

Host-plant preference of *Brachyterolus pulicarius*, an inadvertently introduced biological control insect of toadflaxes

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Abstract

Brachyterolus pulicarius (L.) (Coleoptera: Kateridae) is an inadvertently introduced biological control agent that can reduce seed set in two North American invasive species, yellow (*Linaria vulgaris* P. Mill.) (Scrophulariaceae) and Dalmatian toadflax (*Linaria genistifolia* (L.) P. Mill. ssp. *dalmatica*). The beetles are more common on yellow toadflax than on Dalmatian toadflax. To understand their distribution on the two host plants, we investigated whether they prefer one host to the other and whether individuals aggregate toward conspecifics. In field and laboratory experiments where beetles were presented with a choice of both toadflax species, *B. pulicarius* sampled from both host plants preferred yellow toadflax. However, in the laboratory experiment, beetles collected from Dalmatian toadflax showed a weaker preference for yellow toadflax than beetles collected from yellow toadflax. In the field experiment, all beetle populations sampled showed similar preferences. When given a choice between yellow toadflax plants with and without trapped adult *B. pulicarius*, beetles preferred plants with conspecifics, suggesting aggregation toward beetle pheromones or host-plant volatiles induced by beetle activity. These results do not support the current practice of redistributing North American *B. pulicarius* onto Dalmatian toadflax because of their preference for yellow toadflax.

Introduction

A striking pattern among insect herbivores is that most species feed on only a few plant hosts. Even those that are considered to be generalists may actually be comprised of populations that are locally specialized on only one to a few species of plants (Fox & Morrow, 1981). Preference can have a genetic basis (e.g., Via, 1990), or be a result of non-genetic factors, such as maternal effects or learned behavior (e.g., Mousseau & Fox, 1998; Barron, 2001). In either case, host preference affects the distribution and abundance of many herbivorous insects (Strong et al., 1984).

For the biological control of weeds, a suitable degree of preference for the target weed(s) is central to both safety and efficacy (Messenger et al., 1976). Agents need to be sufficiently specialized on the target host(s) to minimize

the probability of non-target effects, but be broad enough in their host range to attack all host genotypes or species within a target group (Force, 1967; Hopper et al., 1993; Lym et al., 1996). Aggregation behavior could contribute to this specificity. It has been suggested that monophagous or stenophagous insect species should rely on strong early discrimination of different potential hosts (Courtney & Kibota, 1990). A strong attraction that includes an aggregation factor therefore has the ability to limit the herbivore to a preferred host species. For example, the leaf-feeding beetle, *Altica carduorum* (Coleoptera: Chrysomelidae), has the ability to develop on several *Cirsium* species, but in its native range is monophagous to *Cirsium arvense*, in part because of its aggregation behavior (Wan & Harris, 1996).

The host preferences of organisms that are unintentionally introduced are rarely known. Thus, it is important to quantify their preference to determine if such inadvertently introduced populations pose a risk or show promise. This paper presents the results of laboratory and field experiments designed to investigate the host-plant preference of several populations of an inadvertently introduced insect for its

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host plants, two North American invasive weed species in need of effective control.

Study system

Yellow toadflax (*Linaria vulgaris* P. Mill.) (Scrophulariaceae) and Dalmatian toadflax (*Linaria genistifolia* (L.) P. Mill. ssp. *dalmatica*) were brought to North America from Eurasia as ornamentals. They escaped cultivation and have since spread throughout North America. Both species compete with other plants for water, nutrients, and space, reducing the grazing capacity and diversity of rangeland and natural areas (Lajeunesse, 1993). These plants tend to establish in disturbed areas and in environments without continuous groundcover, but also occur in other habitat types (Arnold, 1982; Saner, 1991). Once plants are established, aggressive vegetative growth by rhizomes enables toadflax to increase in density (Nadeau & King, 1991; Nadeau et al., 1991). Seed dispersal and the ability of seeds to remain dormant for at least 10 years (Carder, 1963; Robocker, 1974) seem to play an especially important role in both the establishment of toadflax into new communities and re-establishment of previously infested areas (Zilke, 1954; Lajeunesse, 1993). Dalmatian toadflax plants can produce up to 500,000 seeds per individual per year (Robocker, 1974), and a single yellow toadflax plant can produce up to 30,000 seeds per year (McClay, 1992). Chemical control programs have met with mixed results, and re-establishment from the seed bank results in the continual need for yearly applications of herbicides (Lajeunesse, 1993). For these reasons, biological control of both species is a well-studied option for long-term control (Nowierski et al., 1996).

Brachypterolus pulicarius (L.) (Coleoptera: Kateridae) is a univoltine beetle that was inadvertently introduced to North America and has spread across the continent through human and natural dispersal. Adults feed on both growing vegetative shoot tips and flower parts of yellow and Dalmatian toadflax, and the larvae feed on all of the inner structures of flowers, including developing ovaries (Hervey, 1927). On potted plants, *B. pulicarius* has reduced seed set in yellow toadflax individuals by up to 90% (McClay, 1992), and similar results are seen for Dalmatian toadflax (Grubb et al., 2002). This beetle is thought to be a factor in the decline of yellow toadflax in Alberta, Canada during the 1950s (Harris & Carder, 1971), and its promise as a biological control agent has made it a prescribed target for collection and redistribution onto uncolonized patches of both species of toadflax (Nowierski, 1995). Unfortunately, while these beetles are almost ubiquitous on yellow toadflax, low beetle densities, localized extinctions, and uncolonized plant patches are common on Dalmatian toadflax even after redistribution efforts (Nowierski et al., 1996, DK MacKinnon, unpubl.).

We examined beetle preference for yellow or Dalmatian toadflax to evaluate if differences in preference could help explain the observed lower densities on Dalmatian toadflax. Further, we examined if populations of *B. pulicarius* collected from either Dalmatian or yellow toadflax varied in their preference, indicating the potential for local specialization. Finally, we investigated the aggregation behavior of *B. pulicarius* toward conspecifics.

Materials and methods

Laboratory preference experiment

Plant and beetle collection. In the spring of 2001, we collected plants from three populations of yellow toadflax and three populations of Dalmatian toadflax in Colorado and southern Wyoming. We excavated roots and transplanted them into 3.8-l pots containing potting soil (Scotts® 350 Metro Mix) and about 15 ml of slow-release fertilizer (Osmocote® Vegetable and Bedding Slow Release Plant Food).

Adult *B. pulicarius* were collected from three yellow toadflax and six Dalmatian toadflax populations in Colorado and Southern Wyoming. We caged all the beetles collected from each population in a single bucket in the laboratory for up to 1 week with fresh foliage and flowers from their original host species.

Experimental design. We presented beetles with a choice of both host plants in a plastic cylindrical cage (height 28 cm and diameter 20 cm) with one rectangular 16 × 28 cm mesh window on the side and one 15 cm diameter circular mesh window on the lid. We placed shoots containing similar numbers of flowers and buds from each toadflax species in 50 ml flasks of water. The numbers of flowers and buds were not recorded. Each toadflax species was in a separate flask and Parafilm® was used to cover each flask to reduce water evaporation and limit beetle drowning. We released 6–10 *B. pulicarius* from one field collection site into each cage. At 3, 22, 30, and 40 h after their release, we recorded the location of each beetle as being on yellow toadflax, Dalmatian toadflax, or on the walls of the cage. After 40 h, adult beetles were removed and we dissected all of the foliage to determine the proportion of eggs on yellow toadflax. Depending on the number of beetles collected at each site, we repeated this several times for each beetle population, and individual beetles were used only once. During the experiment, lights were kept on, but cages were covered with black plastic bags to minimize positive phototaxis of the beetles.

We used a multivariate, repeated measures mixed-model logistic regression with a binomial error distribution and a logit link function to assess the proportion of beetles or eggs found on yellow toadflax (Glimmix Macro, SAS version 8,

SAS Institute Inc., 2001). The unit of replication on which repeated measures were taken was the arena containing 6–10 beetles. The date that the beetles were collected (trial) was treated as a random factor, and host plant from which the beetles were collected was fixed.

Field preference experiment

Plant and beetle collection. In March 2002, we sowed yellow and Dalmatian toadflax seeds collected from New York, Wisconsin, Colorado, and Wyoming into flats and placed them in a greenhouse. Seedlings were transplanted to 3.8-l pots filled with a mixture of Scotts® Metro Mix 350 and about 15 ml of Osmocote® slow release fertilizer. In June, we placed them outside.

For this experiment we collected beetles from two yellow and two Dalmatian toadflax populations in northern Colorado and southern Wyoming. We held beetles from different populations in separate cages, with all the beetles collected from each population in a single cage. To identify the beetles' collection site, a small drop of Testor® paint was placed onto the elytra or thorax of each beetle, making sure not to paint the beetles' wings shut. We chose the paint color randomly for each population and for each mark and recapture trial. Paint did not seem to alter adult behavior. We marked 150 beetles per population (600 total/trial) on the day of collection. After painting, beetles were then placed back into their cages overnight and used in the trial the following morning.

Experimental design. We performed the mark and recapture experiment in a fallow field at the Colorado State Park Tree Nursery in Fort Collins, CO. The field consisted mainly of weedy species (e.g., *Bromus tectorum* and *Cirsium arvense*), but did not have either toadflax species. We placed eight patches of potted toadflax (four yellow and four Dalmatian) in a circle 7.5 m away from a central beetle release point. Plants were randomly chosen for inclusion in the experiment 1 week before running each of the three trials. At this time we pruned each patch so that they were similar in the number of vegetative shoots, inflorescences, total flowers, and total buds. No plant was taller than 30 cm from the top of its pot. Because of the inherently large differences in flower number between toadflax species, Dalmatian toadflax patches contained 10 plants, while yellow toadflax patches contained nine plants. At approximately 8:00 AM, the morning after beetles were collected and marked, we released them from the center of the circular arena. At 24, 48, and 72 h after release, we searched each toadflax patch for 6 min, enough time to examine each plot thoroughly and look inside each flower. We recaptured all observed beetles, brought them back to the laboratory, and identified

them to their original collection source by paint color. Because plants had grown since pruning, we recorded total number of flowers and flower buds, and number of inflorescences for each plot at the time of release, and 24, 48, and 72 h after release. After 72 h, we removed all toadflax inflorescences, and randomly sampled and dissected a total of 240 inflorescences from the first two trials to estimate *B. pulicarius* egg density. Trials were run at least 1 week apart to allow remaining uncaptured beetles from the previous run within the field to disperse.

We analyzed the data for our response variables (number of recaptured adults per trial and number of eggs per flower at the end of the experiment) using mixed linear models (Proc Mixed, SAS version 8, SAS Institute Inc., 2001). For recaptured beetles per trial, we treated the species of toadflax from which the beetles were initially collected (host plant) and the species of toadflax on which the beetles were recaptured (recapture plant) as fixed effects. Random effects were each mark and recapture trial and source population nested within source species. For egg density we treated toadflax species and flower number as fixed effects. Trial and trial by toadflax species were treated as random effects.

The numbers of flowers and flower buds might affect beetle behavior, so we assessed whether differences existed between patches of the two toadflax species in the number of buds and flowers at the beginning of the experiment. We treated toadflax species and total number of buds and flowers as fixed effects and trial and patch nested within species as random effects.

Aggregation experiment

Plant and beetle collection. Plants were randomly chosen from the group of plants described previously for the field choice experiment, and were not used in both experiments. We collected beetles from yellow and Dalmatian toadflax populations across Colorado and southern Wyoming, and held them in cylindrical cages (described previously) for 1 night before their release into the experimental arena.

Experimental design. Beetles were given a choice between yellow toadflax plants with and without other *B. pulicarius* present. We ran this experiment in two field release and recapture trials in June 2002 in Fort Collins, CO. In the first trial, the elytra of 120 beetles were glued together with fingernail polish to prevent movement to other plants and we placed 20 of these beetles on each of six yellow toadflax plants. Plants with glued beetles were spaced alternately with plants without glued beetles and placed in two parallel rows. Plants within rows were spaced approximately 1 m apart and the two rows were 9 m apart. We placed glued

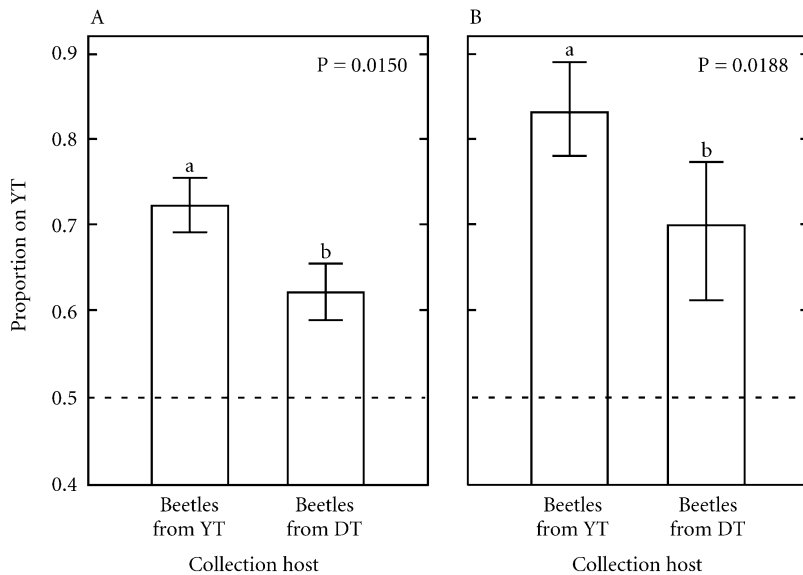


Figure 1 Proportion \pm SE of (A) adult *Brachypterosus pulicarius* beetles recaptured and (B) eggs oviposited on yellow toadflax (YT), *Linaria vulgaris*, in the laboratory experiment. Adults from both hosts preferred to occur and oviposit on yellow toadflax. Proportions also differed between collection hosts ($P < 0.001$), with beetles collected from Dalmatian toadflax (DT), *Linaria genistifolia dalmatica*, showing a less pronounced preference for YT. Proportions labeled with different letters are significantly different from each other using F statistics and SE obtained by backtransforming values obtained from the logit model in SAS.

beetles on the appropriate plants at 9:00 PM and the following morning at 6:00 AM, they appeared to be feeding and mating normally. At that point, we released 150 unglued beetles from the center of the two rows of yellow toadflax. Beetles were not grouped or marked according to the host plant from which they were collected. By 9:00 AM, most beetles had left the release container. At 10:00 AM, plants were individually bagged in 57-l plastic trash bags, brought back to the laboratory and all glued and unglued beetles in each bag were counted. The second trial of this experiment was repeated as previously mentioned except that we confined beetles to test plants using organdy sleeve cages on a single inflorescence of each treatment plant instead of using glued beetles.

We analyzed the number of beetles found on the plants with and without conspecifics using a mixed model (Proc. Mixed, SAS version 8, SAS Institute Inc., 2001). Treatment (plants with *B. pulicarius* and plants without *B. pulicarius*) was considered a fixed effect, and trial (each release and recapture event) was considered a random effect.

Results

Laboratory preference experiment

In the laboratory choice experiment, beetles collected from both yellow and Dalmatian toadflax were found more often on yellow toadflax (Figure 1A, Table 1). Beetles sampled from Dalmatian toadflax, however, showed a weaker preference for yellow toadflax than beetle populations sampled from yellow toadflax (72% compared to 62%, $P = 0.0112$). There were no significant differences in preference of beetles from individual sample sites within collection host.

Oviposition results were similar. Beetles laid more eggs on yellow toadflax (Figure 1B) and this preference was less pronounced in beetles collected from Dalmatian toadflax (83% compared to 69%, $P = 0.0188$). For beetles collected from Dalmatian toadflax, the proportion of eggs on yellow toadflax was only significantly different from 50% when using $\alpha = 0.10$ (Figure 1B). There was no significant trial effect for the adult choice results, but a trial effect was seen in the oviposition results (Table 1).

Field preference experiment

In the field experiment, beetles collected from yellow and Dalmatian toadflax were found more often on yellow toadflax (Figure 2, Table 2). There were no significant differences

Table 1 Statistics for the laboratory preference experiment, including both fixed and random effects. The significance of fixed effects is tested with F tests that account for both the variance from the random effects and the error variance. The significance of each random effect is tested using likelihood ratio tests, and our use of the Satterthwaite approximation to determine the degrees of freedom for the F tests may cause the degrees of freedom to be fractional for the F tests (Littell et al., 1996)

Effect	d.f.	F value	χ^2	d.f. (χ^2)	Prob. > F
Adults					
Host plant	1, 36.4	7.13	—	—	0.0112
Trial	—	—	0.233	1	0.3147
Eggs					
Host plant	1, 28.1	6.21	—	—	—
Trial	—	—	5.822	1	0.0079

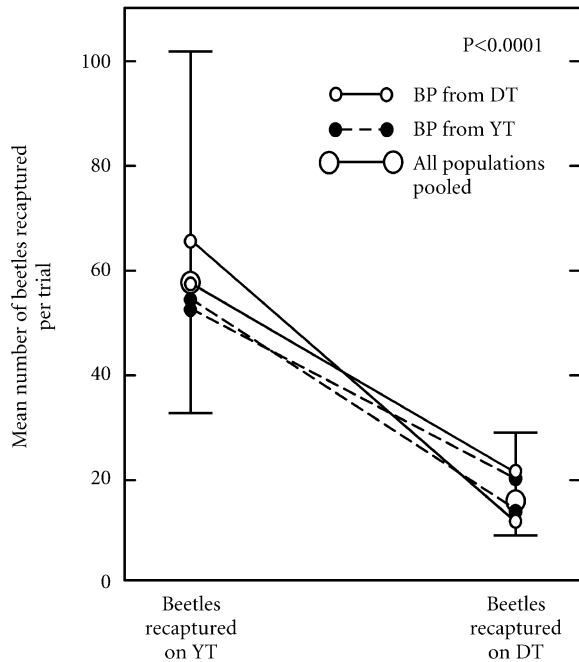


Figure 2 Preference of four *Brachyterolus pulicarius* (BP) populations toward yellow toadflax (YT), *Linaria vulgaris*, in a field choice experiment. Results include average number of beetles collected per block on yellow and Dalmatian toadflax (DT), *Linaria genistifolia dalmatica*, by population and when pooling all populations together, with \pm SE for pooled data. All populations, whether collected off DT or YT, preferred YT (all four $P < 0.001$).

in host-plant choice among populations of beetles, and oviposition rates corresponded with adult recapture results. All four populations studied laid more eggs on yellow toadflax (Table 2), and there were no significant differences among beetle collection sites. There were significant trial effects in both adult beetle recapture results and oviposition

Table 2 Statistics for the field preference experiment, including both fixed and random effects

Effect	d.f.	F value	χ^2	Prob. > F
Adults				
Recapture plant	1, 14	246.58	–	<0.0001
Host plant	1, 14	0.86	–	0.3696
Population (source)	2, 14	2.08	–	0.1616
Source by recapture	1, 14	0.68	–	0.4233
Plant				
Trial	1	–	9.0	0.0079
Eggs				
Host plant	1	9	–	0.0015
Trial	1	–	4.9	0.0134

results. Flower and flower bud and shoot tip numbers were not significantly different between yellow and Dalmatian toadflax patches in any repetition, and none of these variables explained a significant amount of variation in the number of beetles recaptured (all $P > 0.05$).

The laboratory and field preference experiments produced different results. In the laboratory experiment adult beetles collected from Dalmatian toadflax showed a weaker preference for yellow toadflax than those beetles collected from yellow toadflax. In the field experiment, both groups of beetles, those collected from yellow toadflax, and those collected from Dalmatian toadflax, showed similar preferences for yellow toadflax. The experiments occurred at different spatial scales, and differences between them could be attributable to biological differences in how the beetles make choices at these two scales. To evaluate whether the differences between the laboratory and field experiments can be interpreted biologically, or are caused simply by imprecise measurements and high variances, we performed a two-sided t-test. For this t-test we used the estimates of the difference between laboratory and field preference for adult beetles collected from yellow and Dalmatian toadflax and their standard errors from the laboratory and field experiments:

$$t = \frac{(\text{estimate}_{\text{DT}(\text{field})-\text{YT}(\text{field})} - \text{estimate}_{\text{DT}(\text{laboratory})-\text{YT}(\text{laboratory})})}{\sqrt{\text{SE}(\text{estimate}_{\text{field}})^2 + \text{SE}(\text{estimate}_{\text{laboratory}})^2}}$$

This test statistic was significant ($t_4 = -2.82$, $P = 0.047$), indicating that the differences between the field and laboratory experiments are likely to have a biological interpretation (see Discussion).

Aggregation response experiment

Beetles were recaptured at a greater rate on yellow toadflax plants with trapped beetles (Figure 3), indicating that beetles tend to aggregate with conspecifics. There was no significant trial effect ($\chi^2_1 = 1.2$, $P = 0.1367$).

Discussion

Our preference experiments show that *B. pulicarius* is a phytophagous insect that, unlike many others (Mopper & Strauss, 1998 and references therein), does not seem to be comprised of populations locally specialized on different hosts, at least in terms of preference. Rather, although the beetles can be found on Dalmatian toadflax in the field and they are known to develop successfully on it (McClay, 1992; DK MacKinnon & RA Hufbauer, unpubl.), they consistently prefer yellow toadflax regardless of collection host. In addition to preferring yellow toadflax to Dalmatian, our aggregation experiment suggests that *B. pulicarius* aggregates toward conspecifics.

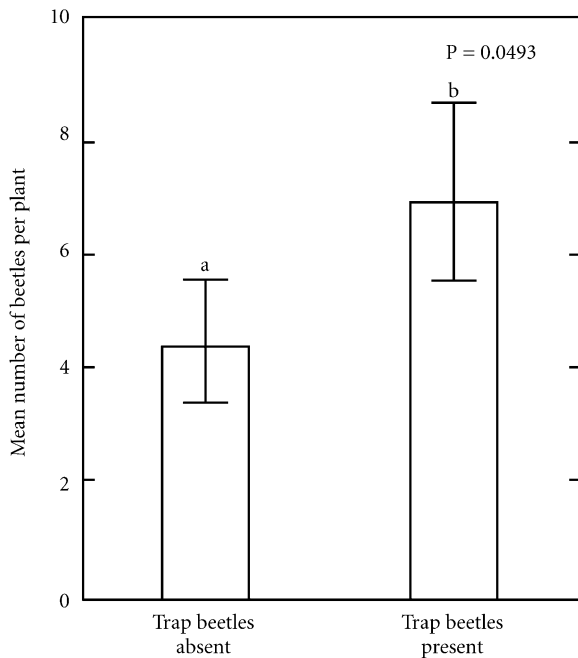


Figure 3 Average number of released *Brachypterus pulicarius* beetles recaptured on yellow toadflax (YT), *Linaria vulgaris*, without trapped beetles and with trapped beetles per block (\pm SE). Averages labeled with different letters show a statistically significant difference using F statistics.

Our laboratory and field preference experiments contained a subtle difference in the degree of preference for yellow toadflax. In the laboratory results, beetles from Dalmatian toadflax were found on yellow toadflax less often than beetles from yellow toadflax, a difference not found in the field experiment. This disparity in results could be the result of the different setting and scale of each experiment. In the laboratory, beetles were enclosed in a small environment where aggregation factors (possibly beetle pheromones or plant volatiles associated with beetle activity) could have filled the entire experimental arena. This would minimize the influence of aggregation factors on behavior, and the beetles may have been able to respond more directly to the potential host plants. In the field experiment, beetles had the ability to disperse, and factors influencing aggregation were likely to accumulate in a more realistic way according to beetle or plant activity. This would allow beetles to respond to both aggregation factors and the two host plants.

The low preference for Dalmatian toadflax contributes to the observations that this species is less abundant on Dalmatian toadflax (Hervey, 1927; Saner, 1991; Lajeunesse, 1993; Grieshop & Nowierski, 2002). However, the scales at which we performed our experiments are much smaller than those that beetles experience in the field. Beetles are likely to travel much greater distances to choose host plant patches,

and yellow and Dalmatian toadflax do not normally co-occur in the field. If beetles do colonize a patch of Dalmatian toadflax, a low performance on this host would contribute to their continued scarcity on Dalmatian toadflax. Indeed, laboratory tests of larval performance show that beetles reared on Dalmatian toadflax weigh less (DK MacKinnon, RA Hufbauer & AP Norton, unpubl.). Thus, the current populations of this beetle in North America are unlikely to contribute to effective control of Dalmatian toadflax. Harris & Carder (1971) suggested that *B. pulicarius* contributed to the control of yellow toadflax, but no similar observations have been published for Dalmatian toadflax. In addition, this beetle may not even commonly occur on Dalmatian toadflax in its native Eurasian range; Hervey (1927) lists plants utilized by *B. pulicarius* and cites European authors. Dalmatian toadflax is not mentioned.

Dalmatian toadflax is an ever-increasing concern across western North America, and the collection and redistribution of *B. pulicarius* onto uncolonized Dalmatian toadflax patches was previously recommended as part of an integrated control plan (Nowierski, 1995). While *B. pulicarius* has the ability to significantly reduce seed set of individual Dalmatian toadflax plants in caged plots (Grubb et al., 2002), this is unlikely to be the case in the field where beetles are able to disperse. The preference that North American *B. pulicarius* exhibits for yellow toadflax indicates that redistribution efforts to produce large beetle populations on Dalmatian toadflax may fail, especially when considering their aggregation behavior. When a beetle such as *B. pulicarius* has the ability to disperse and is attracted to conspecifics, the likelihood that it will choose a sparsely populated patch of a lesser-preferred host is low. Time may be better spent exploring the native range of this beetle for populations that prefer Dalmatian toadflax, or by redirecting efforts toward other more promising biological control insects, such as *Mecinus janthinus* (De Clerck-Floate & Miller, 2002).

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