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Karen E. Rose
Imperial College, Ascot, UK, k.rose@ic.ac.uk

Svata M. Louda
University of Nebraska - Lincoln, slouda1@unl.edu

Mark Rees
Imperial College, Ascot, UK

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DEMOGRAPHIC AND EVOLUTIONARY IMPACTS OF NATIVE AND INVASIVE INSECT HERBIVORES ON *CIRSIUM CANESCENS*

KAREN E. ROSE,[1,2,4] SVATA M. LOUDA,[3] AND MARK REES[1,2]

[1]*Department of Biological Sciences and NERC Centre for Population Biology, Imperial College, Silwood Park, Ascot SL5 7PY, UK*
[2]*Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, UK*
[3]*School of Biological Sciences, University of Nebraska, Lincoln, Nebraska 68588 USA*

Abstract. Invasive species have the potential to alter trade-offs leading to selection in the populations they invade. Here we quantify the demographic and selective effects of herbivory by native insects and the introduced floral feeder *Rhinocyllus conicus* on Platte thistle (*Cirsium canescens*), a sparse monocarpic thistle endemic to North America. *Rhinocyllus* first invaded the Platte thistle population in 1993. Since then, its numbers have increased exponentially, while the Platte thistle population size has decreased. Data from 11 years were analyzed to determine how demographic rates varied with plant size and damage by native insects and *Rhinocyllus*. Individual growth, survival, flowering probability, and seed set were all size dependent. Damage to vegetative structures did not influence demographic rates; damage to flower heads did because Platte thistle is seed limited. These analyses were used to parameterize a series of integral projection models (IPMs) that investigated the effects of floral herbivory on the population growth rate λ, equilibrium population size, and the evolutionary stable (ES) flowering strategy. The IPMs showed that native insects have significant impact on the equilibrium population size and λ, but not the ES flowering strategy, because they use the flowers of different-sized plants indiscriminately. In contrast, *Rhinocyllus* has the potential to drive Platte thistle extinct. *Rhinocyllus* preferentially fed and oviposited on the flowers of larger plants and therefore selected for a reduction in flowering size. However, as the thistle population went into decline, this pattern reversed. Thus, selection imposed by an invader may be complex and will reflect behavioral interactions between herbivore and host, as well as demographic changes in the host population.

Key words: biological control; Cirsium canescens; *evolutionary stable strategy; insect herbivore; integral projection model; invasive species; life history evolution; monocarpic perennial; Platte thistle;* Rhinocyllus conicus; *selection.*

INTRODUCTION

That insect herbivores can have considerable effects on plant performance is widely acknowledged (Janzen 1971, Crawley 1983, Hendrix 1988, Louda 1989, Louda et al. 1990, Doak 1992, Ehrlen 1995*a*, *b*, Louda and Potvin 1995). For example, insect herbivores can reduce plant growth rate, increase development time, delay or prevent flowering and, in turn, reduce seed set. However, understanding how these changes in performance affect population size can be complicated. For example, in a microsite-limited population, where seed production is more than sufficient to colonize all available microsites, herbivores that reduce seed production may have no effect on population density (Turnbull et al. 2000). However, even in microsite-limited populations, herbivores may influence plant fitness provided that the level of herbivore attack varies between plants, resulting in variation in seed set. The number of microsites captured depends on an individual's seed set relative to that of the other plants competing for microsites, so any variation in seed set generated by herbivores will influence plant fitness even when the plant population is microsite limited.

Therefore, in order to understand the ecological and evolutionary effects of herbivores, we need to quantify how herbivores influence plant performance and also understand what limits the population. Platte thistle (*Cirsium canescens* Nutt.) is ideal in this context because we have long-term data quantifying plant demography and the effects of herbivory, and experimental studies have demonstrated that the population is seed limited (Potvin 1988, Louda et al. 1990). This study is unique in that, since 1993, Platte thistle has been attacked by the invasive inflorescence-feeding weevil *Rhinocyllus conicus* (Louda et al. 1997, Louda 1998, Louda and Arnett 1999), allowing us to quantify demographic changes as the invasion proceeds.

Platte thistle is a strictly monocarpic species (i.e., reproduction is fatal). There is no vegetative spread and reproduction depends entirely upon current seed output for establishment and persistence (Lamp 1980,

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[4] E-mail: k.rose@ic.ac.uk

Lamp and McCarty 1981, Louda and Potvin 1995). In such species, the probability of flowering is typically size dependent and is a key determinant of fitness (Metcalf et al. 2003). In a constant environment, the main benefit of flowering at a large size is increased seed production, but this comes at a cost because the longer an individual waits to flower, the greater the chance of dying before reproducing (de Jong et al. 1987). The evolutionarily stable (ES) flowering size is determined by balancing these costs and benefits. Herbivores that change this balance can lead to evolutionary change in the ES flowering size. Damage to vegetative tissues that increases mortality or decreases growth will select for smaller sizes at flowering. In contrast, herbivores that damage reproductive structures only affect the evolution of flowering size, if their attack is size dependent. A few studies have reported cases of floral-feeding insects that selectively attack larger plants (Bullock et al. [1994] and references therein). Thus if pre-dispersal seed predation by *Rhinocyllus* changes the size-related seed production of Platte thistle, it could select for changes in the ES flowering strategy.

Rhinocyllus conicus was introduced to Nebraska in 1969–1972 for the biological control of invasive Eurasian thistles, especially *Carduus* spp. The original releases were made even after initial feeding trials indicated that the weevil's host range included the native North American genus *Cirsium* (reviewed in Zwölfer [1984] and Gassmann and Louda [2001]). Strong oviposition preference and more successful larval development on most *Carduus* species were expected to limit the use of North American native plants by *Rhinocyllus* (Zwölfer and Harris 1984); instead, the weevil has shown increased host range and geographical expansion (Louda et al. 1997, Gassmann and Louda 2001). *Rhinocyllus* did not appear on flower heads of Platte thistle until 1993. Since then, however, its numbers have increased exponentially (Louda 1998), with dramatic effect (Louda et al. 2003). For example, in 1996 the average number of viable seeds produced by Platte thistle flower-heads with weevils was 14.1% of that produced by similar heads with no *Rhinocyllus* or only native insects: ~35 seeds per head with no weevil present, compared to five seeds per head when the weevil was present (Louda et al. 1997). The impact of this decline in seed production on the long-term demography of Platte thistle has been postulated (Louda and Arnett 1999), but this hypothesis has not been quantified until now.

The *Rhinocyllus* range expansion, like all biological invasions, offers an ideal opportunity to quantify shifting selection pressures and microevolutionary change. To date, the research focus of most evolutionary studies of invasions has been the invader. For example, Müller-Scharer and Steinger (2004) list the outcome of a number of attempts to experimentally assess genetic changes in plants introduced into novel habitats. Less common are studies of evolutionary change in native species in response to an exotic invader. The best known example is that of the North American soapberry bug *Jadera heamatoloma*, which has evolved host preference for introduced golden rain trees *Koelreuteria elegans* in some areas of its range (Carroll and Dingle 1996). The populations using the novel host have evolved increased mouthpart length within the last 50 years, and cross-breeding experiments have revealed large amounts of genetic variation for this trait and also for host preference (Carroll et al. 1997). For other examples, see Mooney and Cleland (2001). However, such evidence is still relatively rare and our study system provides an unusual snapshot of the demographic and evolutionary forces at play as an invasion proceeds.

Here, we examine and model the effects of floral herbivory by *Rhinocyllus conicus* and native insects on the demography and evolution of flowering size in Platte thistle, using data on individual demography and herbivory collected continuously since 1990 (Louda and Potvin 1995, Louda et al. 1997, Louda 1998, 2000, Louda and Arnett 1999). First, we present detailed statistical models of the effects of plant size and insect herbivory on the growth, survival, flowering probability, and fecundity of Platte thistle. Then we present a series of integral projection models (Easterling et al. 2000, Rees and Rose 2002, Childs et al. 2003) that examine the demographic and evolutionary consequences of herbivory. This approach is particularly suited to the study of plant populations as it allows individuals to vary continuously in size, variation in growth between individuals of the same size, and size-dependent demographic rates, all essential features of plant populations (Metcalf et al. 2003). In addition, because regression models are used to parameterize the models, it is straightforward to include size-dependent herbivory and the distribution of attack across individuals of the same size.

Materials and Methods

Biology of Platte thistle

Platte thistle (*Cirsium canescens* Nutt: Asteraceae) is an indigenous monocarpic perennial in the midgrass sand prairie of central North America. It is sparsely distributed throughout the Sand Hills of Nebraska (Great Plains Flora Association 1986) as well as Colorado, Wyoming, and South Dakota, USA (Harrington 1954). Densities are highest in moderately disturbed sites. Plants also occur within the grassland matrix, but more sparsely, suggesting that the population is in part microsite limited. The life cycle is typical for a monocarpic perennial. Individuals delay flowering until at least their second year, and all individuals die after flowering (Lamp 1980, Lamp and McCarty 1981, 1982). Seedlings establish in early spring from seed released in the previous season. Seeds are relatively large and have a dehiscent pappus, leading to restricted seedling shadows (Louda et al. 1990). No germination

has been observed in autumn (S. M. Louda, *personal observation*) and there is no seed bank (Potvin 1988, Louda et al. 1990). After establishment, plants grow and persist as a tap-rooted rosette for one or generally more years. During their final year, individuals bolt, flower, and die. Platte thistle does not reproduce vegetatively, and none of the individuals in the Louda and Potvin (1995) study survived after flowering. In another experimental population grown from 4600 seeds planted in 1993, two individuals were still alive in 2003 and thus the maximum life span is at least 10 years. Flowering is determinate, with heads produced sequentially from apex to lower branch terminals and from terminals to subsidiary heads within branches (Louda and Potvin 1995).

In addition to herbivory by the exotic *Rhinocyllus conicus*, the flower heads of Platte thistle are attacked by a number of native insects that feed on the developing flower head tissues. The main inflorescence feeders include the larvae of two tephritid flies, *Orellia occidentale* (Snow) and *Paracantha culta* (Wiedeman), and several pyralid moths, *Pyrausta subsequalis* subs. *plagialis*, *Homeosoma impressale*, and *H. ardaloniphas* (Lamp 1980, Lamp and McCarty 1981, 1982; G. Balogh, *personal communication*). Common foliage-feeding and stem-boring insect herbivores include the nymphalid *Vanessa cardui*; *Pyrausta subsequalis* subs. *plagialis*; the curculionids *Baris* sp. nr. *subsimilis* and *Thecesternus affinis*; the tinged *Corythuca distincta*; as well as several aphids, chrysomelids, myrids, and grasshoppers.

Data collection

The study was conducted at Arapaho Prairie, a Nature Conservancy Preserve in the Sand Hills of Nebraska (Bleed and Flowerday 1989). Life table parameters and insect herbivory were measured on individually numbered (''plot'') plants in five 144-m^2 demography plots in 1990–2002. The information from the demography plots was complemented each year (1990–2000) with performance data for supplemental flowering (''census'') plants that were monitored over the growing season and then sampled destructively at the end of the season to estimate seed production. Although sections of the prairie are mowed each season after Platte thistle has completed flowering and senesced, the demography plots were not mowed during this study. The prairie at Arapaho has not been grazed since 1978. Seed continues to limit seedling recruitment in these plots (S. M. Louda et al., *unpublished data*).

Throughout the study, new plants in each of the demography plots received a uniquely numbered aluminum tag. They were censused each year early in the growing season (20–30 May) and again later (12–20 July). On each sampling date, the data collected included: number and identity of live and dead plants, growth stage, size, and herbivore damage. We used the maximum annual observation for each parameter for each plant. For all live plants, we measured: root crown diameter (millimeters) at the soil interface; the number of green leaves, the number of damaged green leaves (i.e., any amount of damage), and the number of leaves with ≥25% leaf area damaged. Estimates of damage were expressed as proportions of the total number of green leaves.

For flowering plants we also recorded the total number and damage of all flower heads (≥2 mm diameter) present. The external evidence of insect feeding damage to flower heads was scored as follows: 0–1%, none to possible slight damage; 2.5%, definite small amount of insect feeding (<5% of the surface area of the head); 15%, an intermediate amount of insect feeding damage (5–24% of the surface area); 75%, a large amount of insect feeding (≥25% of the surface area); 85%, stem-mining within 1 cm of the base of the flower head of sufficient magnitude to potentially jeopardize the further development of the flower head; and 100%, a hole chewed completely into or out of the flower head (no viable seeds were ever produced by flower heads with a hole chewed completely through).

The supplemental plants were located early in each season (5–20 May) by walking transects and labeling each plant found that showed signs of developing a flowering stem, until a predetermined number had been located in at least 2–3 areas of the prairie (20–30 plants, in total, per year). Flower heads were bagged with fine mesh after flowering in order to prevent dispersal of seed. The plants were sampled as previously described and then their flower heads were dissected to provide counts of viable seeds and quantitative information on insect damage within the inflorescences. Destructive sampling was not carried out in or near the demography plots. In dissecting flower heads, we recorded: the flower head size (diameter, in millimeters), the number of viable seeds, and insect pupal cases, *Rhinocyllus* pupal chambers, and other evidence of insect feeding within each flower head. For each plant, we summed over all flower heads to get individual plant totals for viable seeds, damage by native insects, and *Rhinocyllus* eggs laid.

Integral projection models

The integral projection model (IPM) can be used to describe how a continuously size-structured population changes in discrete time (Easterling et al. 2000). The state of the population is described by a function, $n(x, t)$ that gives the distribution of size x at time t; so the number of individuals between size x and $x + \delta x$ is $n(x, t)\delta x$ with error going to zero as δx decreases to zero (Easterling et al. 2000). This is the continuous size analogue of the population vector $n(t)$ in matrix models (Caswell 2001). The population dynamics at time $t + 1$ are then

$$n(y, t + 1) = \int_{\Omega} [p(x, y) + f(x, y)]n(x, t)\, dx \quad (1)$$

where $p(x, y)$ represents survival and growth, resulting

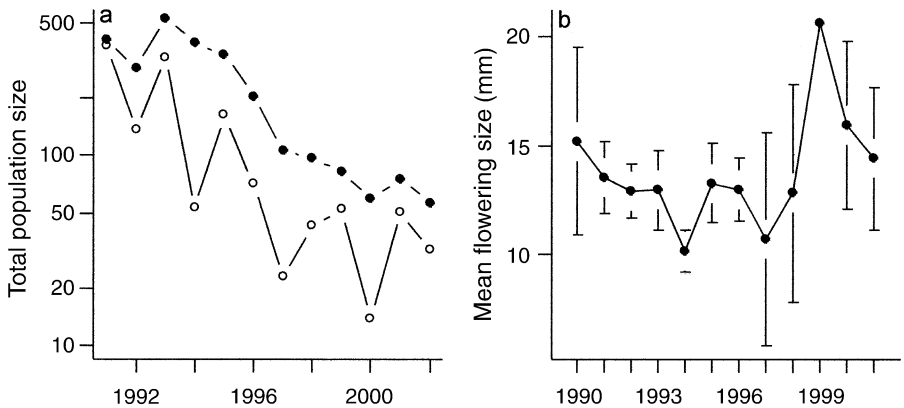

FIG. 1. (a) Changes in population size for all plants (solid circles) and recruits (open circles) over the course of the study, 1991–2002; note the log scale. (b) Mean size at flowering for each year of the study; bars are 95% confidence intervals. Note that only one plant flowered in 1999; hence, the absence of a confidence interval for that year.

in movement of individuals from size x to size y, and $f(x, y)$ is the number of size y seedling recruits produced by a size x plant. The range of possible sizes, Ω, was set at 0.9 times the minimum and 1.1 times the maximum size observed.

In order to apply the model, we must specify the dependence of survival, growth, flowering probability, and seed set on plant size and herbivory. The fecundity function is given as

$$f(x, y) = s(x)p_f(x)f_n(x)p_e f_d(y), \quad (2)$$

where $s(x)$ is the probability of survival of a size x individual, $p_f(x)$ is the probability that an individual of size x flowers, $f_n(x)$ is the number of seeds produced by an individual of size x, and p_e is the probability of seedling establishment. Data were not available on the size of recruits derived from plants of different sizes, but evidence from other systems suggests a low maternal effect on recruit size (Weiner et al. 1997, Sletvold 2002), so the distribution of recruit size, $f_d(y)$, was assumed to be independent of parental size.

The survival–growth function is given by

$$p(x, y) = s(x)[1 - p_f(x)]g(x, y) \quad (3)$$

where $s(x)$ is the size-dependent survival probability and $g(x, y)$ is the probability that an individual of size x grows to size y. The probability of flowering, $p_f(x)$, enters the survival function because reproduction is fatal in monocarpic species. Under assumptions similar to those required by a matrix model, the IPM predicts the population growth rate λ, given by the dominant eigenvalue of the kernel, which can be calculated using standard matrix software. Corresponding to λ are the dominant right and left eigenvectors $w(x)$ and $v(x)$ that give the stable size distribution and size-specific reproductive value of adult plants (Easterling et al. 2000).

We used the long-term field data to parameterize the various functions that define the kernel $[K(y, x) = p(x, y) + f(x, y)]$, in particular to specify how they vary with individual size and herbivory. In all analyses, size was log-transformed using natural logarithms. Data management, analyses, and modeling were done using R Version 1.8.0 (R Development Core Team 2004).

RESULTS

Changes in population size, recruitment, and flowering size over time

Although demographic data collection began in 1990, total population size was not estimated for all of the study plots in that year; hence population size is plotted from 1991 onward. During this period, the total population size ranged from 56 to 529 individuals (Fig. 1a), while the number of new recruits ranged from 14 to 376. Although there was considerable variation between years in population size in the early years of the study, the numbers of plants in each category declined consistently after 1993.

The mean size at flowering was reasonably consistent up to 1998. There is some evidence that the mean has increased during the period after 1998 (Fig. 1b; $F_{1, 213} = 6.12$, $P < 0.02$).

Variation in demographic rates with size and herbivory

Changes in size from one year to the next were well described by a simple linear model; $y = a_g + b_g x$ where y and x are log root crown diameter in successive years ($F_{1, 793} = 779.7$, $P < 0.0001$, Fig. 2a). The probability of survival and flowering were analyzed using a binomial GLM, and a log link function (McCullagh and Nelder 1989). Survival was strongly size dependent, with larger plants being more likely to survive than smaller ones ($\chi^2_1 = 205.1$, $P < 0.0001$; Fig. 2b). The probability of flowering was also strongly size dependent ($\chi^2_1 = 651.9$, $P < 0.0001$; Fig. 2c). Neither measure of foliar herbivory entered any of these regressions significantly, nor did their additive effect when combined ($P > 0.20$ in all cases). This was despite ~10%

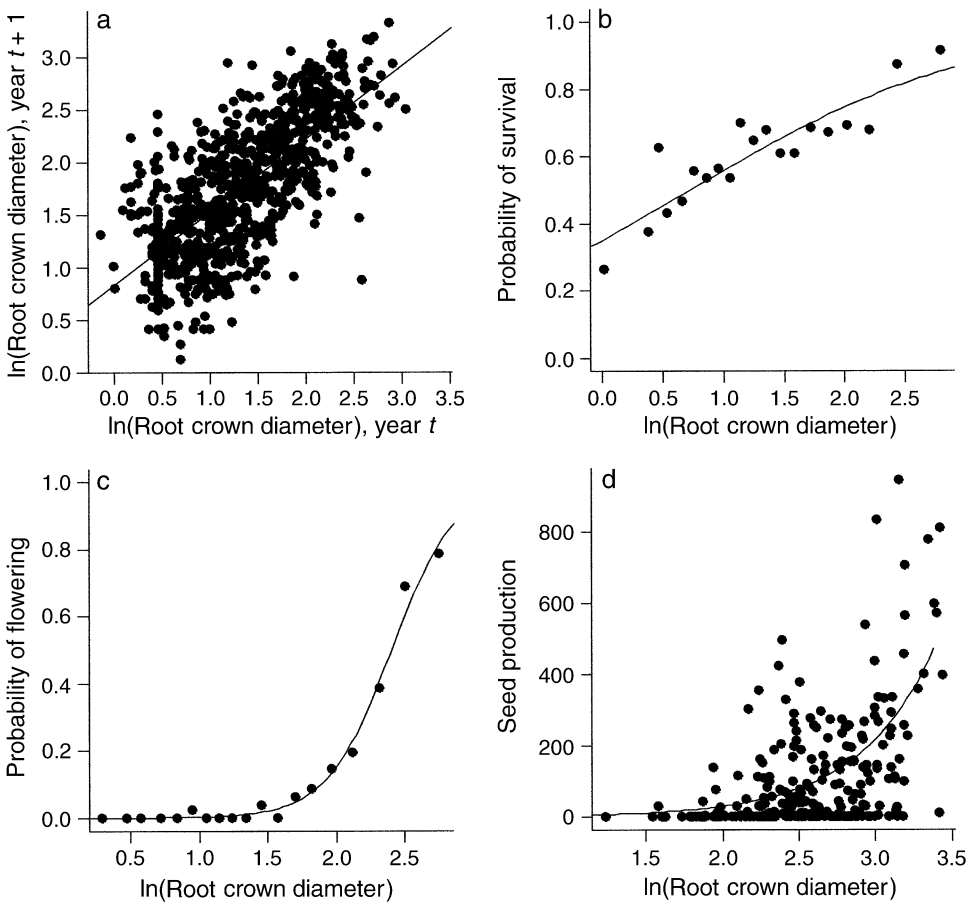

FIG. 2. Patterns of size-dependent plant demography: (a) changes in size (natural log scale; diameter originally measured in millimeters) from one year to the next, (b) the probability of survival, (c) the probability of flowering, and (d) seed production. Note that for panels (b) and (c) we divided the data into 20 equal-sized categories and calculated the probability and mean size for each category; the analysis, however, was performed on the binary data. Parameter values for the fitted functions are given in Table 2.

of leaves having at least 25% of their leaf area damaged. These terms were consequently dropped from the models.

The data from the census plants, where all flower heads have been dissected, allow the relationship between seed production and plant size and herbivore attack to be quantified. Individual seed production is clearly size dependent and highly variable (Fig. 2d). We therefore fitted a negative binomial GLM with a log link function (Venables and Ripley 1997); the fitted model was of the form

$$f_n = \exp(0.37 + 2.02x - 0.02e - 1.96D) \qquad (4)$$

where x is log root crown diameter, e is the number of *Rhinocyllus conicus* eggs, and D is the level of damage by native herbivores. Significance was tested using likelihood ratio tests (Venables and Ripley 1997). This analysis is in agreement with the experimental work of Louda and Potvin (1995), which showed that seed production was decreased by ≈60% by native floral feeding herbivores; our regression model (Eq. 4) predicts a reduction of 65%.

Data from the census plants were also used to explore how the number of *Rhinocyllus* eggs varied with plant size and year. As the invasion progressed the number of eggs per plant increased, and larger plants received more *Rhinocyllus* ovipositions than smaller plants (Fig. 3). Across individuals, the egg distribution was very strongly skewed, with most individuals having no or very low numbers of eggs and only a small number having many eggs. Therefore we modeled this relationship using a negative binomial GLM and a log link function (Venables and Ripley 1997). The effect of year was highly significant ($\chi^2_{10} = 114.5$, $P < 0.0001$), as was the effect of plant size ($\chi^2_1 = 21.7$, $P < 0.0001$); parameter estimates are given in Table 1.

The experimental work of Louda and Potvin (1995) demonstrated that Platte thistle is seed limited; we would therefore expect a positive relationship between this year's seed production and recruitment the follow-

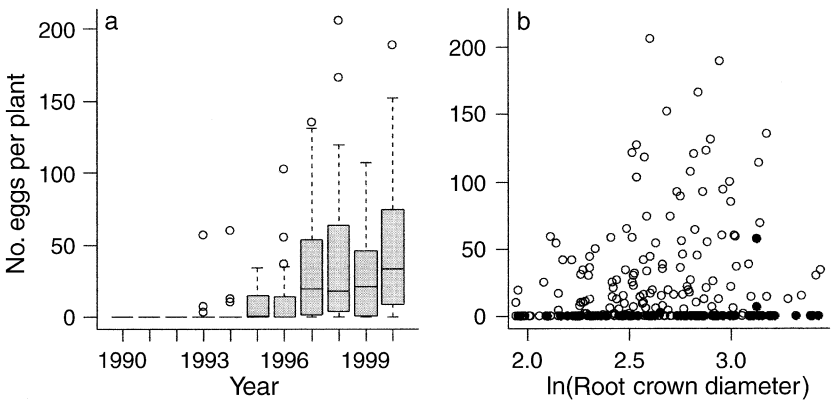

FIG. 3. Box plot of the number of *Rhinocyllus* eggs laid per plant (a) for different years of the study and (b) in relation to plant size (diameter measured in millimeters); open circles come from years after 1993.

ing year. To explore this relationship, we used the regression models (Eq. 4 and Table 1) to predict the seed production of the demography plots. There was a significant positive correlation between seed production and subsequent recruitment (Spearman rank correlation, $r_S = 0.71$, $P = 0.009$; Fig. 4), reinforcing the view that recruitment is indeed seed limited. To quantify this relationship, we fitted negative binomial regression models of the form

$$\ln(R_{t+1}) = \alpha \ln(S_t) \tag{5}$$

where R_{t+1} is the number of recruits in year $t + 1$, S_t is the seed production in year t, and α is the slope of the regression line (estimated $\alpha = 0.67$(1 SE = 0.03)).

TABLE 1. Negative binomial GLM model for the mean number of *Rhinocyllus* eggs per plant, *e*, in relation to plant root crown diameter, *x* (natural-log-transformed).

Year	Parameter estimates
1990	$\ln(e) = -17.30 + 1.71x$ (56.86) (0.36)
1991	$\ln(e) = -16.97 + 1.71x$ (82.90) (0.36)
1992	$\ln(e) = -16.71 + 1.71x$ (87.00) (0.36)
1993	$\ln(e) = -3.74 + 1.71x$ (1.15) (0.36)
1994	$\ln(e) = -3.39 + 1.71x$ (1.06) (0.36)
1995	$\ln(e) = -2.81 + 1.71x$ (1.12) (0.36)
1996	$\ln(e) = -1.64 + 1.71x$ (0.85) (0.36)
1997	$\ln(e) = -0.96 + 1.71x$ (0.97) (0.36)
1998	$\ln(e) = -0.75 + 1.71x$ (1.02) (0.36)
1999	$\ln(e) = -1.24 + 1.71x$ (1.01) (0.36)
2000	$\ln(e) = -0.52 + 1.71x$ (0.99) (0.36)

Notes: Values in parentheses are standard errors. Estimated *k* (the clumping parameter) for the negative binomial distribution = 0.32 (0.04).

Given this relationship, we can then calculate the probability of establishment, p_e, which is given by

$$p_e = \frac{R_{t+1}}{S_t} = \frac{S_t^{\alpha}}{S_t} = S_t^{\alpha-1} \tag{6}$$

and which is density dependent, provided $\alpha < 1$. We also fitted models with an asymptote, but these never improved the fit (assessed using AIC, Akaike's Information Criterion). The parameter values for the various fitted functions are given in Table 2.

Integral projection models

We defined four different integral projection kernels, parameterized using the data analyses previously described. These were: (1) a plant-only kernel that excluded the effects of all types of herbivory; (2) a native-

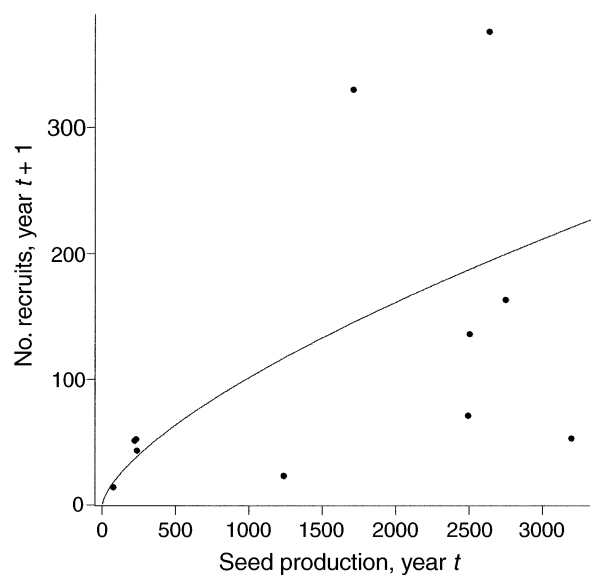

FIG. 4. The relationship between seedling recruitment in year $t + 1$ and estimated seed production in year t. The line is from the fitted negative binomial model (Eq. 5).

TABLE 2. Parameter estimates for the statistical models describing the demography of Platte thistle.

Demography	Equation†	n	P	Other statistics‡
Growth	$y = 0.83 + 0.69x$ (0.04) (0.02)	795	<0.0001	$\sigma_g^2 = 0.19$ $r^2 = 0.50$
Survival	$\text{logit}(p_s(x)) = -0.62 + 0.85x$ (0.08) (0.06)	2643	<0.0001	
Flowering	$\text{logit}(p_f(x)) = -10.22 + 4.25x$ (0.62) (0.27)	1593	<0.0001	
Seed set	$f_n = \exp(0.37 + 2.02x - 0.02e - 1.96D)$ (0.95) (0.32) (0.004) (0.63)	260	<0.0001	$k = 0.24$ (0.02)
Seedling size distribution	Gaussian; mean 0.75, variance 0.17 (log scale)	992		
Recruitment	$\ln(R_{t+1}) = 0.67\ln(S_t)$ (0.03)	11	<0.001	$k = 2.14$ (0.87)
Probability of establishment	$p_e = 0.067$ (mean) or $p_e = S_t^{-0.33}$			

† Variables: x, size, a function of ln(root crown diameter); y, subsequent size after growth of a plant of size x; e, the number of *Rhinocyllus conicus* eggs; D, damage by native insects; S_t, seed production at time t; f_n, the number of seeds produced by an individual of size x; p_s, p_f, p_e, probabilities of survival, flowering, and establishment, respectively; R_{t+1}, recruitment at time $t + 1$. Values in parentheses below the equations are 1 SE.

‡ Statistics: σ_g^2, variance about the growth curve; k, negative binomial distribution clumping parameter.

insects-only kernel that included the effect of floral tissue feeding by native insects; (3) an average-size-related *Rhinocyllus* kernel that examined the effect of floral feeding by *Rhinocyllus* and native insects, assuming that all plants receive the average number of *Rhinocyllus* eggs, allowing for plant size; and (4) a negative binomial *Rhinocyllus* kernel that examined the effect of floral feeding by the *Rhinocyllus* and native insects, assuming a negative binomial distribution of *Rhinocyllus* eggs (see Appendix). Scenario (3) represents a deterministic world where individuals of the same size always receive exactly the same number of eggs. Scenario (4) represents the more realistic alternative, where plants of the same size receive widely differing number of eggs, depending upon the host plant selection behavior of the weevil. Note that because vegetative herbivory did not significantly influence growth or the probability of surviving or flowering, the four kernels differ only in their fecundity functions (Table 2).

Finite rates of increase and equilibrium population size

Setting the probability of establishment, p_e, equal to its average value over the duration of the study (estimated by dividing the number of recruits by estimated seed production) removes all density dependence from the system, allowing comparison of the finite rate of increase, λ, under the four scenarios just described. In the absence of any type of herbivory, λ = 1.38, so we would expect the population to increase rapidly. Analysis of the native-insects-only kernel showed that floral herbivory by native insects decreases λ to 1.05, consistent with the experimental work of Louda and Potvin (1995). Under both of the *Rhinocyllus* scenarios, the effect of the invader increases as the invasion proceeds, reducing λ to less than one for all years after 1995 (Fig. 5a). The negative effect of *Rhinocyllus*, however, is smaller when we allow for the variable distribution of eggs across plants (Fig. 5a). In either case, based on

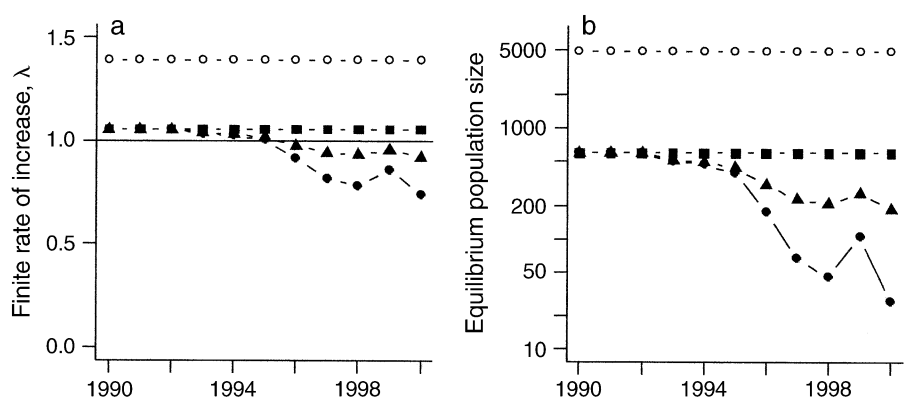

FIG. 5. Predicted finite rate of increase (λ) and equilibrium population size for Platte thistle in each year of the study, 1990–2002. The symbols refer to different kernels: open circles, plant-only; solid squares, native-insects-only; solid diamonds, average-size-related *Rhinocyllus* oviposition; and solid triangles, aggregated (negative binomial) *Rhinocyllus* oviposition.

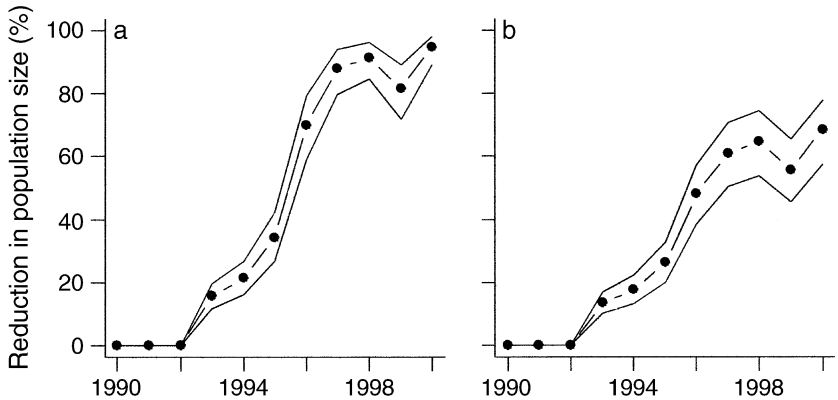

FIG. 6. Predicted reduction in equilibrium Platte thistle population size, assuming that the distribution of *Rhinocyllus* eggs is: (a) even across all plants, each receiving the mean number of eggs, and (b) aggregated (negative binomial), with some plants receiving more eggs than other plants of the same size. The points are the means of the bootstrapped samples; the lines are the 2.5 and 97.5 percentiles (see *Finite rates of increase and equilibrium population size* for details).

this analysis, we conclude that *Rhinocyllus* is capable of driving Platte thistle extinct.

When the probability of establishment, p_e, is density dependent, the equilibrium population size can be predicted for the four scenarios (Fig. 5b). In the absence of native floral herbivores, the predicted equilibrium population size is ~5000, much larger than ever observed in the field. Incorporating the effect of native floral herbivores reduces the equilibrium to ~600 plants, in reasonable agreement with that observed in the field prior to invasion by *Rhinocyllus*, ~500 plants (Fig. 1a). Comparing the effects of *Rhinocyllus* with those of the native insects, specifically, shows that a reduction in predicted equilibrium density of up to 95% by the weevil is possible, assuming that all plants receive the mean number of eggs. The effect is reduced but the trend is not altered, if we allow for an aggregated (negative binomial) distribution of *Rhinocyllus* eggs across plants, with a maximum reduction to date (2002) of 69% (Fig. 5b).

Prediction of the possible impact of *Rhinocyllus* is critically dependent upon the relationship between seed production and subsequent recruitment (Fig. 4). To explore how uncertainty in this relationship influenced the predicted impact of *Rhinocyllus*, we used a computer-intensive approach. First we generated 1500 bootstrapped samples of the data by sampling with replacement from the observed seed production recruitment data pairs. We then re-estimated Eq. 5 using the bootstrapped sample and used this new relationship to recalculate the equilibrium population size predicted for each year of the study. Approximate 95% confidence intervals were constructed using the percentiles of the bootstrapped equilibrium population size distribution. This analysis shows that the percentage reduction in population size is reasonably well characterized (Fig. 6).

To explore how well the models described the data, we calculated the predicted stable size distribution for the whole population and for flowering plants only (see Rees and Rose [2002] for details of the calculation). Provided that $\lambda \approx 1$, all of the kernels have excellent descriptive power (Fig. 7) in terms of the size distribution of all plants and also of those that flower.

Herbivory and the evolutionarily stable flowering size

To explore how herbivory influences the evolution of flowering size, we use the evolutionarily stable (ES) approach. Early evolutionary studies assumed that some measure of population growth, such as λ, is maximized by evolution (Stearns 1992). In contrast, the ES approach is based on the idea of invasibility and seeks to define a strategy that cannot be invaded by any alternative strategy. To do this, we apply the results of Mylius and Diekmann (1995), who demonstrate that when density dependence acts at the recruitment stage, the ES flowering strategy, out of a range of varying strategies, is that which maximizes R_0. In Platte thistle, the probability of establishment is density dependent (see previous section), so these methods are appropriate. The net reproductive rate, R_0, is the mean number of offspring by which a newborn individual will be replaced by the end of its life, and thus the rate by which the population increases from one generation to the next (Caswell 2001). To calculate R_0 for the IPM, we apply the methods of Cochran and Ellner (1992) and Caswell (2001) that allow age-based life history statistics to be calculated from stage-based models. This is straightforward using matrix software (see Caswell [2001] for details of the calculations).

We calculated the ES flowering strategy assuming that the size-dependent slope of the flowering function, β_s, was fixed at the estimated value, in order to prevent the flowering surface from becoming a step function, whereby all individuals in a population flower above the same critical size. There are several reasons why a step function might not be biologically realistic: (1)

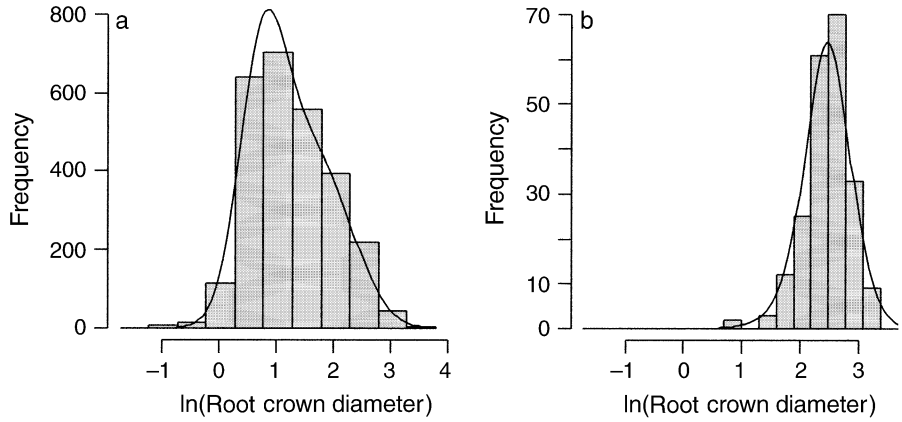

FIG. 7. Observed (bars) and predicted (line) stable size distributions (natural-log-transformed; diameter measured in millimeters) from the native-insects-only kernel for: (a) all plants and (b) only flowering plants.

there is variable growth between the commitment to the flower being made and when plant size is measured; (2) plant size may not be perfectly correlated with the threshold condition for flowering; and (3) there may be genetic variation in the threshold condition for flowering. To predict the ES flowering size under the different scenarios, we used a quasi-Newton algorithm to find the intercept β_0 that maximized R_0. For the two different *Rhinocyllus* models, we calculated the ESS (evolutionarily stable strategy) separately for each year, based on the specified distribution of weevil eggs and the appropriate annual parameter from the model of weevil egg load (Table 1). To aid interpretation of the results, we converted the ES intercepts into mean flowering sizes. To do this, we constructed a kernel using the predicted ES intercept and the observed slope, β_s, and then calculated the stable size distribution of flowering plants $w^*_{\mathrm{fl}}(y)$ using the following equation:

$$w^*_{\mathrm{fl}}(y) = \frac{s(y)p_{\mathrm{f}}(y)w(y)}{\int_{\Omega} s(y)p_{\mathrm{f}}(y)w(y)}\,dy \tag{7}$$

where $w(y)$ is the stable size distribution (right-hand eigenvector); the arithmetic mean size at flowering is then

$$\mu_{\mathrm{fl}} = \int_{\Omega} w^*_{\mathrm{fl}}(y)\exp(y)\,dy. \tag{8}$$

The plant-only and native-insect-only kernels predict the same ES size at flowering (~20 mm) for all years. This prediction is considerably larger than the observed mean flowering size (~13 mm; Fig. 8a). The ES flowering size is the same for both strategies because native floral herbivores did not act in a size-dependent manner. In contrast, *Rhinocyllus* laid its eggs preferentially on

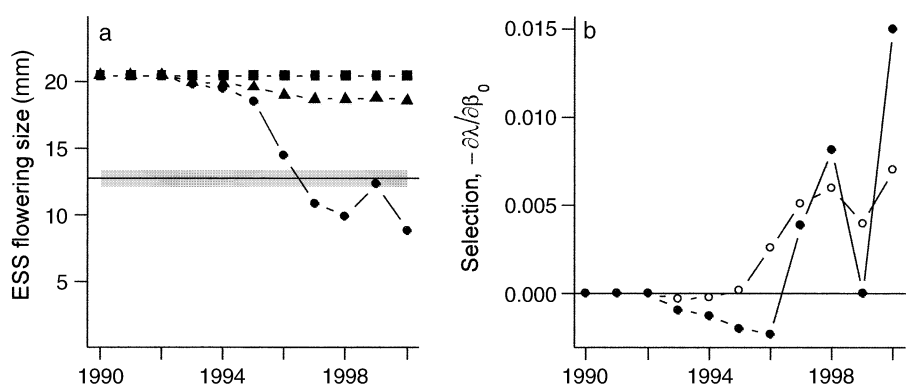

FIG. 8. (a) Predicted ESS (evolutionarily stable strategy) flowering size for the different scenarios, 1990–2000; the symbols refer to different kernels; open circles, plant-only; solid squares, native-insects-only; solid circles, average-size-related *Rhinocyllus* oviposition; and solid triangles, aggregated (negative binomial) *Rhinocyllus* oviposition. The horizontal line is the mean size at flowering; the shaded area indicates the 95% confidence interval. The plant-only and native-insect-only kernels give the same ES prediction because native insect attack is not size dependent. (b) Patterns of selection, measured as $-\partial\lambda/\partial\beta_0$, for the average-size-related *Rhinocyllus* oviposition (solid circles) and aggregated (negative binomial) *Rhinocyllus* oviposition (open circles) kernels, 1990–2000.

larger plants, which reduces the fitness gains from flowering at a larger size and thereby selects for smaller sizes at flowering. The exact effect of the invasive weevil, however, is strongly influenced by the pattern of attack. If all plants of the same size receive the average number of eggs, then the minimum ES prediction is 8.9 mm. Alternately, if the distribution of eggs across plants is aggregated (negative binomial) then the minimum ES prediction is 18.6 mm (Fig. 8a).

The average size at flowering in Platte thistle is approximately proportional to $-\beta_0$, so $-\partial\lambda/\partial\beta_0$ provides a measure of the force of selection on the flowering strategy. Assuming that the population is initially at the demographic and evolutionary equilibrium ($\lambda = 1$ and β_0 is at the ES prediction of the plant only model, so $-\partial\lambda/\partial\beta_0 = 0$) allows exploration of the pattern of selection imposed by *Rhinocyllus* as it invades the Platte thistle population. Initially there is selection for smaller sizes at flowering, but as the invasion proceeds, the direction of selection is reversed, leading to selection for larger sizes at flowering (Fig. 8b; see *Discussion*). As with the ES predictions, the magnitude of selection imposed by *Rhinocyllus* is affected by the distribution of eggs: the predicted selection is much stronger for the average-size-related, compared to the negative binomial, distribution of weevil eggs (Fig. 8b).

Discussion

Invasive species have long been the subject of concern. Applied research has aimed to identify the factors that make some habitats more invasible than others and some species better invaders than others, as well as to find methods of managing the impact of biological invasions in the increasing number of ecosystems that they threaten. In addition, recognition is increasing that population ecology and life history theory are important in understanding invasions (e.g., Sakai et al. 2001). Here, we used life history and evolutionary (ESS) theories to estimate the selection imposed by the introduced floral herbivore *Rhinocyllus conicus* on size at flowering, a key component of fitness (Metcalf et al. 2003), of its adopted native plant host, *Cirsium canescens*. We estimated the effects of native insects at the same time. Although the invasion has been well documented (Louda et al. 1997, Louda 1999, Louda and Arnett 1999), we present here the first analysis of this invasion using a quantitative, predictive framework. We use data on individual size-related demography and herbivory by native insects and *Rhinocyllus* to parameterize integral projection models (IPMs; Easterling et al. 2000, Rees and Rose 2002) of the system. These models provide a precise, flexible methodology for developing new insights into demography and evolution in size-structured populations. Complex aspects of biological interactions, for example, attack by *Rhinocyllus*, which is size-related and highly variable, are easily accommodated within this framework, allowing an assessment of their impact on plant demography and evolution.

Despite the growing literature documenting changes in established invaders by drift, hybridization, or response to selection (e.g., Müller-Scharer and Steinger 2004), evidence for recent evolutionary change in invaded communities or species is still relatively rare. Exceptionally, Singer et al. (1993) presented evidence for rapid evolution of host preference in two populations of the butterfly *Euphydryas editha*. Individuals in each population expanded their host preference to include an introduced plant species in their diet. At both sites, the proportion of insects using the novel host increased, and some individuals were found that no longer had a preference for their ancestral host plant species. Choice tests were used to demonstrate genetic variation underlying these changes in behavior. Similarly, the North American soapberry bug *Jadera heamotoloma* has evolved host preference for introduced golden rain trees (*Koelreuteria paniculata*) in some areas of its range (Carroll and Dingle 1996). The populations using the novel host have evolved increased mouthpart length within the last 50 years, and cross-breeding experiments have revealed large amounts of genetic variation for this trait and also for host preference (Carroll et al. 1997). In both of these studies the native insect herbivores must have responded to selection-created differences in fruit size of native and introduced host plants. As far as we know, ours is the only study that has quantified current changes in selection on a native species imposed by an invasive species. Perhaps it is not coincidental that, including our study, much of the evidence for selection and evolutionary change in native species in response to an exotic invader comes from studies that cross trophic levels. Because such interspecific interactions are the basis of community organization, some (e.g., Thompson 1998) argue that these connections between species will naturally evolve rapidly and, when invasive species are involved, will have potentially major effects on communities.

The pattern of selection on flowering size imposed by *Rhinocyllus* is complex (Fig. 8b). Initially, before *Rhinocyllus* has had a substantial demographic impact, there is selection for smaller sizes at flowering because larger plants receive higher egg loads. However, as the invasion proceeds and the population goes into decline, the direction of selection changes, leading to selection for larger sizes at flowering. This is probably a consequence of selection for increased generation time in the declining population (Charlesworth 1994); larger flowering sizes occur as smaller individuals are eliminated through mortality and flowering, and this increases generation time and increases the average time that it takes individuals to reach the critical size for flowering. There is some evidence for this effect in Platte thistle, as size at flowering has increased since 1995 (Fig. 1b). Also, we found that the effect of *Rhin-*

ocyllus was strongly mediated by the distribution of eggs across plants. To better visualize why selection for increased generation time should occur in the declining population, consider a population in which recruitment is prevented completely. Initially the population is made up of a mix of phenotypes with small and large threshold sizes for flowering; as time goes by, all of the plants with small threshold sizes are lost from the population as individuals become large enough to flower, leaving a population dominated by plants with large threshold sizes for flowering. As this pattern continues, theory suggests that average threshold size should increase.

Quantifying selection by calculating $-\partial\lambda/\partial\beta_0$ allows us to get around the problem that flowering size is only expressed in plants that survive to reproduce, the ''invisible fraction'' problem (Grafen 1988). Using regression approaches (Lande and Arnold 1983, Arnold and Wade 1984*a*, *b*) to detect phenotypic selection on such characters is misleading because only individuals that survive to reproduce are included in the analysis. We cannot measure flowering size for individuals that die before flowering, which means that the cost of flowering at large size is ignored. This problem led Blanckenhorn (2000) to conclude that ''Detection of pre-reproductive viability selection against large body size . . . is therefore difficult.'' By using models, we are viewing Darwinian fitness as a property of a design (Williams 1966), not of an individual; thus we can account for the costs of delayed flowering as well as the benefits. Ignoring such mortality costs would lead to the general conclusion that there is strong directional selection for larger sizes at flowering, as lifetime reproductive success increases with flowering size (Rees and Crawley 1989, Metcalf et al. 2003), even in systems where we know the population is close to the ESS (Rees et al. 1999, Rees and Rose 2002, Childs et al. 2004).

Attack by *Rhinocyllus* is predicted to continue to decrease both λ and the expected equilibrium population size, as a result of the population being seed limited. These effects have been calculated assuming that the current level and distribution of attack do not change through time. If levels of attack continue to increase through time (Fig. 3), then the models will underestimate the already substantial impact of *Rhinocyllus*. However, field observations suggest that *Rhinocyllus* rates of attack are declining on Platte thistle individuals at the low density, while increasing on the closely related, later flowering wavyleaf thistle *Cirsium undulatum* (S. M. Louda, *unpublished data*). Russell and Louda (2004) recently demonstrated that egg load on wavyleaf thistle is reciprocally related to the availability of Platte thistle flower heads. The models presented here clearly indicate the need to quantify not only mean levels of attack but also the distribution of attack across plants when assessing the role of herbivores (Fig. 5). Failure to do this could lead to a substantial overestimate of the impact of insects on plant populations. In this case, this is because fecundity is a decreasing exponential function of egg load (Eq. 4), which means that $E[f_n(e)] > f_n(\bar{e})$, where $\bar{e}$ is the mean egg load (Jensen's inequality). Biologically, this stems from the fact that plants that have small egg loads have disproportionately higher fecundities, whereas those that receive high egg loads all have fecundities close to zero.

In addition to estimating the effects of *Rhinocyllus*, we also quantified the demographic and selection effects of seed damage by native floral-feeding herbivores. Our analyses show these to have a substantial negative impact on λ and the equilibrium population size, in agreement with the experimental studies of Louda and Potvin (1995). In the absence of even the native floral-feeding herbivores, the predicted population size of Platte thistle is an order of magnitude higher ($\sim$5000 compared to $\approx$500–600 plants); this assumes that no other density-dependent forces would come into effect at high densities. However, given the experimental data demonstrating both significant effects of the native floral herbivores and lower rates of recruitment per viable seed for plants in the grass-covered microhabitat vs. in more disturbed microhabitat (Louda and Potvin 1995), we expect that interspecific competition would supplement insect seed limitation and lead to somewhat lower densities than predicted by the model. In contrast, our analyses demonstrate that native herbivores attacking vegetative tissues had no discernible effect on the subsequent growth or survival of Platte thistle; thus they had no effect on predicted population size. However, this interaction may be subtler. If there is a cost of tolerance or resistance to native vegetation-feeding herbivores, in terms of decreased growth or survival, then these may have an effect on abundance, which is not easily evaluated using the existing data; an exclusion experiment is needed. If such hidden costs exist and were quantified, however, then their impact could be easily assessed within the current framework.

Given our parameterized model of size-dependent demography and knowledge of the nature of density dependence, we can use the results of Mylius and Diekmann (1995) to characterize the ES flowering strategy. Previously, we used these results for recruitment-limited populations where the probability of establishment was inversely proportional to seed production, $p_e \propto 1/S_t$ (Rees et al. 1999, 2000, Rees and Rose 2002, Rose et al. 2002). These results are also applicable to Platte thistle because $p_e = 1/S_t^{0.33}$. The predicted ES flowering size with aggregated oviposition by *Rhinocyllus* (18.9 mm) is substantially larger than that observed in the field ($\sim$13 mm); this discrepancy suggests that either (1) the observed flowering strategy is maladaptive, or that (2) important selection pressures were not included in the model. We explore these options briefly as a guide for further research.

The current flowering strategy could be maladaptive due to recent changes in the environment or lack of genetic variation. The cattle grazing at Arapaho, which ended in 1978, would have selected for smaller flowering sizes through decreased growth rates and increased mortality. The population could still be flowering at a suboptimal small size if some lack of genetic variation prevented adaptation to the new conditions. However, several studies have demonstrated that natural populations harbor extensive genetic variation for threshold flowering size (Wesselingh and de Jong 1995, Wesselingh and Klinkhamer 1996, reviewed in Metcalf et al. 2003). Consequently, we hypothesize that an important aspect of the selective environment remains to be incorporated into our models. Two factors occur as possibilities for further exploration. First, better data are required on the mortality caused by root crown herbivory, which is higher on large juvenile plants; mortality that increases with plant size has been documented on a close relative of Platte thistle (Stanforth et al. 1997). Alternatively, previous studies of monocarpic species (Rees et al. 1999, 2004, Rose et al. 2002, Childs et al. 2004) have suggested that temporal variation in growth, survival, and recruitment can have a substantial impact of the evolution of flowering decisions; we are currently developing stochastic integral projection models to explore this. In sum, floral herbivory by both native and invasive floral herbivores is predicted to be a significant factor in predicting the ES flowering strategy for Platte thistle, in addition to other selective factors in the environment.

Acknowledgments

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APPENDIX

A description of the negative binomial distribution for aggregated oviposition by *Rhinocyllus conicus* on flower heads of Platte thistle is available in ESA's Electronic Data Archive: *Ecological Archives* E086-022-A1.