2005

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EVALUATION OF ECOLOGICAL RISK TO POPULATIONS OF A THREATENED PLANT FROM AN INVASIVE BIOCONTROL INSECT

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Abstract. Controversy exists over estimation of ecological risk in biological control. At present, the risk to the rare, federally listed Pitcher's thistle (*Cirsium pitcheri*) in North America from *Rhinocyllus conicus*, a biological control weevil now feeding on many native thistles, is unknown. We hypothesized that quantification of host specificity and potential phenological overlap between insect and plant would improve assessment of the magnitude of risk. In laboratory host specificity tests, we found no significant difference in *R. conicus* feeding or oviposition preference between the rare *C. pitcheri* and the targeted exotic weed (*Carduus nutans*) or between *C. pitcheri* and Platte thistle (*C. canescens*), a closely related native North American species known to be affected by *R. conicus*. In a garden environment, *R. conicus* spontaneously found, oviposited, and developed completely on *C. pitcheri*. Taller plants with more flower heads were significantly more vulnerable, suggesting that the greatest impact is likely to be on individuals that generally contribute the most to recruitment and population persistence. For eight sites in two national parks over three years, the calculated period of expected *R. conicus* activity overlapped 99% and 78% of the flower heads initiated by *C. pitcheri* in the southern and the northern park, respectively. A demographic model suggests that population growth rate (λ) of *C. pitcheri* will decrease from 0.9897 to 0.8686, while time to halve the population will decrease from 66.9 to 4.9 years, under the conservative assumption that oviposition by *R. conicus* on *C. pitcheri* will occur at the same rate as on the related *C. canescens*. Calculated decreases in λ and $t_{0.5}$ are larger if the rate of oviposition actually observed in the laboratory tests is used. These results indicate that the weevil poses a serious quantitative, demographic risk to the threatened *C. pitcheri*. The study supports the suggestion that ecological data can be used to improve the quantification of risk to native nontarget plant populations within the potential physiological host range of a biological control insect.

Key words: Cirsium pitcheri; ecological risk assessment; insect–plant interactions; nontarget effects; plant demography; rare plants; Rhinocyllus conicus.

INTRODUCTION

Increased awareness of the threat posed by invasive exotic plants to natural and agronomic ecosystems (McKnight 1993, Office of Technology Assessment 1993, 1995, Pimentel et al. 2000, National Research Council 2002, Myers and Bazely 2003) has renewed interest in the potential of classical biological control to limit exotic weed densities (Kauffman and Nechols 1992, Hokkanen and Lynch 1995, Pimentel 1995, Delfosse 2000). Classical biological control involves the introduction of exotic species, usually insects, as natural enemies of the weed (DeBach and Rosen 1991, Van Driesche and Bellows 1996). However, controversy continues over the ecological risks associated

with such introductions (Hoddle 2004, Louda and Stiling 2004). While viewed as a ''reestablishment of natural enemies'' (Hoddle 2004), the process by definition involves the deliberate introduction of alien species into new communities in new environments. Quantification of the associated risks is still a scientific frontier.

Few dispute that deliberate introductions of any exotic species entail a risk (Simberloff 1981, 1992, Turner 1985, Howarth 1991). The controversy is over the magnitude of the risk and over the information needed to evaluate it (Simberloff and Stiling 1996, 1998, Frank 1998, Marohasy 1998, McFadyen 1998, Strong and Pemberton 2001, Arnett and Louda 2002, Hoddle 2004, Louda and Stiling 2004). In weed projects, where host specificity tests are now standard (McEvoy 1996, Secord and Kareiva 1996, Thomas and Willis 1998), the controversy revolves around the degree to which current protocols characterize and quantify the likely mag-

nitude of ecological risk to native species (Gonzalez and Gilstrap 1992, Simberloff and Stiling 1996, 1998, Frank 1998, Marohasy 1998, McFadyen 1998, Louda 1999, 2000a, Schaffner 2001, Arnett and Louda 2002, Louda et al. 2003a).

A critical, unresolved issue is the degree to which the host specificity paradigm, used to predict the host range of the exotic insect, can also be used to predict the actual magnitude of the ecological risk to a native species identified as a partial, less preferred, or secondary host in the testing. The preference and performance tests that form the host specificity evaluation compare insect response to a phylogenetically centrifugal series of plant species (McEvoy 1996, Thomas and Willis 1998, Schaffner 2001). Relative performance of individuals in these tests is used to define the species' "physiological host range" (Pemberton 2000b, Louda et al. 2003b). When some feeding or oviposition occurs on native plant species in these trials, relative preference and performance have been used to infer the magnitude of the threat expected in the field, or "ecological host range" (e.g., Zwölfer and Harris 1984, McClay 1990, Blossey et al. 1994).

However, recent findings of unexpected or unexpectedly large ecological effects in the field caused by insect weed control agents (Louda et al. 1997, Callaway et al. 1999, Pearson et al. 2000, Louda and O'Brien 2002) suggest that additional criteria are needed to estimate the likely ecological host range and impact subsequent to host specificity tests that show native species are accepted as secondary hosts (Louda 1999, 2000a, Arnett and Louda 2002, Benson et al. 2003, Louda et al. 2003a, b). If risk is defined as the product of hazard and exposure (Bouskila and Blumstein 1992, Secord and Kareiva 1996), then host specificity can be viewed as one measure of potential hazard from an exotic insect. However, additional data appear necessary to quantify likely exposure, the expected intensity of interaction, and so the total risk to native species.

Parameters that influence interaction intensity of herbivores with their host plants have been proposed as additional criteria for exposure, and so the prediction of ecological host range (Louda et al. 1998, 2003a, b, Louda 1999, 2000b). Multiple studies of plant–insect interactions have suggested that phenological synchrony, the relative timing of development of insect and potential host plant species, can explain a large portion of the variation in insect impact on plant performance and population impacts, including for thistle–insect interactions (Goeden and Ricker 1986a, b, 1987a, b, Maddox et al. 1991, Louda 1998, 2000a, Herr 2000, Russell and Louda 2004; F. L. Russell and S. M. Louda, *unpublished manuscript*). Thus, we hypothesized that evaluation of the expected phenological synchrony, in addition to host specificity testing as a fundamental dimension of exposure and ecological host range estimation, would increase the precision of the assessment of potential ecological impact on listed species

from a biological control insect, at least within the ecological time frame. The system in which we evaluated this hypothesis takes advantage of an extensive existing database (e.g., Louda 2000a, Gassmann and Louda 2001), which includes the best quantification available to date of the demographic effects of nontarget feeding by a biological weed control agent.

This study had two major aims. The first aim was to quantify probable risk to the rare Pitcher's thistle (*Cirsium pitcheri* [Torr.] Torrey & Gray), which is listed as federally "threatened" in the USA and "endangered" in Canada, from *Rhinocyllus conicus* Frölich, a weevil introduced for the biological control of exotic thistle species; this weevil has become invasive on native thistles in sand prairies of the central USA (Louda et al. 1997, 1998, Louda 1998, 2000a). To date, *R. conicus* has not been reported from Pitcher's thistle habitat in the intermittent sand dune ecosystem along the shores of the Great Lakes of North America (U.S. Fish and Wildlife Service 2002). However, it now occurs both north and south of these populations (Gassmann and Louda 2001). Our second aim was to evaluate the phenology hypothesis described in the paragraphs above.

Pitcher's thistle is a very close relative of Platte thistle, *Cirsium canescens* Nutt., a species whose densities have declined dramatically since first exposure to *R. conicus* in 1993 (Louda 2000a, Louda and Arnett 2000, Rose et al. 2005). Phylogenetic analyses suggest that the two species are sister species, with Platte thistle the likely progenitor for Pitcher's thistle (Johnson and Iltis 1963, Loveless and Hamrick 1988), and the species have striking ecological similarities (Keddy and Keddy 1984, Loveless 1984, McEachern 1992, Louda 1994). These facts led to the inference that *R. conicus* likely represents a significant new threat to Pitcher's thistle persistence if it reaches the *C. pitcheri* habitat (Louda et al. 1997). This inference was challenged since no direct evaluation had been done (Boldt 1997). Thus, our study was motivated by the lack of direct evidence and by the opportunity to evaluate the hypothesis that quantitative evaluation of ecological parameters, such as phenological synchrony, would improve the quantitative assessment of exposure and probable ecological risk to rare plant species from invasive phytophagous insects.

With these two aims in mind, we addressed five questions that focus on the critical parameters defining potential use and demographic impact of *R. conicus* on *C. pitcheri*. First, given the opportunity, does *R. conicus* recognize Pitcher's thistle as a feeding and oviposition host? "No-choice" acceptance tests are critically important in this context, since the coevolved targeted weed, *Carduus nutans* L., does not occur within *C. pitcheri*'s protected dune habitat. Second, if *C. pitcheri* is an acceptable host, how strong are the weevil's feeding and oviposition responses to Pitcher's thistle relative to its responses to other thistles, such as its coevolved host, the targeted weed, *Carduus nutans*, and

its close relative *Cirsium canescens* that is already being affected negatively by *R. conicus*? Third, can the weevil complete development on Pitcher's thistle plants? Fourth, what is the likely magnitude of phenological overlap between the projected *R. conicus* oviposition period with flower head availability of Pitcher's thistle within the thistle's protected habitat of two national parks in the USA? Fifth, using a simple demographic model, would the weevil's use of *C. pitcheri* suggested in laboratory and garden data have significant population-level consequences?

We used laboratory host specificity tests, garden exposure of potted *C. pitcheri* plants within the current range of North American populations of *R. conicus* in Canada, and field data on flowering phenology of *C. pitcheri* plants in their protected habitat in Indiana and Michigan, USA, and on weevil activity dates in locales to the north and south of this habitat to parameterize both the hazard and the exposure components of environmental risk. These data and demographic parameters from the literature allowed us to model the population consequences of an interaction. The host specificity tests in the laboratory and garden clearly demonstrate host recognition, colonization, feeding, oviposition, and development of *R. conicus* on Pitcher's thistle. The field data suggest a high probability of significant phenological overlap between *R. conicus* and reproductive effort of *C. pitcheri* within its protected habitat. Finally, the model predicts a significant demographic effect by *R. conicus* is likely on this threatened plant species.

Natural history and background

The flowerhead-feeding weevil, *Rhinocyllus conicus*, was introduced into North America from its indigenous region in Europe in July 1968 to control Eurasian *Carduus* spp. thistles, especially musk thistle *C. nutans* (Zwölfer and Harris 1984, Gassmann and Louda 2001). Weevils from eastern France were released in Nebraska early in the program, 1969–1972 (McCarty et al. 1981). Over-wintering adults of *R. conicus* emerge in late spring, feed, and oviposit on thistle flower heads, leaving easily observed external egg cases (Rees 1982, Zwölfer and Harris 1984). Timing of adult weevil activity in spring is best predicted by a combination of winter and spring growing degree-days and spring precipitation (Russell and Louda 2004; F. L. Russell and S. M. Louda, *unpublished manuscript*). Phenological synchrony between this insect and its host plant species has been hypothesized to be a key mechanism in determining relative use among thistle species by *R. conicus*, both in its indigenous environment (Zwölfer and Preiss 1983, Klein 1991) and in its nontarget host use in North America (Goeden and Ricker 1986*a*, *b*, 1987*a*, *b*, Louda 1998, Herr 2000, Russell and Louda 2004). The larvae feed for 14–30 days, destroying the receptacle, florets, and seeds within a developing flower head. After the pupal stage (14–21 days) and a qui-

escent period (7–14 days) within distinctive chambers within the flower head, new adults emerge and disperse to over-wintering sites.

In 1993, *R. conicus* invaded well-studied prairie grasslands in the Sand Hills of central Nebraska, USA (Louda et al. 1997, Louda 2000*a*), in sites without the targeted exotic thistles (Lamp and McCarty 1981, Louda et al. 1990). Weevil numbers in the flower heads of Platte thistle (*C. canescens*) increased exponentially over three years (Louda 1998) and have remained high, reducing seed production by 86% (Louda 2000*a*, Louda and Arnett 2000, Louda et al. 2003*a*). Since 1993, population density of Platte thistle in demography plots has declined over 80% (Louda and Arnett 2000, Louda et al. 2003*a*). Demography plot data and integral projection model methods (Easterling et al. 2000, Rees and Rose 2002) demonstrate that the decline of Platte thistle (*C. canescens*) is related to this invasion. Our model predicts significant long-term demographic effects for Platte thistle (Rose et al. 2005), consistent with experimental evidence demonstrating the significant effect of native floral herbivores on density and lifetime maternal fitness of this native thistle (Louda et al. 1990, 1992, Louda and Potvin 1995).

The rare Pitcher's thistle (*Cirsium pitcheri*) is a state and federally listed "threatened" species in the USA (U.S. Fish and Wildlife Service 2002) and an "endangered" species in Canada (Environment Canada, Schedule 1: List of species at risk, *available online*).[7] This species is restricted to the intermittent coastal sand dune ecosystem around the Great Lakes of North America (Keddy and Keddy 1984, Loveless 1984, McEachern 1992, U.S. Fish and Wildlife Service 2002). Similarities between Pitcher's thistle and its close congener Platte thistle include life history; both are long-lived, monocarpic perennials with determinant flowering. Juvenile rosettes of both species persist 2–11 years (McEachern 1992, Louda and Potvin 1995; S. M. Louda, *unpublished data*). Both initiate reproductive development early, in May (Lamp and McCarty 1981, Loveless 1984), and have similarly sized flower heads. Most plants release seed in mid-summer: Platte thistle by July (Louda and Potvin 1995) and Pitcher's thistle by August (Loveless 1984). Floral herbivory by native insects can be extensive on both species (Keddy and Keddy 1984, Loveless 1984, Louda and Potvin 1995, Bevill et al. 1999), and seed limits seedling recruitment for both species (Louda et al. 1990, Louda and McEachern 1995, Louda and Potvin 1995; S. M. Louda and A. K. McEachern, *unpublished data*).

METHODS

Laboratory tests of host recognition and preference

We evaluated host recognition, feeding acceptance, and oviposition preference of *Rhinocyllus conicus* for

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[7] ⟨http://www.sararegistry.gc.ca/species/schedules_e.cfm?id=1⟩

Pitcher's thistle in the laboratory at Cedar Point Biological Station in Ogallala, Nebraska (NE), using contemporary protocols for evaluation of host specificity (McClay 1990, McEvoy 1996). These tests paralleled our evaluation of the acceptance and preference of *R. conicus* for Platte thistle (*Cirsium canescens*) relative to the targeted exotic musk thistle (Arnett and Louda 2002). Sample size for some tests with *C. pitcheri* necessarily was limited by its threatened status. However, the tests were repeated in two years and the results were consistent (see *Results*).

In each year (1999, 2000), we collected 30 inflorescence branches, each with a single large unopened flower head of Pitcher's thistle, from two sites in Sleeping Bear Dunes National Lakeshore (Empire, Michigan [MI]): Good Harbor Bay (*n* = 15 per year) and Peterson Beach (*n* = 15 per year) on 7 June 1999 and 12 June 2000 (U.S. Fish and Wildlife Service Permit TE 009673, State of Michigan Permits 1086 and 1225, U.S. National Park Service Permits SLBE-1999/2000-154). Stems were re-cut and kept in water in a refrigerator overnight. The next day they were packed in plastic with moist paper towels and shipped in an insulated container (one-day delivery) to Cedar Point Biological Station, near field sites with naturalized populations of *R. conicus* in Nebraska. Branches of *C. nutans*, and, in 2000, branches of *C. canescens* as well, also were harvested at the same time from sites near the station in Nebraska (7 June 1999, 12 June 2000) to make sure that time since cutting was comparable among all species to be tested.

The day after shipping (9 June 1999, 14 June 2000), five branches were chosen randomly for no-choice tests in the laboratory. The remaining 25 branches were used in the choice tests, paired with branches of musk thistle (*Carduus nutans* spp. *leiophyllus*) with a similarly sized flower head (*n* = 25 in 1999, *n* = 20 in 2000) as the main contrast, or with a similar branch from Platte thistle (*Cirsium canescens*) as a subsidiary contrast (*n* = 5 in 2000). For choice tests, two flasks filled with nutrient solution, one containing a branch of Pitcher's thistle and the other containing one matched branch of the exotic *C. nutans* or alternative thistle species, were placed inside each of 30 insect cages (30 × 30 × 30 cm; 0.5-mm mesh). We added two mating pairs of *R. conicus* adults to each cage. Weevils had been collected during the week prior to the experiment from musk thistle (Lincoln County, NE) and Platte thistle (Arthur County, NE); these weevils were kept and allowed to mix freely in an insect cage in the laboratory. For no-choice tests, one flask with nutrient solution in a cage received one mating pair of *R. conicus* adults.

We recorded the number of 3-mm² feeding scars and the number of eggs laid on each head by examining plants every morning, afternoon, and evening in 1999 and every afternoon in 2000, for the next 5 d. We used the maximum number of egg cases observed by the end of the third day to quantify oviposition preference, for two reasons. First, most of the weevils (90%) had laid eggs by the end of the second day; and, second, egg cases dropped off as they dried and a large number had dropped off by the end of the fourth day. The results of these tests were also compared directly to those from similar tests done with Platte thistle (Arnett and Louda 2002).

The response variables (area chewed, and number of *R. conicus* eggs oviposited) were transformed as necessary to reduce heterogeneity of variances. Area of feeding damage, based on the number of chewing scars per inflorescence, was square-root transformed. Counts, such as cumulative number of eggs laid per head, were $\ln(X + 0.5)$-transformed. Area chewed and numbers of *R. conicus* eggs were analyzed using analysis of covariance (ANCOVA), with flower head diameter as the covariate (as in Arnett and Louda 2002). Flower head diameter was used as a covariate, since egg deposition could have varied with flower head size differences among replicates, even when heads within replicate trials were similar.

Weevil colonization, development, and impact under garden conditions

To supplement laboratory tests for host acceptance and preference, we used quantitative evidence on discovery, oviposition, development, and eclosion success by *R. conicus* on Pitcher's thistles spontaneously colonized by the weevil in 1999 on the Alberta Research Council grounds in Vegreville, Alberta, Canada. These plants were started from seed in 1997 and grown outside in pots, intermixed with other native and exotic *Cirsium* spp. being raised for use in host specificity tests of other thistle-feeding insects (McClay et al. 2000). The Pitcher's thistle plants (*n* = 13) were harvested at the end of the 1999 growing season and shipped to the University of Nebraska, Lincoln, NE, USA.

In the laboratory, we measured stem heights and counted the total number of flower heads initiated (>3.5 mm diameter) per stem. We then dissected each flower head and recorded evidence of weevil oviposition, feeding, and chamber development, as well as the number of larvae, pupae, and adults of *R. conicus*. Feeding scars could not be quantified accurately on the dried material. Voucher specimens were preserved. We also counted viable seed. These methods parallel those used in multiple field studies of thistles: Platte thistle (Louda and Potvin 1995, Louda and Arnett 2000, Rand and Louda 2004, Russell and Louda 2004; F. L. Russell and S. M. Louda, *unpublished manuscript*); wavyleaf thistle, *Cirsium undulatum* var. *undulatum* (Nutt.) Spreng. (Louda 2000*a*, F. L. Russell and S. M. Louda, *unpublished manuscript*); Tracy's thistle, *C. undulatum* var. *tracyi* (Rydb.) Welsh (Louda and O'Brien 2002); as well as Pitcher's thistle (Louda and McEachern 1995, Bevill et al. 1999).

We analyzed the patterns of weevil attack, quantified as *R. conicus* development, damage, and occurrence within *C. pitcheri* flower heads, on plants in the garden in two ways. First, we used analysis of variance to test for differences in plant traits for stems with vs. without *R. conicus*, treating plant as a blocking variable. In addition to number of *R. conicus* per stem, the response variables were number of viable seeds per head per stem, number of flower heads per stem, mean stem height (cm), mean diameter per head per stem (mm), and mean of flowering success (final stage of development). Flowering stage was indexed, using: 1 = small flower head bud (<12 mm), 2 = large bud (>12 mm, but no florets exerted), 3 = partial flower (at least one floret exerted), 4 = full flower (>50% florets exerted and with color), 5 = maturing seed (florets brown, dried, seeds undispersed), and 6 = released (>50% seeds dispersed), following Lamp and McCarty (1981, 1982). Less than 5% of the heads dissected had dispersed seed prior to collection and examination.

Counts were square-root transformed and measurements were $\ln(X + 0.5)$-transformed when necessary to decrease heterogeneity of variances. Probabilities were corrected for multiple comparisons using the Bonferroni procedure (Systat; SPSS 2000). Second, we analyzed weevil response in relation to plant size (tall, >25 cm; short, ≤25 cm) with number of *R. conicus* per stem as the response variable. We analyzed transformed counts, as described in the previous paragraph, using analysis of covariance to control for potential covariation in numbers and sizes of flower heads among stems within plants.

Phenology and potential synchrony with resource availability

Estimation of the likely oviposition period for *R. conicus* at latitudes that include Pitcher's thistle in protected habitat along the shores of Lake Michigan was a direct, linear interpolation by latitude between dates of observations of *R. conicus* activity to the north (A. S. McClay, *unpublished data*) and to the south (F. L. Russell and S. M. Louda, *unpublished manuscript*). This interpolative approach is consistent with the observed variation in *R. conicus* phenology in Europe (Aeschlimann 1999, Gassmann and Louda 2001). A likely mechanism for latitudinal variation in activity is temperature, since activity and fecundity of *R. conicus* respond to temperature variation (Smith et al. 1984, Smith and Kok 1987; F. L. Russell and S. M. Louda, *unpublished manuscript*). The interpolative method should lead to a conservative estimate of the likely temporal overlap of *R. conicus* with *C. pitcheri*, since lower temperatures in the *C. pitcheri* habitat along the lakeshore than predicted from inland continental sites available would be expected to delay *R. conicus* activity and so increase the likelihood of overlap with the documented flowering period of *C. pitcheri*. Female *R. conicus* were counted biweekly from early May through

June in 1997 to 2001 on Platte thistle in the Nebraska Sand Hills (Arapaho Prairie, 40°56′ N), south of the National Lakeshores with *C. pitcheri* (Russell and Louda 2004; F. L. Russell and S. M. Louda, *unpublished manuscript*). To the north in Vegreville, Alberta (53°30′ N), *R. conicus* was observed on plants from the first week of June through the last week of July (A. S. McClay, *unpublished data*). These dates are consistent with other observations of dates of *R. conicus* activity in the eastern USA (Frick 1978, Surles and Kok 1978).

Estimation of the proportion of Pitcher's thistle flower heads that would be available during the calculated oviposition period for *R. conicus* used three years of field data on flowering phenology of Pitcher's thistle (S. M. Louda and A. K. McEachern, *unpublished data*). We quantified the number and timing of flower head production (1993–1995) in two U.S. national parks in which Pitcher's thistle is protected: four sites were at Indiana Dunes National Lakeshore (Porter, Indiana [IN]; 42°6′ N) and five sites were in Sleeping Bear Dunes National Lakeshore (Empire, MI; 44°47′ N) (Louda and McEachern 1995; S. M. Louda and A. K. McEachern, *unpublished data*). In Indiana Dunes, the local sites were: Big Blowout Inner (n = 48, 61, 24 plants in 1993, 1994, 1995, respectively), Big Blowout Outer (n = 27, 29, 0 plants), Howe's Beach (n = 109, 120, 24 plants), and West Beach (n = 57, 49, 0 plants). In Sleeping Bear Dunes, the local sites were (south to north): Platte River mouth (n = 161, 156, 24 plants), Peterson Beach (n = 158, 104, 24 plants), Aral Dunes (n = 160, 156, 24 plants), Sleeping Bear Plateau (n = 104, 104, 24 plants), and Good Harbor Bay (n = 103, 94, 24 plants).

Early each season (7–15 May), we identified large rosettes that were likely to flower throughout the sand dune ecosystem at each site. Rosettes were numbered, mapped, and the number of flower heads recorded. We remeasured plants at ~3-wk intervals. Sampling dates over all years at Indiana Dunes were 6–14 May, 1–11 June, and 5–16 July; and at Sleeping Bear Dunes the dates were 28 May–7 June, 25–30 June, and 27–31 July. In our analysis, we averaged the total number of flower heads (>3.5 mm diameter) available on each date at each site over the three years to determine the average pattern of flowering by locale. Curves of plant flower head development were fit statistically as third order polynomials using Systat 10.0 (SPSS 2000). To determine the overlap between the interpolated weevil oviposition period and the availability of Pitcher's thistle flower heads as resources for the weevil, we calculated the proportion of the total flower heads initiated per plant by the end of the calculated oviposition period.

Demographic consequences

A four-stage matrix model (Caswell 2001) for Pitcher's thistle was developed to assess whether the effects predicted at a particular life stage, seed production,

would generate any corresponding demographic effects. The life-cycle diagram and stage transition matrix for *C. pitcheri* included four stages: seedling (with cotyledons), small juvenile (1–4 leaves), large juvenile (>4 leaves), and flowering adult (Loveless 1984). All of the demographic parameters were extracted from Loveless (1984) for Sleeping Bear Dunes National Lakeshore, MI, except the proportion of seeds surviving predation by native insect floral herbivores, which came from Louda and McEachern (1995, and *unpublished data*). The value of *f*, the number of seedlings established per plant, includes the effect of *R. conicus* on seed production; it was calculated using alternative assumptions about attack rate with co-occurrence based on the laboratory test results.

RESULTS

Host recognition and feeding

Pitcher's thistle was accepted by *R. conicus* for feeding in both no-choice and choice tests (Fig. 1A). In no-choice tests, the mean area of *R. conicus* feeding scars per inflorescence averaged 59.6 mm² (Fig. 1A). Average weevil feeding did not differ significantly between years: 62.0 ± 9.86 mm² (means $\pm$ 1 SE) in 1999 vs. 56.3 ± 8.91 mm² in 2000 (Table 1A). In choice tests with the coevolved exotic weed musk thistle (*C. nutans*), *R. conicus* showed no strong or consistent preference for musk thistle over the native Pitcher's thistle (Fig. 1A). Neither species ($P < 0.75$), nor year ($P < 0.19$) was a significant factor in the analysis of covariance (Table 1B). However, a significant species × year interaction ($P < 0.01$) suggested that the trend toward higher feeding on Pitcher's thistle in 1999 differed significantly from the trend toward higher feeding on musk thistle in 2000 (Fig. 1A).

The relative susceptibility of *C. pitcheri*, compared to its severely affected relative *C. canescens*, can be assessed both directly and indirectly. The direct measure is based on the small choice test conducted in 2000 ($n = 5$). In this test, the mean level of feeding on Pitcher's thistle (28.5 ± 10.44 mm²) appeared to be lower than on the affected Platte thistle (46.5 ± 11.48 mm²), but the difference in this small test was not statistically significant (ANCOVA, $F_{1,9} = 1.480$, $P < 0.26$, with head diameter as a covariate). The indirect measure is based on a comparison of *R. conicus* acceptance of Pitcher's thistle or of Platte thistle (Arnett and Louda 2002) relative to musk thistle in laboratory choice tests. In these tests, the area chewed by *R. conicus* on averaged 57.4 ± 7.40 mm² on Pitcher's thistle vs. 63.9 ± 13.97 mm² on Platte thistle (Fig. 1A). These feeding responses by *R. conicus* to the two native species relative to musk thistle were not significantly different (Table 1C). Neither species, nor year was a significant factor in the variation observed. Together, these data strongly suggest that *R. conicus* feeding response to
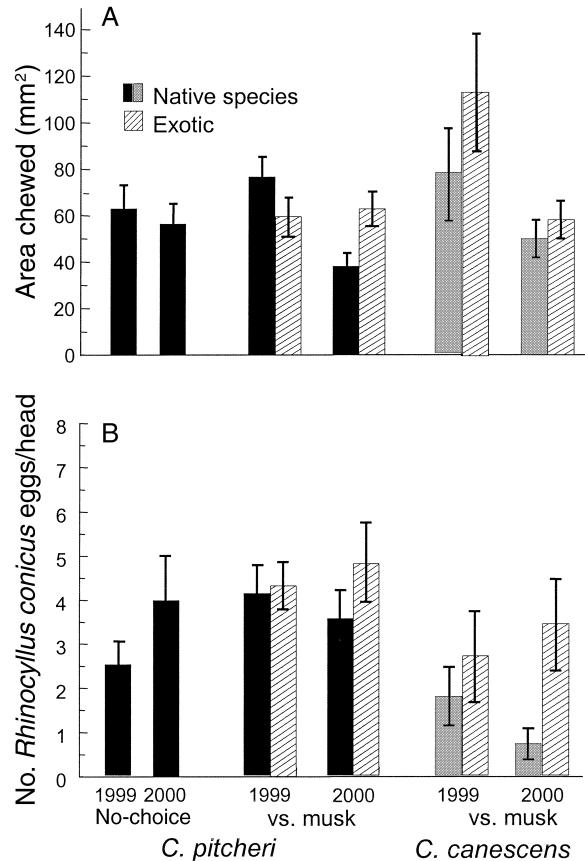

FIG. 1. Response of *Rhinocyllus conicus* to *Cirsium pitcheri* in laboratory feeding and oviposition tests in 1999 and 2000, under no-choice conditions (alone) vs. under choice conditions, with either the targeted exotic weed *Carduus nutans* (musk or nodding thistle) or its closely related congener *Cirsium canescens* (Platte thistle): (A) area of flower head and adjacent stem chewed by *R. conicus* over three days, and (B) maximum number of egg cases per flower head observed over each three-day test. The solid bars are native thistle types (black is the threatened *Cirsium pitcheri*, and gray is the closely related *C. canescens*), and the crosshatched bars are the exotic thistle, *Carduus nutans*. Shown are means $\pm$ 1 SE.

Pitcher's thistle is comparable to its response to Platte thistle.

Oviposition

Pitcher's thistle was accepted for oviposition, in both no-choice and choice tests (Fig. 1B). In no-choice tests, there was a mean of 2.5 ± 0.60 eggs laid/inflorescence on Pitcher's thistle in 1999 and 4.0 ± 0.97 eggs laid/inflorescence in 2000, exhibiting significant rather than chance oviposition acceptance in both years (95% confidence intervals exclude zero) and no significant difference between years (Table 2A). In choice tests with its coevolved exotic host species, *Carduus nutans*, a trend toward higher preference for musk thistle (overall mean 4.8 vs. 3.8 eggs/head; Fig. 1B) was not significant (Table 2B). Neither species ($P < 0.14$) nor year ($P <$

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TABLE 1. Feeding (area chewed) by *Rhinocyllus conicus* on *Cirsium pitcheri*; ANCOVA results with flower head diameter as the covariate.

Factor	SS	df	MS	F ratio	P
A) No-choice tests: *C. pitcheri* alone, 1999 vs. 2000 ($R^2 = 0.01$)					
Year	0.361	1	0.361	0.084	0.777
Head diameter	0.044	1	0.044	0.010	0.921
Error	55.995	13	4.307		
B) Choice tests: *C. pitcheri* vs. *C. nutans*, 1999 vs. 2000 ($R^2 = 0.12$)					
Species	0.670	1	0.670	0.103	0.749
Year	11.491	1	11.491	1.771	0.187
Species × year	52.589	1	52.589	8.104	0.006
Head diameter	4.546	1	4.546	0.701	0.405
Error	551.592	85	6.489		
C) Choice tests: *C. pitcheri* vs. *C. canescens* with musk thistle, 2000 ($R^2 = 0.03$)					
Species	0.104	1	0.104	0.007	0.931
Year	1.860	1	1.860	0.133	0.716
Species × year	16.707	1	16.707	1.196	0.279
Head diameter	9.869	1	9.869	0.706	0.404
Error	796.309	57	13.970		

0.48), nor their interaction ($P < 0.92$) was significant in explaining the variation observed (Table 2B).

We also compared *R. conicus* oviposition response to Pitcher's thistle with its oviposition response to its more common relative Platte thistle. First, in the small, direct, choice test in 2000, we observed twice as many eggs oviposited on Pitcher's thistle (2.5 ± 1.26 eggs/head) as on Platte thistle (1.3 ± 0.56 eggs/head) on average, but the difference was not statistically significant, likely reflecting our limited sample size ($n = 5$; ANCOVA, with head diameter as the covariate, $F_{1,9} = 0.295$, $P < 0.60$). Second, in comparing choice tests for each of the native species against musk thistle, we unexpectedly found a significantly higher level of oviposition on Pitcher's thistle than on Platte thistle (4.1 ± 0.64 eggs/head vs. 1.8 ± 0.66 eggs/head in 1999,

TABLE 2. Oviposition by *Rhinocyllus conicus* on *Cirsium pitcheri* in laboratory tests; ANCOVA results with head diameter as the covariate.

Factor	SS	df	MS	F ratio	P
A) No-choice test with *C. pitcheri*: 1999 vs. 2000 ($R^2 = 0.12$)					
Year	0.696	1	0.696	0.805	0.386
Head diameter	0.095	1	0.095	0.110	0.745
Error	11.232	13	0.864		
B) Choice test: *C. pitcheri* vs. *C. nutans*: 1999 and 2000 ($R^2 = 0.03$)					
Species	1.304	1	1.304	2.253	0.137
Year	0.292	1	0.292	0.504	0.480
Species × year	0.007	1	0.007	0.012	0.914
Head diameter	0.357	1	0.357	0.617	0.434
Error	49.214	85	0.579		
C) Choice tests: *C. pitcheri* vs. on *C. canescens* in choice tests with musk thistle, 2000 ($R^2 = 0.13$)					
Year	0.385	1	0.385	0.337	0.564
Species	7.900	1	7.900	6.916	0.011
Year × species	0.033	1	0.033	0.029	0.866
Head diameter	0.003	1	0.003	0.003	0.959
Error	65.110	57	1.142		

and 3.6 ± 0.73 vs. 0.7 ± 0.29 eggs/head in 2000) in the presence of musk thistle in the respective choice tests (Fig. 1B). No significant effect of year, and no interaction between species and year occurred (Table 2C).

Finally, a meta-analysis of the three experiments in which data on *R. conicus* oviposition rates on Pitcher's thistle were available (no choice, choice with musk, choice with Platte) showed no effect of experiment on oviposition rate (ANOVA, $F_{5,61} = 0.734$, $P \leq 0.60$). Thus, Pitcher's thistle was as acceptable an oviposition host for *R. conicus* as its coevolved targeted species, *C. nutans*, and seemingly even more preferred for oviposition than its more common, affected relative, Platte thistle.

Development

Successful larval growth and pupal development to eclosion and emergence occurred on adventitiously colonized two-year-old flowering Pitcher's thistle plants in pots in the Alberta Research Council grounds in Vegreville, Alberta, in 1999. We found a total of 107 *R. conicus* developed successfully from the 398 flower heads (≥3.5 mm diameter) on 125 stems of the 13 potted Pitcher's thistle plants grown from seed. Nine of the 13 plants (69.2%) were colonized, and 52 of the 125 stems (41.6%), as well as 137 of the 398 flower heads (34.5%), had evidence of *R. conicus* oviposition and development. There was an average of 1.0 overall and 2.1 *R. conicus* per plant stem for attacked stems only (Fig. 2A). These data provide additional evidence of both host recognition and oviposition acceptance of Pitcher's thistle by *R. conicus*, and expand it to more natural outdoor conditions.

The data collected were sufficient to quantify the rates of spontaneous oviposition and successful development in relation to plant traits, as well as the effect of *R. conicus* on seed production by Pitcher's thistle
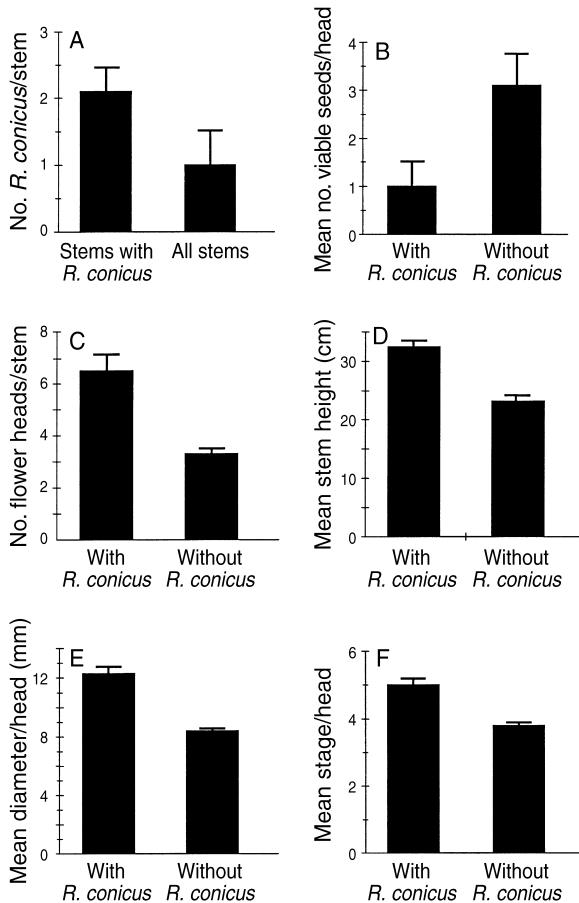
FIG. 2. Contrast between *Cirsium pitcheri* plants with vs. without evidence of spontaneous colonization by *Rhinocyllus conicus* of potted plants in the Alberta Research Council grounds in Vegreville, Alberta, Canada (n = 51 vs. 74 stems and 81 vs. 272 flower heads, with vs. without internal evidence of *R. conicus* feeding and development, respectively): (A) number of *R. conicus* that developed on plants with evidence of colonization, (B) number of viable seeds per flower head with vs. without evidence of *R. conicus*, (C) number of flower heads on stems with vs. without *R. conicus* colonization, (D) stem height of stems with vs. without *R. conicus*, (E) flower head diameter for heads with vs. without evidence of use by *R. conicus*, and (F) stage of flower head development for flower heads attacked by vs. not attacked by *R. conicus*. Stages are categorized as: 1, small bud (<15 mm diameter); 2, large bud (>15 mm diameter, with no florets exerted); 3, partial flower (1 < florets exerted < 25); 4, full flower (florets past receptivity); and 6, releasing or dispersing seed (following Lamp and McCarty [1981] and Bevill et al. [1999]). Shown are means + 1 SE.

in the garden context. Comparison of stems with vs. without *R. conicus* suggested plants with more flower heads (Fig. 2C) on taller stems (Fig. 2D) were most susceptible to colonization by *R. conicus*, as is also the case for Platte thistle (Rose et al. 2005). To verify the role of plant height, we analyzed *R. conicus* numbers on tall (>25 cm) vs. on shorter (≤25 cm) *C. pitcheri* stems. We found that weevil colonization of and successful development on Pitcher's thistle was signifi-

cantly greater on the tall stems than on the short ones (Table 3B), especially as the number of heads per stem increased (interaction of stem height × number of heads, $P < 0.001$).

Colonization by *R. conicus* of Pitcher's thistle in the garden also varied significantly among plants (Table 3B). The plants colonized by *R. conicus* had more flower heads (ANCOVA, $F_{1, 122} = 24.370$, corrected $P < 0.01$; Fig. 2C) on taller stems on average (ANCOVA, $F_{1, 122} = 41.335$, corrected $P < 0.01$; Fig. 2D). In addition, the flower heads on which oviposition occurred were generally larger (ANCOVA, $F_{1, 350} = 81.147$, corrected $P < 0.01$; Fig. 2E) and more phenologically advanced (ANCOVA, $F_{1, 354} = 22.247$, corrected $P < 0.01$; Fig. 2F). The number of *R. conicus* per head of *C. pitcheri* (Table 3A) reflected a highly significant effect of flower head size (1 mm diameter classes), when flower head position and plant were taken into consideration ($R^2 = 0.95$; Table 3A). This result is consistent with the fact that 75.9% of the *R. conicus* egg cases and 74.2% of the weevils that were observed occurred on or in the terminal heads of the main stem and of the first two branches. These first three heads comprised almost 50% of the average 6.5 heads/stem-branch of *C. pitcheri* with *R. conicus* (Fig. 2C) in this study.

Colonization, feeding, and development by *R. conicus* resulted in a 67% decrease, from 3.1 ± 0.66 to 1.0 ± 0.48 viable seed produced/head by *C. pitcheri* in the garden context (Fig. 2B), a significant drop (Table 3C). Production of viable seed was related to mean flower head size (Fig. 2E, Table 3D) as well as plant size. Flower heads colonized by *R. conicus* averaged 12.3 ± 0.39 mm in diameter, while the heads that were not colonized averaged 8.4 ± 0.19 mm. Stems bearing these flower heads averaged 32.4 ± 1.09 cm, whereas stems that were not colonized and bore the smaller heads averaged only 23.1 ± 0.86 cm (Fig. 2E). The model that best predicted the production of viable seed by *C. pitcheri* heads included the highly significant effect of flower head size (diameter) and *R. conicus* presence (Table 3C). Also, addition of *R. conicus* to the flower head guild in the garden environment significantly reduced the slope of the line relating increase in viable seed with increase in flower head diameter (Fig. 3).

Thus, the largest, most vigorous plants, expected to contribute most to recruitment in the protected habitat, were the most vulnerable to *R. conicus* colonization and impact. Oviposition by *R. conicus* was greater on more vigorous plants, with vigor represented as stature (height) and flower head production and resource availability. Flower head resource availability was measured as greater number of flower heads per stem, larger sized heads, and earlier, upper flower heads on the taller plants. Significantly, the interaction with *R. conicus* led to lower production of viable seed by *C. pitcheri*.

TABLE 3. Results of ANCOVA for *Rhinocyllus conicus* occurrence on *Cirsium pitcheri* in pots in the Agricultural Experiment Station garden, Vegreville, Ontario, Canada in 1999.

Factor	ss	df	ms	*F* ratio	*P*
A) No. *R. conicus* per *C. pitcheri* head with vs. without *R. conicus* ($R^2 = 0.95$)					
Head diameter	124.078	296	0.419	2.395	0.001
Plant	0.081	1	0.081	0.466	0.499
Head position	0.193	1	0.193	1.101	0.300
Error	7.351	42	0.175		
B) No. *R. conicus* per stem on *C. pitcheri* by stem height class ($R^2 = 0.72$)					
Stem height class	31.516	1	31.516	28.859	0.001
No. heads	5.976	6	0.996	0.912	0.490
Stem height × heads	48.302	5	9.660	8.846	0.001
Plant	4.972	1	4.972	4.553	0.035
Error	110.301	101	1.092		
C) No. viable seeds per *C. pitcheri* head with vs. without *R. conicus* ($R^2 = 0.84$)					
Rhinocyllus presence	2166.302	1	2166.302	21.680	0.001
Head diameter	5534.579	1	5534.579	55.389	0.001
Plant	34.489	1	34.489	0.345	0.557
Error	34872.617	349	99.922		

Phenological overlap

For the weevil, the likely activity and oviposition period in the Indiana Dunes and Sleeping Bear Dunes National Lakeshore Parks along Lake Michigan, interpolated between observed dates in latitudes to the south and north, occurred between early-to-middle May and middle-to-late July (Fig. 4A). Specifically, the expected oviposition period of *R. conicus* in the southern portion of *C. pitcheri* range, such as at Indiana Dunes National Lakeshore (Porter, IN), should be at least from the second week of May through the last week of June into the first week of July (Fig. 4A). In a more northern area, such as Sleeping Bear Dunes National Lakeshore (Empire, MI), the interpolation leads to a conservative expectation of oviposition from the third week of May
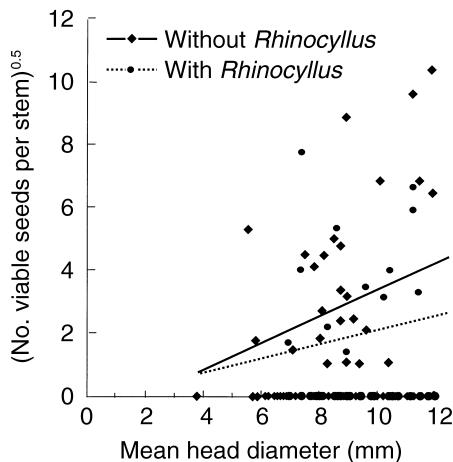

FIG. 3. Number of viable seeds per plant stem (square-root transformed) for *Cirsium pitcheri* in relation to flower head diameter (mm) for stems both with and without evidence of *Rhinocyllus conicus* colonization in the Alberta Research Council grounds in Vegreville, Alberta (*n* = 51 and *n* = 74 stems with and without *R. conicus*, respectively).

through at least the first or second week of July (Fig. 4A). Cooler weather along the lakeshore could delay and lengthen the estimated activity period to the end of July.

For flower head resource availability, the field data on development of flower heads on *C. pitcheri* plants in situ available from those two National Lakeshore Parks suggest that the vast majority of its flower heads will be available and susceptible to oviposition during the expected *R. conicus* activity period. In the south, at four sites within or near the Indiana Dunes National Lakeshore, >93% of the flower heads per plant, on average, were initiated before the end of the calculated *R. conicus* oviposition period there (end of June): 99.9%, 93.8%, 94.8%, 97.0% at the sites BBI, BBO, HWE, and WBE, respectively, from east to west within the park (Fig. 4B). These heads included all of the upper, larger flower heads that have the highest probability of setting viable seed (S. M. Louda and A. K. McEachern, *unpublished data*), such as those most damaged by *R. conicus* in Alberta (Table 3, Fig. 4). In the northern part of lower Michigan State, at five sites within the Sleeping Bear Dunes National Lakeshore, from 78% to 90% of all flower heads per plant at the park were initiated on average before the end of the conservatively calculated *R. conicus* oviposition period there (second to third week of July): 90.5%, 80.6%, 81.6%, 78.1%, and 85.0% at the sites GH, SBP, AD, PB, and PR, respectively, from north to south within the park (Fig. 4C). This number also included the larger, usually more successful flower heads (S. M. Louda and A. K. McEachern, *unpublished data*). Extending the activity period there by one to two weeks would increase the portion of heads exposed on the order of 5%, to 95.0%, 84.6%, 85.7%, and 89.2% respectively.

Demographic model

A life-cycle diagram and 4 × 4 matrix model for Pitcher's thistle are shown in Fig. 5. Each arrow rep-
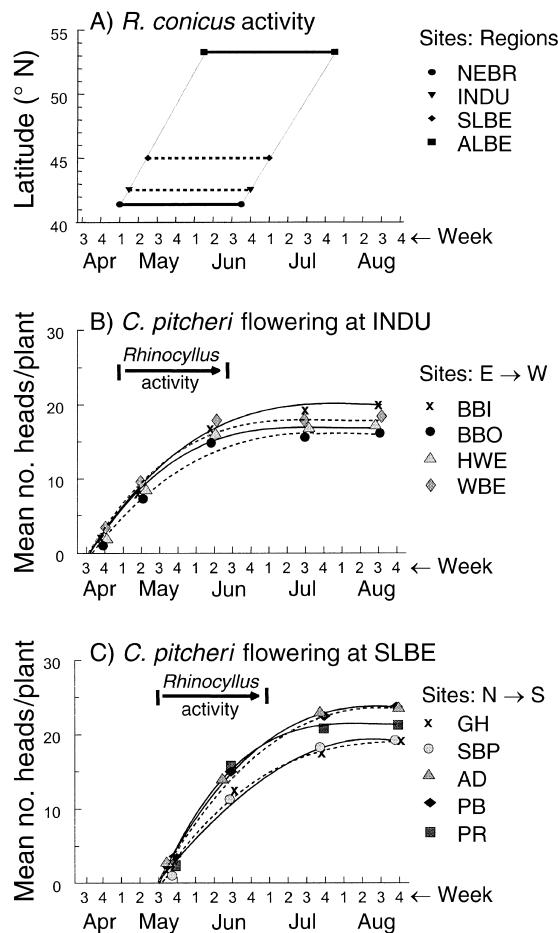
FIG. 4. (A) Phenology of *Rhinocyllus conicus* activity period with latitude. (B, C) Phenology of flowering by *Cirsium pitcheri*, averaged for 1993, 1994, and 1995, along southern Lake Michigan (B) at four sites in protected habitats of Indiana Dunes National Lakeshore in the south and (C) at five sites in protected habitats of Sleeping Bear Dunes National Lakeshore farther north. In (A), the latitudinal sites were (south to north): Arapaho Prairie Preserve, Arthur County, Nebraska, USA (NEBR; 40°56′ N); Indiana Dunes National Lakeshore, Porter, Indiana, USA (INDU; 41°36′ N); Sleeping Bear Dunes National Lakeshore, Empire, Michigan, USA (SLBE; 44°47′ N); and Vegreville, Alberta, Canada (ALBE; 53°29′ N). The solid lines are reported activity periods; the dashed lines are interpolated activity periods in the parks where *R. conicus* does not occur yet. In panel (B), the expected *R. conicus* activity period is from panel (A), and the local sites were, from east to west: Big Blowout Inner (BBI; $n = 48, 61, 24$ plants in 1993, 1994, 1995, respectively), Big Blowout Outer (BBO; $n = 27, 29, 0$ plants), Howe's Beach (HWE; $n = 109, 120, 24$ plants), and West Beach (WBE; $n = 57, 49, 0$ plants). In panel (C), the expected *R. conicus* activity period is from panel (A), and the local sites were, from north to south: Good Harbor Bay (GH; $n = 103, 94, 24$ plants), Sleeping Bear Plateau (SBP; $n = 104, 104, 24$ plants), Aral Dunes (AD; $n = 160, 156, 24$ plants), Peterson Beach (PB; $n = 158, 104, 24$ plants), and Platte River mouth (PR; $n = 161, 156, 24$ plants). Sampling dates across all years were 6–14 May, 1–11 June, and 5–16 July at Indiana Dunes, and 28 May–7 June, 25–30 June, and 27–31 July at Sleeping Bear Dunes. Curves were fit statistically as third-order polynomials (all $R^2 > 0.99$).
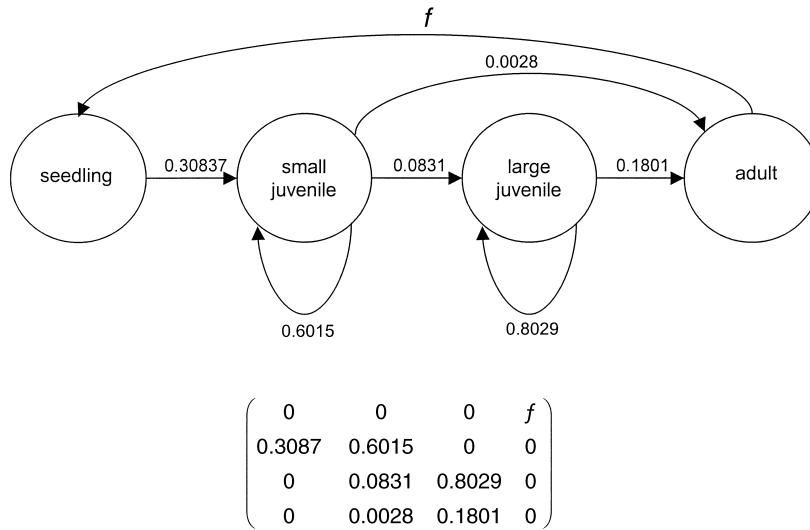
resents the contribution of one individual in a stage to any other stage one year later. The parameter f represents the number of new seedlings in the second year from one adult in the first year, incorporating seeds initiated, floral and seed predation, and seedling germination. In the presence of native floral predators only, the value of f is 14.85 seedlings/adult. With *R. conicus* added to the native floral insects, and assuming conservatively that the relative proportion of seeds lost to both native insects and *R. conicus* scale as for Platte thistle, the value of f is reduced 80.9%, to 2.83 seedlings. Furthermore, if relative impact also includes the relative oviposition preferences shown for Pitcher's thistle vs. for Platte thistle in the choice tests with the targeted musk thistle above (Fig. 1B), then the value of f becomes 1.32 seedlings (91.1% reduction).

With native predators only, the dominant eigenvalue for Pitcher's thistle is $\lambda = 0.9897$; the population size is declining very slowly or is nearly steady. With the non-native weevil (*Rhinocyllus conicus*) added, the dominant eigenvalue declined 12% to $\lambda = 0.8686$, assuming equal preference for Pitcher's thistle as for Platte thistle (*C. canescens*). Alternately, the dominant eigenvalue declined 15% to $\lambda = 0.8395$, using the relatively higher preference of *R. conicus* for Pitcher's thistle observed in the laboratory oviposition tests (Fig. 1B). The cumulative consequences of these annual estimates of λ can be compared by examining their effect on time to halve the population ($t_{0.5}$). Under current conditions without *R. conicus*, the time to halve the population ($t_{0.5}$) is 66.9 years. However, with *R. conicus* added to the floral insect herbivore guild, the estimated time to halve the population ($t_{0.5}$) is only 4.9 years, assuming equal preference for Pitcher's thistle as for Platte thistle, or 4.0 years, assuming the relatively higher preference for Pitcher's thistle than Platte thistle observed in the laboratory tests.

DISCUSSION

Likelihood of ecological impacts

Rhinocyllus conicus can recognize and use Pitcher's thistle as a potential feeding and oviposition host, in both laboratory tests and the garden environment. The "no-choice" laboratory tests showed significant feeding and oviposition. This finding suggests Pitcher's thistle is vulnerable to *R. conicus* in the absence of its targeted plant, an important finding since musk thistle does not occur within the U.S. National Parks with *C. pitcheri* in protected dune habitat (U.S. Fish and Wildlife Service 2002). Furthermore, in the "choice" situation with musk thistle (*C. nutans*), *R. conicus* unexpectedly showed no significant or consistent acceptance and oviposition preference for its coevolved weedy host plant relative to Pitcher's thistle. In addition, *C. pitcheri* was at least as acceptable to *R. conicus* as its close, severely impacted relative Platte thistle,

$$\begin{pmatrix} 0 & 0 & 0 & f \\ 0.3087 & 0.6015 & 0 & 0 \\ 0 & 0.0831 & 0.8029 & 0 \\ 0 & 0.0028 & 0.1801 & 0 \end{pmatrix}$$

Herbivores	Rate of attack assumption	f	λ
Native insects only	Field data from 1993–1995	14.85	0.9897
Natives + R. conicus	Rate observed on Platte thistle	2.83	0.8686
Natives + R. conicus	Relative rate from oviposition test	1.32	0.8395

FIG. 5. Life-cycle diagram and stage-transition matrix for *Cirsium pitcheri* at Sleeping Bear Dunes National Lakeshore, Michigan, USA, including four stages: seedling (with cotyledons), small juvenile (1–4 leaves), large juvenile (>4 leaves), and flowering adult (Loveless 1984). All of the demographic parameters were extracted from Loveless (1984), except the proportion of seeds surviving predation by native insect floral herbivores (Louda and McEachern 1995, and *unpublished data*). The value of *f*, the number of seedlings established per adult plant, was calculated using alternative assumptions about attack rate with co-occurrence (assumptions detailed in *Results: Demographic model*).

suggesting a high probability of comparable or greater impact on Pitcher's thistle populations.

Also, *R. conicus* found and developed successfully on *C. pitcheri*, a prerequisite for the development of a population build up on Pitcher's thistle. Despite being rare in the area of Vegreville, Alberta (A. S. McClay, *personal observation*), *R. conicus* appeared in large numbers on potted *C. pitcheri* and other *Cirsium* spp. in the garden plot, suggesting that the weevil can efficiently locate and orient to suitable host plants from a considerable distance. The only other available hosts growing nearby are the exotic *Cirsium arvense* (L.) Scop. and the native *C. flodmanii* (Rydb.) Arthur. Rates of oviposition by *R. conicus* on *C. arvense* in the area appear to be very low, and the weevil has not yet been found attacking the later flowering *C. flodmanii* at Vegreville (A. S. McClay, *personal observation*). Development of *R. conicus* was complete on *C. pitcheri*, demonstrating that the weevil population can build up on this rare species once it is found.

Most of the Pitcher's thistle flower heads on plants within the protected habitats along Lake Michigan were initiated and available during the calculated *R. conicus* oviposition period. These results contrast to the only

other quantitative study of the threat posed by *R. conicus* to a rare native thistle (*C. hydrophilum* var. *vaseyi* (Gray) J. T. Howell, Mt. Tamalpais thistle) in California (Herr 2000). In that study, low overlap between *R. conicus* and total flowering effort of this seep-dependent species was hypothesized to limit the weevil's numerical effect on the population. In the case of Pitcher's thistle, however, the phenological data provide strong, unequivocal evidence that the likely activity period of *R. conicus* will overlap the availability of the majority of flower heads produced by *C. pitcheri*. Depending upon specific site, at least 78–85% to 99% of all flower heads initiated by plants within the two protected parks would be exposed to *R. conicus* during its estimated oviposition period. This exposure rate is similar to that for Platte thistle (90–99%), and so suggests that a similar strong negative impact on seed production and seedling recruitment of *C. pitcheri* is likely. These findings also support the hypothesis that quantification of likely temporal overlap can help predict the ecological interaction intensity of a biocontrol agent with a native species when host specificity tests show that the native species is within the larger host range. Indication of a temporal overlap also provides a basis for a po-

tential long-term evolutionary increase in interaction intensity.

Finally, the demographic model shows that the projected loss of seed production is likely to have a major negative effect on population growth rate and persistence through its effect on seedling establishment. An annual decrease of 12–15% in population growth rate (λ) from the current level of relative stability, observed in the model, has the potential of driving this already rare, federally listed species into decline. The cumulative effect, estimated as time to halve the population (66.9 to 4.0 or 4.9 years), is severe. Given the already limited range and population size of Pitcher's thistle (U.S. Fish and Wildlife Service 2002), such severe reductions in population growth rates also increase the likelihood and potential importance of other detrimental processes, such as Allee effects based on inbreeding depression or effects of pollen limitation, in small populations.

The results here provide direct evidence for the vulnerability of Pitcher's thistle to *R. conicus* at least of the same order of magnitude as its close, declining relative, Platte thistle (Louda and Arnett 2000, Rose et al. 2005; T. A. Rand and S. M. Louda, *unpublished manuscript*). We conclude that the data are sufficient to predict that *R. conicus* poses a major, serious risk to protected populations of *C. pitcheri*, an already exceptionally rare North American endemic species.

Ecological parameters in the prediction of ecological risk

Determining the direct ecological risk posed by an exotic insect herbivore species for native plant species necessarily includes at least two components. The most obvious one is a quantitative estimate of the dietary range of host plants, those likely to be recognized and potentially used by the insect. In weed projects, this physiological host range is well approximated by careful host specificity testing (Pemberton 2000a, Louda et al. 2003b). Contemporary evaluations of ecological risk rely primarily on this determination. Definition of this "physiological host range" is done by documenting patterns of host use in the indigenous environment and by testing the key components of host specificity (McEvoy 1996, Pemberton 2000a, Schaffner 2001, Louda et al. 2003a, b).

The basic set of parameters that define host specificity is adult host recognition, feeding acceptance and preference, oviposition acceptance and preference, plus successful larval and pupal development (DeBach and Rosen 1991, McEvoy 1996, Secord and Kareiva 1996). Adult insect behavior plus developmental success of the immature stages are considered the fundamental information needed to predict the potential for host range expansion by alien insects (McEvoy 1996, Marohasy 1998). Our laboratory and garden tests used the standard strategy to evaluate host range, and we found

that Pitcher's thistle is unambiguously within the physiological host range of *R. conicus*.

The second, apparently less obvious, need is a quantitative estimate of the interaction intensity and magnitude of effect when feeding or oviposition on native species could occur. Assessment of the likely magnitude of interaction when a native species has been identified as a less preferred, or secondary, host species has lagged behind evaluations of host range. Expert opinion has been used to infer the likely magnitude of the ecological risk to populations of less preferred host plants in the field (Zwölfer and Harris 1984, McClay 1990, Blossey et al. 1994). However, expert opinion was not consistent with the magnitude of subsequent ecological impacts documented in the several cases for which quantitative data on nontarget effects are now available (Louda et al. 1997, 2003b, Arnett and Louda 2002, Louda and O'Brien 2002).

It is not surprising, with hindsight, that the estimation of the magnitude of ecological risk to a native species identified as a potential host requires ecological data (Louda et al. 2003a, b). However, even though ecological data are acknowledged as potentially important (Follett and Duan 2000, Wajnberg et al. 2001), no such data are now required as a standard part of the ecological risk assessment protocols, even when a native species is identified as a less preferred, potential secondary host by the specificity tests. Although a petition to release a biological control insect should "present as clear a picture as possible of the long-term ecological consequences that could possibly result from the successful establishment of this agent in the North American environment" (USDA PPQ TAG guidelines; USDA 2001), no explicit guidance or criteria are proposed.

Quantification of phenological synchrony was hypothesized to be a critical parameter in the estimation of interaction intensity for less preferred native species that are accepted as secondary hosts. Temporal overlap between an herbivore and its plant resource has often been hypothesized to be critically important in plant–herbivore interactions, including prediction of ecological host range and potential nontarget impact in biological control (Crawley 1997, Gassmann and Louda 2001, Louda et al. 2003b, Russell and Louda 2004; F. L. Russell and S. M. Louda, *unpublished manuscript*). Further, temporal overlap between potentially interacting species is considered a critical parameter for the prediction of ecological outcomes in general (Rathcke and Lacey 1985; F. L. Russell and S. M. Louda, *unpublished manuscript*). Our comparison of the phenologies of the insect and the rare plant indicate that significant phenological overlap is likely, providing the first quantitative estimate of likely ecological interaction intensity before contact between a native host plant and a biocontrol herbivore. These results demonstrate a novel, realistic way to use ecological information to develop a quantitative estimate of the likely interaction

intensity for native species identified as possible host plants in host specificity testing. The outcome also provides data that support the suggestion that additional, ecological parameters are needed in risk assessment (Louda et al. 2003*a*, *b*). The main constraint on a reliance on the use of phenological overlap as a criterion for potential impact is that it is a measure of only contemporary, not evolutionary, overlap. Complete asynchrony would be required to predict no evolutionary potential for increased overlap, since even some phenological overlap would leave open the option for host switching.

Biological control practitioners have argued that phenological synchrony should be examined in prerelease assessments to increase the likelihood of weed control (Harris 1973, Goeden 1983). This study suggests that such assessment could be expanded to aid in the evaluation of the magnitude of potential nontarget side effects. Such information provides a quantitative way to better define exposure, as well as hazard, refining our ability to predict the risk of potentially significant demographic nontarget effects on populations of native species. Thus, we conclude that such information should be standard in assessments of magnitude of ecological risk for species within the potential host range of a biological control insect.

This study also demonstrated the utility of the experimental garden approach for evaluating plant traits that influence potential colonization, feeding, oviposition, and impact on performance of sensitive native species. This approach of using potted plants of the protected or rare species of interest, but done in an environment where the insect is established, provided critical insight on potential interaction intensity if overlap is established.

Biological control and conservation of species in natural areas

The study results are relevant also to the current interest in using biological control efforts against invasive exotic weeds in natural areas (Roush 1990, Quimby et al. 1991, Kauffman and Nechols 1992, Malecki and Blossey 1994, Office of Technology Assessment 1995, Pimentel 1995, Pimentel et al. 2000, Hoddle 2004). One motivation for advocates of more biological control efforts is the perception that the method, by definition, will restore natural enemy limitation, even in an entirely new community. It is also viewed as effective, cheap, and environmentally benign. However, success in biological control is elusive. For example, only 20% of weed projects show evidence of substantial decrease in weed density (Williamson and Fitter 1996), and another 20% were judged partially successful since the insect was established without evidence on weed limitation (Office of Technology Assessment 1995, Julien and Griffiths 1998). Furthermore, all successful introductions, whether effective or not, leave alien species in new environments (Simberloff 1986).

Also, recent studies have found unanticipated or higher than expected interaction intensities with nontarget native species by some insects used as biological control agents (Johnson and Stiling 1996, Louda et al. 1997, Boettner et al. 2000, Follett and Duan 2000, Stiling et al. 2000, Henneman and Memmott 2001, Wajnberg et al. 2001, Louda and O'Brien 2002). Unanticipated indirect and cascading ecological effects of biological control introductions on recipient native communities also have been reported recently (Callaway et al. 1999, Louda and Arnett 2000, Pearson et al. 2000). Thus, recent studies of nontarget effects (Follett and Duan 2000, Wajnberg et al. 2001, Louda et al. 2003*b*) challenge the automatic acceptance of this perception of safety in the conservation context.

Introduction of exotic species into new environments is a form of ecological engineering (Louda et al. 2003*a*). The relevance and applicability of ecological research on determinants of interaction intensities for biological control and invasive species management is clear (Crawley 1986, 1989, Follett and Duan 2000, Wajnberg et al. 2001, Shea and Chesson 2002). While perceived as ''reestablishment of natural enemies'' (Hoddle 2004), it is a more complex ecological manipulation, since the alien species are being introduced into new communities in new environments without their own natural enemies (Louda and Stiling 2004). The unexpected ecological outcomes, including unexpected interaction intensities, altered food webs, indirect and cascading effects, now known suggest the environment can alter expectations based on preference, and that serious, unexplored environmental costs can be associated with exotic species introductions, even when done with the best intentions.

Our results suggest that natural enemies that might affect sensitive and rare species, such as *C. pitcheri*, need to be tested for ecological host range, as well as physiological host range, and our study illustrates one way to expand testing in this direction. Furthermore, our results suggest that managers of natural areas should use great caution in releasing exotic insects for biological control when close relatives of target weeds (especially rare ones) exist in the preserve (Louda and Stiling 2004). We conclude that quantitative studies need to be done prior to release in any new habitat and that these studies should include ecological criteria for quantifying likely interactions and interaction intensities in native communities, especially in the conservation context.

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