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Evaluation of the field impact of an adventitious herbivore on an invasive plant, yellow toadflax, in Colorado, USA

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Abstract Although some introduced plants arrive into their new range without their generalist and specialist herbivores, for others, their herbivores arrive prior to, with, or after the introduction of the plant, reestablishing the link between natural enemies and invaders in the introduced range. Research documenting the effects of adventitiously introduced herbivores on their target plants in the introduced range, and the mechanisms by which those effects occur, can provide insight into potential biological weed control. We studied the effects of an accidentally introduced beetle *Brachypterolus pulicarius* on the growth and reproduction of its host, the invasive plant *Linaria vulgaris* (yellow toadflax), growing under field conditions across multiple years and sites in western Colorado, USA. We found that feeding by *B. pulicarius* on *L. vulgaris* was variable among 3 years (2002–2004) and across eight local sites. Part of the variation in damage was explained by ramet density; sites with greater ramet density experienced a higher proportion of damage. In an observational study across 2 years, damage was positively correlated with estimates of sexual reproduction, ramet growth, and clonal shoot production. However, opposite trends were observed in an experiment; damage by *B. pulicarius* decreased estimates of sexual reproduction. Differences between the results of the observational and experimental studies were likely driven by selective feeding by *B. pulicarius* on larger ramets. Nonetheless, the ability of *B. pulicarius* to control established *L. vulgaris* population growth remains uncertain under the environmental conditions we studied. In both the observational and experimental study, *B. pulicarius* did not affect *L. vulgaris* survival, and we found no evidence that established *L. vulgaris* populations were seed limited, suggesting that reductions in seeds may not translate into demographic changes in heavily infested populations. Interactions among insect foraging behavior, individual plant responses to damage, and the demographic consequences of seed input may help to explain the varying degrees to which herbivores affect plants and populations in this and other systems.

Keywords Biological Control · *Brachypterolus pulicarius* · Herbivory · Insect behavior · Invasive · *Linaria vulgaris*

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Introduction

Herbivores consume as much as 18% of terrestrial plant biomass (Cyr and Pace 1993), and in some natural systems, herbivory can regulate primary productivity, plant reproductive success, and plant population dynamics (reviewed in Crawley 1989; Marquis 1992; Danell and Bergström 2002). The top-down control of plants by herbivores is the supposition upon which biological control of invasive plants is based. Classical biological control (hereafter biocontrol) assumes that invasive plants are successful because they have escaped natural enemies from their native range (e.g., Elton 1958; Keane and Crawley 2002) and that the addition of one or more of these natural enemies will regulate or decrease their population growth in the invaded range (Wilson and McCaffrey 1999). Many non-native plants, however, do not arrive to their introduced range alone. Instead, both generalist and coevolved specialist herbivores of non-native plants are also often introduced accidentally prior to, with, or after their plant hosts, reestablishing the link between natural enemies and invaders in the introduced range. Research documenting the effects of adventitiously introduced herbivores on their target plants in the introduced range, and the mechanisms by which those effects occur, can provide insight into how particular herbivores or modes of feeding influence potential biological weed control. Such efficacy assessment of types of herbivores or modes of feeding on plants in the introduced range may help screen out ineffective potential classical biocontrol agents prior to introduction (McClay and Balciunas 2005).

A major challenge in the study of plant ecology is assessing if and how herbivores affect plant populations. For example, although studies have documented that herbivores, including some biocontrol agents, can decrease individual plant survival, growth, and reproduction in greenhouse and field conditions (e.g., James et al. 1992; McClay 1992; Grubb et al. 2002), reductions in individual components of plant performance may not translate into population-level effects (Maron and Crone 2006). Most studies assume a positive correlation between seed production and offspring recruitment. Such a positive link may be realized in some natural systems (Louda and Potvin 1995; Maron et al. 2002), but not others (Crawley and Nachapong 1985; Eriksson and Ehrlén 1992). A diversity of factors, including limited safe sites for seedling germination, can override seed numbers in determining population size. Detailed demographic studies of plant invasions are accumulating and provide predictive insight into the conditions under which invasion is mostly likely to occur (Parker 2000; Shea et al. 2005) and the life-history stages and transitions to target by biocontrol (Koop and Horvitz 2005; Davis et al. 2006). As a complement to demographic studies, field data linking observations and manipulations of adventitiously introduced herbivores with plant and population responses may provide a means to evaluate the efficacy of potential types of biocontrol agents and, more generally, the ecological conditions that determine the difference between successful and failed biocontrol.

The objective of this study was to assess the degree to which the accidentally introduced beetle *Brachypterolus pulicarius* L. (Coleoptera: Kateretidae) affected the growth and reproduction of its host plant, the invasive rangeland weed *Linaria vulgaris* Mill. (Scrophulariaceae), growing under field conditions across multiple years and sites in the introduced range. The interaction between *B. pulicarius* and *L. vulgaris* provides a good system for investigating the success of an accidentally introduced herbivore on its host plant: *L. vulgaris* shares common characteristics with other exotic weeds (it reproduces by seed and clonal growth and invades a variety of habitat types), the population biology of *B. pulicarius* and *L. vulgaris* are well described (Harris 1961; Saner et al. 1995), and *L. vulgaris* has economic impacts in the western USA (Lajeunesse 1999). We addressed four questions. (1) To what degree does herbivory by adult *B. pulicarius* on *L. vulgaris* vary among years and sites? We focused on local site variation in damage by adult *B. pulicarius* on *L. vulgaris* and assessed the relationships between local site characteristics and damage levels over 3 years. (2) What are the plant reproductive consequences of *B. pulicarius* herbivory on *L. vulgaris* ramets? We used an observational study with natural damage and an experiment in which we added *B. pulicarius* to plants in a common garden. Finding that the observations and experiments yielded different results, we asked (3) whether the differences might be driven by selective feeding by *B. pulicarius* on larger ramets. Selective feeding by herbivores on larger plants is

a common phenomenon (e.g., Bullock et al. 1994; Gómez 2003; Louda et al. 2005; Rose et al. 2005) and may be a general mechanism driving ambiguity in the effects of natural enemies on target weeds. Finally, because *B. pulicarius* affected estimates of sexual reproduction and not mortality of *L. vulgaris*, we asked: (4) Does variation in seed input into established populations of *L. vulgaris* affect seedling recruitment? By combining observations and experiments with an exploration of mechanism and seedling recruitment, this study provides a comprehensive analysis of the effects of an adventitiously introduced herbivore on weed performance in the introduced range.

Methods

Study system

We studied *L. vulgaris* and *B. pulicarius* in subalpine meadows in the West Elk Mountains of Colorado near the Rocky Mountain Biological Laboratory (RMBL), Gothic, Gunnison County, CO, USA.

Linaria vulgaris was introduced into North America from southeastern Europe and southwestern Asia at least 300 years ago (Saner et al. 1995) and is now considered a noxious pest in natural areas and rangelands throughout western North America. *Linaria vulgaris* is a rhizomatous perennial, reproducing sexually as an obligate outcrosser (Arnold 1982), and is common in disturbed open habitats (Lajeunesse 1999; Pauchard et al. 2003). Single clonal stalks (hereafter referred to as ramets) produce (mean ± 1 SE) 26.8 ± 2.6 yellow, zygomorphic, typically bee-pollinated flowers over 3–6 weeks in mid-summer (early July to early September; R. E. Irwin, unpublished data). Individual flowers are hermaphroditic and bloom for ~4 days (Arnold 1982). Ramets vary in the number of seeds they produce, ranging from 0 to 6,000 seeds per year, and genets can produce up to 30,000 seeds annually (reviewed in Saner et al. 1995). The majority of seeds fall within 0.5 m of the parent plant (Nadeau and King 1991). Seed viability can be as low as 40% (Nadeau and King 1991), and seeds can remain dormant in the soil for a number of years prior to germination (Carder 1963). Along with reproduction by seed, *L. vulgaris* also reproduces vegetatively by producing adventitious shoots from both the main and lateral roots. The shoots (ramets) die back at the end of each growing season, and the root system sends up new ramets each spring. Plants in their second year of growth can produce as many as 250 ramets through vegetative reproduction (reviewed in Saner et al. 1995). Around the RMBL, infestations of *L. vulgaris* range from 109 to 428 ramets m^{-2} with a mean ± 1 SE across 18 sites of 239 ± 97 ramets m^{-2} (R. E. Irwin, unpublished data).

A number of natural enemies have been inadvertently or intentionally released to control *L. vulgaris* (Saner et al. 1995), including the beetle *B. pulicarius*, which is common in *L. vulgaris* infestations around the RMBL. *Brachypterolus pulicarius* was accidentally introduced into North America in the early 1900s and subsequently spread via natural and human-mediated dispersal (reviewed in Sing et al. 2005). Adults are black, oval beetles, 2.2- to 2.6-mm long and 1.0- to 1.2-mm wide; larvae are 1- to 4-mm long (Hervey 1927). Adults emerge from the soil in late spring and feed on *L. vulgaris* ramets, boring into the vascular tissue just beneath the apical buds, causing stooling (stunted growth). Adults also feed on buds and flowers later in the season. The adults mate in late June, and females lay eggs inside *L. vulgaris* flowers. Larvae primarily feed on *L. vulgaris* pollen, anthers, ovaries, and developing fruits. In mid-August, larvae drop to the soil to pupate, and *B. pulicarius* overwinter as pupae or adults (Hervey 1927; Harris 1961). *Brachypterolus pulicarius* is likely to be univoltine across most of its distribution in North America (McClay 1992). In several field studies, the presence of *B. pulicarius* has been correlated with reduced seed production and rates of spread of *L. vulgaris* in Alberta and Saskatchewan, Canada (Harris 1961; Darwent et al. 1975; Nadeau and King 1991). In Alberta, damage by *B. pulicarius* on potted *L. vulgaris* delayed flowering and reduced viable seed production by 74% (McClay 1992). In greenhouse and field studies in Montana, USA, using *L. genistifolia* ssp. *dalmatica* (a closely related species), feeding by *B. pulicarius* decreased plant height and reduced branching and seed production by up to 95% (Grubb et al. 2002). Here, we focused on the effects of *B. pulicarius* on established populations of *L. vulgaris* in the West Elk Mountains of Colorado, where establishment and spread of this invasive plant into wilderness areas have been of recent concern (Sutton et al. 2007).

Field methods

To what degree does damage by adult B. pulicarius *on* L. vulgaris *vary among years and sites?*

From 2002 to 2004, we conducted field censuses of *B. pulicarius* damage to *L. vulgaris* ramets in eight sites located in and around the RMBL (Appendix 1). At the beginning of the growing season, we haphazardly ran a 7-m transect through each site. For the 2002 and 2004 censuses, 90–100 ramets were randomly selected and marked at ~0.1-m intervals along the transect in each site. In 2003, 25–50 ramets were marked in each site along the transects at 0.14–0.28-m intervals. We focused on *L. vulgaris* ramets because ramets are extensively connected underground, and it was not possible to identify genets in the field. Ramet dynamics have been successfully compared to genet dynamics in other systems (e.g., Caswell 1985; but see Munzbergova et al. 2005). Moreover, an experimental and ^{13}C-labelling study suggests that there is competition for resources within *L. vulgaris* genets, and undamaged ramets may not direct resources toward damaged ramets (Hellström et al. 2006).

To examine variation in *B. pulicarius* damage among years and sites, we measured shoot damage by adult *B. pulicarius*. Shoot-boring scars of adult *B. pulicarius* are distinctive, and damaged ramets exhibit a conspicuous hole near the top of the plant along with dried, chewed shoot tissue. Focal ramets were not extensively damaged by other natural enemies (Appendix 2). Ramets were censused for damage by *B. pulicarius* weekly in 2002 and monthly in 2003 and 2004 and were assigned a value of damaged or not damaged. Once a ramet experienced stem boring by *B. pulicarius*, it was considered damaged for the rest of the season. Because adults bore into the vascular tissue, the severity of damage was hidden within the shoot, and there was no meaningful way to record the magnitude of damage without destroying the ramet. We also counted eggs and larvae of *B. pulicarius* inside flowers during the damage surveys. However, because both the eggs and larvae are small and difficult to find, we had few instances of observed larval presence or damage (data not shown). Therefore, the estimates of *B. pulicarius* damage reported here should be viewed as conservative estimates that only reflect stem boring by adults and do not incorporate larval or adult florivory.

We hypothesized that ramet density may be important in affecting site and ramet probability of damage by *B. pulicarius*. We measured the density of ramets at 1-m intervals along each transect using a 625-cm^2 quadrat. Each year, we calculated average ramet density per site.

Data analyses. Variation in damage among years and sites was analyzed using an ANCOVA with year as a fixed factor, site as a random factor (here and in univariate analyses below), ramet density as a covariate, and proportion of ramets damaged in each site as the response variable. We also tested whether damage levels were correlated between sites and across years using correlation.

What are the plant reproductive consequences of B. pulicarius *damage to* L. vulgaris *ramets?*

Observational study. We measured the reproductive consequences of *B. pulicarius* damage to the marked *L. vulgaris* ramets in the 2002 and 2003 damage surveys. As a covariate, we measured initial ramet height to the nearest 0.1 cm as an estimate of initial ramet size in mid- to late-June, a time in the season generally before *B. pulicarius* damage occurs. To estimate ramet performance, we measured survival and whether or not surviving ramets flowered. On all surviving ramets, we counted the number of branches. Once ramets senesced, above-ground ramet biomass was collected, dried at 60°C, and weighed to the nearest 0.01 g. In 2002, we collected above-ground ramet biomass from four sites (Appendix 1), and in 2003, from all sites. In 2002, we also dug the ramets up in the same four sites in which we estimated above-ground biomass and counted the number of new stalks emerging from the focal root mass as an estimate of clonal growth.

For ramets that flowered, we collected mature fruits in early September. Capsules were classified as expanded (seed-bearing) or aborted. Proportion fruit set was calculated as the number of expanded fruits divided by the number of expanded plus aborted capsules. We used seed weight to estimate number of seeds per fruit. We counted and weighed a subsample of seeds from each site, and these data were used to estimate seed number from seed weight.

Data analyses. We tested the effect of damage (yes, no), year, site, and their interactions on survival and whether or not ramets flowered using nominal

logistic regression. For each response variable, we tested the relative fit of multiple hierarchical models (with main effects and one or more interaction terms) to the main (saturated) model with all main effects and interaction terms using goodness-of-fit (Hosmer and Lemeshow 1989).

For ramets that survived and flowered, we tested whether *B. pulicarius* damage was associated with *L. vulgaris* sexual reproduction using a MANCOVA with damage (yes, no), year, and site as factors; initial ramet height as a covariate; and number of flowers produced (square-root transformed), proportion fruit set (arcsine square-root transformed), and mean seeds per fruit (square-root transformed) as response variables. Ramet height in June is positively correlated with root-stalk diameter ($r = 0.59$, $n = 470$ ramets, $P < 0.0001$) and final ramet size (see "Results"). By including the covariate, we could tease apart the potential variation in plant reproduction caused by initial ramet size from potential variation caused by *B. pulicarius* damage. We only included data from sites in which we had response variables measured for both damaged and undamaged ramets; thus, we excluded two sites in 2002 and four sites in 2003. We did not have measures of sexual reproduction for damaged and undamaged plants from some site–year combinations because, for example, some sites did not receive damage or undamaged plants did not flower. Because we had to exclude some sites, we could not include interactions among site and any other factor due to the unbalanced design. A significant MANCOVA was followed by univariate ANCOVAs (Scheiner 1993; Rencher 1995).

To assess whether *B. pulicarius* damage was associated with final ramet size (both flowering and non-flowering ramets), we used a MANCOVA as above and number of branches (square-root transformed) and above-ground ramet biomass (square-root transformed) as response variables. We only included data from sites in which we collected measures of final ramet size on both damaged and undamaged ramets. We had to exclude two sites in 2003 because one site did not receive damage and one site was buried by an early snowfall. Finally, to assess how *B. pulicarius* damage influenced the number of new clonal ramets (square-root transformed) in 2002, we used an ANCOVA with damage and site as factors and initial ramet height as a covariate.

Experimental garden. We used an experimental garden at the RMBL in 2003 in which we assigned *L. vulgaris* to damaged and undamaged cage treatments. From the five *L. vulgaris* sites located in the RMBL town site (Appendix 1), 80 undamaged single-stalked ramets were transplanted individually into 10-cm^2 peat pots (Griffin, Tewksbury, MA) in early summer. Ramets were watered with a root stimulator (Green Light, San Antonio, TX) on the first 2 days following transplant and subsequently with a 20:20:20 NPK fertilizer (Alaska Fish Fertilizer Co., Renton, WA) as needed.

Each ramet was randomly assigned to one of two caging treatments: undamaged control (no *B. pulicarius* damage) or *B. pulicarius* damage. We used five replicate cages per treatment; each cage had eight *L. vulgaris* ramets in separate pots. Cages were 90 cm × 50 cm × 50 cm, covered with netting (ca. 246 holes cm^{-2}), and arranged in the garden ca. 1 m apart. Treatment cages within the garden were assigned randomly. The pots were sunk into the ground and covered with the cages by 16 July, 2003, and we measured initial ramet height (to the nearest 0.1 cm) and stem diameter (at the base of the plant to the nearest millimeter). Ramets in the undamaged and damage treatments did not differ significantly in initial ramet size (MANOVA: $\lambda = 0.53$, $F_{2,7} = 1.84$, $P = 0.23$). We wrapped the pots in agricultural cloth to deter *L. vulgaris* root growth into the surrounding environment.

In mid-July, we released 80 unsexed beetles into each damage cage. We then censused the cages for *B. pulicarius* adults and larvae once per week for 6 weeks. *Brachypterolus pulicarius* ranged from 0 to 20 individuals per ramet on any given census date, with a mean (±1 SE) of 0.7 ± 0.2 individuals per ramet (0–3 individuals per ramet in the 10th to 90th quantiles). The adults likely moved among ramets within cages as the counts per ramet varied among census periods. It is likely that some *B. pulicarius* also died or escaped from the cages because we never found all 80 beetles in a cage in a census period. The number of *B. pulicarius* per ramet observed in the censuses was similar to numbers found in the field. For example, in 2004, we observed a range of 0–17 beetles per ramet in the field with a mean number of beetles per ramet under one (0–1 individuals per ramet in the 10th to 90th quantiles). In the undamaged cages, no beetles were added, and in no census did we find *B. pulicarius* adults or larvae or evidence of damage.

Because *L. vulgaris* are self-incompatible, we had to ensure that ramets were outcrossed for fruit production. Thus, when at least one ramet in a cage came into flower, twice per week for 2 h, we introduced two legitimately pollinating *Bombus* spp. into the cages along with four recently picked, flowering ramets of *L. vulgaris* but with no adult or larval *B. pulicarius*.

To estimate the consequences of *B. pulicarius* damage to *L. vulgaris*, we recorded the proportion of surviving ramets in each cage. To estimate sexual ramet reproduction, we measured the proportion of surviving ramets that flowered and that produced expanded fruits. In addition, on all surviving ramets, we counted the number of branches produced per stalk and measured final ramet height to the nearest 0.1 cm at the time of plant senescence. Once ramets senesced, we dug the ramets up and counted the number of new stalks emerging from the root mass as an estimate of clonal growth. We counted the number of stalks that had emerged above ground and that were photosynethically active as well as those that were still below ground. Above- and below-ground plant biomass were collected, dried at 60°C, and weighed to the nearest 0.01 g.

Although we watered and fertilized ramets in the garden twice weekly, some ramets died, likely due to transplant shock. Thus, our experiment should be viewed as testing the effects of *B. pulicarius* on *L. vulgaris* under stressed conditions (Heinrichs 1988) and may overestimate the effects of *B. pulicarius* damage to more healthy *L. vulgaris*.

Data analyses. To test how *B. pulicarius* affected *L. vulgaris* sexual reproduction, we used a MANOVA with treatment (undamaged or damaged) as a fixed effect and proportion of ramets that flowered and set fruit as responses (both arcsine square-root transformed). To test how *B. pulicarius* affected ramet growth and clonal reproduction, we used a MANOVA with final ramet height, number of branches, above- and below-ground ramet biomass, and number of new clonal ramets (above and below ground) as responses. Cage was the unit of replication.

Does ramet height influence the probability of damage by B. pulicarius*?*

Because we found that the observational and experimental studies of the effects of *B. pulicarius* on *L. vulgaris* yielded different results (see "Results"), we explored whether the differences might be driven by selective feeding by adult *B. pulicarius* on *L. vulgaris*. We hypothesized that initial ramet height (a proxy for ramet size, see "Results") may affect the probability of damage by *B. pulicarius*. We used data from the observational study in 2002 and 2003 (see "What are the plant reproductive consequences of *B. pulicarius* damage to *L. vulgaris* ramets?") and with multiple logistic regression assessed the degree to which ramet height influenced whether or not a ramet was damaged. One site was excluded in 2003 because there was no damage by adult *B. pulicarius* in that site–year combination. We performed separate analyses for each site–year combination because we were most interested in assessing the selective feeding behavior of *B. pulicarius* within sites and thus wanted to avoid the confounding influence of correlations between height and damage across sites, rather than among ramets within sites (the relevant hypothesis). We did not apply the sequential Bonferroni correction to significance levels because the correction inflates Type II error rate (Moran 2003; Gotelli and Ellison 2004).

Does variation in seed input into established L. vulgaris *sites affect seedling numbers?*

To explore the potential population-level consequences of *B. pulicarius* effects on *L. vulgaris* sexual reproduction, over the course of 3 years (2003–2005) in 10 plots, we estimated the number of seeds naturally input, the number of seeds germinating, and seedling survival. The plots were each 625 cm^2 and located within established *L. vulgaris* populations in the RMBL town site. The plots were likely connected by gene flow via pollen and ranged in total density (flowering and non-flowering ramets) from 240 to 1,056 ramets m^{-2} in 2003 and 96 to 688 ramets m^{-2} in 2004. To estimate seed input, in early September in 2003 and 2004, we counted the number of ramets per plot that flowered and produced fruits. On up to 10 randomly chosen reproductive ramets per plot, we counted the number of expanding fruits. We then haphazardly chose three reproductive ramets of similar size outside of the plots in 2003 and 10 reproductive ramets in 2004, collected three fruits per ramet, and counted the number of seeds per fruit. We collected fruits from ramets outside the plots because we did not want to remove seed-bearing fruits from within the

plots. We estimated the seed input per plot as: (number of reproductive ramets) × (mean number of expanded fruits per reproductive ramet) × (mean number of seeds per fruit from the fruits taken from outside the plot). One concern with this estimate is that some seeds may have dispersed outside of the plots and some seeds may have dispersed into the plots, although we have no reason to believe that seed immigration and emigration did not balance. Nonetheless, the seed input values should be viewed simply as relative and not exact estimates. To measure seed germination in 2004 and 2005, every 2 weeks throughout the growing season we counted the number of seedlings that emerged in each plot. *Linaria vulgaris* seedlings have distinct, spade-shaped cotyledon leaves. Seedlings were marked with toothpicks, and their survival was assessed every 2 weeks.

Because *L. vulgaris* seeds may also remain dormant in the soil for a number of years prior to germination (Carder 1963), we also estimated short-term seed dormancy. We removed all *L. vulgaris* above-ground biomass from 2000 to 2004 in six plots and from 2001 to 2004 in an additional six plots. The plots were 625 cm^2 each and were located in the RMBL town site and thus likely connected by gene flow via pollen. Ramets were removed by pulling at the base. We also removed all *L. vulgaris* around the plots up to 3 m away. Given that up to 96% of seeds fall within 0.5 m of the parent plant with very few seeds moving further than 1.5 m (Nadeau and King 1991), it is likely that we removed the majority of seeds input into plots over the course of the study. Removing the *L. vulgaris* ramets by pulling at the based likely created disturbance to the soil, which may have increased the likelihood of seed germination by loosening the soil and removing competing congeners. We removed the pulled ramets from the plots to avoid mulching effects. In the plots established in 2001, flowering ramet density ranged from 47 to 85 flowering ramets m^{-2}, and in 2002, 66 to 170 flowering ramets m^{-2}. We did not estimate the number of seeds input prior to pulling because any seed germinating from the seed bank likely represents a mixture of seeds input from multiple cohorts across a decade. Here, we were simply interested in whether seeds still germinated in established *L. vulgaris* sites at least 2 years (or greater) after removing seed input. Every 2 weeks throughout the growing season from 2003 to 2005, we counted the number of seedlings and the survival of those seedlings, as described above. One caveat is that because we did not quantify how many seeds were left in the soil after 2005, we simply estimated seedling emergence and not seed mortality (Maron and Crone 2006).

Results

To what degree does damage by adult *B. pulicarius* on *L. vulgaris* vary among years and sites?

The proportion of ramets damaged per site by *B. pulicarius* ranged from 0 to 86% with a mean ± 1 SE across all years and sites of 39.5 ± 5.4% of ramets damaged. We found that proportion of ramets damaged varied among years (ANCOVA: $F_{2,11} = 5.06$, $P = 0.03$). Damage in 2004 (mean ± 1 SE: 30.5 ± 6.0%) was 10% lower than damage in 2002 (41.5 ± 9.9%) and 17% lower than damage in 2003 (47.9 ± 11.9%). In addition, we also found that proportion of ramets damaged varied up to six times among sites across years (ANCOVA: $F_{7,11} = 3.53$, $P = 0.03$; Fig. 1). The covariate, ramet density, explained some of the variation in damage by adult *B. pulicarius* (ANCOVA: $F_{1,11} = 5.51$, $P = 0.04$). Sites with higher ramet density received a higher proportion of ramets damaged by *B. pulicarius* ($\beta \pm 1$ SE $= 0.015 \pm 0.006$). Finally, damage levels were positively associated within sites and across

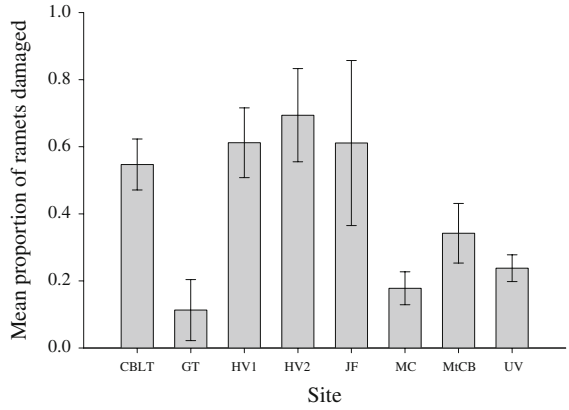

Fig. 1 Proportion of *Linaria vulgaris* ramets damaged by *Brachypterolus pulicarius* differed significantly among sites. Bars are means over 3 years ± SE. Site abbreviations as in Appendix 1

years ($r > 0.73$, $0.02 > P < 0.10$), suggesting that sites with consistently more damage in 1 year had more damage in subsequent years.

What are the plant reproductive consequences of *B. pulicarius* damage to *L. vulgaris* ramets?

Observational study

For both survival and flowering, the model that included year, site, damage, and interactions between site by year and site by damage provided the best fit to the observed data (survival: $\chi^2 = 9.52$, df = 5, $P = 0.09$; flowering: $\chi^2 = 7.68$, df = 5, $P = 0.17$). Damage had no effect on ramet survival (Table 1). Across all sites and years, 86% of damaged ramets survived and 87% of undamaged ramets survived. However, the probability of ramet survival varied among sites, and there was a significant site by year interaction, suggesting that year affected the degree to which probability of survival varied among sites (Table 1). In addition, there was a marginally significant site by damage interaction, suggesting that damage may differentially affect the probability of survival among sites (Table 1).

Damage was associated with a greater likelihood that ramets flowered (Table 1). Across all sites and years, damaged ramets were 11% more likely to flower than undamaged ramets (percent of ramets that flowered damaged versus undamaged: 34 vs. 23%). In addition, site and interactions between site by year and site by damage affected the probability of ramet flowering (Table 1), suggesting that in some sites and years, damaged ramets were more likely to flower.

Table 1 Best fit nominal logistic regressions showing the effects of year, site, damage, and interactions between site by year and site by damage on probability of survival and flowering of *Linaria vulgaris* ramets naturally damaged and undamaged by *Brachypterolus pulicarius*

	df	Survival		Flowering	
		χ^2	P	χ^2	P
Year	1	<0.01	0.96	<0.01	0.99
Site	7	87.13	<0.0001	63.58	<0.0001
Damage	1	<0.01	0.98	21.36	<0.0001
Site × year	5	62.42	<0.0001	31.35	<0.0001
Site × damage	7	12.74	0.08	20.46	0.005

For plants that survived and flowered, damage by *B. pulicarius* was associated with variation in estimates of *L. vulgaris* sexual reproduction ($\lambda = 0.15$, $F_{3,80} = 3.99$, $P = 0.01$). Damaged flowering ramets produced double the number of flowers as undamaged flowering ramets ($F_{1,111} = 5.39$, $P = 0.02$; Fig. 2a) and significantly more seeds per fruit ($F_{1,82} = 7.60$, $P = 0.007$). However, damage had no significant effect on proportion fruit set ($F_{1,110} = 0.06$, $P = 0.81$; mean ± 1 SE, damaged: 0.45 ± 0.04, undamaged: 0.52 ± 0.03). There was a significant effect of the covariate, initial ramet size, on *L. vulgaris* sexual reproduction ($\lambda = 0.14$, $F_{3,80} = 3.76$, $P = 0.01$). Ramet height was positively associated with flower production ($F_{1,111} = 7.34$, $P = 0.008$) and seeds per fruit ($F_{1,82} = 8.86$, $P = 0.004$) but not proportion fruit set ($F_{1,110} = 0.14$, $P = 0.71$). There was no significant effect of year on ramet sexual reproduction ($\lambda = 0.04$, $F_{3,80} = 1.20$, $P = 0.31$). However, there was a significant damage by year interaction ($\lambda = 0.17$, $F_{3,80} = 4.58$, $P = 0.005$). The year of study affected the degree to which damage influenced seeds per fruit ($F_{1,82} = 12.34$, $P = 0.0007$). Because damaged ramets produced more flowers but proportion fruit set did not vary with damage, damaged ramets also produced almost two times more expanded fruits than undamaged ramets ($F_{1,110} = 4.59$, $P = 0.03$; Fig. 2b). Finally, estimates of sexual reproduction varied among sites ($\lambda = 0.56$, $F_{12,212} = 4.39$, $P < 0.0001$). Flower production per ramet varied by at least five times among sites ($F_{4,111} = 4.13$, $P = 0.004$) as did seeds per fruit ($F_{4,82} = 8.09$, $P < 0.0001$). There was no one site that had higher measures of all estimates of sexual reproduction.

For all surviving ramets (both flowering and non-flowering), damage by *B. pulicarius* was also associated with variation in final ramet size (number of branches and above-ground ramet biomass; $\lambda = 0.22$, $F_{2,389} = 42.62$, $P < 0.0001$). Damaged ramets produced over three times more branches ($F_{1,520} = 155.87$, $P < 0.0001$; Fig. 2c) and weighed twice as much ($F_{1,391} = 21.46$, $P < 0.0001$; Fig. 2d) as undamaged ramets. We also found an association between initial ramet size and final ramet size ($\lambda = 0.49$, $F_{2,389} = 95.51$, $P < 0.0001$). Initial ramet height was positively associated with number of branches ($F_{1,520} = 63.05$, $P < 0.0001$) and above-ground biomass ($F_{1,391} = 194.04$, $P < 0.0001$). Final ramet size varied between years ($\lambda = 0.02$,

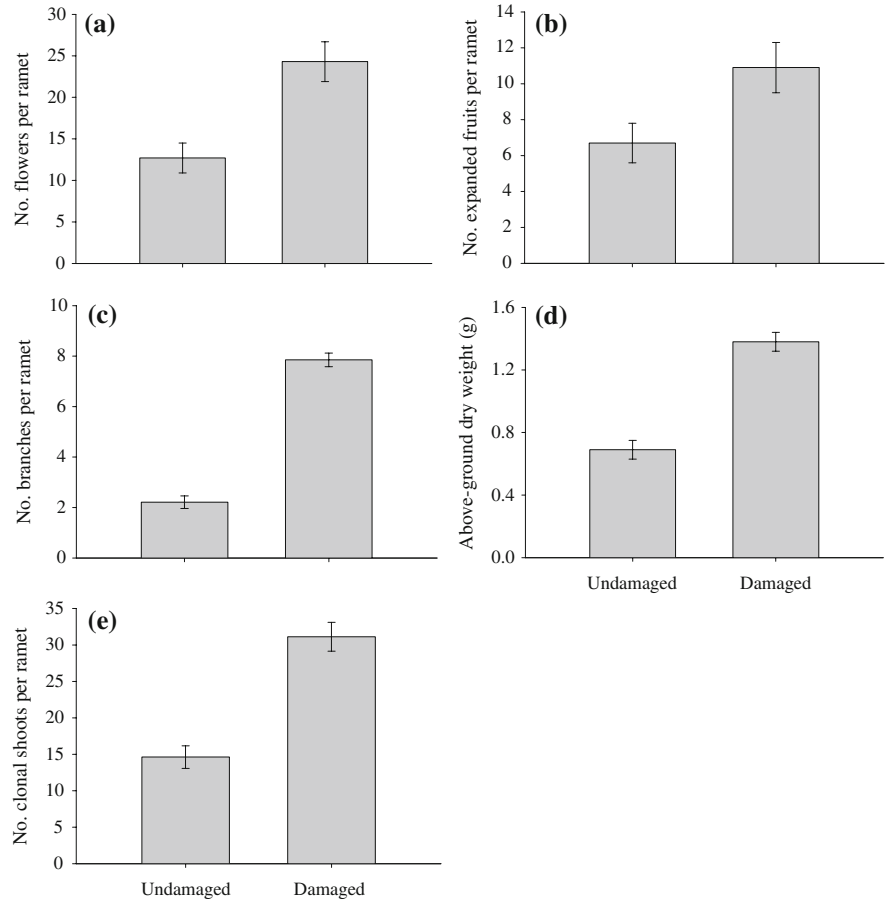

Fig. 2 Damaged *Linaria vulgaris* ramets in the observational study produced significantly more (**a**) flowers and (**b**) expanded (seed-bearing) fruits, (**c**) branches, (**d**) above-ground biomass, and (**e**) clonal shoots than undamaged ramets. In (**a**–**d**), bars are means across sites over 2002 and 2003 ± SE; in (**e**), bars are means across sites in 2002 ± SE

$F_{2,389} = 3.62$, $P = 0.03$), but there was no significant damage by year interaction ($\lambda = 0.01$, $F_{2,389} = 1.02$, $P = 0.36$). Final ramet size also varied among sites ($\lambda = 0.81$, $F_{12,778} = 7.30$, $P < 0.0001$). Number of branches varied by four times among sites ($F_{6,520} = 5.96$, $P < 0.0001$), as did above-ground biomass ($F_{6,391} = 6.90$, $P < 0.0001$). Finally, in 2002 (the only year in the observational study in which we estimated clonal growth), damaged ramets produced two times more clonal shoots than undamaged ramets ($F_{1,242} = 18.86$, $P < 0.0001$; Fig. 2e), but there was no significant effect of initial ramet size on clonal shoots ($F_{1,242} = 1.76$, $P = 0.19$). Clonal shoot production varied by almost three times among sites ($F_{3,242} = 3.83$, $P = 0.01$). Taken together, results from the observational study suggest that damage by *B. pulicarius* was associated with *higher* estimates of sexual reproduction (number of flowers and expanded fruits), final ramet size (number of branches per stalk and above-ground ramet biomass), and clonal shoot production even with the covariate, initial ramet size, included in the model.

Experimental garden

Damage treatment had no effect on the percent of ramet mortality per cage ($F_{1,8} = 0.93$, $P = 0.36$). In cages with *B. pulicarius*, damage significantly affected estimates of sexual reproduction ($\lambda = 2.73$, $F_{2,6} = 8.20$, $P = 0.02$). Damage by *B. pulicarius* reduced the probability of flowering by 10 times ($F_{1,7} = 14.77$, $P = 0.006$; Fig. 3a), and the probability of producing expanded fruits by almost eight times ($F_{1,7} = 6.64$, $P = 0.04$; Fig. 3b). Damage treatment had no effect on estimates of final ramet size or clonal ramet production ($\lambda = 2.12$, $F_{5,3} = 1.27$, $P = 0.45$). Hence, results from the experimental study suggest that damage by *B. pulicarius* was associated with *decreased* estimates of sexual reproduction (probability of flowering and producing

fruits) with no effect on estimates of ramet or clonal mortality and size.

Does ramet height influence the probability of damage by *B. pulicarius*?

We found that in six of seven sites in 2002, taller plants were significantly more likely to be damaged by *B. pulicarius* (logistic regression: $\beta < -0.10$, $\chi^2 > 6.49$, $P < 0.01$). The Upper Valley site was the only site in which there was no relationship between plant height and whether or not a plant was damaged ($\chi^2 = 0.09$, $P = 0.77$). In 2003, taller plants were significantly more likely to be damaged by *B. pulicarius* in three out of six sites ($\beta < -0.38$, $\chi^2 > 13.41$, $P < 0.0002$). In the other three sites, there was no significant relationship between plant height and likelihood of damage ($\beta > -0.01$, $\chi^2 < 1.99$, $P > 0.16$). These results suggest that in some years and in some sites, ramet height may affect the probability of damage by *B. pulicarius*.

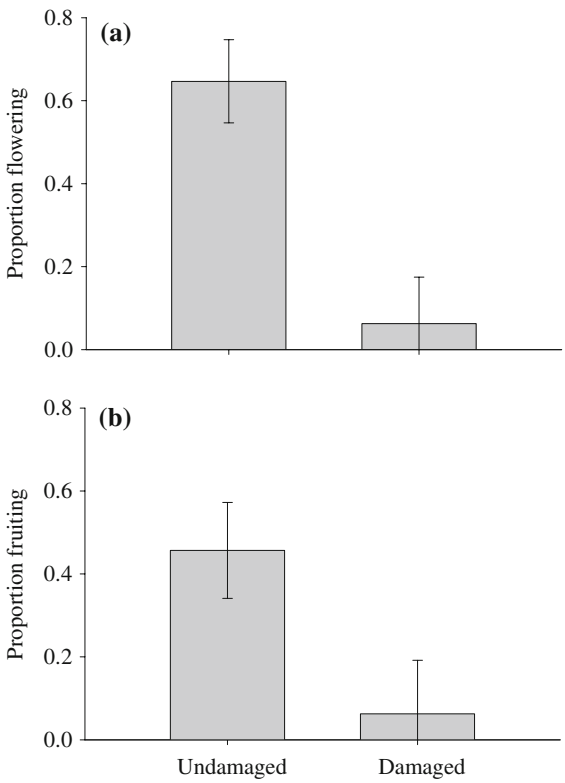

Fig. 3 Undamaged *Linaria vulgaris* in the experiment had a higher probability of (**a**) flowering and (**b**) fruiting compared to damaged *L. vulgaris*. Bars are means ± SE

Does variation in seed input into established *L. vulgaris* sites affect seedling numbers?

In 2003, the number of seeds input into plots ranged from 0 to 13,755 seeds per 625 cm^2 (or 0 to 220,080 seeds m^{-2}), and in 2004, the number of seeds input into plots ranged from 0 to 9,032 seeds per 625 cm^2 (or 0 to 144,512 seeds m^{-2}). In 2004 and in 2005, we found no seedlings in any of the plots. These results suggest that in established *L. vulgaris* populations, seed input likely contributes little to population size in the subsequent year in the study plots.

In our assessment of short-term seed dormancy, we found one plot with two seedlings on 29 May, 2003. One of the seedlings died by 30 June; the other seedling survived throughout the growing season, putting on multiple new true leaves. No other plots in 2003 had seedlings. In 2004, we found one plot with two seedlings on 17 June. Both seedlings died by 1 July. No other plots in 2004 had seedlings. Finally, in 2005, we found no seedlings in any of the plots. These results suggest that over the short-term, seeds from the seed bank contribute little to overall population size in established *L. vulgaris* sites.

Discussion

Many non-native plants arrive into their new range with natural enemies from their native range. What impact do these natural enemies have on their host plants in the introduced range? Here we show that feeding by *Brachypterolus pulicarius* on *Linaria vulgaris* was variable among years and sites. In the observational study, damage was positively associated with sexual reproduction (number of flowers and expanded fruits), final ramet size (number of branches produced and above-ground ramet biomass), and clonal shoot production, even with initial ramet size (height) included as a covariate. However, opposite trends were observed in the experiment; damage by *B. pulicarius* decreased estimates of sexual reproduction (probability of flowering and producing fruits) with no effect on final ramet size or clonal growth. Nonetheless, the ability of *B. pulicarius* to affect established *L. vulgaris* population growth remains doubtful under the environmental conditions that we studied. In neither

the observational nor experimental study did *B. pulicarius* affect *L. vulgaris* survival. In the experimental study, we found no evidence that *B. pulicarius* affected clonal growth. Moreover, we found no evidence that seed input contributed to established *L. vulgaris* populations. Thus, even though damage in the experiment decreased estimates of sexual reproduction, it is unlikely that variation in seed input will translate into a demographic consequence in established populations of *L. vulgaris*, a result mimicking demographic patterns observed for related *L. genistifolia* spp. *dalmatica* (Grieshop and Nowierski 2002).

Methodological considerations

Three caveats are important in the interpretation of the results of this study. First, *L. vulgaris* and *B. pulicarius* are widely distributed across North America and beyond, and it is inappropriate to assume that *B. pulicarius* damage will have no effect on *L. vulgaris* across all environmental conditions. The populations of *L. vulgaris* we studied were dense and well established. Established infestations of *L. vulgaris* are more likely to expand by vegetative reproduction than by seed (Nadeau et al. 1992). For example, in six established *L. vulgaris* infestations around the RMBL near areas where we measured seedling emergence (in the same meadows), we observed an increase in ramet density over 4 years (2001–2004) but we observed no seedling emergence (Appendix 3); this increase in ramet density was solely driven by vegetative production. Even on the edge of established *L. vulgaris* populations, expansion may be driven by vegetative spread. We observed a site over 4 years (2004–2007) that was on the edge of an *L. vulgaris* infestation; the expansion of *L. vulgaris* into the new site was solely driven by ramets (Appendix 3). Thus, the management of established populations requires control of vegetative growth (Lajeunesse 1999). Nonetheless, damage-induced reductions in estimates of sexual reproduction may reduce the probability that *L. vulgaris* will spread to new, isolated sites by reducing the number of seeds available for dispersal. Reductions in sexual reproduction due to herbivore damage may also reduce the number of seeds buried in the seed bank, although the seed bank may be relatively unimportant to the demography of established sites.

A second caveat is that we measured the effects of *B. pulicarius* on *L. vulgaris* within a year. However, herbivores can have cumulative effects on plant fitness when perennials are damaged over multiple years (Strauss 1991; Doak 1992). Because we did not keep track of individual genets across seasons, we do not know whether genets damaged in 1 year are likely to be damaged in subsequent years. If damage levels are consistent within genets, we may have underestimated the potential cumulative effects of *B. pulicarius* on *L. vulgaris* genets.

A third caveat is that additional field studies would help elucidate potential mechanisms driving differences between the observational and experimental studies testing the effects of *B. pulicarius* on *L. vulgaris*. In particular, sites that are more productive for *L. vulgaris* also harbor a higher proportion of damaged ramets. Could this positive co-variation be associated with the positive relationship between beetle damage and *L. vulgaris* success in natural populations? Manipulations of *B. pulicarius* on *L. vulgaris* using insecticide or cage exclosures in a field setting are needed to test this question further.

Spatiotemporal variation in damage

Damage of *L. vulgaris* by *B. pulicarius* varied both among sites and among years; however, sites that had higher levels of damage in 1 year generally had higher levels of damage in subsequent years. Some of the variation in *L. vulgaris* damage by *B. pulicarius* was explained by a positive relationship between the percent of ramets damaged in a site and ramet density. Other studies of weeds and their natural enemies suggest similar patterns in some, albeit not all, cases. For example, the density of both the cinnabar moth (*Tyria jacobaeae*) and the ragwort flea beetle (*Longitarsus jacobaeae*) increased with increasing density of their target weed, *Senecio jacobaea* (McEvoy et al. 1993). Conversely, the number of *Hypericum perforatum* stems per site in northern Idaho was not strongly correlated with the number of eggs laid by the introduced root-boring beetle *Agrilus hyperici* (Campbell and McCaffrey 1991). Aggregation behavior of *B. pulicarius* (MacKinnon et al. 2005) could explain the positive association between *L. vulgaris* density and damage by *B. pulicarius*. It is important to note, however, that if *B. pulicarius* has no effect on *L. vulgaris* in dense,

established sites, then *B. pulicarius* may be damaging sites most intensely where it may be most ineffective. Finally, because ramet density did not explain all of the local spatiotemporal variation in *B. pulicarius* damage, other factors may also be important in influencing the probability that sites (and ramets) experience *B. pulicarius* damage in given years, including climate, phenological synchrony between weed and insect, and the availability of other potential host plants (reviewed in Russell and Louda 2005).

Observations, experiments, and selective feeding

That qualitatively and quantitatively different results were obtained from the observational and experimental studies examining the effects of *B. pulicarius* on *L. vulgaris* reaffirms the importance of both observations and manipulations in the study of plant–insect interactions and weed control (McEvoy 1985). Interpretation of the observational study alone may have suggested that *L. vulgaris* overcompensates for damage, producing higher estimates of sexual and vegetative reproduction in the damaged compared to the undamaged state (Maschinski and Whitham 1989; Paige 1992). However, in the experimental study, we found that damage reduced the probability of flowering by 10 times and producing fruit by eight times and had no effect on vegetative production.

One mechanism that may explain, in part, differences in the observational and experimental studies is selective feeding by *B. pulicarius*. In six of seven sites in 2002 and three of six sites in 2003, taller ramets were more likely to be damaged. Thus, damaged plants in the observational study were associated with higher estimates of sexual and vegetative production compared to undamaged plants likely because damaged plants were larger before feeding by *B. pulicarius*. Selective feeding of insects on larger, or more vigorous, plants is common (e.g., Price 1991; Rose et al. 2005). Insects may selectively feed on larger plants for a variety of reasons, including plant apparency and quantity and quality of nutrition provided. Predicting the ecological, evolutionary, and management consequences of selective feeding on larger ramets is not straightforward. Preferential feeding by insects on larger plants may remove the largest, most fecund individuals from the population, individuals which may be contributing the most to population recruitment and persistence (Louda et al. 2005). Size-selective harvesting has been hypothesized to alter the pattern and rate of evolutionary change in the size of both animals (Coltman et al. 2003) and plants (McGraw 2001), although patterns of selection can change as host population size declines (Rose et al. 2005). However, preferential feeding by insects on larger plants may have little individual- or population-level consequences if the largest plants are also most tolerant to damage. The ecological and evolutionary consequences of size-selective foraging on *L. vulgaris*, and invasive plants in general, warrant further experimental attention.

Management considerations

Results from this study suggest that damage by the natural enemy *B. pulicarius* reduces estimates of *L. vulgaris* sexual reproduction, but the weak link between seed production and recruitment attenuates the effects of *B. pulicarius* in managing established populations. Based on these results, damage by *B. pulicarius* alone, and likely stem- and flower-feeding herbivores similar in feeding mode to *B. pulicarius*, will not be effective in managing established *L. vulgaris* populations. Management is required that targets vegetative reproduction. Studies of the effects of *B. pulicarius* on the management of newly established *L. vulgaris* populations and of the life-history transitions most strongly linked to population growth will yield additional management insights.

Our results echo the patterns and processes observed in other weed biocontrol programs suggesting (1) spatiotemporal variation in damage by natural enemies (De Clerk-Floate and Miller 2002), (2) selective feeding by natural enemies (Rose et al. 2005), (3) negative effects of natural enemies on estimates of plant reproduction (McClay 1992), but (4) ambiguous effects of natural enemies on plant population spread and weed management (Shea et al. 2005), and (5) weak effects of flower- and seed-feeders on hosts whose populations are not seed limited (McClay and Balciunas 2005). To understand how, when, and why natural enemies will affect invasive plant populations, research is needed on the reproductive and demographic stages of weeds most amendable to management and the coupled population dynamics of insects that target those vulnerable

plant stages (McEvoy and Coombs 1999; Buckley et al. 2005). For practical and economic reasons, there is a critical need for multidisciplinary efforts that combine studies of plant–insect interactions and plant demography to test causality and predict and measure the consequences of interactions between invasive plants and their natural enemies.

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Appendices

Appendix 1 Location of sites used in field censuses

Site (abbreviation)	Location	Elevation (m)	Biomass and clonal growth in 2002	Sweep netting	Pitfall traps (dates traps open in 2002)
Crested Butte Land Trust (CBLT)	38°53′21.8″ N, 106°59′40.3″ W	2,717	Y	N	Y (11–19 July)
Gates (GT)	38°57′31.8″ N, 106°59′11.7″ W	2,923	Y	Y	Y (10–19 July)
Happy Valley 1 (HV1)	38°57′33.1″ N, 106°59′23.5″ W	2,897	Y	Y	Y (11–19 July)
Happy Valley 2 (HV2)	38°57′32.4″ N, 106°59′24.8″ W	2,902	N	Y	Y (11–19 July)
Judd Falls (JF)	38°57′33.0″ N, 106°59′20.2″ W	2,905	N	N	N
McLeod (MC)	38°57′27.8″ N, 106°59′24.8″ W	2,898	Y	Y	Y (10–19 July)
Mt. Crested Butte (MtCB)	38°54′35.5″ N, 106°58′03.7″ W	2,903	N	N	Y (11–19 July)
Upper Valley (UV)	38°59′45.6″ N, 107°00′53.1″ W	2,997	N	N	Y (12–22 July)

Five sites (Gates, Happy Valley 1, Happy Valley 2, McLeod, and Judd Falls) were in the RMBL town site and were likely close enough to be connected by gene flow via pollen. The Upper Valley site was ~5 km north of the RMBL town site. The Mt. Crested Butte site was located in a disturbed roadside habitat, and the Crested Butte Land Trust site was at the lowest elevation along a riparian zone. The Upper Valley, Mt. Crested Butte, and Crested Butte Land Trust sites were separated from all other sites by several kilometers. The Biomass column refers to whether ramets in the sites were collected for above-ground biomass and clonal growth in 2002. In 2003, above-ground ramet biomass was harvested at all sites, but clonal growth was not estimated due to an early September snowfall. Some sites were also sampled for other herbivores and arthropods associated with *L. vulgaris* (Appendix 2) using sweep netting and pitfall traps

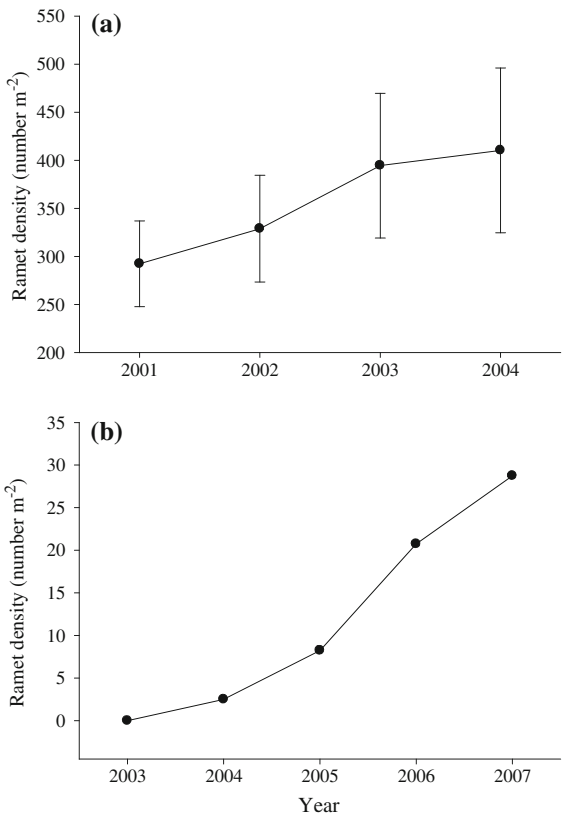
Appendix 2

Field measurements of other arthropods associated with *Linaria vulgaris*

To ensure that marked ramets were not extensively damaged by other natural enemies, we used a combination of sweep netting, pitfall traps, and observations of leaf-feeding and other arthropods associated with *L. vulgaris* during censuses of marked plants. In 2002, we used sweep netting in four sites near the RMBL (Appendix 1) once in mid-July. Also in 2002, pitfall traps were placed at ~1-m intervals along the 7-m transects (see "To what degree does damage by adult *B. pulicarius* on *L. vulgaris* vary among years and sites?") in seven sites and left open for 8–9 days. Most specimens from the sweep netting and pitfall traps were preserved in ethanol and identified to Order or Family. Sweep-net samples were dominated by leafhoppers and several Chrysomelid beetle species. Pitfall traps contained primarily Carabid beetles, ants, spiders, and mites. During field censuses, the only arthropods consistently associated with *L. vulgaris* were *B. pulicarius*, the non-native seed-feeding weevil *Gymnaetron antirrhini*, pollen-feeding thrips and Chrysomelids, and several species of ants feeding on nectar or other arthropods. Besides *B. pulicarius* and

G. antirrhini, none of the arthropods that we commonly observed on *L. vulgaris* are known biocontrol agents or closely related to known herbivores of *L. vulgaris* (Saner et al. 1995; Julien 1998). We never observed significant foliar feeding or other types of herbivore damage besides stem boring by adult *B. pulicarius* and flower feeding by the larvae. Thus, it is likely that the stem damage we observed was exclusively caused by *B. pulicarius*.

Appendix 3



Expansion of *Linaria vulgaris* by vegetative growth (**a**) in established populations ($n = 6$ sites over 4 years, points are means ± 1 SE) and (**b**) on the edge of an established population ($n = 1$ site over 5 years, points are means). We did not observe *L. vulgaris* seedlings in the sites

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