Ten-year impacts of the biological control agents *Galerucella pusilla* and *G. calmariensis* (Coleoptera: Chrysomelidae) on purple loosestrife (*Lythrum salicaria*) in Central New York State

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Abstract

More than a decade has passed since the biological control agents *Galerucella pusilla* and *G. calmariensis* (Chrysomelidae) were introduced into North America for biological control of the wetland weed purple loosestrife (*Lythrum salicaria*). This study provides an assessment of impact of these beetles at 36 sites in Central New York where they were released in 1994. Measurements of stand area, plant density, and plant height were made at the time of release and again in 2004. Plant heights were found to be significantly reduced, but there were no changes in stand area or plant densities, even when the presence or absence of beetles was included as a factor. The relative abundances of the two beetle species were also compared between 2004 and the last observation made in 1997. *G. pusilla* was found to be more abundant than *G. calmariensis*, but *G. calmariensis* had increased in relative frequency as compared to the earlier survey. Both species were more likely to be present in sites where larger releases were made in 2004. In addition to the 36 release sites, 22 non-release sites were surveyed for *Galerucella* and their damage. Only 27% of non-release sites were found to be occupied by *Galerucella*. Beetle abundance and damage levels were lower at these sites than at release sites. The results suggest that any regional, population-level decline in purple loosestrife in the Central New York region will require more time before it can be detected and that the biocontrol program could be expedited with human aided dispersal of *Galerucella* to areas not yet occupied.

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1. Introduction

The impacts of introduced biological control agents on target weed populations can be difficult to measure, especially when they are subtle, slow to arise, and spatially sporadic (Crawley, 1989). In such cases, measuring changes in the plant population at a regional scale can require a large number of sites monitored over a long time period. Impacts on individual plants such as plant size or reproductive capacity typically appear early on, while population-level change such as declines in abundance can take much longer, especially for long-lived perennial weeds. Unfortunately, program funding is often cut short or researchers move on to other projects before monitoring is complete. A reasonable alternative to continuous monitoring is to return after a number of years have passed to measure the cumulative change.

This study examines the changes in size and abundance of the invasive wetland plant *Lythrum salicaria* L. (purple loosestrife) at 36 sites in Central New York State where the biological control agents *Galerucella calmariensis* (L.) and *Galerucella pusilla* (Duft.) (leaf beetles) were released 10 years prior. The releases were made as part of a 4-year (1994 through 1997) experiment to test the influence of release size on establishment, the details of which can be found in Grevstad (1999). The releases also served to supply this region, which is heavily infested with purple loosestrife, with agent populations. As part of the original
experiment, the size of each purple loosestrife stand and the density and height of purple loosestrife stems were measured in 1994, the year when agents were released. In 2004, a decade after the Galerucella releases, I returned to all 36 sites to re-survey plant and insect populations. Moreover, I visited 22 non-release sites within the same region to assess occupancy and damage to purple loosestrife by Galerucella.

The two Galerucella beetles are ecologically and behaviorally similar (Blossey, 1995). In New York State, they usually have one generation per year. Adults overwinter in a photoperiod induced diapause, emerging in early May to lay eggs on the leaves. Larvae feed on the leaves and pass through 4 instars before pupating in the soil. The new generation of adults feeds for approximately 2 weeks in late July and early August before entering the leaf litter for the winter.

While the primary objective of this study was to determine the impact that Galerucella spp. have had on purple loosestrife in the Central New York region, a secondary objective was to determine the occurrence and relative abundance of the two Galerucella species in comparison to the last observations at these sites, which were made in 1997. G. pusilla and G. calmaiensis are ecologically and behaviorally similar, making them prone to competitive interactions (Blossey, 1995). The Central New York releases are unique from others across the continent in that both species were released simultaneously at each site using equal numbers of individuals. Most other releases used just one species or uneven mixes of the two (Hight et al., 1995) and monitoring programs usually have not distinguished the two species. With the even starting conditions used in these New York releases, it was possible to determine which species, if any, tends to dominate over time. Also of interest was whether the initial release size had a long-term influence on the biocontrol agent population persistence or impact to purple loosestrife.

In general, biological control programs for weeds take many years, even a decade or longer, to attain the maximum level of control. The purple loosestrife biological control program has already been hailed as a success by some reports with regard to specific sites in North America where substantial declines in purple loosestrife have been observed after only a few years (e.g., Blossey and Skinner, 2000; Lindgren, 2000; Dech and Nosko, 2002; Lindgren, 2003; Landis et al., 2003; Denoth and Myers, 2005). However, in some areas, including parts of the Northeastern United States, the plant is still plentiful in spite of some local successes. This study serves as a quantitative, 10-year assessment of progress for biological control of purple loosestrife at a regional scale in Central New York. The results help to identify future needs and directions for this program.

2. Materials and methods

In May of 1994, Grevstad (1999) released adult stages of both species of Galerucella into each of 36 release sites throughout the Hudson River, Mohawk River, Oneida Lake, Syracuse, and Binghamton areas of New York State (Fig. 1). Four release sizes of 20, 60, 180, and 540 individuals were randomly assigned to sites within each of 9 regional blocks. Both species were simultaneously released at each site using the same release number of for each species. The release sites each contained an isolated, well-defined patch of purple loosestrife (rather than a sprawling expanse), with the exception that two sites contained continuous linear arrangements of purple loosestrife along a canal. During the summer of 1994, the area of each purple loosestrife stand, stem densities, and end-of-season plant heights were measured. These site characteristics were used in the original study as possible covariates of beetle performance. Each release site was at a distance of at least 10 km from any other release site. The beetle populations were followed for three full generations with the last survey of the original study taking place in late May 1997. Out of 36 releases of each species, 21 G. pusilla and 12 G. calmaiensis populations persisted into the fourth year (Grevstad, 1999).

These 1994 Galerucella releases were the first in the eastern-central region of New York State. Other early releases in or near New York State include the Tonawanda Wildlife Management Area in northeastern New York (Genesee County) in 1992, Philadelphia, Pennsylvania in 1992 (Hight et al., 1995), Howland Island Wildlife Management Area (Cayuga County, NY) in 1994 (Grevstad, 1998), and Ithaca, NY area (Tompkins County) beginning in 1994 (e.g., Grevstad and Herzig, 1997).

In late July of 2004, 10 years and 2 months after release of Galerucella spp. and 7 years after last surveying the beetle populations, I returned to all 36 sites. At each site, I surveyed for the two beetle species and measured stand area, stem heights, and stem densities. To quantify beetle abundance, I used 10-min searches, noting the number of adults of each species found during the period. Timed searches have been shown to accurately measure relative densities of Galerucella spp. on purple loosestrife and have been recommended for monitoring (Blossey and Skinner, 2000; Lindgren, 2003). The approach is especially appropriate in late season when complete direct counts on the large, bushy plants are difficult. The method and time of year of these beetle surveys differed from those made in 1995–1997. The earlier surveys were made in late May, when plants were small and complete direct counts were possible. Because of this difference, direct comparisons of beetle abundance within sites between 1997 and 2004 are not appropriate. Rather, a comparison was made for presence/absence and the abundance of each species relative to the other for each site.

Plant measurements were made at approximately the same time of year and using the same methodology used 10 years before (Grevstad, 1999). Stand area was determined by approximating the shape of the stand with a polygon and measuring its dimensions. For height measurements, 20 stems were selected at random along a transect bisecting the stand by blindly pointing a stick at the ground at each
of 20 equal intervals along the transect and choosing the nearest stem. Stem heights were measured from the ground to the highest point on the stem including the inflorescence, if present. Stem densities were measured in five 1-m² quadrats that were evenly spaced along the same transect. Additionally, I qualitatively recorded the degree of damage visible in each stand as follows: 0, no damage visible; 1, light damage on only some of the plants; 2, most or all plants damaged, but plenty of flowers present and few if any architectural changes such as increased branching; 3, some browning of leaves, few flowers, some architectural changes; 4, some stems entirely browned, very few or no flowers, extensive architectural changes; and 5, mostly dead stems, no flowers.

To determine the extent to which the biocontrol agents had spread beyond the release sites and throughout the landscape, I haphazardly selected 22 additional patches of purple loosestrife (Fig. 1) in which I carried out 10-min searches for Galerucella spp. and assessed damage as above. The easiest way to find purple loosestrife stands at this time of year is to look for the bright purple flowers. However, doing so would bias the sampling against sites that were not flowering because of beetle damage. Instead, sites were selected by the wetland habitats (e.g., the presence of other wetland plants or standing water). Then it was determined if there was purple loosestrife at the site (flowering or not) and if so, the beetle survey was carried out.

During the interim between 1997 and 2004 three release sites were demolished by construction. One was filled and converted into a parking lot, one was bulldozed, and the third was converted into an equestrian center. Measurements of stand area, stem heights, and stem densities were not taken at these sites in 2004 and they were omitted from the analyses for these measures. However, two of these sites still had purple loosestrife on the perimeter of construction and beetle counts were made on these plants.

All statistical analyses were carried out using SPSS version 10.1. Changes in stand area, stem density, and plant height were analyzed using a repeated measures analysis of variance with survey year as the repeated within-site factor and beetle presence a between-site factor. Area measures were log-transformed prior to analysis. The assumption of similar covariance among pairs of measurements is met in this case because there is only one pair of measures (Mauchly’s $W = 1.00$). A significant interaction between survey year and beetle presence would support the hypothesis that changes in plant measures were due to Galerucella. Fisher’s exact test was used to compare occupancy categories between years and between species. The effects of original release size on long-term establishment were analyzed using logistic regression with the inclusion of the blocking design from the original experiment. Each block included 4 releases (one of each treatment) made in the same region on the same day (see Grevstad, 1999). This blocking structure was also used in an analysis of variance to investigate long

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**Fig. 1.** Map of New York State showing locations of release sites where purple loosestrife plants and Galerucella beetles were surveyed and non-release sites where Galerucella beetles were surveyed.
term effects of release size on change in plant measurements.

3. Results

3.1. Beetle presence or absence

Galerucella pusilla was found to be present at 22 of 36 sites and G. calmariensis was found at 10 sites (Table 1). These overall occupancy rates are similar to what were found during surveys in 1997. At that time, 21 sites were occupied by G. pusilla and 12 by G. calmariensis. A total of 23 sites kept the same occupancy status for both Galerucella spp. between surveys, whereas 13 had a change in occupancy. Thus, sites that had beetles in 1997 were more likely than other sites to have beetles in 2004. This tendency was highly significant for G. pusilla (Fisher’s exact $df = 1$, $P = 0.00053$) for which 18 of 21 sites remained occupied, but only marginally so for G. calmariensis (Fisher’s exact $df = 1$, $P = 0.052$), for which 6 of 12 sites remained occupied.

Changes in occupancy were as follows. Four out of 15 sites that had no G. pusilla in 1997 now have a population of this species, and 3 populations that were present in 1997 were not found in 2004. For G. calmariensis, 4 out of 24 sites unoccupied in 1997 now have a population of this species, and 6 of 12 populations that were present in 1997 were not found in this latest survey. It is possible that some populations were present, but not detected. This might happen if densities were low or if the beetles had already entered overwintering sites. As evidence against the latter possibility, in no cases was beetle damage found without also finding at least some adults.

In contrast to results found in 1997, there was no longer a significant spatial correlation between the two species. In 1997, each Galerucella spp. was more likely to be present if the other species was also present (Fisher’s exact test, $df = 1$, $P = 0.0049$). In 2004, the two beetle species assorted independently among sites (Fisher’s exact, $df = 1$, $P = 0.255$).

3.2. Relative abundance of beetles

The number of beetles found in a 10-min period ranged from 0 to 120 for G. pusilla and 0 to 59 for G. calmariensis. The mean (+1 standard error) recorded per site (for sites that had populations) was similar for both species: 17.09 ± 8.60 ± for G. pusilla and 16.00 ± 4.36 for G. calmariensis. Because they occupied more sites, the total number of G. pusilla (485) found at all sites was greater than G. calmariensis (144). However, compared to 1997, the relative abundance of G. calmariensis has increased from 6.5% to 22.9% of the total Galerucella individuals found.

3.3. Plant measures

The sizes of many of the purple loosestrife patches changed during the period from 1994 to 2004, but there was not a consistent pattern to the change. Seven out of 31 sites experienced stand area increase, 11 sites decreased, and 13 sites remained approximately the same (10% change or less). Overall, the average stand area did not differ significantly between 1994 and 2004 (Fig. 2A; Table 2). A lack of interaction between beetle presence and survey year indicates that the presence of beetles did not influence the direction of change. These analyses exclude 3 sites that were demolished by construction and two sites with a continuous linear orientation (area in calculable). At only one site (near Frankfort, NY) did purple loosestrife completely disappear due to apparent natural causes. Before its disappearance, this was a fairly small (185 m² patch with a moderately low stem density 17.4 ± 3.4 stems per m² and diverse vegetation). Beetle abundance at last check (May, 1997) was relatively high (311 beetles found in entire patch) so it is possible that the beetles caused the decline.

The mean stem density also did not change significantly between 1994 and 2004 (Fig. 2B; Table 2). This was true even when beetle presence was included as an interacting factor.

Unlike stand area and stem density, a significant reduction in stem height was found between 1994 and 2004. The overall average stem height declined by 25.8% from 1.45 to 1.07 m and the decline was significantly greater for sites with beetles (significant interaction term) (Table 2). Part of the decline was assumed to be due to year to year differences in growing conditions and the timing at which measures were taken (early August, 1994 vs. late July, 2004). In order to tease apart the magnitude of decline that was due to beetles, the mean difference found for sites not attacked by beetles (24.23 cm) was added to the 2004 measurements and the 1994 heights were compared with the adjusted 2004 heights for sites with beetles (Fig. 2C). The average adjusted change in height for sites with beetles ($N = 9$) was $-20.65 ± 6.99$ cm. This adjustment in the plant height data eliminates the effect of year, but the effects of beetle presence and beetle by year interaction remain identical to those reported with the unadjusted data in Table 2.

3.4. Qualitative assessment of damage and flowering

For all 36 release sites, the mean damage level score was 2.06 ± 0.281 (Fig. 3). For the subset of those sites with beetles present, the mean damage level was 2.92 ± 0.227. All sites with beetles had at least some damage and all sites
with no beetles had zero damage. The highest level (5) of damage was found at only one release site.

Flowering frequency was not quantified in 2004 because it was not quantified in 1994. However, reduced flowering frequency is one of the consistent and obvious results of beetle feeding. Sites with damage levels of 4 or above had essentially no flowers and sites with damage levels of 3 had very few flowers. Thus, nearly half of the sites with beetles exhibited substantial or complete reduction in flowering (those scoring 3, 4, or 5).

Table 2
Results of repeated measures analysis of variance for effects of survey year, presence of Gallerucella spp., and their interaction on three plant responses: stand area, stem density, and stem height

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
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<tr>
<td><strong>Area</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year (within site)</td>
<td>1</td>
<td>0.536</td>
<td>1.947</td>
<td>0.174</td>
</tr>
<tr>
<td>Beetle presence</td>
<td>1</td>
<td>3.925</td>
<td>1.866</td>
<td>0.183</td>
</tr>
<tr>
<td>Year x beetle presence</td>
<td>1</td>
<td>0.164</td>
<td>0.596</td>
<td>0.447</td>
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<tr>
<td><strong>Density</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year (within site)</td>
<td>1</td>
<td>220.462</td>
<td>1.715</td>
<td>0.200</td>
</tr>
<tr>
<td>Beetle presence</td>
<td>1</td>
<td>158.397</td>
<td>0.664</td>
<td>0.422</td>
</tr>
<tr>
<td>Year x beetle presence</td>
<td>1</td>
<td>23.587</td>
<td>0.184</td>
<td>0.671</td>
</tr>
<tr>
<td><strong>Height</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year (within site)</td>
<td>1</td>
<td>13144</td>
<td>21.616</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Beetle presence</td>
<td>1</td>
<td>6874.25</td>
<td>5.161</td>
<td>0.030</td>
</tr>
<tr>
<td>Year x beetle presence</td>
<td>1</td>
<td>3126.24</td>
<td>5.141</td>
<td>0.031</td>
</tr>
</tbody>
</table>

Fig. 2. Mean plant measurements taken in 1994 and 2004 at 36 sites throughout Central New York State. Sites with and without Gallerucella leaf beetles are summarized separately in each graph. Open circles, beetles absent; solid circles, beetles present. (A) Area of the purple loosestrife stand; (B) purple loosestrife stem densities; and (C) stem heights. Error bars represent one standard error. The height measures depicted are standardized for year to year difference that was not due to beetles (see text).

Fig. 3. Histogram of the frequency of sites in each damage class, for (A) 33 release sites (excludes 3 sites destroyed by construction) and (B) 22 sites where beetles were not released.
3.5. Beetles and damage at non-release sites

Galerucella spp. adults were found at only 6 of the 22 haphazardly selected survey locations away from the points of release. Two sites had G. californiensis only, 2 sites had G. pusilla only, and 2 sites had both species. At a seventh site, only eggs were found (species undeterminable). Where beetles were present, they were approximately half as abundant as they were at release sites, the average being 8.00 ± 3.34 G. pusilla and 8.00 ± 1.22 G. californiensis found in a 10 min period.

Damage levels at these non-release sites were lower on average than at the release sites (Fig. 3). The average score was 0.682 ± 0.274 for all non-release sites (N = 22) and 2.33 ± 0.615 (N = 6) for non-release sites with beetles. The site with the highest level of damage (a score of 5) was a large marsh south of Athens, New York, which had high plant diversity. It was later learned that releases of Galerucella had been made directly into this marsh (B. Blomsey, Cornell University, personal communication).

3.6. Long-term effects of initial release size on establishment and plant impact

A significant effect of initial release size on population persistence, first reported in 1997, was still apparent in 2004 (Tables 3 and 4). Populations of both G. pusilla and G. californiensis were more likely to be present at sites where larger releases were made. The log of the odds ratio (establish/fail) increased by an estimated 0.007 ± 0.003 for each additional G. pusilla and 0.008 ± 0.003 for each additional G. californiensis introduced (Table 4).

Table 3
Number of populations of Galerucella pusilla and G. californiensis established from each of 4 sizes of releases made in 1994

<table>
<thead>
<tr>
<th>Release size</th>
<th>Number of established populations in 2004</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>G. pusilla</td>
</tr>
<tr>
<td>20</td>
<td>5</td>
</tr>
<tr>
<td>60</td>
<td>4</td>
</tr>
<tr>
<td>180</td>
<td>5</td>
</tr>
<tr>
<td>540</td>
<td>8</td>
</tr>
</tbody>
</table>

A total of 9 releases were made for each release size.

Table 4
Results of logistic regression analysis for effects of release size on long-term establishment of Galerucella populations

<table>
<thead>
<tr>
<th>Source</th>
<th>B</th>
<th>SE</th>
<th>Wald $\chi^2$</th>
<th>$df$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>G. pusilla</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Release size</td>
<td>0.007</td>
<td>0.003</td>
<td>4.87</td>
<td>1</td>
<td>0.027</td>
</tr>
<tr>
<td>Block</td>
<td></td>
<td></td>
<td>3.71</td>
<td>8</td>
<td>0.882</td>
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<tr>
<td>Constant</td>
<td>−2.79</td>
<td>1.68</td>
<td>2.75</td>
<td>1</td>
<td>0.097</td>
</tr>
<tr>
<td>G. californiensis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Release size</td>
<td>0.008</td>
<td>0.003</td>
<td>7.29</td>
<td>1</td>
<td>0.007</td>
</tr>
<tr>
<td>Block</td>
<td></td>
<td></td>
<td>2.56</td>
<td>8</td>
<td>0.96</td>
</tr>
<tr>
<td>Constant</td>
<td>−3.361</td>
<td>1.887</td>
<td>3.171</td>
<td>1</td>
<td>0.075</td>
</tr>
</tbody>
</table>

The analysis included the blocking structure (by region and release date) from the original experimental design (Grevstad, 1999).

The significant effect of release size on establishment, in combination with the above reported effect of beetle presence on plant height, suggests a possible long-term effect of release size on plant impact. However, this was not the case. Within-site differences in plant height, stem density statistically and stand area were not significantly affected by the release size used in 1994 (Table 5).

4. Discussion

Surveys of 36 purple loosestrife stands in Central New York before and after 10 years of exposure to Galerucella spp. revealed significant impacts at the level of individual plants but not at the population level. Plants were found to be shorter on average, especially in sites with beetles present, and they sustained various levels of current beetle damage. However, no change was found in overall plant density or in the size of the purple loosestrife stands. This was true even when the presence or absence of Galerucella populations was taken into account. Some of the sites surveyed probably did experience declines in stem densities due to the beetles, but these declines were countered by sites that had increasing stem densities. Thus there was no net reduction at the regional scale.

These results are consistent with other published studies on the impacts of Galerucella on purple loosestrife. Impacts to individual plants in the form of reduced plant height and flowering rates are frequently reported (e.g., Lindgren, 2003; Denoth and Myers, 2005; Blomsey and Skinner, 2000; Landis et al., 2003), but measured declines in plant abundance are limited to sporadic cases. For example, Landis et al. (2003) found significant declines in stem density in only one of 8 sites in Michigan where stem densities were measured over a 6-year period. Similarly, Denoth and Myers (2005) measured declines in 1 of 6 sites over a 4 year period in Coastal British Columbia. In these studies, the impacts were assessed separately for each site. Because purple loosestrife may be expanding at some sites while being controlled at others, conclusions about regional impacts cannot be drawn from isolated examples of local success. To date, no studies have presented landscape-level declines in abundance of purple loosestrife by analyzing the collective changes in many sites at once.
Several factors may contribute to a lack of impact at the population level. First, 10 years may not be long enough. Purple loosestrife is a long-lived perennial with a large capacity for storing energy in its bulky roots and crown. A plant must be completely defoliated many times before death occurs. Katovich et al. (1999) found that even after two years of near complete defoliation by high densities of caged Galerucella spp., an average of 31.6 and 49.9% (in two separate trials) of the root crown biomass still remained in comparison to undamaged controls.

Second, densities of Galerucella may not be high enough. At most of the sites surveyed in Central New York, Galerucella did not cause complete defoliation. Many sites were found to be unoccupied by Galerucella and those that were occupied sustained sub-maximal levels of feeding damage. Of the 58 sites surveyed (release sites and non-release sites), only two exhibited Galerucella damage at the highest possible level, in which the plants were nearly completely defoliated. Other studies suggest that densities of Galerucella may be limited by predation (Nechols et al., 1996; Wiebe and Obrzycki, 2002; Hunt-Joshi et al., 2005).

Third, year to year or seasonal variation in beetle abundance may limit impacts. Some beetle populations that were present in 1997 were not detected in 2004 and other populations appeared at sites where they were previously undetected. During years when the beetles are absent or low, purple loosestrife could recover lost energy stores and recruit new seedlings. The plants also experience a seasonal refuge from herbivory each year in late summer. In most North American locations, Galerucella adults diapause in early August after completing just one generation. This allows plants to recover for approximately 2 months without herbivory.

Even if the density of purple loosestrife has not (yet) declined, a reduction in the size and flowering of individual plants may be already reducing its environmental impacts. Shorter plants are likely to be less competitive, allowing a more diverse plant community to intermix with purple loosestrife. Hunt-Joshi et al. (2004) found that purple loosestrife plants damaged by Galerucella allowed greater light penetration of the canopy and this in turn allowed neighboring native plants to grow larger than they did in the presence of healthy purple loosestrife. Reduction in flowering is likely to result in reduced local recruitment and reduced spread to new areas. Over a longer time scale, it may contribute to population-level declines. Another benefit of reduced flowering is that it will prevent purple loosestrife from competing with native plants for pollinator services. Brown et al. (2002) found that the abundant and showy flowers of L. salicaria attracted pollinators away from the native L. alatum (winged loosestrife) reducing seed set in this plant. Moreover, when L. salicaria grows intermixed with L. alatum, pollinators deliver a mix of the two pollens to L. alatum and this also contributed to lower seed set (Brown and Mitchell, 2001). Other native plant species may be affected in this way as well.

Surveys for Galerucella away from release sites revealed limited spread of beetles to new areas. Site occupation rates were surprisingly low given the amount of time passed and the proximity of sampled sites to successful releases. In a previous study, G. calmaniensis individuals were found capable of dispersing 847 m over a period of a few days to colonize an isolated host patch (Grevstad and Herzig, 1997). But this was in a situation where beetles were released at that distance from the nearest patch of their host. It may be that Galerucella spp. are not prone to dispersing if their host plant is locally plentiful. Within contiguous stands of purple loosestrife, published rates of spread are slow. For example, in Ontario, populations of G. calmaniensis spread just 26.5 m through a contiguous stand in 3 years and G. pusilla spread only 8.5 m in 3 years (Dech and Nosko, 2002). Initial spread rates were similar in a Virginia population (McAvoy et al., 1997). Moreover, when Galerucella spp. do disperse, they have a strong propensity for colonizing sites already occupied by conspecifics and congeners (Grevstad and Herzig, 1997; Grevstad, 1998) and this may limit the rate at which new sites are colonized.

Galerucella pusilla occurred at more sites and was more abundant than G. calmaniensis suggesting that this species has played a larger role in impacting purple loosestrife in this region. However, since the 1997 survey, the frequency of G. calmaniensis increased from 6.5 to 23% of the total beetles counted. Outside of the original releases, G. calmaniensis occupies the same number of sites and occurs at equal abundance to G. pusilla. Thus, the relative importance of the two beetles may be changing with time. Galerucella calmaniensis is known to disperse more than G. pusilla (Grevstad, 1998; Dech and Nosko, 2002) and has been observed to be the first to colonize outlying host patches when spreading into new areas (E. Coombs, Oregon Department of Agriculture). The ability of an agent to colonize outlying patches can be crucial to the success of biocontrol programs (Isaacs et al., 1996). Thus, it is difficult to conclude whether one or the other species is most important for long term control. It is possible that both species will remain compatible cohabiters as is the case in their native range (Blossey, 1995).

Given that a decade has passed with limited beetle dispersal and minimal impacts on the plant population, actions to increase effectiveness of the biocontrol program are warranted. The results of this study suggest that the regional impact could be improved by releasing Galerucella into more locations. The insects could be easily collected in large numbers from established populations and re-released across the landscape at intervals of a few kilometers or so. Previous work has shown that release sizes of 500 are suitable to achieve a high probability of establishment (Grevstad, 1999). Another approach is to release a potentially complementary biocontrol agent, the root weevil Hylobius transversovittatus Goze, into sites with Galerucella. The larvae of H. transversovittatus feed on the root mass that remains after defoliation by Galerucella. While availability of this insect was limited early in the program, it is
becoming more available with advances in rearing technology and expanding field populations (Piper et al., 2004). In the near term, these actions will result in more widespread reductions in plant vigor and flowering. In the long term, they will expedite any future population-level impacts.

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