the raccoon roundworm (*Baylisascaris procyonis*). *Canadian Journal of Zoology*,79, 4: 616-622.

Parker I and Gilbert G. 2007. When there is no escape: the effects of natural enemies on native, invasive, and noninvasive plants. *Ecology*, 88, 5:1210-1224.

Pearson D, Callaway R, and Maron J. 2011. Biotic resistance via granivory establishment by invasive, naturalized, and native asters reflects generalist preference. *Ecology*, 92, 9: 1748-1757.

Rejmánek M and Richardson D. 2004. Conifers as invasive aliens: a global survey and predictive framework. *Diversity and Distributions*, 10: 321–331.

Rejmánek M, Richardson D M, Higgins S I, Pitcairn M J, and Grotkopp E. 2005. Ecology of invasive plants: state of the art. *Washington, DC: Island Press*, 104–61.

Richardson D, Pysek P, Rejmanek M, Barbour M, Panetta F, and West C. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, 6:93–107.

Ritchie J and MacDonald M. 1986. The patterns of post-glacial spread of white spruce. *Journal of Biogeography*, 13, 6: 527-540.

Shahid A, Garneau D, and McCay T S. 2009. Selection of Seeds of Common Native and Non-native Plants by Granivorous Rodents in the Northeastern United States. *The American Midland Naturalist*, 162(1):207-212.

Stohlgren T, Binkley D, Chong G, Kalkhan M, Schell L, Bull K, Otsuki Y, Newman G, Bashkin M, and Son Y. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs*, 69, 1: 25-46.

Turner A K. 1982. Optimal foraging by the swallow (*Hirundo rustica*, L): Prey size selection. *Animal Behaviour*, 30 3: 862–872.

U.S. National Arboretum, United States Department of Agriculture. 1999. Invasive plants. Available: http://www.usna.usda.gov/Gardens/invasives.html. (May 15, 2012)

U.S. National Arboretum, United States Department of Agriculture. 2012a. PLANTS Profile: *Picea pungens Engelm*. Available: http://plants.usda.gov/java/profile?symbol=PIPU&mapType=nativity&photoID=pipu_001_ahp.jpg. (July 16, 2012).

U.S. National Arboretum, United States Department of Agriculture. 2012b. PLANTS Profile: *Picea glauca*. Available: http://plants.usda.gov/java/profile?symbol=PIGL. (July 17, 2012).

Vander Wall, S B. 1994. Removal of wind-dispersed pine seeds by ground-foraging vertebrates. *Oikos*, 69,1: 125-132.

Vander Wall, S B. 2003. Effects of seed size of wind-dispersed pines (Pings) on secondary seed dispersal and the caching behavior of rodents. *Oikos*, 100: 25-34.

Waldron R M. 1965. Cone production and seedfall in a mature white spruce stand. *Forestry Chronicle* 41,3 :314-329.

Werner E and Hall D. 1974. Optimal foraging and size selection of prey by the bluegill sunfish (*Lepomis macrochirus*) *Ecology*, 55:1042-1052.

Zasada J C. 1980. Some considerations in the natural regeneration of white spruce in interior Alaska on forest regeneration at high latitudes. USDA Forest Service, *General Technical Report PNW* 107: 25-29.