Conservation of a rare Block Island wildflower: Herbivory, seed predation, and Allee effects in Northern blazing star (*Liatris scariosa* var. *novae angliae*)

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Thesis

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Abstract

Northern blazing star (*Liatris scariosa* var. *novae angliae*, Asteraceae) is a rare wildflower, endemic to the northeastern United States. It is a state-endangered (S1) plant in Rhode Island, and Block Island is home to all but one of this state's Northern blazing star populations. Habitat fragmentation, deer grazing, and seed predation are three threats experienced by Northern blazing star on Block Island, and throughout New England. This study examines the effects of patch size and isolation, herbivory, and seed predation on reproductive success. Deer grazing was found to significantly inhibit reproductive success, and appeared to be reducing the proportion of seedlings in populations experiencing high herbivory rates. Two species of moth larva were found eating seeds of Northern blazing star, but these seed predators do not appear to be significantly affecting the demographic structure of populations. Patch size and isolation were important in determining herbivory and seed predations rates, and may affect reproductive success. Deer grazing is a major threat to Block Island populations of Northern blazing star.

Introduction

Twenty-five percent of the 250,000 vascular plant species in the world may become extinct in the next 50 years (Schemske *et al* 1994). This study examines the case of one rare plant species, Northern blazing star (*Liatris scariosa* var. *novae angliae*). I investigate threats to reproductive success in Northern blazing star on Block Island, an island 12 miles off the coast of southern Rhode Island, and I use the data from this study to make recommendations for conservation of this species.

Development is a primary cause for extinction of many species. Development leads to habitat fragmentation, which increases the risk of extinction in many species (Schemske *et al* 1994). Both models and empirical data have shown that small, fragmented plant populations are more likely to go extinct than larger, continuous populations (Groom, 1998; Menges, 1992).

Reproductive success can be negatively impacted by fragmentation and small size through Allee effects, which may cause local extinction in some rare or sparse plant species (Groom, 1998). Allee effects are low per capita reproductive rates found in small populations (Allee, 1951). Allee effects can occur in response to low density, small patch size, or patch isolation. Among plants, these decreased reproductive rates are particularly pronounced in species with animal pollinators (Groom, 1998). Small, isolated patches may be less attractive to pollinators. A lower degree of pollinator visitation may cause Allee effects due to insufficient pollen transfer. This is especially significant among plants that cannot self-fertilize, because they depend on pollen arrival from a different individual, but pollen limitation has been observed in fully self-compatible species as well (Groom, 1998). Low density patches, in which the species is surrounded mostly by other plant species, may also experience Allee effects due to transfer of the wrong species' pollen. Allee effects may also result from inbreeding depression (Groom, 1998).

Empirical data have confirmed that patch size, density, and isolation have significant effects on reproduction of plant populations. Population models that incorporate Allee effects show that extinction rates increase as density decreases, and below some density threshold, extinction is certain. Groom (1998) confirmed the existence of such a threshold in her study of *Clarkia concinna*. Furthermore, in a study of *Centaurea corymbosa*, Colas *et al.* (1997) found lower fertilization rates in areas with a low density of flowering plants. Isolation is also an important determinant of reproductive success. Groom (1998) found that seed set decreased with isolation distance. She further discovered that, among small populations of *Clarkia concinna*, extinction rates increased with isolation, or distance to the nearest patch of this species.

There are many biotic factors that influence the reproductive success of a population. Herbivores, such as deer and other grazers, and seed predators, which often consist of moth and other insect larva, can influence population size and distribution of plants (Harper, 1977; Louda, 1983; Louda and Potvin, 1995). Conversely, the degree of herbivory and seed predation may depend on population size, density, and isolation. Large, dense populations may be more attractive to herbivores and therefore have higher herbivory and seed predation rates, which may decrease reproductive success. However, the food source may be plentiful enough in large patches that herbivores are satiated and herbivory does not significantly affect the population size or structure (Janzen, 1971). Groom (1998) reported that tiny patches experienced much lower levels of deer grazing than larger patches, suggesting that deer located larger patches with greater ease than smaller ones. Seed predation rates have been correlated with variation in density among populations (Sheppard et al, 1994).

The impact of grazers and seed predators on plant populations is often significant. Seed predation rates vary widely from one population to another, and from one individual plant to another within a population. Seed predation can destroy 100% of produced seeds at an individual plant level (Briese, 2000).

When the impact of seed predators and herbivores reaches such high levels, the demographic structure of a population is drastically changed. Demographic structure plays a large role in determining the long-term success of a population, and demographic information is often extremely useful in assessing the status of rare plant populations and their reproductive success, and developing recovery strategies (Schemske *et al*., 1994). In fact, Schemske *et al*. (1994) maintain that in rare and declining plant populations, "only after the demographic status is known can the underlying ecological and genetic causes of decline be identified and considered efficiently."

The negative effects of herbivory and seed predation, and their effects on demographic structure, have been widely observed, but the roles of population size and isolation in herbivory and seed predation rates are not well-described or well-understood, particularly in association with rare plants (Louda and Potvin, 1995). These factors undoubtedly play a major role in determining the reproductive success of rare plants and may significantly affect extinction risks. I studied the effects of population size and isolation, mammal herbivory, and insect seed predation on reproductive success in Northern blazing star (*Liatris scariosa var. novae angliae*), a rare wildflower endemic to the northeastern United States. This plant, about which very little is known, was studied at 21 patches on Block Island, an island 12 miles off the coast of southern Rhode Island. In order to study the threats to reproductive success of Northern blazing star at this site, my specific study questions were:

1) Is Northern blazing star self-fertilizing?
2) Does Northern blazing star experience seed predation on Block Island?
3) Does deer grazing on Block Island inhibit reproduction of Northern blazing star?
4) Are seed predation and deer grazing altering the demographic structures of Northern blazing star populations on Block Island?
5) How do patch size and isolation affect reproductive success, seed predation, and herbivory of Northern blazing star?

Northern blazing star (*Liatris scariosa* var. *novae angliae*)

Northern blazing star, *Liatris borealis* (Lunnell) or *Liatris scariosa* var. *novae angliae* (Nutt.) is endemic to the northeastern United States. Its global range is limited to Connecticut, Massachusetts, Maine, New Hampshire, New Jersey, New York, Pennsylvania, and Rhode Island. The plant is state endangered in Maine, New Hampshire, and Rhode Island, and is listed as a Division 1 species in need of conservation by the New England Plant Conservation Program (Brumback and Mehrhoff, 1996).

Northern blazing star is an early successional species that inhabits coastal plains, grasslands, and disturbed areas. The major threat to Northern blazing star is habitat loss due to human development and succession to a closed canopy, but other significant threats include extensive deer grazing and predispersal seed predation (Kane, 2001).

Northern blazing star is an herbaceous perennial in the Aster family (Asteraceae). It has one to several flowering stems with rose-purple, thistle-like flowering heads, which are pollinated by bees, moths, butterflies, and other insects (Sawyer, 1996; Kane, personal observation). Northern blazing star overwinters as a corm, comes up in May or June, flowers in August and September, and sets seed in late September or October.

Northern blazing star grows in dry open woods, clearings, and barrens of coastal plains, morainal grasslands, and roadsides. The plant appears to be disturbance-dependant, as seed germination and seedling recruitment of the plant are low in absence of disturbance (Vickery, 1997). Fire increases flowering, seed production, seed germination, and seedling establishment in Northern blazing star (Vickery, 1997; Peteroy, 1997). At some sites, Northern blazing star has low juvenile recruitment, which may be due to poor seed viability (Vickery, 1997). Vickery found that some Northern blazing star seed heads lost up to 90% of their seeds to predation by moth larvae. Vickery also discovered that seed predation rates declined by 70% following a burn treatment. Fire has historically been important to the coastal plains and grassland habitat of Northern blazing star (Vickery and Dunwiddie, 1997), and fire suppression may be another threat to the plant and its rare habitat.

Study Site

Block Island

Block Island is a 9.7 square mile (2600 ha) island, located 12 miles south of Narragansett Bay in southern Rhode Island. The island was formed when the Laurentide ice sheet retreated 20,000 years ago, leaving a large moraine that extended from Cape Cod, Massachusetts to Long Island, New York (Sirkin, 1996). Today Block Island consists of glacial till and outwash material; there is no exposed bedrock on the island (Collins, 1999).

Because of this geology, morainal grassland communities exist on Block Island. Morainal grassland, characterized by sparse low herbaceous cover, frequent occurrences of mosses and lichens, sandy soil, and exposed knolls or low slopes, is considered a globally-endangered natural community type (Henderson, 1994). These communities are home to rare plant species, including Northern blazing star and bushy rockrose (*Helianthemum dumosum*), on Block Island. Over the past half-century, large-scale abandonment of agriculture, suppression of fire and other disturbance regimes, and infestation of invasive exotic species have led to a rise in shrubland, which has become the dominant community type on Block Island (Collins, 1999).

Morainal grasslands, and the rare plants inhabiting these communities, are threatened by this conversion to shrubland, as well as by pressures from development and recreation. Although the year-round population of Block Island is under a thousand, up to 15,000 people visit the island daily in the summer (Collins, 1999). Since 1970, the number of houses on the island has more than doubled to 1500 units, and zoning regulations for the island allow for 800 more. Although 30% of the island is protected as open space, development remains a threat to habitat for Northern blazing star on Block Island (Littlefield *et al*. 2001).

There are 28 known Northern blazing star patches on Block Island, all located in the south-central area of the island. Twenty of these patches occur on protected open space, including land owned by conservation organizations and land in conservation easements. The table in Appendix 2 summarizes the number of plants and ownership type of all Northern blazing star patches on Block Island. I surveyed 21 of these patches (See Appendix 1 maps; * in Appendix 2) for this study.

Deer were introduced to Block Island in 1968 by the Rhode Island Department of Environmental Management (Enser, 2001; Morin, 1997). In February 2001, the annual deer count, conducted by helicopter, found 196 deer on the island, a 57% increase from the 1999 count (Weaver, 2001). Deer eat the flowers of Northern blazing star (Littlefield, 2000; personal observation; MA and RI Natural Heritage Program records), and may dig up the corm, or root-like starch storage structure, for a winter food source (Littlefield, 2000). The Nature Conservancy-Block Island Program observed deer grazing on 97% of Northern blazing star stalks at Turnip Farm (Comings, 2000). In order to protect some plants from grazing, a 51 by 21 m deer exclosure was constructed in 1997 at the largest Northern blazing star patch on Block Island, the Turnip Farm site. The fence encloses approximately half of the area of the entire population at that site.

Methods

Self-fertilization

Little is known about the mating system of *Liatris scariosa* var. *novae angliae*. This is important information for conservation of rare plants because of the different threats associated with different mating systems. Reproduction of plants that do not self-fertilize, such as species with self-incompatibility mechanisms that prevent fertilization by genetically similar pollen, can be threatened by pollen-limitation, as discussed in the Introduction. Plants that are able to self-fertilize may not experience pollen-limitation, but fitness may decrease due to inbreeding.

In order to determine if Northern blazing star is self-fertilizing, 20 treatment (‘bagged’) plants were bagged with nylon to prevent pollinator visitation. These bagged plants were paired with 20 control (‘unbagged’) plants. Pairing was done spatially: two adjacent plants were considered paired and each received a different treatment. Seedheads were collected, and seed set, or number of seeds per inflorescence head, was measured for treatment and control plants.

Reproductive success

Individual plant reproductive success was measured as seed set. Of the 21 surveyed patches, four did not contain any successful seed-setting adult plants. I thus collected seedheads from only 17 patches. At each patch, I collected one seedhead from each of 20 plants located at random distances along a transect through the center of the population. Some patches had fewer than 20 fruiting plants, due to small size, extensive herbivory, or mowing. In these cases, one seedhead was collected from each of the fruiting plants. Reproductive success was also measured at the patch level as flowering rate (flowering rate = number of flowering plants/ total number of plants per patch). Flowering rate was measured at all 21 patches. Flowering rate data was collected at all patches over a one-week period in August, when flowering of Northern blazing star appeared to peak.

Seed predation

I collected seedheads from 17 of the 21 patches, as described above. I measured both total seed set and "viable" or unpredated seed set, determined by subtracting predated seeds from total seeds. Predated seeds were defined as seeds that were visibly eaten by larvae (See photo, Appendix 5). I counted seed set, number of predated seeds, and number of seed predators for each seedhead. Seed predators were defined as any insect larvae found within the seedhead. I also determined patch-level seed predation rates (seed predation rate = number of predated plants/total number of plants per patch).

Herbivory

I scored all plants for presence or absence of herbivory at the 21 Northern blazing star patches I surveyed on Block Island. Presence of herbivory was recorded when the vegetative and/or flowering parts of the plant were clearly grazed or nibbled by a mammal. Deer have been widely observed eating Northern blazing star, and they are the only mammal on Block Island known to graze on this plant. I calculated patch-level herbivory rates by dividing the number of grazed plants per patch the total number of plants per patch (herbivory rate=grazed plants/total plants).

To determine if herbivory has a significant negative impact on reproduction of Northern blazing star, I set up 18 one-m^2 plots at the Turnip Farm site. Nine of these plots were inside the deer exclosure ('fenced'), and nine plots were in the adjacent area outside the exclosure ('unfenced'). I calculated herbivory rates (herbivory rate = number of grazed plants/ total number of plants per plot), flowering rates (flowering rate = number of flowering plants/ total number of plants per plot), fruiting rates (fruiting rate = number of plants with seedheads/ total number of plants per plot), and average seed set for all plots.

Demographic Data

In order to determine the demographic structure of Northern blazing star populations, I collected baseline demographic data in the summer of 2000. I tagged 50 plants per patch at 14 patches ($^{+}$ in Appendix 3) and tracked them over the course of the summer. Plants were selected at random distances along a transect through the center of the population, and visited three times over the growing season. Because Northern blazing star is a perennial, several years of data are needed to calculate transition rates between life stages. However, I was able to calculate mortality of each stage over one season.

I recorded the stage (seedling, juvenile, or adult), number of stalks, number of flowering stalks, number of seed stalks, and number of seedheads. I defined seedlings as plants with two or fewer leaves, juveniles as vegetative plants, and adults as reproductive plants. Evidence of deer browsing was also recorded for each plant. I collected one seedhead from every tagged fruiting adult and counted seed set. I also recorded number of seed predators and number of predated seeds for each seedhead collected.

At the Turnip Farm site, I tagged all plants in the established one by one meter study plots in the fenced (total number tagged plants=196) and unfenced areas (total number plants=326). The characteristics described above were recorded for every tagged plant in these plots throughout the summer.

For all patches, I counted total population size, determined each stage's proportion of the total population, and calculated herbivory and mortality rates for each stage over the summer . I also calculated the seedling to adult ratio (number of seedlings/number of adults) at all patches. Both deer grazing, which may reduce the number of flowerheads that produce seed, and seed predation, which may reduce the number of viable seeds, affect seedling establishment by reducing the number of viable seeds. The seedling to adult ratio was thus used to compare the effects of herbivory and seed predation on patch demography.

Patch Size and Isolation

Patch size was determined by counting the total number of plants in a patch. I defined a patch as a group of plants separated by at least 5 m from other Northern blazing star individuals. Because seed dispersal distance is not known for Northern blazing star, I could not use this information to determine a distance to distinguish patches. I thus used the 5m separation distance utilized by Groom (1998). For the three largest patches, patch size was estimated from density and area measurements. In these patches, density was measured in random 1 x 1 m areas throughout the patch. A Global Position System (GPS) unit was used to map area and location of each patch. From these measurements, area and isolation, or distance to the closest patch, was calculated using Arcview software.

Statistical Analyses

I used a two-tailed t-test for unequal variances to analyze self-fertilization results, and to analyze effects of herbivory in the fenced and unfenced area at Turnip Farm. I used the multiple regression SAS general linear model (Type III) to perform ANOVAs of the patch size and isolation on reproductive success, seed predation, and herbivory. I used the SAS regression model to analyze the effects of herbivory and seed predation rates on the seedlings to adult ratio. Prior to these statistical analyses, all proportions were normalized by an arcsine square root transformation [$p_n = \sin^{-1}(\sqrt{p_0})$, where p_n= normalized proportion and p_0= raw proportion].

Results

Northern blazing star patch size ranged from six to 11,000 plants (mean =1720, S.E. = 770). Patch area ranged from 1 to 18,425 m^2 (mean =1235, S.E. = 855) and isolation ranged from 10 to 1052 m (mean =102, S.E. = 52). All proportions were normalized to perform statistical analyses, using the above transformation, but all figures display the raw, untransformed data.

Self-fertilization

There was no significant difference in the seed set of bagged and unbagged flowerheads (Figure 1, two-tailed t-test for unequal variances: $p=0.293$). This indicates that bagged flowerheads self-fertilized and successfully produced seed.

Reproductive Success

As shown in Table 1, there appear to be no significant effects of patch size ($p=0.1812$, Figure 2) or isolation ($p=0.3583$, Figure 3) on seed set. However, there may be a threshold patch size, above which average seed set increases. This threshold appears to be around a patch size of 400 individuals (Figure 2).

Flowering rate (number of flowering stalks/total number of stalks in a patch) is correlated with patch size and isolation (Table 1, Figures 4 and 5). There were a significant positive relationships between patch size and flowering rate (p=0.0021) and patch isolation and flowering rate (p=0.0001). This suggests that larger, more isolated patches have a higher proportion of flowering stalks small, less isolated patches.

Seed predation

Northern blazing star experiences seed predation on Block Island. Of the 17 patches where I collected seedheads, seed predators were found at 13 of them. Among the 13 patches experiencing seed predation, the predation rate, or proportion of plants in a patch experiencing seed predation, ranged from 0.05 to 0.72, with a mean of 0.32. The proportion of predated seeds per seedhead of an individual plant ranged from 0 to 0.95, with a mean of 0.074 (S.E.=0.01).

I observed two different seed predators in the seedheads that I collected. The most abundantly found seed predator, shown in Appendix 5c, is the larval stage of a moth of the genus *Isophrictis* in the Gelechiidae family (Roberts, 2000). This genus has also been identified as a seed predator of Northern blazing star in southern Maine. In this study, 81% of the observed seed predators were *Isophrictis*. The second seed predator, making up the remaining 19%, was tentatively identified as a species of *Idia*, in the Noctuidae family (Roberts, 2000).

Seed predation was positively correlated with patch size(Table 1, Figure 6), indicating that a greater proportion of plants experience seed predation at larger patches.

There was also a significant correlation of seed predation rate and isolation (Table 1, Figure 7). Although seed predators were observed at the majority of surveyed patches and predation rates reached 95% in some seedheads, there was a very low mean seed predation rate over all patches and seed predation does not seem to be significantly limiting populations on Block Island. This is supported by the demographic data, and is discussed more extensively in that section.

Herbivory

The Turnip Farm data show that deer grazing occurs extensively in the unfenced area, and it significantly reduces flowering and fruiting (Figure 8). Reproductive stalks, at both flowering and fruiting stages, make up a significantly smaller proportion of total plants in unfenced (grazed) area compared with the fenced area, where deer grazing was prevented. There also appears to be a relationship between grazing and seed predation. There were significantly higher rates of seed predation in the fenced area, where grazing did not occur, than in the unfenced area ($t=4.2099$, $p=0.0004$, Figure 9). As displayed in Table 1 and Figure 10, deer grazing was not significantly correlated with patch size ($p=0.0693$). There was a significant negative relationship between patch isolation ($p=0.0230$, Table 1; Figure 11). Thus, it appears that deer are less likely to graze at isolated patch.

Demographic Data

When all populations on Block Island are considered together, seedlings make up 21.8% of all Northern blazing star plants, juveniles make up 33.6%, and adults make up the remaining 44.6%. These numbers represent the population at the beginning of the summer, prior to mortality over the growing season. As shown in Figure 12, mortality rates were extremely high among seedlings (0.79), moderately high among juveniles (0.56), and minimal among adult plants (0.03). The demographic structure of each of the 14 surveyed patches is summarized in Appendix 4.

There appear to be two distinct demographic structures among the populations of Northern blazing star. At the majority of patches sampled (nine of the 14), seedlings make up less than 15% of the populations, while adults dominate (Figure 13). The remaining 5 patches seem to have a more equal stage distribution. Note that Patch 1 and Patch 2 have similar demographic structures. This was unexpected because Patch 1 is the fenced area, where deer grazing did not occur, and Patch 2 is the adjacent unfenced area at Turnip Farm. The previous section indicates that deer are limiting the reproductive success of that population and I expected to find a lower proportion of seedlings in the unfenced area.

Among all patches, the average seedling to adult ratio = 0.49, indicating that there are approximately twice as many adults as seedlings on Block Island. At severely grazed patches, however, this ratio was zero, indicating that none of the sampled plants were seedlings. The seedling to adult ratio is negatively correlated with patch herbivory rate (Figure 14a), indicating that as herbivory increases, seedling recruitment is lower and seedlings make up significantly smaller proportion of all plants. The seedling to adult ratio was not correlated with seed predation rates (Figure 14b), suggesting that, while herbivory appears to limit seedling recruitment, seed predation does not. Thus, the demographic data offer powerful evidence that seed predation is not currently a threat on Block Island. Deer grazing is the stronger negative force affecting Northern blazing star here.

Discussion

There was no difference in seed set between bagged and unbagged heads, indicating that Northern blazing star is self-fertilizing (Figure 1). Thus, even small, remote patches of the plant will successfully set seed and reproduce. However, because Northern blazing star is able to self-fertilize, these small patches may experience higher self-fertilizing rates and thus higher rates of inbreeding.

Inbreeding seems to reduce fitness among both plants and animals (Hedrick and Kalinowski, 2000). For plants, inbreeding can result in reduced seed set, germination, survivorship, and growth (Hokanson and Hancock, 2000; Sheridan and Karowe, 2000). This is of particular concern among small populations of randomly mating individuals, such as those typical of many rare and endangered species. In these cases, plants can suffer from inbreeding depression due to effects of genetic drift that may decrease the fitness of all individuals in the population (Hedrick and Kalinowski, 2000).

Although inbreeding often causes reductions in reproductive success and fitness, it can also lead to a purging, or disappearance through natural selection, of deleterious mutations. Cheptou et al. (2000) showed that, among populations of *Crepis sancta* with varying levels of self-compatibility, more highly self-compatible populations had reduced inbreeding depression. In fact, the most self-fertile population showed a complete absence of inbreeding depression, indicating that purging may have taken place.

More studies need to be performed on Northern blazing star to determine if small populations exhibit inbreeding depression, or if these populations are self-compatible enough that purging has reduced deleterious alleles. Because of the often severe negative impacts of inbreeding depression, it is important to know such information in managing rare and sparse plant populations such as those of Northern blazing star on Block Island.

Although inbreeding depression could be a threat to Northern blazing star, the data in this study do not conclusively demonstrate that the patches of Northern blazing star are experiencing Allee effects, due to inbreeding or any other factors, on Block Island. Seed set was not significantly reduced in patches of small size or with high degrees of isolation (Table 1). While there was no linear relationship, there may be a threshold effect. If there is a patch size threshold, below which average seed set decreases, the seed set data might support the presence of Allee effects. Groom (1998) found this threshold effect in isolation: small populations beyond a certain distance from the closest patch received less pollen and were more likely to go extinct than less isolated patches.

It is also possible that the ability of Northern blazing star to self-fertilize helped the species avoid Allee effects due to low pollinator visitation at these small patches. If this is the case, and plants of small patches are forced to self-fertilize, then one might expect to observe lower reproductive success in small populations due to inbreeding depression. However, this pattern is not observed in the seed set data, so it appears that inbreeding depression is not occurring in the smaller patches. Insects were observed visiting Northern blazing star plants at all patches, and this absence Allee effects may be due to high pollinator visitation to the showy, brightly colored inflorescences. Alternatively, if small populations of Northern blazing star on Block Island are highly self-compatible, this lack of evidence for inbreeding depression and Allee effects could be due to purging of deleterious alleles. Finally, it is possible that none of the patches are far enough apart to prevent pollen exchange with other populations.

The flowering rate data provide a patch-level measure of reproduction. There is a significant positive correlation between flowering rate and patch size. This relationship could be explained by a link between flowering rate and herbivory rate. (Herbivory rates and flowering rates are negatively correlated). Deer often prevent flowering, as they graze the plants continuously throughout the growing season. If the increased flowering rates at large populations are an artifact of reduced herbivory rates, this could be due to predator satiation. Deer are less destructive, i.e. they do not decrease flowering rates as much, in large populations compared with small populations because the deer are satiated before eating a significant proportion of the flowering stalks.

Flowering rate data further suggest that there is a significant relationship between isolation and flowering rate (Figure 4). The positive correlation between flowering rate and isolation is probably due to the decreased herbivory rates in more isolated patches ($p=0.0889$). Thus, while patch size and isolation may not directly affect individual reproductive success, as measured by seed set, these factors may affect reproduction by altering flowering rates.

Patch size also appears to affect seed predation of Northern blazing star. Seed predation rates are positively correlated with patch size (Figure 6). This may be because moths are more attracted to larger patches and thus lay their eggs on individuals in these populations, leading to higher rates of predation by their seed-eating progeny. Studies have shown that the number of flowers per plant may influence seed predation rates (Stephenson, 1981). Ehrlen (1996) found increased seed predation in plants with many flowers. He suggested that inflorescence size may thus be subjected to opposing selective pressures, as seed predation selects for inflorescences with fewer flowers, while pollinator attraction and reproductive success select for larger inflorescences. This difference in seed predation rates appears to be occurring in Northern blazing star at the patch level, and is probably due to seed predator attraction.

While seed predation is occurring on Block Island, particularly at larger patches, the demographic data indicate that seed predation is not limiting seedling recruitment (Figure 14). Thus, seed predation does not appear to be a significant threat to the species on Block Island. However, if seed predation rates increase and appear to be inhibiting growth of Northern blazing star populations, managers may want to consider exclusion of insects. In the past fifty years, studies have shown that seed losses due to insect feeding are significant and that exclusion of such insect herbivores increases viable seed set and maturation (Louda, 1983; Briese, 2000, Bevill et al. 1999). Several studies have shown insecticides, such as Isotox, to be successful means of increasing viable seed set and decreasing plant mortality (Bevill et al. 1999; Louda 1983)

In this case, however, there are several reasons that suggest insecticide exclusion is not an appropriate management strategy for Northern blazing star on Block Island. First, it remains unknown if seed predation is limiting this species. The only definitive method of determining effects of predispersal seed predation on seedling establishment, demography, and lifetime fitness is predator exclusion. This can be done with cages, but insecticides are more frequently used. The problems associated with predator exclusion are that the chemicals in insecticides may have direct effects on plant performance and frequent repeated applications of insecticide are often necessary (Louda and Potvin, 1995). Furthermore, nontarget insects, including pollinators, could be affected by insecticide application.

Insecticide exclusion on Northern blazing star may also be inappropriate because so little is known about the insects associated with this plant. As Lesica and Atthowe (2000) point out, “Most plants directly or indirectly support a large number of arthropods, including herbivores and their predators and parasites.” Furthermore, a seed predator found on Northern blazing star plants in Maine is believed to be a previously unidentified species, in the Tortricidae family, which may be an obligate feeder on Northern blazing star (Roberts, personal communication 2000). If this is the case, Northern blazing star may be a required food source for an endangered insect species, and this would further underscore the need to protect this rare plant.

Deer grazing appears to have a much more significant negative effect on reproduction of Northern blazing star than seed predation. Seedling to adult ratios are correlated with herbivory rates (Figure 14), indicating that deer grazing is altering the demographic structure of Northern blazing star populations. If these high rates of herbivory continue to limit seedling recruitment, the species will be unable to sustain itself on Block Island and populations will decline.

Islands such as Block Island often support unique ecosystems, rich in endemic species, and introduced herbivores have been a major cause of extinction of plants on islands(Bowen and van Vuren, 1997). This may be because herbivorous mammals were absent from most islands until human arrival, and plants thus evolved in absence of herbivores. Because plants evolve chemical, physical, and structural defenses to herbivory in direct proportion to the risk of herbivory, island plants that evolved in absence of herbivores may lack defenses against herbivory (Bowen and van Vuren, 1997). Northern blazing star populations on Block Island may be a victim of high herbivory rates because they have not evolved defenses to introduced deer.

There may be an interaction between herbivory and seed predation rates. Herbivory reduces reproductive success and may also reduce seed predation by reducing flowering rates and thus rendering the patch less attractive to seed predators. The data from the fenced and unfenced area at Turnip Farm (Figure 9) support this hypothesis.

Although herbivory rates may reduce seed predation, this relationship is unlikely to be ultimately important to the survival of Northern blazing star patches on Block Island because deer grazing has a much more significant effect on reducing seedling recruitment than seed predation. Based on these data, deer are the major threat to Northern blazing star on Block Island. Neither Allee effects nor seed predation appear to be playing a significant role in reproduction or demographic structure of the plant. If the deer herd on the Island continues to increase, as has been observed since 1999 (Weaver, 2001), the effects of herbivory on Northern blazing star will only be exacerbated. The town of New Shoreham is currently considering reducing the deer herd (Comings, personal communication). The data from this study add to the list of negative impacts from deer on Block Island, including a high instance of Lyme disease, and strengthen the need for a significant reduction of the deer herd.

The demographic data provide important information about the importance of herbivory and seed predation in determining the current stage distribution, as described above. These data also reveal that many populations on Block Island have extremely low proportions of seedlings and juveniles (Figure 13). In nine of the 14 surveyed patches, seedlings make up less than 15% of the total population, while 50% to 86% of the population consists of adult plants. Figure 13 describes the patches before mortality that occurred over the summer. Seedlings experienced high growing season mortality rates (0.79, over all patches) compared with adult plants (0.03), as shown in Figure 14 (See Appendix 4 for mortality rates of all stages, among all patches).

It is likely that the adult life history stage in Northern blazing star, which is a perennial that may be able to reproduce for multiple seasons, is longer than the seedling stage, which lasts only one season. This may partially explain why adults make up a much larger percentage of most patches. However, it is likely that most of this difference is due to reduced seedling recruitment caused by deer grazing.

The demographic data support the hypothesis that deer grazing is a threat to Northern blazing star populations on Block Island (Figure 14). The negative correlation of the seedling to adult ratio and herbivory rates (Figure 14a) show that seedling recruitment is probably limited by herbivory. Because predation rates are uncorrelated with the seedling to adult ratio (Figure 14b), it is likely that seed predation plays a minimal role. In order to understand definitively if seedling recruitment is limiting population growth, and populations are declining, increasing, or stable, several more years of demographic data need to be collected.

In five Northern blazing star patches, the proportion of plants in each stage class is equally distributed (Figure 13). This stage structure differs greatly from the one exhibited in the other nine patches. It makes sense that the stage structure is equally distributed in patch 1, the fenced area at Turnip Farm, because deer grazing is prevented. However, reduced herbivory rates cannot explain this stage distribution in all five patches, as herbivory rates do not differ significantly from the reduced seedling patches to the equally distributed patches. Furthermore, the stage structures of patch 1, the fenced area at Turnip Farm, and patch 2, the unfenced area, are equal. Even though deer grazed 80% of stalks in patch 2 and no stalks in patch 1, seedlings make up about one third of the population. This may be due to seed dispersal from patch 1 to patch 2. Thus, the seed production of plants in patch 2 could be low due to grazing, but seeds produced within the fenced area are dispersed outside the fence, elevating the proportion of seedlings.

Demographic studies play a crucial role in determining causes of rarity and population decline (Schemske *et al.*1994). Demographic data are often incorporated into population viability analyses, or PVAs, to provide assessments for extinction risks, or population persistence, for populations. They usually involve matrix projection methods that incorporate demographic data collected over several years. PVAs can be used to asses population characteristics, such as the finite rate of increase (λ), and threats, such as environmental and demographic stochastisity. PVAs can also be used to predict time to extinction and future population size or structure (Menges, 2000). The populations observed and individuals tagged in this study should be followed for several more years to determine extinction risks, threats, and sensitive life history stages so that conservation efforts can be effectively and efficiently targeted to the necessary areas.

Conclusions

In conclusion, deer grazing seems to be the major threat to Northern blazing star populations on Block Island and herbivory is significantly altering the demographic structure of many populations by reducing reproductive success. More research is needed to determine if Northern blazing star populations are decreasing, and, if so, what life history stage is limiting growth. Such studies could help determine for certain if deer grazing is limiting populations, and what effect seed predation has, if any, on demographic structure. Further research is also needed to understand more about the biology and life cycle of this plant, including studies on average lifespan, time to reproduction and reproductive life span of plants, and seed bank existence. Although my data do not suggest that Allee effects are reducing reproductive success of small, isolated populations, Northern blazing star patches on Block Island should be further studied to determine this for certain. A severe threat to this rare plant on Block Island is deer herbivory, and this threat must be addressed to ensure the protection of Northern blazing star populations.

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Numerous people and organizations made this thesis possible and helped me tremendously. I would like to thank the following people:

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- The Rhode Island Wild Plant Society for funding;
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Figures and Tables

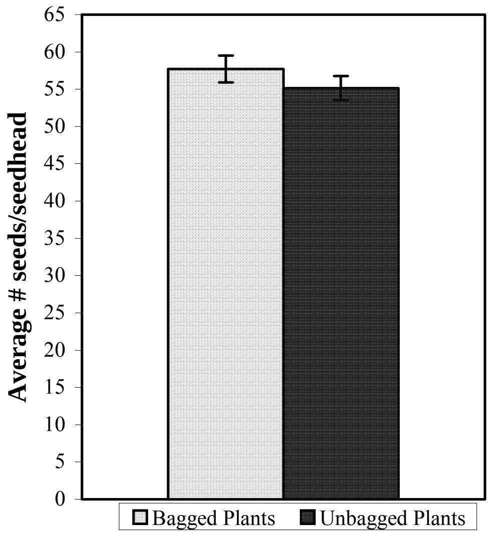


__Figure 1. Seed set of bagged and unbagged plants.__ There is no significant difference in seedset of bagged (mean=57.7; S.E.=1.8) and unbagged flowerheads (mean=55.1; S.E.=1.6) (two-tailed t-test for unequal variances, df=18, p=0.2925).

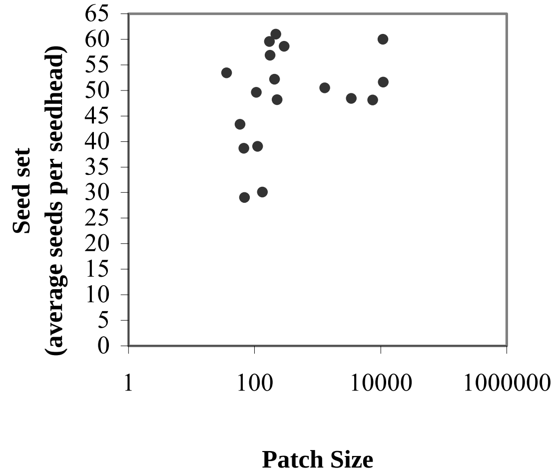


__Figure 2. Seed set and patch size.__ There appears to be a threshold patch size above which average seedset increases.

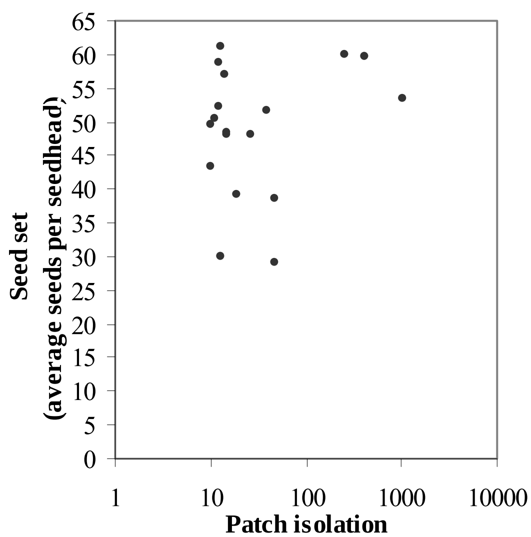


__Figure 3. Seed set and patch isolation.__ There is no linear relationship between patch isolation and seed set.

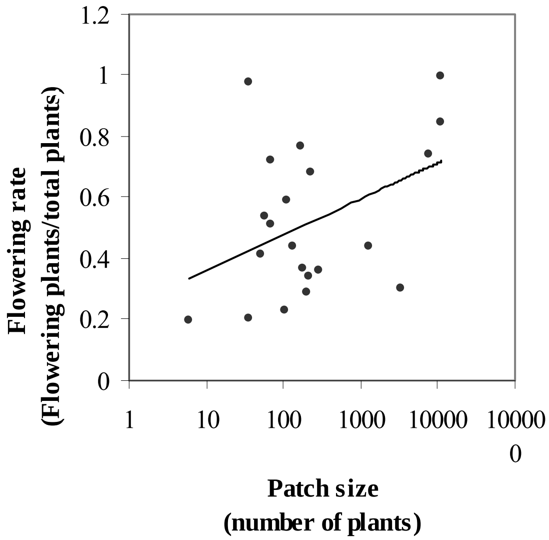


Figure 4. Flowering rate and patch size. *Flowering rate is positively correlated with patch size.*

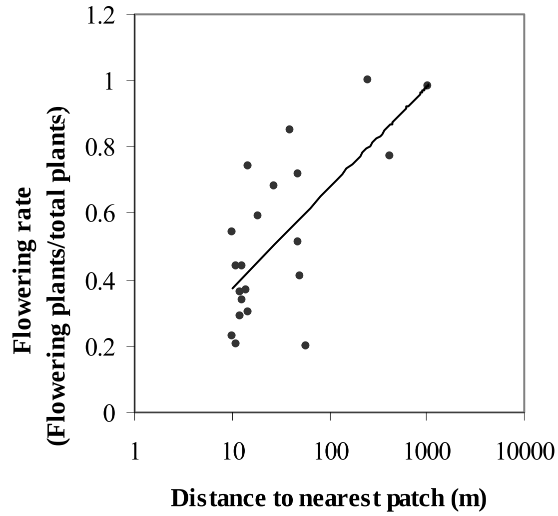


Figure 5. Flowering rate and patch size. *Flowering rate is positively correlated with patch isolation.*

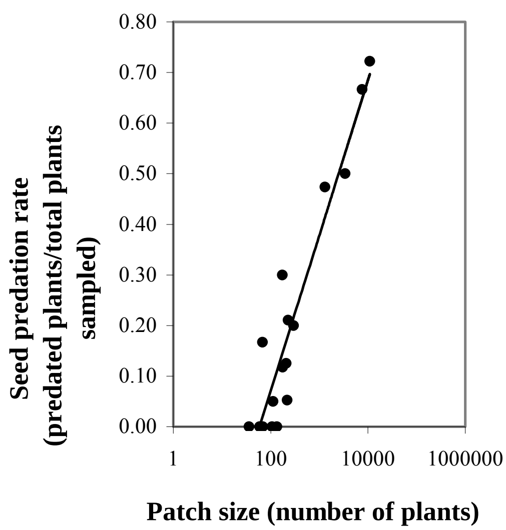


Figure 6. Seed predation as a function of patch size. *Seed predation rates increase with patch size. This graph shows raw seed predation rates.*

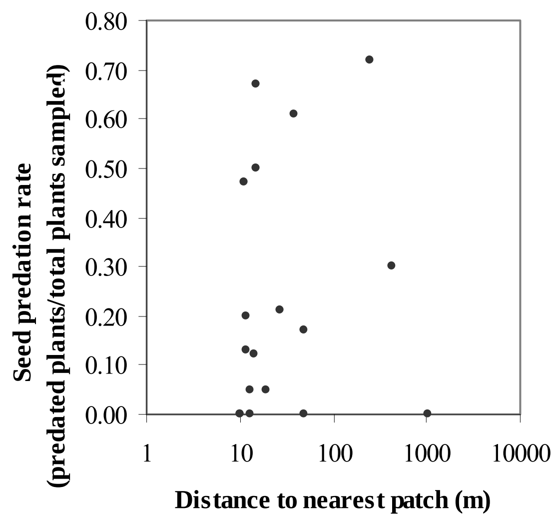
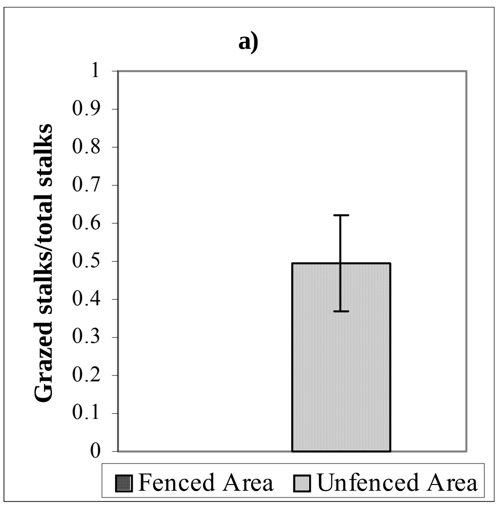
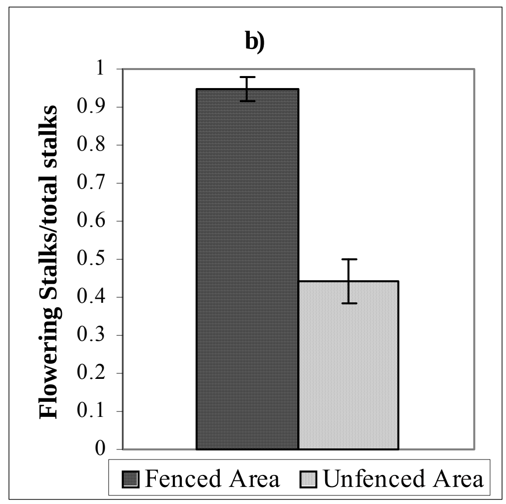


Figure 7. Seed predation and patch isolation. *There is no significant relationship between patch isolation and seed predation rate.*

	Seed set		***Viable seed set*** (total seeds-predated seeds)		***Flowering rate*** (fl. stalks/total stalks)		***Seed predation rate***		***Herbivory rate*** (herb. stalks/total stalks)	
	Slope	P-value	Slope	P-value	Slope	P-value	Slope	P-value	Slope	P-value
Patch size (logsize)	3.935	0.1812	-0.858	0.7721	0.156	**0.0021**	0.395	**0.0001**	-0.140	0.0693
Patch isolation (logisolation)	3.990	0.3583	2.070	0.6424	0.432	**0.0001**	0.099	0.1558	-0.309	**0.0230**

Table 1. Reproductive success, seed predation, and herbivory as functions of patch size and isolation. *Patch size is significantly correlated with flowering rate and seed predation rate, and weakly correlated with herbivory rate and seedset. Isolation is significantly correlated with flowering rate and seed predation rate. All proportions have been arcsine square root transformed for this ANOVA. P-values≤0.05 are in bold type.*





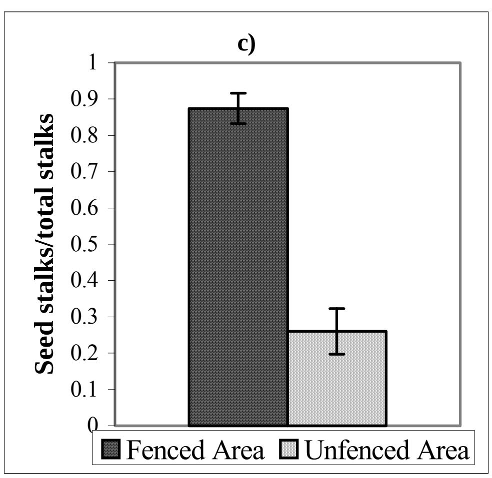


Figure 8. Effects of herbivory on reproduction of Northern blazing star. *One-m^2 plots in the fenced(n=9) and unfenced area (n=9) showed significant decreases in the proportion of flowering and fruiting stalks in the unfenced area compared with the fenced are. a)Average herbivory rates in the fenced area were 0.002 (S.E.= 0.002) and 0.496 (S.E.= 0.127) in the unfenced area (df=8, t=-3.8863, p=0.0046). b)The average proportion of flowering stalks in the fenced area is 0.947 (S.E.=0.031), compared with only 0.440 (S.E.=0.058) in the unfenced area (df=12.1, t=7.7063, p=0.0001). c)The average proportion of seed-producing stalks is0.874 (S.E.= 0.043) in the fenced area and 0.260 (S.E.=0.062) in the unfenced*

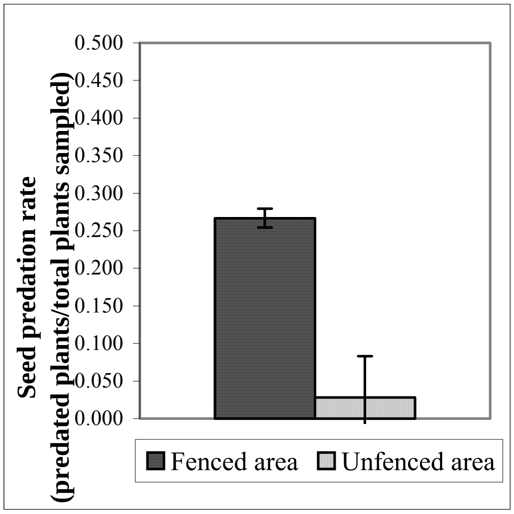


Figure 9. Seed predation rates in fenced and unfenced areas. *Seed predation rates were higher in the fenced area, where grazing did not occur, than the unfenced area (t=4.2099 , p=0.0004), where deer grazed half of all Northern blazing star (see Figure 8).*

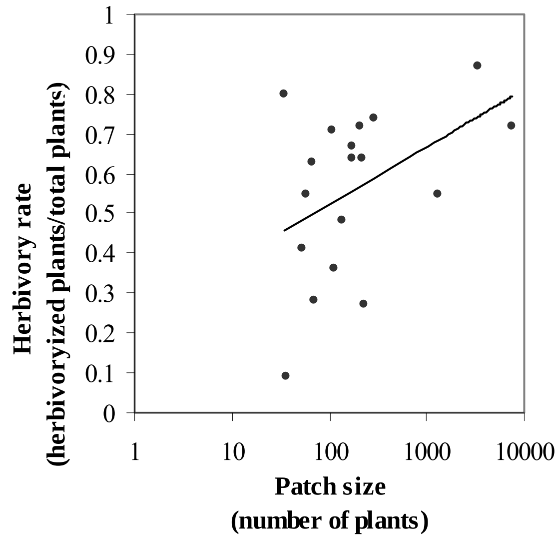


Figure 10. Herbivory and patch size. *Herbivory rates may be correlated with patch size.*

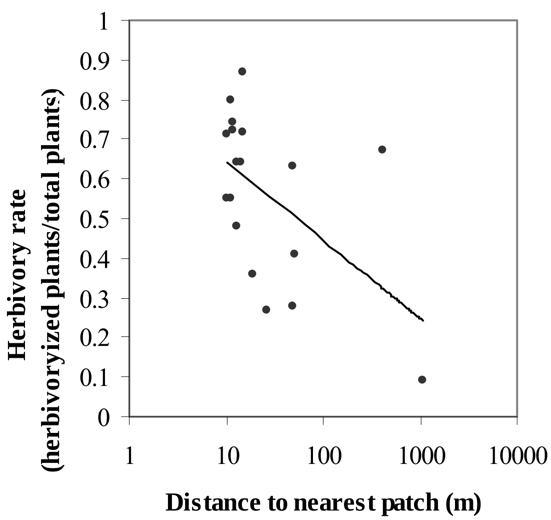


Figure 11. Herbivory and patch isolation. *Herbivory rates are significantly positively correlated with isolation.*

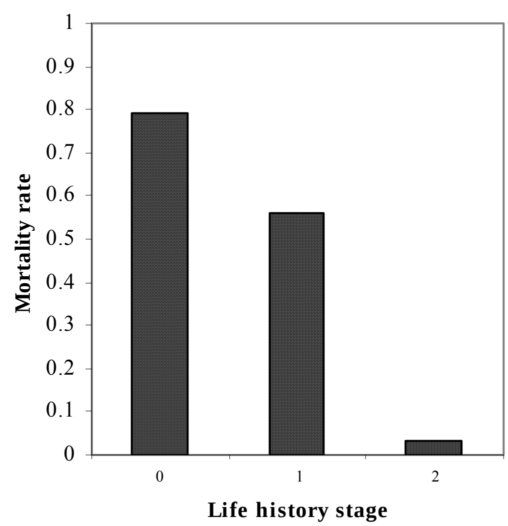


Figure 12. Mortality rates of seedlings (0), juveniles (1), and adults (2). *From June to early October, the mortality rate of seedlings, juveniles, and adults was 0.79, 0.56, and 0.03, respectively.*

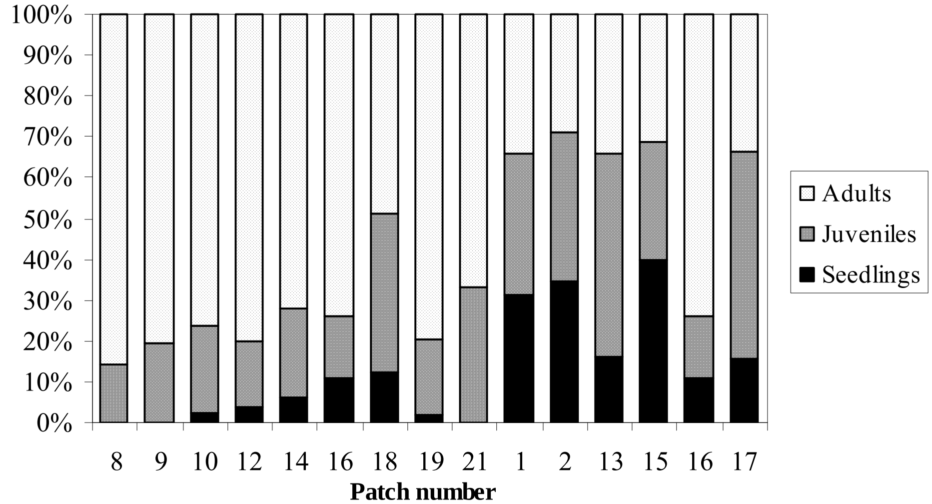


Figure 13. Demographic structure of 14 Northern blazing star patches on Block Island. *In nine of the patches (8,9,10,12,14,16,18,19, and 21), seedlings make up less than 15% of all plants (before mortality over the season is included) and adults make up the majority of these populations. In the remaining five patches (1 and 2,13,15,16, and 17), populations are more equally distributed between the three stages. Patches 1 and 2 are the large patch at Turnip Farm; Patch 1 is the fenced area and Patch 2 is the unfenced area. (See Appendix 4 for patch characteristics and demographics).*

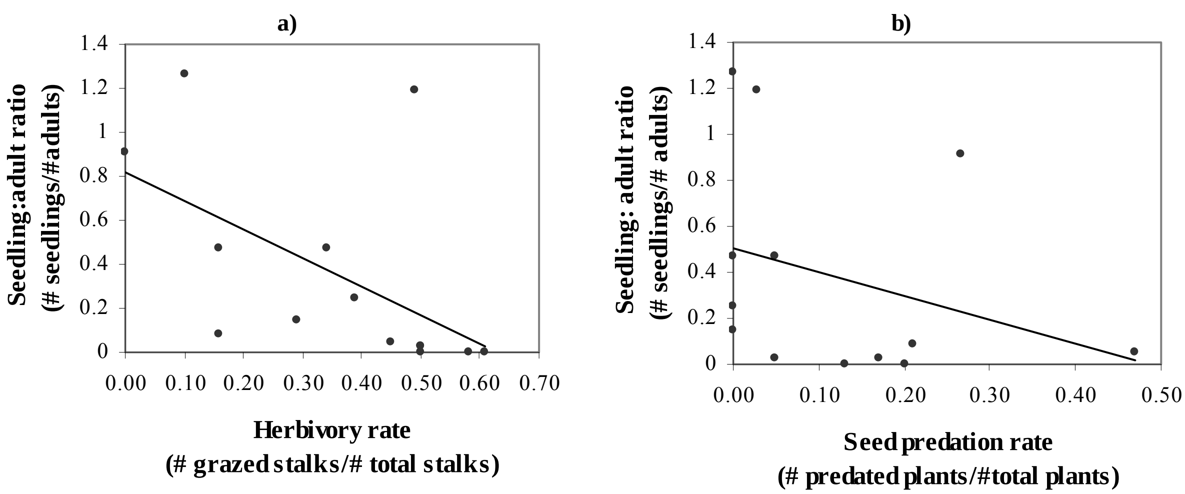


Figure 14. Demographic effects of herbivory and seed predation: the seedling to adult ratio in 14 patches on Block Island. *a) Herbivory is significantly negatively correlated with the seedling:adult ratio (n=14, r^2=0.3035, p =0.0412), suggesting that herbivory may be significantly reducing seedling recruitment. b) Seed predation is not significantly correlated with the seedling:adult ration in (n=13, r^2=0.0976, p=0.2986). The number of patches is reduced to 13 in this graph because one patch produced no seedheads, due to high grazing rates.*

New graphs

Appendices

Appendix 1. ***Northern blazing star populations on Block Island.***

Appendix 2. ***Herbivory in Northern blazing star populations on Block Island.***

Appendix 3. ***Known Block Island Northern blazing star occurrences.***

Appendix 4. ***Demographic Data.***

Appendix 5. ***Seed predation in Northern blazing star..***

Appendix 1. ***Northern blazing star populations on Block Island.***

Appendix 2. ***Herbivory in Northern blazing star populations on Block Island.***

Appendix 3: Known Block Island Northern blazing star patches.

Site Number	Number of Plants	Ownership type
1*+	11029	Protected
2*+		Protected
3*	10918	Private
4*	3415	Private
5*	7531	Private
6*	173	Private
7*	36	Private
8*+	295	Protected
9*+	208	Protected
10*+	218	Protected
11*	176	Protected
12*+	1307	Protected
13*+	112	Protected
14*+	227	Protected
15*+	69	Protected
16*+	134	Protected
17*+	107	Protected
18*+	59	Protected
19*+	68	Protected
20*	35	Protected
21*+	6	Protected
22*	52	Protected
23	100	Protected
24	100	Protected
25	23 (all mowed)	Protected
26	5 (all mowed)	Town
27	200-250[1]	Private
28	Thousands	Private
29	Few[2]	Town

*Studied populations

+Demographic data collected

[1]Data from 1992 Rhode Island Natural Heritage Program records.

[2]Comings, personal communication.

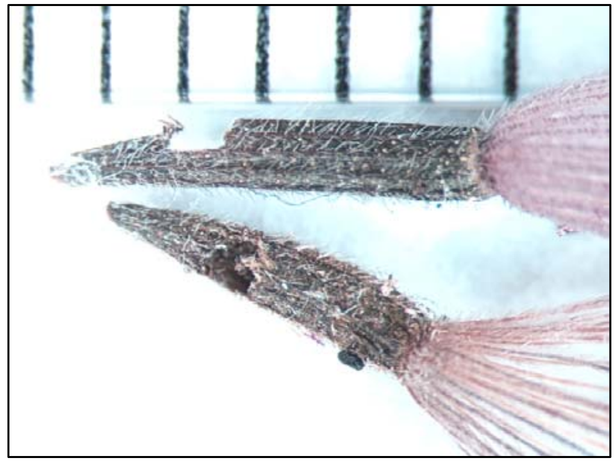
Appendix 4. Demographic Data.

Patch	Stage	N	Proportion of population	Mortality rate	Proportion of grazed plants	Seedling:adult ratio	Total N sampled	Herbivory rate (of total population)
1	0	61	0.31	0.80	0	0.91	195	0.00
	1	67	0.34	0.60	0			
	2	67	0.34	0.03	0.01			
2	0	112	0.35	0.87	0.08	1.19	324	0.49
	1	118	0.36	0.58	0.19			
	2	94	0.29	0.19	1.2			
8	0	0	0	--------	0	0.00	42	0.61
	1	6	0.14	0.33	0			
	2	36	0.86	0.11	0.92			
9	0	0	0	---------	0	0.00	46	0.58
	1	9	0.2	0	0.11			
	2	37	0.8	0	0.95			
10	0	1	0.02	1	0	0.03	46	0.50
	1	10	0.22	0	0.1			
	2	35	0.76	0	0.91			
12	0	2	0.04	0	0	0.05	50	0.45
	1	8	0.16	0	0.25			
	2	40	0.8	0.05	0.9			
13	0	8	0.16	0.13	0	0.47	50	0.16
	1	25	0.5	0.52	0.08			
	2	17	0.34	0	0.76			
14	0	3	0.06	0.67	0	0.08	50	0.16
	1	11	0.22	0.45	0			
	2	36	0.72	0.028	0.58			
15	0	19	0.4	0.90	0	1.27	48	0.10
	1	14	0.29	0.5	0			
	2	15	0.31	0.27	0.73			
16	0	5	0.11	0.20	0	0.15	46	0.29
	1	7	0.15	0.71	0			
	2	34	0.74	0.09	0.94			
17	0	24	0.16	0.88	0	0.47	152	0.34
	1	77	0.51	0.69	0.04			
	2	51	0.34	0.22	0.76			
18	0	6	0.12	0.50	0	0.25	49	0.39
	1	19	0.39	0.63	0.11			
	2	24	0.49	0.04	0.96			
19	0	1	0.02	0	0	0.03	49	0.50
	1	9	0.18	0.33	0.11			
	2	39	0.8	0.15	0.9			
21	0	0	0	---------	0	0.00	6	0.50
	1	2	0.33	0.5	0.5			
	2	4	0.67	0.25	1			

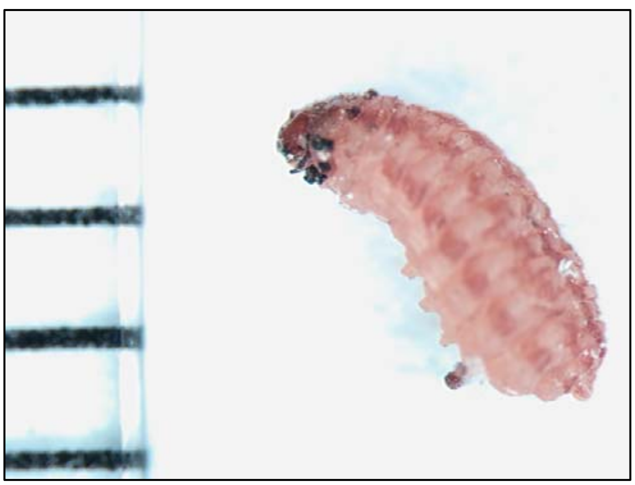
Life stages: **0**=seedling
1=juvenile
2=adult

Appendix 5. Seed predation in Northern blazing star.

a) *Unpredated Northern blazing star seeds.*



b) *Predated Northern blazing star seeds.* These seeds were predated by moth larva of the genus *Isophrictis*. A millimeter scale appears along top of photo.



c) *Isophrictis moth larva.* This was the moth larva most abundantly found on Block Island. A millimeter scale appears