

Evaluating host use of an accidentally introduced herbivore on two invasive toadflaxes

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Abstract

The distribution of phytophagous insects is influenced by their preference for and performance on their host plants. Biological control agents of invasive plants that prefer and perform better on their target hosts are more likely to be both effective and safe. *Brachyterolus pulicarius* is an herbivore used in North America to combat two invasive plants, yellow toadflax and Dalmatian toadflax (*Linaria vulgaris* and *Linaria dalmatica*). Adult beetles prefer yellow toadflax over Dalmatian toadflax, and when beetles are redistributed onto Dalmatian toadflax, populations do not consistently establish. This leads to the hypothesis that beetle larvae will perform best on yellow toadflax. A reciprocal transfer experiment was conducted to test this hypothesis. Development rate, pupal mass and percent survival were measured to assess larval performance. Development time was influenced by an interaction between the source host and the test host, a pattern suggesting that it is important to consider both the collection host and redistribution host when releasing this beetle for the control of toadflax. Pupal mass of larvae reared on yellow toadflax was, on average, 13% greater than that of larvae reared on Dalmatian toadflax, supporting the hypothesis. Survival rate was not significantly influenced by source host, test host, or their interaction, suggesting that survival rates will be similar no matter the combination of collection host and redistribution host. These results, along with the preference that adult beetles show for yellow toadflax, do not support the redistribution of *B. pulicarius* onto Dalmatian toadflax in North America. © 2007 Elsevier Inc. All rights reserved.

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1. Introduction

Most populations of phytophagous insects are restricted in the number of species they can use (Thompson, 1994). Many insect species that are considered generalist feeders across their range actually are comprised of local populations that feed on only a subset of the suitable hosts to which they are exposed (Fox and Morrow, 1981). For these reasons, the distribution and abundance of phytophagous insects can depend strongly on local patterns of host use (Jaenike, 1978; Rausher, 1984; Futuyama and Moreno, 1988; Diehl and Bush, 1989; Futuyama, 1991).

Two traits provide insight into the host use of phytophagous insects; the behaviors that influence host choice, and the physiological characteristics that influence an insect's performance (fitness) during development (Via, 1986; Thompson, 1988). Behavior is commonly measured as the rate of oviposition, occurrence, or feeding by adults to determine a preference for a particular host over others. Physiology is quantified by measuring the performance of larvae on prospective hosts in terms of development time, pupal mass and survival rate. When insects prefer one host over others and perform better on that same host, this host is likely to be used to the exclusion of other potential hosts (Rausher, 1984; Via, 1984). Via (1986) and Singer et al. (1988) have not only demonstrated that a link can exist between the behavior and physiology of insects on different hosts, but that adult preference and offspring performance can be genetically correlated.

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One characteristic of many phytophagous insect species that can link adult behavior and offspring performance is that often larvae do not have the mobility to choose the host on which they develop. The host on which larvae feed is often chosen at the discretion of their mothers, especially for species that oviposit directly onto the host. This can provide a direct link between preference and performance, with natural selection strongly favoring females that lay their eggs on hosts that confer a fitness advantage to their offspring (Wiklund, 1975; Courtney and Kibota, 1990). A positive correlation between female oviposition and larval performance characteristics has been found in several systems (see Thompson, 1994). However, this correlation does not always exist, even in systems where females determine their offspring's host (Futuyma and Moreno, 1988; Thompson, 1988, 1994; Price, 1994).

This potential link between oviposition preference and larval performance gives scientists studying biological control of invasive plants a valuable tool to evaluate candidate insect agents both before and after their release. Before the release of an agent, individual populations of the candidate can be sampled and their preference for and performance on the target and nontarget hosts can be studied to evaluate both the risk to nontarget plants and efficacy. After the release of an insect agent, preference and performance studies may help determine which populations of the agent are best to collect for redistribution onto uncolonized patches of the target host. In this way releases of insect biocontrol agents may have a decreased potential for nontarget effects and an increased chance for success (Messenger et al., 1976).

This study focuses on the larval performance of an inadvertently introduced insect (*Brachyterolus pulicarius* L., Coleoptera: Kateridae) that feeds on two plants that have invaded North America; yellow toadflax (*Linaria vulgaris* P. Mill., Scrophulariaceae) and Dalmatian toadflax (*Linaria dalmatica* (L.) P. Mill. ssp. *dalmatica*). The females of this beetle oviposit directly on the host, and the larvae are not mobile enough to choose the host on which they develop, suggesting that selection may lead to a correlation between preference and performance. Previous studies of *B. pulicarius* in North America have found that adult beetles prefer yellow toadflax over Dalmatian toadflax, and this is true even when they are collected from Dalmatian toadflax (MacKinnon et al., 2005). This preference matches well with the beetles' distribution: *B. pulicarius* is almost ubiquitous on yellow toadflax in North America (making redistribution onto this plant species unnecessary), but is much less common on Dalmatian toadflax. Its potential as a biological control agent on Dalmatian toadflax (see Study System, below), has made it a recommended insect for collection and redistribution onto Dalmatian toadflax (Nowierski, 1992; Grubb et al., 2002). Collecting and selling this beetle as a biological control agent for Dalmatian toadflax has also been a successful commercial enterprise (N. Poritz, owner, Biological Control of Weeds, Inc., Bozeman, MT, personal communication).

However, the consistent preference of *B. pulicarius* for yellow toadflax over Dalmatian toadflax regardless of the host species from which the beetles were collected leads to the hypothesis that beetles collected from both hosts will perform better on yellow toadflax. If both preference for and performance on Dalmatian toadflax are low, then redistributions on to Dalmatian toadflax are not likely to be successful. However, a positive relationship between adult preference and larval performance does not always exist with insects (Courtney and Kibota, 1990), and therefore it is possible that within Dalmatian toadflax populations, *B. pulicarius* may have high performance, and even exhibit local adaptation. If populations of the beetle exist within North America that show a performance advantage on Dalmatian toadflax, they could be used as collection sites for redistribution onto uncolonized patches of Dalmatian toadflax. We test the hypothesis that *B. pulicarius* from both hosts will perform better on yellow toadflax and to evaluate whether there is sufficient evidence to warrant collecting and redistributing this beetle onto populations of Dalmatian toadflax that are not yet colonized by the beetle.

1.1. Study system

Yellow toadflax and Dalmatian toadflax are perennial plants that were introduced to North America from Eurasia as ornamentals and medicinal plants. They escaped cultivation and now infest rangelands, wild lands, and agricultural crops across North America. Seed dispersal and the ability of seeds to remain dormant for at least 10 years (Carder, 1963; Robocker, 1974) may play an especially important role in both the establishment of these toadflax species into new communities and reestablishment of previously infested areas (Zilke, 1954; Lajeunesse, 1993). A single Dalmatian toadflax plant 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). Once plants become established, aggressive vegetative growth by rhizomes enables toadflax to increase in density (Nadeau and King, 1991; Nadeau et al., 1991). For these reasons, biological control may be the only long-term solution for the management of these invaders (Nowierski et al., 1996).

Brachyterolus pulicarius is a univoltine beetle that was inadvertently introduced to North America along with its hosts and now occurs across the continent. Adults feed on both the growing vegetative shoot tips and flower parts of yellow toadflax and Dalmatian toadflax, and the larvae feed on all of the inner structures of flowers, including ovules and developing ovaries (Hervey, 1927). Although this beetle does not cause direct mortality of toadflax plants, it is thought to be a factor in the decline of yellow toadflax in Canadian agricultural fields during the 1950s due to its potential to significantly reduce yellow toadflax seed production (Harris and Carder, 1971).

Two studies have quantified the impact this beetle can have on both toadflax species. When caged on individual

hosts, *B. pulicarius* can reduce seed set of Dalmatian toadflax by up to 93% (Grubb et al., 2002), and of yellow toadflax by 74% (McClay, 1992). While these studies show the potential for *B. pulicarius* to reduce the seed set of both species of toadflax, these results might not accurately represent how it affects natural populations of the hosts when beetles are able to disperse freely. In the two experiments, Grubb et al. (2002) and McClay (1992) caged 10 beetles on each plant. While 10 *B. pulicarius* per plant is not unusual in natural populations of yellow toadflax, the same is not true of Dalmatian toadflax. Beetle densities can be quite low on Dalmatian toadflax (less than 1 beetle per plant), and *B. pulicarius* often becomes locally extinct, and patches of Dalmatian toadflax without any *B. pulicarius* are common, even after repeated attempts to establish it (Nowierski et al., 1996; Grieshop and Nowierski, 2002; D. MacKinnon, personal observation). If populations of the beetle exist within North America that perform well on Dalmatian toadflax, they could be used as collection sites for redistribution efforts, potentially increasing rates of establishment.

2. Materials and methods

An experiment was performed in the summers of 2003 and 2004 and set up as a reciprocal transfer: adult beetles were collected from both hosts and their offspring were reared on both hosts (Fig. 1). Larvae were reared through to pupation on both hosts. Response variables measured included larval development time, pupal mass, survival rate and the number of flowers fed upon. Development time, pupal mass and survival rate are common measures of larval physiology (Thompson, 1994). The number of flowers fed upon is used here as an indirect way to assess how much damage the larvae inflict on their host over the course of development.

2.1. Plant and beetle collection

Plants were collected from six sites (three sites of each plant species) in April and early June in 2003 and 2004. Plants were not harvested at random; rhizomes were excavated from the most robust plants. After excavation, the vegetative growth was cut off and single rhizomes were transplanted into 11.5-l pots or pairs of rhizomes were transplanted into 19-l pots. Plants were grown in Scotts Metro Mix 350™ (The Scotts Company, Marysville, OH) potting soil and one tablespoon of Osmocote™ Vegetable

and Bedding Slow Release Plant Food (The Scotts Company, Marysville, OH) per plant was added to each pot. Plants were then placed outside and watered as needed. Each pot was fertilized a second time using the same amount of the Osmocote™ in late August. These plants were used as a source of inflorescences in the reciprocal transfer experiment.

In late June of 2003, 25–30 adult *B. pulicarius* were collected from 8 sites in Colorado and southern Wyoming (four sites of each plant species). In June 2004, adult beetles were collected from 4 locations, a subset of the 2003 collection sites (two sites of each plant species). Collected beetles were brought back to Fort Collins, Colorado. One Dalmatian toadflax collection site in our study was within 2 km of a yellow toadflax collection site. All other beetle collection sites did not have any known populations of the alternative species of toadflax within 10 km. All collections were treated as isolated populations of beetles and toadflaxes.

2.2. Egg collection

Beetles from each population were placed in a translucent, cylindrical cage (height 28 cm, diameter 20 cm) with two mesh windows for ventilation. Each cage contained 100 ml flasks with freshly cut inflorescences and vegetative sprigs of both yellow toadflax and Dalmatian toadflax. Parafilm™ was stretched around the neck of each flask to limit water evaporation and beetle drownings. These toadflax sprigs were cut from the potted plants described earlier and were free of *B. pulicarius* eggs before they were placed in the cage. Eighteen to 24 beetles from each collection site were placed in separate cages (collection sites were not mixed within cages). Over the next 72 h, adult beetles mated and females oviposited on either species of toadflax. After 72 h, the toadflax was removed from the cage and examined twice daily for first instar larvae of *B. pulicarius*. Each first instar larva was placed within a petri dish to develop as described below. This egg-collecting process was repeated three times per year for each *B. pulicarius* population.

2.3. Larval transfer and development

Each larva used in this study was reared within an 8.5 cm diameter ventilated petri dish with a smaller petri dish (3.75 cm in diameter) glued inside. The stem of a freshly cut toadflax inflorescence was placed through a hole into the smaller dish and kept moist with a cotton ball saturated with tap water. First instar larvae (<12 h old) were transferred with a paintbrush or pin into a bud of this toadflax inflorescence. The inflorescences in which the larvae developed matched the toadflax species from which it hatched. This petri dish was then placed into a growth chamber. A light regime of 18 h:6 h was used to simulate summer day-length at our latitude. Humidity was maintained at 85%, to prolong the life of the plant shoots. Additionally, the humidity is appropriate for the beetles, as the insides of flowers on intact plants are humid environments. The

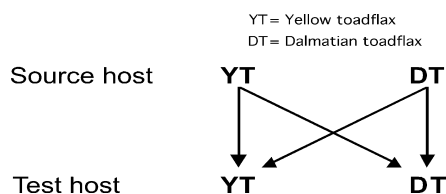


Fig. 1. Reciprocal transfer design. Larvae from each source host were reared on both hosts.

temperature regime was set at 25°C (light) and 22°C (dark). For the first 8 days the toadflax inflorescence was replaced every fourth day. After the 8th day, each petri dish was examined every day and toadflax sprigs were changed every 3rd or 4th day, as needed. On the 8th day, 3 cc of Metro Mix 350™ potting soil was placed within the larger petri dish to provide larvae with a substrate for pupation. Larvae within this soil were considered to be pupating, and were not fed further.

Wild *B. pulicarius* colonized the potted toadflax planted for this experiment in July 2003, so inflorescences collected from the field were also used during this trial. Each inflorescence was searched for *B. pulicarius* larvae and eggs. If any were found, the inflorescence was discarded. The experiment then proceeded as described above. Upon subsequent observation, if more than one larva was found in a petri dish, the larvae in that dish were discarded immediately.

2.4. Pupal mass measurements

When pupae appeared, they were placed in folded and labeled 10 cm × 10 cm weighing paper and dried in an oven at 75°C for a minimum of 24 h. After drying, the pupal mass was measured to within 0.00001 g.

2.5. Statistical analysis

The number of days it took for the larvae to develop into pupae (development time), pupal mass, and the number of flowers the larvae consumed were analyzed using mixed linear models (Proc Mixed, SAS Version 8.2: SAS Institute, 2000). Data on development time were log transformed and data on the number of flowers consumed were square-root transformed to normalize the residuals. For each analysis, the plant species from which the adults were collected (source host), the plant species on which the larvae were reared (test host), and the interaction between source host and test host were treated as fixed effects. Year and its interactions with source host and test host, and population nested within source host were treated as random effects.

A mixed-model logistic regression with a binomial error distribution and a logit link function was used to examine the roles of source host, test host and their interaction on survival rates (Glimmix Macro, SAS Version 8.2: SAS Institute, 2000). Source host, test host and their interaction were treated as fixed effects and year and population nested within source host were treated as random effects for the survival rate analysis.

3. Results and discussion

Development time showed a significant interaction between source host and test host such that beetles developed more quickly on their source host than the alternative host (Table 1, Fig. 2). For example, beetles collected from yellow toadflax developed faster on yellow toadflax than on Dalmatian toadflax. This suggests that there is a physiolog-

Table 1
Mixed-model analysis of the reciprocal transfer experiment^a

Effect	d.f.	F value	χ^2	Prob > F
<i>Development time</i>				
Source plant	1, 3.84	0.07	—	0.6704
Test plant	1, 106	0.71	—	0.4025
Source plant * test plant	1, 106	4.39	—	0.0385
Year	1	—	0	0.5000
Pop(source)	1	—	0	0.5000
<i>Pupal mass</i>				
Source plant	1, 3.12	0.32	—	0.8257
Test plant	1, 60.3	0.17	—	0.0129
Source plant * test plant	1, 64.0	1.58	—	0.2462
Year	1	—	9.0	0.0014
Pop (source)	1	—	2.2	0.0690
<i>Survival rate</i>				
Source host	1, 301	0.06	—	0.5749
Test host	1, 305	6.57	—	0.6772
Source plant * test plant	1, 304	1.37	—	0.2104
Year	1	—	6.9	0.0202
Pop (source)	1	—	0.5	0.5000
<i>Nos. flowers consumed</i>				
Source plant	1, 104	0.14	—	0.7083
Test Plant	1, 105	8.87	—	0.0036
Source plant * test plant	1, 104	1.03	—	0.3117
Year	1	—	0.9	0.1714
Pop (source)	1	—	0.0	0.5000

^a Mixed-model analyses of the reciprocal transfer 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. 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). The significance of each random effect is tested using likelihood ratio tests.

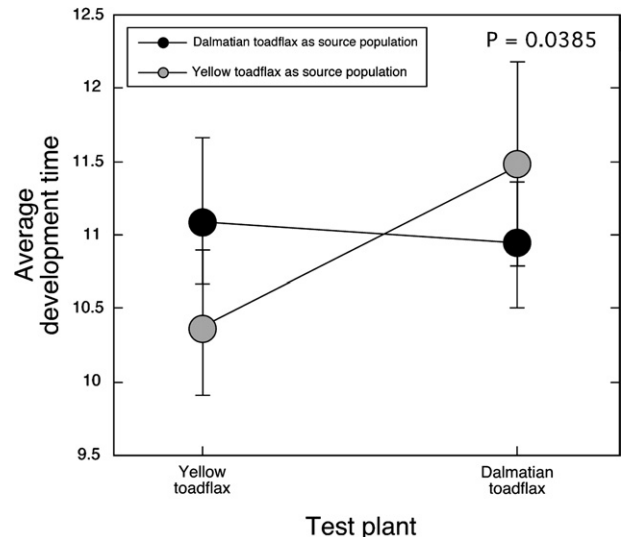


Fig. 2. The average development time (number days from first instar to pupa). CL of larvae collected from yellow toadflax and Dalmatian toadflax. Larvae showed a significant source host by test host interaction ($P = 0.0385$), providing evidence to support a physiological difference between beetles collected from yellow toadflax and Dalmatian toadflax.

ical difference between beetles collected from Dalmatian toadflax and those collected from yellow toadflax, and the success of redistribution efforts might be influenced both by

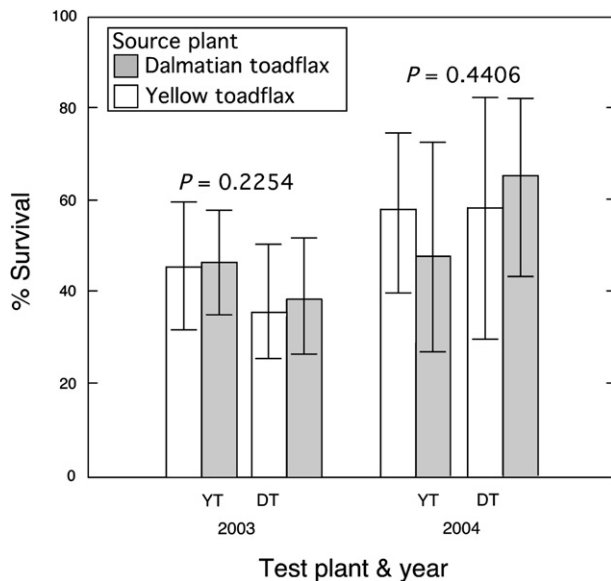


Fig. 3. Percent survival of *B. pulicarius* larvae when reared on their source host and the alternate host. *P* values are for the interaction source species by test species. There is no significant source host by test host interaction in years 2003 or 2004. Combine titles of footnotes.

the host from which beetles are collected and the host on which they are released. Independently, the main effects of source host and test host did not significantly affect the rate of larval development.

Unlike development time, pupal mass was not influenced by an interaction between source host and test hosts. Rather, all beetles grew, on average, 13% larger (0.965 mg vs. 0.839 mg) when reared on yellow toadflax, even those collected from Dalmatian toadflax (Table 1). This supports the hypothesis that beetles collected from either host would perform better on yellow toadflax, and suggests that it does not matter from which toadflax species beetles are collected; *B. pulicarius* will perform well on yellow toadflax and poorly on Dalmatian toadflax.

The third measurement, beetle survival rate, was not significantly influenced by which host the beetles were collected from, which they were tested on, or the interaction between the source host and test host (Table 1). This suggests that it does not matter from which species beetles are collected or released; all beetle collection sites will have similar survival rates on either host species. However, survival did differ between the two experimental years. Therefore, we ran the same statistical model for each year separately. Within the two years, survival again did not vary significantly by source host, test host, or their interaction (Table 1, Fig. 3). While this study was not designed to test why the survival rate might differ between years, our results may be due to the larger sample size in 2003 (232 individuals) than in 2004 (87 individuals), the number of collection sites used between years (8 locations vs. 4 locations), or the type of toadflax used (wild vs. potted) between years.

It is not uncommon for development time, pupal mass, and survival rate to exhibit different patterns

(Rauscher, 1984; Mayhew, 1998). There is evidence to suggest that each of these three developmental characteristics can be at least partially under separate genetic control in other phytophagous insects (Thompson, 1996). Pupal mass and survival rate most likely play a larger role in the overall fitness of *B. pulicarius* than development time for two main reasons. First, natural selection for a shorter development time is likely to be weaker for univoltine insects than for multivoltine insects (Tauber et al., 1986; Masaki and Walker, 1987; Ishihara, 1998), and *B. pulicarius* is univoltine in North America (Hervey 1927). Second, both adult size and survival rate tend to be strongly correlated with fitness for both male and female insects (Peters, 1983; Thornhill and Alcock, 1983; references therein). While this hierarchy of developmental characteristics may provide more support for the hypothesis that *B. pulicarius* larvae will perform better on yellow toadflax, it decreases the likelihood of finding beetle populations that would establish well on Dalmatian toadflax.

On average, larvae reared on yellow toadflax consumed approximately one more flower per larva (3.77 flowers vs. 2.87 flowers, Table 1), whether they were collected from Dalmatian toadflax or yellow toadflax. We did not quantify the amount of tissue consumed by each larva, thus this difference may reflect differences in flower size or in consumption rate. Yellow toadflax flowers and inner structures are smaller than those produced by Dalmatian toadflax (Saner et al., 1995; Vujnovic and Wein, 1997). We can, however, use these data as an indirect measure of the relative effectiveness of this beetle as a biological control agent on these two species of toadflax. The smaller number of flowers damaged when feeding on Dalmatian toadflax supports the view that *B. pulicarius* is likely to be a less effective biological control agent on Dalmatian toadflax than on yellow toadflax.

Collecting *B. pulicarius* from colonized patches of Dalmatian toadflax and releasing it on uncolonized patches of Dalmatian toadflax is a common and commercially successful practice. However, establishment of this beetle on Dalmatian toadflax is uncommon, even if beetles are originally collected from Dalmatian toadflax (Nowierski, 1992; Grieshop and Nowierski, 2002). The data presented here, along with the results in MacKinnon et al. (2005) illustrate two underlying factors that appear to play a role in the distribution of *B. pulicarius*. First, adult beetles from both hosts prefer yellow toadflax and therefore are not likely to remain on Dalmatian toadflax (MacKinnon et al., 2005). Second, the larvae of adults from both hosts grow larger, on average, on yellow toadflax and this is likely to slow the population growth of beetles that colonize Dalmatian toadflax relative to yellow toadflax. This higher preference for and performance on yellow toadflax suggests that establishment on Dalmatian toadflax is likely to remain low. Concentrating biological control efforts on candidate agents that show both a preference for and a performance advantage on Dalmatian toadflax and have the ability to cause direct mortality to existing plants, such as *Mecinus janthinus*

Germar (Coleoptera: Curculionidae) (De Clerck-Floate and Miller, 2002), should take higher priority than redistributing *B. pulicarius*.

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