CHAPTER 26

Biological Control of Invasive *Linaria* spp. in the Western United States

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NON-TECHNICAL SUMMARY

Anecdotal reports indicate that invasive yellow or common toadflax (*Linaria vulgaris*) and Dalmatian toadflax (*Linaria dalmatica*) (Plantaginaceae) were deliberately introduced to North America for ornamental purposes. They were also accidentally introduced as a seed contaminant, as was the case for many early-introduced invasive plants in North America (Mack, 1986, 2003; Mack and Erneberg, 2002; Lehan et al., 2013). In the absence of laws regulating the importation of exotic plants (as opposed to plant pests) into the United States, plant-lovers ranging from homesteaders and miners to horticultural enthusiasts imported and shared non-native flora, including toadflax (Mack, 2004). Widespread co-invasion by both toadflax species in North America resulted in their hybridization, which was first suspected in the early 2000s (Pauchard et al., 2003) and later molecularly confirmed in many western U.S. states (Ward et al., 2009; Boswell et al., 2016).

Most unintentionally introduced toadflax-specialist insects, as well as the approved toadflax biocontrol agents, were initially thought to exploit both *L. vulgaris* and *L. dalmatica*, with preferences for exact toadflax species becoming apparent only after insect establishment in North America (Sing et al., 2016; Smith et al., 2018). In response to this new understanding of agent specificity, concerted efforts were made to find, evaluate, and release host races or biotypes of previously approved toadflax biocontrol agents (Winston et al., 2022). Molecular diagnostics have confirmed the previous introduction of cryptic species, which in turn has explained localized issues with establishment and inconsistent efficacy of agents that, at the time of their introduction, were presumed to attack both *L. dalmatica* and *L. vulgaris* (Toševski et al., 2018). The earliest species introduced for control of toadflax (some flower- or seed-feeding beetles and a defoliating moth) provided minimal control. However, the more recent introductions and establishment of

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stem-mining insects have significantly suppressed toadflax populations throughout North America, which has resulted in widespread and sustained rangeland improvement, reduced weed management costs, and increased protection of non-target organisms.

HISTORY OF INVASION AND NATURE OF PROBLEM

The native range of yellow or common toadflax (*Linaria vulgaris*, Plantaginaceae) (**Fig. 1**) includes temperate areas of Europe and Asia, extending from Scandinavia and the British Isles through northern, central, and southern Europe including the Balkan and Mediterranean regions, to Turkey and southwestern areas in the Russian Federation and China (Saner et al., 1995; CABI, 2022; ISSG, 2022). *Linaria vulgaris* was imported for ornamental, medicinal, and textile dying purposes by early American settlers; it became naturalized in the eastern American colonies of England by 1671, and it was considered a significant agricultural weed both in the mid-western and eastern United States by 1849 (Darlington, 1849; Leighton, 1970; Mack, 2003). First reported in Canada in the early 1800s in southern Quebec, *L. vulgaris* became widespread in the North American prairie regions of Canada by the mid-1900s (Rousseau, 1968; Saner et al., 1995). Historically, *L. vulgaris* spread as a contaminant of crop seed, in baled hay, along railway corridors, and in the ballast of ships (Mitich, 1993; Saner et al., 1995; USDA-NRCS, 2022a). Dissemination of this species as a popular ornamental and medicinal plant was also facilitated by commercial nurseries and seed catalogs (Sing et al., 2016). It is now found throughout North America other than in the Canadian provinces of Nunavut and Labrador (USDA-NRCS, 2022a), and it is considered a nuisance or noxious species as far north and west as Yukon Territory in Canada and Alaska in the United States (Yukon Invasive Species Council, 2020; Alaska Department of Natural Resources, 2021).

Dalmatian toadflax (*Linaria dalmatica*) (**Fig. 2**) was reportedly first introduced in North America in the northeastern United States by 1894, approximately 200 years after *L. vulgaris* was first reported (Alex, 1962). This plant is a Eurasian species from the Mediterranean region, extending from the Balkans to Iran (Robocker, 1974). Like *L. vulgaris*, *L. dalmatica* was introduced as an ornamental plant, both in the United States (to Massachusetts in 1894) and Canada (to Ontario in 1901) (Hatfield, 1894, 1897; Macoun, 1908; Alex, 1962). Escape from horticultural settings has contributed to its current widespread distribution (USDA-NRCS, 2022b), infesting rangelands, open forests, and transportation corridors throughout North America (Lange, 1958; Robocker et al., 1972; De Clerck-Floate and Miller, 2002). The rapid westward spread of *L. dalmatica* is

Figure 1. Yellow toadflax, *Linaria vulgaris.* (Linda Wilson, University of Idaho, Bugwood.org CC BY-NC 3.0 US)

Figure 2. Dalmatian toadflax, *Linaria dalmatica.* (K. George Beck & James Sebastian, Colorado State University, Bugwood.org CC BY-NC 3.0 US)

confirmed by voucher specimens from populations that escaped cultivation: collected in California near Sturtevant Camp, Angeles National Forest in 1920, in Washington State near Spokane in 1926, and in Alberta in the towns of Bingen in 1927 and Edmonton in 1933 (Alex, 1962).

Persistent populations of hybrid toadflax (**Fig. 3**), which resulted from cross-pollination of *L. vulgaris* and *L. dalmatica*, have been confirmed since the late 2000s from many sites in Montana, Washington, Idaho, Wyoming, and Colorado, creating a third invasive toadflax target requiring additional management at some locations (Ward et al., 2009; Sing et al., 2016). Hybrid toadflax is not a single defined taxon and is more accurately described as a hybrid complex generated by ongoing cross-pollination between the two parent species (= first generation or F_1 hybrids), crosses of hybrids with other hybrids, and backcrosses of hybrids with one of the parent *Linaria* species (Boswell et al., 2016). Because *L. vulgaris*, *L. dalmatica*, and their hybrid offspring are persistent perennials, there are populations that consist of one or both parent species growing together with multiple-generational hybrids and backcrossed offspring. Controlling these genetically and taxonomically complex populations with biocontrol agents that have specific host preferences can be difficult.

Figure 3. Hybrid toadflax (center) between *Linaria vulgaris* (left) and *L. dalmatica* (right). (Elizabeth Goulet, Cornell University, Bugwood.org CC BY-NC 3.0 US)

WHY CONTROL THESE INVASIVE SPECIES?

Linaria vulgaris can economically harm pastures, rangeland, and cultivated fields, displacing desirable forage and crop plants such as wheat, canola, strawberries, and peppermint (Coupland et al., 1963; Harker et al., 1995; Baig et al., 1999; Volenberg et al., 1999; McClay and De Clerck-Floate, 2002). Yield reductions of 33% in the forage species red fescue (*Festuca rubra*), and 20% in canola and wheat have been recorded in association with yellow toadflax invasions (Darwent et al., 1975; O'Donovan and McClay, 1987; O'Donovan and Newman, 1989).

As a fire-adapted transformer species with the potential to reduce local diversity or transform ecosystems (D'Antonio et al., 2004), *L. dalmatica* has the ability to locally alter vegetation communities following fire (Dodge et al., 2008). Established *L. dalmatica* plants readily regrow from the roots even when their top growth sustains significant burn damage (Smith et al., 2021). Following wildfire, increases in *L. dalmatica* density, cover, reproduction, and distribution have been correlated with reductions in native plant species richness (Dodge et al., 2008) and displacement of native species of concern (Phillips and Crisp, 2001). Jacobs and Sheley (2003) found that prescribed fire increased *L. dalmatica* biomass and seed production without changing toadflax density or percent cover, but it reduced the cover of co-mingled perennial native forbs. *Linaria dalmatica* can also serve as an alternate host for some crop diseases such as Cucumber Mosaic Virus (Pariera Dinkins et al., 2007).

Hybrid toadflax might be a more difficult ecological and management problem than either parent species. Comparisons of *L. vulgaris* x *L. dalmatica* hybrids with the two *Linaria* parent species for traits contributing to invasiveness—including shoot length, flowering stem number, seed capsule production, aboveground biomass, seed germination, and seed viability—all found that hybrids consistently outperformed the parents (Turner, 2012). Results from the same common garden study found that superior adaptation to the local conditions by natural hybrid toadflax genotypes conferred competitive advantages such as earlier emergence from overwintering dormancy and higher rates of seedling germination (Turner, 2012). Species distribution models predict that hybrid toadflax may spread into regions where neither parent species has so far invaded. The potential for increased vigor and rapid adaptation in toadflax hybrids is likely to escalate their threat to native biodiversity in protected areas such as Yellowstone National Park (Pauchard et al., 2003; McCartney et al., 2019).

THE ECOLOGY OF THE PROBLEM

Linaria vulgaris has successfully invaded North American rangelands, grasslands, shrublands, wastelands, agricultural areas (cropland and pastures), and riparian zones subject to chronic, periodic, natural, or anthropogenic disturbance (Coupland et al., 1963; Darwent et al., 1975; Morishita, 1991; Pauchard et al., 2003; Sutton et al., 2007). Although *L. vulgaris* is generally considered a colonizer of disturbed areas, it has also invaded intact native plant communities in remote high-elevation wilderness areas (Sutton et al., 2007). In the Greater Yellowstone Ecosystem, *L. vulgaris* is one of the most invasive plant species, and it remains a significant threat to native biodiversity in open, human- or naturally- disturbed environments in protected areas of the Rocky Mountains (Pauchard et al., 2003).

New invasions of yellow toadflax typically originate from seeds, whereas expansion of established patches occurs primarily through vegetative reproduction (Nadeau et al., 1992; Pauchard et al., 2003). Seeds are produced mid- to late summer, averaging 1,500–30,000 seeds per plant annually, and seeds can remain viable in the soil seedbank for 8–10 years (Carder, 1963; Arnold, 1982). *Linaria vulgaris* is also vegetatively propagated by shoots produced by lateral roots and root fragments (Bakshi and Coupland, 1960; Charlton, 1966; Nadeau et al., 1992). Shoot growth can be initiated from root fragments as small as 10 cm (4 in) and from seedlings as young as three weeks old (Nadeau et al., 1991). Plants can produce 75–694 shoots (typically 90–100) from lateral roots in one growing season, and 200–250 by the second year, with the radius of established patches increasing an average of 1.22 m (4 ft) annually (Nadeau et al., 1991; Saner et al., 1995; Zouhar, 2003; Beck, 2014).

Linaria dalmatica is propagated sexually via seeds produced through obligate outcross pollination and vegetatively by buds formed on the roots of primary and secondary shoots (Vujnovic and Wein, 1997). Mature plants produce up to 500,000 seeds annually, from late June to December, with the seeds remaining dormant but viable in the soil for up to 10 years (Robocker, 1970). Seedling recruitment of *L. dalmatica* is likely limited more by interspecific competition than seed availability (Grieshop and Nowierski, 2002). Vegetative propagation can occur as early as 22 days after seedling emergence, from root and stem fragments as short as 10 mm (0.4 in) (Wilson et al., 2005).

The abundant, small, light-weight seeds of both *Linaria* species shatter out of seed capsules from late summer through winter, and seeds can be further dispersed by wind (Robocker, 1970; Nadeau and King, 1991). Seed viability is largely unaffected by consumption or digestion by livestock or wildlife (Robocker, 1970, 1974), so seed spread in animal droppings may account for isolated invasions or patches in apparently undisturbed areas (Sutton et al., 2007). Dual reproductive modes allow both *Linaria* species to colonize and dominate sites rapidly following disturbance (Pauchard et al., 2003; Dodge et al., 2008). Extensive root systems increase drought tolerance and therefore a competitive advantage over other plants (Sing and Peterson, 2011).

Hybridization between *L. vulgaris* and *L. dalmatica* facilitates introgression of adaptive genes that enhance fitness, expand ecological amplitude, and increase the invasive potential of hybrid and backcrossed genotypes (Ward et al., 2009; Turner, 2012). Gene transfer between invasive populations of both species may be more common than previously realized, as was evident by the frequency with which *L. vulgaris* DNA was detected in field-collected, putative *L. dalmatica* specimens (Boswell et al., 2016). Although *L. vulgaris* and *L. dalmatica* have slightly different habitat preferences (*L. dalmatica* is tolerant of poorer quality soil on dry, open slopes and *L. vulgaris* requires more fertile soil and moister growing conditions), hybrid toadflax readily exploits sites with marginal soil quality and minimal soil moisture, which are common features of Intermountain West rangelands (Boswell et al., 2016; McCartney et al., 2019).

Table 1. List of all biological control species recorded, released, or pending release in the United States, listed according to phase in the history of the toadflax biological control project.

Agent	Order	Site of attack	Introduction				
			Date	Location first record or release	Host found/ released on	Source location	Type of release
Phase 1: First U.S. records of accidentally introduced species							
Rhinusa antirrhini	weevil	seed capsules	1909	MA	yellow toadflax	unknown	adventive introduction
Brachypterolus pulicarius	beetle	flowers	1919	NY	yellow toadflax	unknown	adventive introduction
Rhinusa neta	weevil	seed capsules	1937	CT, NY, NJ, PA, VA, IA	yellow toadflax	unknown	adventive introduction
Rhinusa dieckmanni	weevil	seed capsules	2016–2018	MT	Dalmatian toadflax	unknown	adventive introduction
Phase 2: Introduction of first regulated toadflax biocontrol agent							
Calophasia lunula	moth	foliage	1968	WA	yellow toadflax	Switzerland, via Canada	intentional introduction
Phase 3: Intentional introduction of host-specific biotypes of established agents							
Calophasia lunula	moth	foliage	1990–93	MT, CO, WY, ID	Dalmatian toadflax	Missoula, MT	intentional introduction
Brachypterolus pulicarius	beetle	ovary/ flowers	1992	MT	Dalmatian toadflax	Kamloops, BC	intentional introduction
Rhinusa antirrhini	weevil	seed capsules	1992	MT	Dalmatian toadflax	Canada	intentional introduction
Rhinusa antirrhini	weevil	seed capsules	1996	MT	Dalmatian toadflax	former Yugoslavia	intentional introduction
Phase 4: Intentional introduction of root- or stem-attacking biocontrol agents							
Eteobalea intermediella	moth	roots	1996	MT	Dalmatian toadflax	former Yugoslavia	intentional release
Eteobalea serratella	moth	roots	1996	MT	yellow toadflax	Italy	intentional release
Rhinusa linariae	weevil	roots	1996	MT, WY	yellow toadflax	Rhine Valley, Germany	intentional release
Mecinus janthinus	weevil	stems	1997	MT	yellow toadflax	Germany/France *and* Germany/ France, via Canada	intentional release
Mecinus janthiniformis	weevil	stems	2001	MT	Dalmatian toadflax	former Yugoslavia, via Canada	intentional release
Phase 5: Intentional introduction of cold-adapted agents							
Rhinusa pilosa	weevil	stems	2019	MT	yellow toadflax	Serbia *and* Serbia, via Canada	intentional release
Rhinusa rara	weevil	stems	pending				
Mecinus peterharrisi	weevil	stems	pending				

PROJECT HISTORY THROUGH AGENT ESTABLISHMENT

The history of the toadflax biocontrol project in the United States evolved through five distinct phases and associated insect species or biotypes (**Table 1**). In the first phase, three exotic toadflax seed- or flower-feeding beetle species invaded North America before efforts began to manage invasive toadflax through regulated classical biological control (Smith, 1959). The first recorded unintentional introduction, in 1909, was of the seed capsule-feeding weevil *Rhinusa* (formerly *Gymnetron*) *antirrhini* (Coleoptera: Curculionidae) (**Fig. 4**). It was first recorded in North America as a Massachusetts field-collected specimen in 1909 (Smith, 1959). Specimens collected in Montreal, Quebec and added to the Canadian National Collection in 1917 represent the first Canadian records for this species (Smith, 1959). *Rhinusa antirrhini* was collected during surveys conducted 1951–57 in British Columbia, Washington, Idaho, and Montana (Smith, 1959). Another seed capsule-feeding weevil, *Rhinusa neta* (**Fig. 5**), first recorded in the United States in 1937 from collections made in Connecticut, New York, New Jersey, Pennsylvania, Virginia, and Iowa, was found to be established in Washington and British Columbia by 1955 (Smith, 1959). Field surveys conducted between 1950 and 1959 found that both of these species were primarily associated with *L. vulgaris* in North America (Smith, 1959; Harris, 1961).

Rhinusa antirrhini collected from *L. dalmatica* ssp. *macedonica* was intentionally introduced to Canada in 1993 and thereafter to the United States in 1996 for biological control of *L. dalmatica* (Winston et al., 2022). *Rhinusa neta* was investigated for its toadflax biocontrol potential by CABI Switzerland in 1996–2001, but the species was never formally petitioned for field release in the United States (Pitcairn et al., 2021). This species was likely not formally pursued as a permitted biocontrol agent due to its perceived limited North American distribution (Smith, 1959; Nowierski, 1995). Recent surveys have found *R. neta* associated with *L. dalmatica* in multiple locations in Montana (I. Toševski, pers. comm.) and California (Pitcairn et al., 2021), well outside of its known historic western North American distribution (Smith, 1959).

Another unintentional introduction, recorded in 1919, was of the ovary-feeding beetle *Brachypterolus pulicarius* (Coleoptera: Kateretidae) (**Fig. 6**). This

Figure 4. Toadflax seed capsule-feeding weevil *Rhinusa antirrhini* (Coleoptera: Curculionidae). (Richard W. Hansen, USDA-APHIS-PPQ, Bugwood.org CC BY-NC 3.0 US)

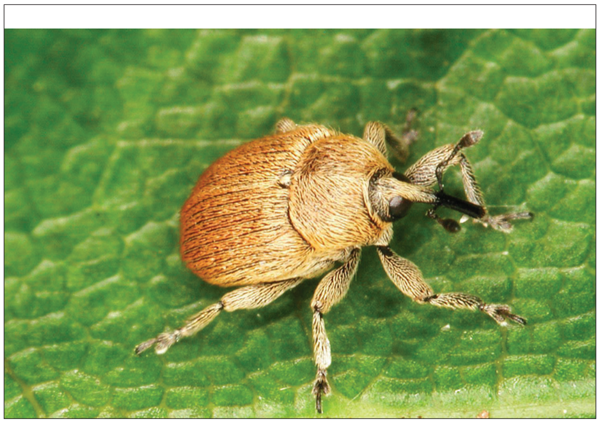

Figure 5. Toadflax seed-feeding weevil *Rhinusa neta* (Coleoptera: Curculionidae). (Gyorgy Csoka, Hungary Forest Research Institute, Bugwood.org CC BY-NC 3.0 US)

Figure 6. Toadflax ovary-feeding beetle *Brachypterolus pulicarius* (Coleoptera: Kateretidae). (Daniel K. MacKinnon, Colorado State University, Bugwood.org CC BY-NC 3.0 US)

beetle was reported in 1922 as a potential (but eventually unsubstantiated) economic pest due to its presence in damaged strawberry blossoms in the Hudson River Valley of New York. It was subsequently recorded in the flowers of *L. vulgaris* and other plants (Hervey, 1927). *Brachypterolus pulicarius* was collected in 1992 from naturally-established populations on *L. dalmatica* in British Columbia. It was later purposefully released on *L. dalmatica* in Montana, where the beetle successfully overwintered and was recovered from all release sites in 1993 (Nowierski, 1995). This species is now ubiquitous in Canada and the United States on both toadflax species (MacKinnon et al., 2005).

Due to the poor control of toadflax species by seed and flower-feeding species, agents with different sites of action were sought to check the continued, rapid spread of *L. vulgaris* in western Canada (Darwent et al., 1975). Survey efforts by scientists at CAB International led to the collection of the defoliating moth *Calophasia lunula* (Lepidoptera: Erebidae) (**Fig. 7**) from *L. vulgaris* in Switzerland. Following host specificity testing, this moth was released in Canada between 1962 and 1968 (Harris and Carder, 1971), and later in the United States. Initial establishment was restricted to *L. vulgaris* (Harris and Carder, 1971). Individuals collected from *L. dalmatica* in the former Yugoslavia were released in 1988 on *L. dalmatica* in British Columbia and Saskatchewan (Winston et al., 2022). The establishment of *C. lunula* on *L. dalmatica* in North America was first reported in 1989 near Missoula, Montana, when larvae were accidentally discovered feeding on roadside *L. dalmatica* plants (McDermott et al., 1990).

Nearly three decades after the intentional release of *C. lunula*, intensification of the toadflax problem in the western United States and Canada led to a concerted joint effort to identify, test, and gain approval for the release of new toadflax biocontrol agents (Nowierski, 1995). Out of the pool of potential agents identified, permits were approved for the release of four new agent species in North America: the two root-boring moths *Eteobalea intermediella* and *E. serratella* (Lepidoptera: Cosmopterigidae) (**Fig. 8**), the root-galling weevil *Rhinusa* (= *Gymnetron*) *linariae* (Coleoptera: Curculionidae) (**Fig. 9**), and the stem-mining weevil *Mecinus janthinus* (Coleoptera: Curculionidae) (**Fig. 10**) (Nowierski, 1995; De Clerck-

Figure 7. Toadflax defoliating moth *Calophasia lunula* (Lepidoptera: Erebidae) larva. (Gary L. Piper, Washington State University, Bugwood.org CC BY-NC 3.0 US)

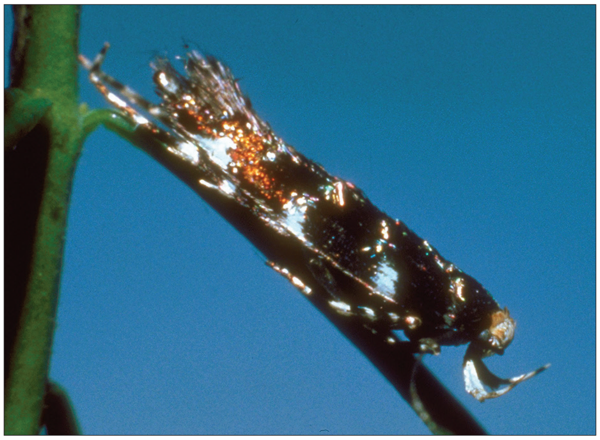

Figure 8. Yellow toadflax root-boring moth *Eteobalea serratella* (Lepidoptera: Cosmopterigidae). (Robert M. Nowierski, Montana State University, Bugwood.org CC BY-NC 3.0 US)

Figure 9. Toadflax root-galling weevil, *Rhinusa linariae* (Coleoptera: Curculionidae). (Bob Richard, USDA-APHIS-PPQ, Bugwood.org CC BY-NC 3.0 US)

Floate and Harris, 2002; McClay and De Clerck-Floate, 2002). These species were selected from the larger pool of potential agents for two reasons. First, no native North American root borers or stem miners were known to attack *L. vulgaris* or *L. dalmatica*. Second, root borers and stem-mining insects were believed to have greater potential for control of toadflax than the defoliators and seed/flower feeders already established in North America (Jeanneret and Schroeder, 1992; Saner and Müller-Schärer, 1994).

Figure 10. Toadflax stem-mining weevil *Mecinus janthinus* s.l. (Coleoptera: Curculionidae). (Bob Richard, USDA-APHIS-PPQ, Bugwood.org CC BY-NC 3.0 US)

Possibly due to their cryptic nature, widespread establishment of the three root-attacking agents has not yet been confirmed in North America (Winston et al., 2022). In 2002, researchers were unable to confirm the continued survival of an *E. intermediella* colony considered established from a 1998 release on *L. dalmatica* in Kamloops, British Columbia (De Clerck-Floate and Turner, 2013). Similarly, although larvae were found one year after a 1995 *E. serratella* release on *L. vulgaris* at Kinsella, Alberta, there was no indication of its continued establishment when the site was resampled in 2007 (De Clerck-Floate and McClay, 2013). Beginning in 2001, *R. linariae* weevils reared from Kamloops, British Columbia propagation plots were abundant enough to make additional field releases on *L. vulgaris* in British Columbia and Alberta (De Clerck-Floate and McClay, 2013) and, later, in Colorado (Winston et al., 2022). Successful overwintering was observed in Colorado in 2016; however, long-term establishment has yet to be confirmed. *Rhinusa linariae* is well-established on *L. vulgaris* at some locations in British Columbia; however, populations have been slow to build and are not widely distributed (Winston et al., 2022).

Twenty-five years after its initial North American release, *M. janthinus* has become widely distributed throughout southwestern and eastern Canada, and the northwestern United States through natural dispersion and active redistribution (Toševski et al., 2018; Winston et al., 2022). Most of the weevils imported under this name from Europe for release in North America are now known to have been *M. janthinus* collected from *L. vulgaris* populations in Western Europe (DeClerck-Floate and McClay, 2013; Toševski et al., 2018). Records indicate that in 1997, 200 weevils of a second, cryptic species (now known to have been *Mecinus janthiniformis*) collected from *L. dalmatica* in Macedonia were shipped for release in Canada (DeClerck-Floate and Turner, 2013; Toševski et al., 2018). This single shipment of *M. janthiniformis* is now believed to have eventually led to outbreak-level populations on *L. dalmatica* throughout western North America (Toševski et al., 2011).

Figure 11. Yellow toadflax stem-galling weevil *Rhinusa pilosa* (Coleoptera: Curculionidae). (R.K.D. Peterson, Montana State University)

Climatic factors in North America, including effects of extreme cold temperatures and lack of insulating snow cover on the overwintering survival of *M. janthiniformis* on *L. dalmatica* (De Clerck-Floate and Miller, 2002) and too short a growing season for *M. janthinus* on yellow toadflax (McClay and Hughes, 2007), spurred a search for additional toadflax biocontrol agents in the 1990s. Several new stem-galling *Rhinusa* weevils, including the closely related *Rhinusa pilosa* on yellow toadflax (**Fig. 11**) and the newly described *Rhinusa rara* on Dalmatian toadflax, were confirmed to be highly host-specific species with good potential as biocontrol agents (Toševski et al., 2015). Newly emerged *R. pilosa* adults aestivate during the hottest part of late summer and then overwinter in leaf litter (Gassmann et al., 2014), which provides them better protection from climatic fluctuations than is the case for the earlier established *Mecinus* species, which are susceptible to freeze-thaw extremes from late fall through late spring and desiccation or physical destruction (when overwintering *Mecinus* adults are in standing toadflax stems). Although *R. pilosa* has been established in Alberta since 2015 (British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development, 2018a), releases made at two sites in southwestern Montana in August 2020 resulted in the first populations of *R. pilosa* to successfully overwinter in the United States, producing galls in 2021 (S. Sing, pers. obs.). *Rhinusa pilosa* adults sourced from a Montana garden-based mass rearing program were released for the first time in 2021 in Oregon, North Dakota, and South Dakota, and at new locations in Montana (S. Sing, unpub. data). Additional *Mecinus* species are also being investigated to discover agents potentially better matched to *L. dalmatica* populations at high-elevation, cooler sites (i.e., *M. peterharrisi*) and for biocontrol of hybrid toadflax and *L. vulgaris* (i.e., *M. heydeni*) (Sing et al., 2016).

HOW WELL DID IT WORK?

Rhinusa antirrhini

A noticeable reduction in *L. vulgaris* infestations in western Canada in the 1950s was attributed to regional build-ups of *B. pulicarius* and *R. antirrhini*, which together exerted population-level impacts on the host weed *L. vulgaris* (Harris, 1961; Darwent et al., 1975). However, attack by *R. antirrhini* alone has not been demonstrated to control *L. vulgaris*.

Brachypterolus pulicarius

Under controlled conditions, exposure of *L. vulgaris* to *B. pulicarius* resulted in significant reductions in total and individual seed weight, percent germination of seeds, and percent viable seeds produced (McClay, 1992). Reductions in stem height, increases of 77% and 95%, respectively in the number of primary and secondary branches, reductions in flower number on a per plant basis of 44–49%, and a 43–93% reduction in seed production were reported for *L. dalmatica* exposed to *B. pulicarius* individuals collected in Kamloops, British Columbia from an adventive population of the beetles established on Dalmatian toadflax (Nowierski, 1995; Grubb et al., 2002). While McClay (1992) found that *B. pulicarius* can reduce flowering and seed production, this beetle generally does not exert enough pressure on plants to effectively control either toadflax species under field conditions.

Calophasia lunula

Although up to 20% defoliation of *L. vulgaris* by larvae of this moth was observed in Ontario (Harris, 1984), only minimal impact was recorded on plant density, possibly because parasitism of the moth's pupae can reach 90% at some sites (McClay and Hughes, 1995). Because defoliation on either toadflax species is seldom lasting, damage by this species alone does not control invasive toadflax.

Eteobalea intermediella, E. serratella, and *Rhinusa linariae*

It has not been possible to assess the impact of either *E. intermediella* or *E. serratella* because long-term North American field establishment has not yet been confirmed for either species (De Clerck-Floate and

Turner, 2013; De Clerck-Floate and McClay, 2013). In an experiment designed to evaluate the potential efficacy of *E. serratella* for control of *L. vulgaris* in commercial mint fields, potted *L. vulgaris* plants receiving the combination of root-mining by the moth *E. serratella* and interspecific competition from inter-planted mint showed reductions in number, weight, and rate of shoot regrowth, following simulated harvest of the mint crop by stem cutting (Volenberg et al., 1999). After multiple field releases of the two *Eteobalea* species resulted in the failure of either species to become truly established, no further attempts were made to establish either of these root-boring moths in the United States or Canada. Consequently, the potential efficacy of *E. serratella* to control *L. vulgaris* infesting mint fields has not yet been field-tested.

In contrast, the third root-feeding species, the beetle *R. linariae*, successfully established in British Columbia where adults feeding on foliage and larvae galling roots both reduce *L. vulgaris* nutrient reserves (British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development, 2018b). This has led to heavy impact on *L. vulgaris* in the immediate vicinity of release sites. However, *R. linariae* populations are slow to build and slow to disperse on their own if *L. vulgaris* patches are widely scattered, so redistributions are made manually every 2–4 years (Winston et al., 2022). *Rhinusa linariae* beetles from British Columbia were shipped to Colorado in 2008 and 2015 to initiate insectaries there for redistribution in the United States. This weevil has successfully overwintered at one Colorado release site, but long-term establishment has not been confirmed (A. Norton, pers. comm.).

Mecinus janthinus/M. janthiniformis

Mecinus janthinus populations were slow to build up in both Canada and the United States compared to the rapid, obvious establishment of *M. janthiniformis* (McClay and De Clerck-Floate, 2002; Toševski et al., 2018), and consequently few studies have evaluated the impact of *M. janthinus*. However in Montana, wherever *M. janthinus* became established (either through intentional releases or natural dispersal), a consistent and dramatic decline in *L. vulgaris* abundance has been observed (S. Sing, unpub. data). *Mecinus janthinus* failed either to establish or significantly increase in number at some locations in western Canada and the western United States despite multiple releases (De Clerck-Floate and McClay, 2013; Sing et al., 2016).

In contrast, for *M. janthiniformis*, studies have documented important reductions in *L. dalmatica* biomass and flower and seed production per m^2 (Goulet et al., 2014). Suppression of seasonal stem height growth (Goulet et al., 2013) has also been attributed to attack by *M. janthiniformis*. Similarly, Cariveau and Norton (2014) found reductions in the number of flowers (33%) and seeds (38%) per plant in Dalmatian toadflax subjected to larval feeding by *M. janthiniformis*, compared to control plants. Larval feeding by *M. janthiniformis* is thought to disrupt water and nutrient transport in infested *L. dalmatica* stems. This disruption results in growth inhibition (Schat et al., 2011) and reduction in photosynthesis and transpiration, leading to a reduction in resources available for flower production (Peterson et al., 2005).

In western Canada, the impact of *M. janthiniformis* on *L. dalmatica* has been demonstrated by the regional dispersal of the agent, significant decline in host plant size and density, and widespread fragmentation of host plant patches (Van Hezewijk et al., 2010). The strongest impacts of *M. janthiniformis* on *L. dalmatica* have typically been seen at release sites where environmental factors, such as higher precipitation, are particularly favorable. Such conditions allow greater increases in agent numbers (Weed and Schwarzländer, 2014). In general, the warmer conditions that are commonly found in British Columbia, Utah, and California (Willden and Evans, 2019; Smith et al., 2021) are also more favorable than those typical of Montana and Alberta (De Clerck-Floate and Miller, 2002; Sing et al., 2008; De Clerck-Floate and Turner, 2013).

Parasitism is another factor influencing the success of biological control by species of *Mecinus*. The first New World record for the Palearctic species *Pteromalus microps* (Hymenoptera: Pteromalidae), which was recovered in Wisconsin from populations of *R. antirrhini* on *L. vulgaris*, was assumed to be the result of the adventive introduction of the parasitoid (Volenberg and Krauth, 1996). This parasitoid was later reported from several sites where *M. janthinus* had been released on *L. vulgaris* in Alberta (McClay and De Clerck-Floate, 2002). Parasitism of *Mecinus* spp. by various parasitoid species has been reported with increasing frequency in the United States in recent years (Willden and Evans, 2019), with the generalist weevil ectoparasitoid *Neocatolaccus tylodermae* (Pteromalidae) being the most commonly recovered species to date, having been recorded from both *M. janthinus* and *M. janthiniformis* (Karimzadeh et al., 2021).

Host Races or Biotypes

The possibility that geographically disparate populations of toadflax-feeding insect species occurring either on *L. dalmatica* or *L. vulgaris* may have evolved distinct host races in response to the locally prevalent *Linaria* species has been investigated. This work eventually resulted in permits to import and release or redistribute host races or host specific biotypes of *B. pulicarius* and *R. antirrhini* (Groppe, 1992; De Clerck-Floate and Harris, 2002; Nowierski, 2004; USDA-APHIS, 2022). Although *B. pulicarius* has been field collected from both invasive toadflax species, even the individuals that naturally established on *L. dalmatica* demonstrated a consistent preference for *L. vulgaris* (MacKinnon et al., 2005). However, molecular analyses were unable to detect any significant genetic differentiation based on host plant association in *B. pulicarius* (Hufbauer and MacKinnon, 2008).

Cryptic Species

As stated previously, based on the results of overseas host-specificity testing, the toadflax stem-mining weevil *M. janthinus* was considered a single species that non-preferentially attacked both *L. vulgaris* and *L. dalmatica*, and it was approved for release in Canada and the United States for biological control of both invasive toadflax species (Jeanneret and Schroeder, 1992; De Clerck-Floate and Harris, 2002; McClay and De Clerck-Floate, 2002). Morphological, molecular, and biological evidence has since shown that in its native range, the agent originally known as *M. janthinus* is two closely-related species that are ecologically segregated by host plant (Toševski et al., 2011, 2013). The native ranges of *M. janthinus* and *M. janthiniformis* do not overlap, reflecting the separate distributions of their natural hosts in central and southern Europe, southern Russia, and southwestern Asia (Jeanneret and Schroeder, 1992; Toševski et al., 2011, 2013). Molecular and morphological analyses confirmed that *Mecinus* weevils currently established on North American toadflax commonly belong to haplotype groups present in the native ranges of their populations (Toševski et al., 2018).

Field and garden observations have suggested a strong preference in North American *R. antirrhini* populations for *L. vulgaris* (Smith, 1959). Host-specificity testing of a potential *L. dalmatica* host race or biotype of *R. antirrhini* found that host acceptance and performance for beetles collected from Dalmatian toadflax in the former Yugoslavia were higher on test plants of *L. dalmatica* that originated from Canada compared to *L. vulgaris* plants of European origin (Groppe, 1992; De Clerck-Floate and Harris, 2002). Analyses of *R. antirrhini* collected across its European native range from five *Linaria* species or subspecies concluded that structuring of genetic variation was best explained by the host plant of field-collected specimens rather than their geographic distribution (Hernández-Vera et al., 2010). A contemporaneous phylogeny of the genus *Rhinusa*, based on adult morphological characters and host plants, grouped *R. antirrhini* with *Rhinusa dieckmanni* (Caldara et al., 2010). Molecular information on *R. antirrhini* s.l. collected from *L. dalmatica*, *L. dalmatica* ssp. *macedonica*, and closely related species at multiple locations in the European native range, and from *L. dalmatica* in Montana in the United States suggests that *Rhinusa* spp. individuals found on *L. dalmatica* and its closest non-*L. vulgaris* relatives are more likely to be *R. dieckmanni* than *R. antirrhini* (I. Toševski, unpub. data).

Non-Target Attack

Rhinusa neta, a toadflax seed-feeding weevil that was unintentionally introduced to North America and recorded in the United States since 1937 and in Canada since 1957 (Smith, 1959), has never been permitted for collection and redistribution (Pitcairn et al., 2021). Host specificity of *R. neta* assessed by CABI-Switzerland beginning in 1996 found that the weevil could successfully complete development on several non-native *Linaria* species (*L. vulgaris*, *L. dalmatica*, *L. supina*, *L. reflexa*, and *L. purpurea*) as well as on the California endemic species *Neogaerrhinum strictum* (USDA-NRCS, 2022c; ITIS, 2022) and the annual invasive species *Chaenorrhinum minus* (dwarf snapdragon) (Gassmann and Paetel, 1998; Gassmann, 2001). *Chaenorrhinum minus*, reportedly introduced and disseminated throughout North America in ballast material that was subsequently re-used in transcontinental railway beds (Arnold, 1981, 1991), is now established throughout North America (USDA-NRCS, 2022d). It provides a widely available alternative food source that may facilitate the distribution of this oligophagous herbivore. In recent years, *R. neta* has also been collected from the seed capsules of another endemic species, *Sairocarpus virga* (USDA-NRCS, 2022e), in five California counties (Pitcairn et al., 2021).

Host-specificity testing under controlled conditions showed that the larval stage of the toadflax-defoliating moth *C. lunula* fed on (Karny, 1963), and to a limited extent was able to complete development on (Harris, 1963), three non-target ornamental species: *Antirrhinum majus* (common snapdragon), *Cymbalaria muralis* (Kenilworth ivy), and *Linaria maroccana* (Moroccan toadflax). The former species is ubiquitous throughout North America, while the latter two have escaped cultivation in various U.S. locations, including California (USDA-NRCS, 2022f,g,h). *Calophasia lunula* is also able to complete development on the California endemic species *S. virga* (Wilson et al., 2005). In this context, the risk of non-target attack on *S. virga* is likely amplified by the presence of abundant additional hosts, including *L. dalmatica*.

Hybrid Toadflax

Data and qualitative observations indicate that the stem-mining weevils *M. janthinus* and *M. janthiniformis* are currently the best widely available classical biological control agents for managing *L. vulgaris* and *L. dalmatica* (Sing et al., 2016; Willden and Evans, 2019; Smith et al., 2021). Both species exhibit extreme fidelity to their natural (native range) host, seldom developing or establishing on the other non-host invasive toadflax species (Toševski et al., 2011, 2018). Hubbard (2016) reported a probable olfactory basis for this observed host fidelity, finding a significant correlation between the semiochemical profile of respective natural hosts and host acceptance in female weevils of both *Mecinus* species. Preliminary tests under containment conditions indicate that a yellow toadflax semi stem-galling weevil, *Mecinus heydeni*, was able to recognize, accept, and successfully develop on its natural host and a range of field-collected and hand-crossed hybrid toadflax genotypes, but it fully rejected *L. dalmatica* as a host for feeding or oviposition (Sing et al., 2016).

BENEFITS OF BIOLOGICAL CONTROL OF INVASIVE TOADFLAXES

Published post-release evaluations of biological control of *L. dalmatica* by *M. janthiniformis* in Canada and in the United States report that successful establishment and build-up of agent populations were correlated with significant reductions in stem length, density, and cover, as well as plant biomass and seed production of the target toadflax species (Van Hezewijk et al., 2010; Jamieson et al., 2012; Weed and Schwarzländer, 2014; Weed et al., 2018; Smith et al., 2021). As stated above, similar accounts of *M. janthinus* suppression of *L. vulgaris* have not yet been widely published, although anecdotal reports of both the target weed and agent disappearing from previously productive collection sites are not uncommon in Montana, where it first became established in the United States (M. Maggio, pers. comm.).

Although permitting of any weed biological control agent requires documentation of stringent host specificity, this aspect of toadflax biological control is also one of its main benefits, in that direct non-target effects and collateral damage are not risks associated with the use of this management tool. The high level of treatment selectivity conferred by toadflax biological control is particularly important when plant species of concern (e.g., Flagstaff pennyroyal, *Hedeoma diffusum* [Phillips and Crisp, 2001]) or of economic value (e.g., peppermint [Volenberg et al., 1999]) are intermingled with *L. dalmatica* or *L. vulgaris*.

Finally, once established, toadflax biological control systems can function as sustainable components of integrated weed management. This is particularly important when weed infestations occur at a landscape scale on low-value land, necessitating the use of low- or no-cost and reduced-input weed treatments. *Mecinus janthiniformis*' ability to self-distribute effectively allows for control of unrecorded or undetected toadflax populations and the re-establishment of agent populations on *L. dalmatica* infestations that often dominate sites following wildfire.

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