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Experimental invasions using biological control introductions: the influence of release size on the chance of population establishment

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Abstract

Introductions of biological control organisms offer a unique opportunity to experimentally study the process of invasion by exotic species. I used two chrysomelid beetles, *Galerucella calmariensis* and *Galerucella pusilla*, which are currently being introduced into North America for the biological control of purple loosestrife (*Lythrum salicaria*), to determine how the initial size of a release affects the probability that the introduced population grows and persists. I released both species into stands of their host plant at 36 sites scattered throughout central New York State using four release sizes: 20, 60, 180, and 540. I returned to these sites over the next 3 years to census the populations. For both species, the probability of population establishment increased with release size. Population growth rates also depended positively on release size. The implication from these results is that the demographic factors whose influence depends on population size or density such as demographic stochasticity, Allee effects, and genetics play important roles in the establishment of invading populations. A second set of releases was used to determine if it was at all possible for a single gravid female to found a population. Out of twenty individual females released, one female (a *G. calmariensis*) founded a population that persisted until the end of the study (3 generations).

Introduction

The study of biological invasions has long been hampered by a lack of experimentation. Clearly, we cannot introduce exotic species into new regions for the sole purpose of testing hypotheses about invasions. A lack of experimentation has meant that some key questions about the invasion process remain unanswered. In order to address two critical questions in invasion biology, I took advantage of a current biological control program in which two European Chrysomelid beetles are being introduced into North America to control the wetland weed, purple loosestrife (*Lythrum salicaria*). I used introductions of these species to determine how the size of the introduction influences whether or not a permanent population establishes and, also, to determine if it is possible for one mated female to found a population.

A small number of colonization experiments have been performed in the past using small islands as release sites with the intent of testing MacArthur and Wilson's (1967) theory of island biogeography. Limited replication in these studies has been a consistent problem. However, 3 independent studies using small mammals (Sheppe 1965; Crowell 1973; Ebenhard 1989) show trends for a greater chance for establishment from larger release sizes. In a similar and better replicated experiment with lizards, T.W. Schoener and A. Schoener (1983) found that population establishment depended more on island size than on the number

of individuals released, an indication that an environmental influence can swamp the effect of population size.

While experiments addressing the relationship between population size and persistence are rare, theoretical studies addressing this relationship abound (MacArthur and Wilson 1967; Richter-Dyn and Goel 1972; Leigh 1981; Shaffer 1981; Soulé 1987; Goodman 1987; Dennis 1989; Gabriel and Bürger 1992; Stephan and Wissel 1994; Grevstad 1999). Collectively, these studies demonstrate that the shape of the relationship can vary greatly depending on what assumptions are made about life histories, stochasticity, carrying capacities, genetics, Allee effects, etc. In general, persistence is predicted to be an increasing function of initial population size. But it is also possible (and consistent with theory) that persistence could instead be largely *independent* of initial population size (as per T.W. Schoener and A. Schoener's (1983) lizards). This independence can be expected if (1) density-independent factors, such as weather, habitat conditions, or the size of the habitat patch are the main determinants of persistence, or if (2) a high rate of population increase allows initially small populations to quickly escape the risk of extinction. Insects are likely to fall into this category, since they tend to have both high biotic potential and high sensitivity to environmental conditions. In support of this view, a number of populations are known to have been founded by remarkably few founders (Allee et al. 1949; Elton 1958; Mayr 1963; Cock 1986; Simberloff 1989). Even cases of a single mated female (or a male–female pair) founding a population are known, but such accounts are anecdotal and not well documented (e.g. Cock 1986).

Retrospective analysis of successful and unsuccessful purposeful introductions have offered another approach to studying the role of initial colony size on establishment (e.g. Hall and Ehler 1979; Beirne 1985; Hopper and Roush 1993; Green 1997). Beirne (1985) reported that 60% of biological control introductions of 800 or more individuals led to establishment but only 15% smaller introductions did so. Hall and Ehler (1979) and Hopper and Roush (1993) report similar correlations. However, these retro-analyses may be misleading. They compare establishment rates *among species* for which different numbers were released rather than comparing the establishment rates of different sized releases *within a species*. Therefore, the number of individuals released in each case is likely to be confounded with species traits that make them easy to obtain in large numbers, such as a high reproductive rate or abundance in their native range; both of these factors have also been shown to correlate with a higher establishment rate (Crawley 1986, 1987). Thus, controlled and well replicated experimental introductions are needed to demonstrate the role of initial colony size on the chance of population establishment.

Only one published study has used biocontrol introductions to experimentally test for an effect of release size on population establishment. Memmott et al. (1998) recently found that the number of thrips (range of 10–810) released onto individual gorse bushes influenced the likelihood of finding thrips one year (one generation) later. Their work also points to a need for longer-term monitoring of populations to ascertain establishment or failure, especially when individual insects are difficult to find.

In the present study, the fates of 92 staged 'invasions' by 2 exotic beetle species were monitored for more than 3 years (3 full generations). One set of releases was used to determine the influence of release size on establishment. A second set of releases tested whether a single gravid female can found a population. In addition to addressing these important issues, this study provides observations of population dynamics during the critical establishment phase of an invasion, a stage that typically passes unobserved and certainly unquantified in almost all biological invasions.

Methods

Study system

L. salicaria is a perennial wetland weed native to Eurasia. It was introduced into North America during the early 1800s (Stuckey 1980). The weed is most abundant in the northeastern US, but it is actively invading wetlands across the continent, often forming expansive monospecific stands that are rarely found in Europe. Habitats occupied by *L. salicaria* include marshes, moist fields, stream sides, pond sides, and ditches. An individual plant consists of multiple stems that resprout each year from a persisting root mass. Plants can grow as tall as 3 m (personal observation) but are more often between 1 and 2 m in height. The inflorescence consists of a terminal spike of bright purple or magenta flowers. The plant is considered a problem because it displaces native plants, clogs waterways, and reduces the quality of habitat for wildlife (Mal et al. 1992).

Galerucella pusilla and *G. calmariensis* are two chrysomelid beetles that are currently being released in North America for control of *L. salicaria* (Hight et al. 1995). These two beetles are very closely related and have similar life histories and habits (Blossey 1995). In the northeastern US, both species have one generation per year. The adult stages overwinter in the leaf litter, emerging in May to mate and lay eggs on the plant surface. The adults continue to lay eggs through the end of June and then die off. Larvae feed and develop on leaves and stems and then burrow into the soil to pupate. The new generation of adults emerges in July and August. These adults feed for a brief period before diapausing for the winter. The two species differ biologically in that *G. calmariensis* has a higher fecundity than *G. pusilla* and is also more mobile (switches plants more frequently) (Grevstad 1998).

Experiment 1: Effect of release size on establishment

Methods of site selection, insect rearing, and release differ in the first and second experiments. Here I describe methods for the experiment to determine the effect of release size. In a later section, I describe the methods used for releases of single females.

Site selection and characterization

I selected 36 stands of *L. salicaria* in the Central New York State region in which to release both *Galerucella* species (Figure 1). I chose stands that formed discrete patches and that had moderate to high plant densities. I avoided sites that were dominated by standing water or that were likely to flood. The stands were variable in size with a mean of $807 \pm 30\,m^2$ ($n = 36$). The mean stem density was 23.6 stems/m^2 with a range

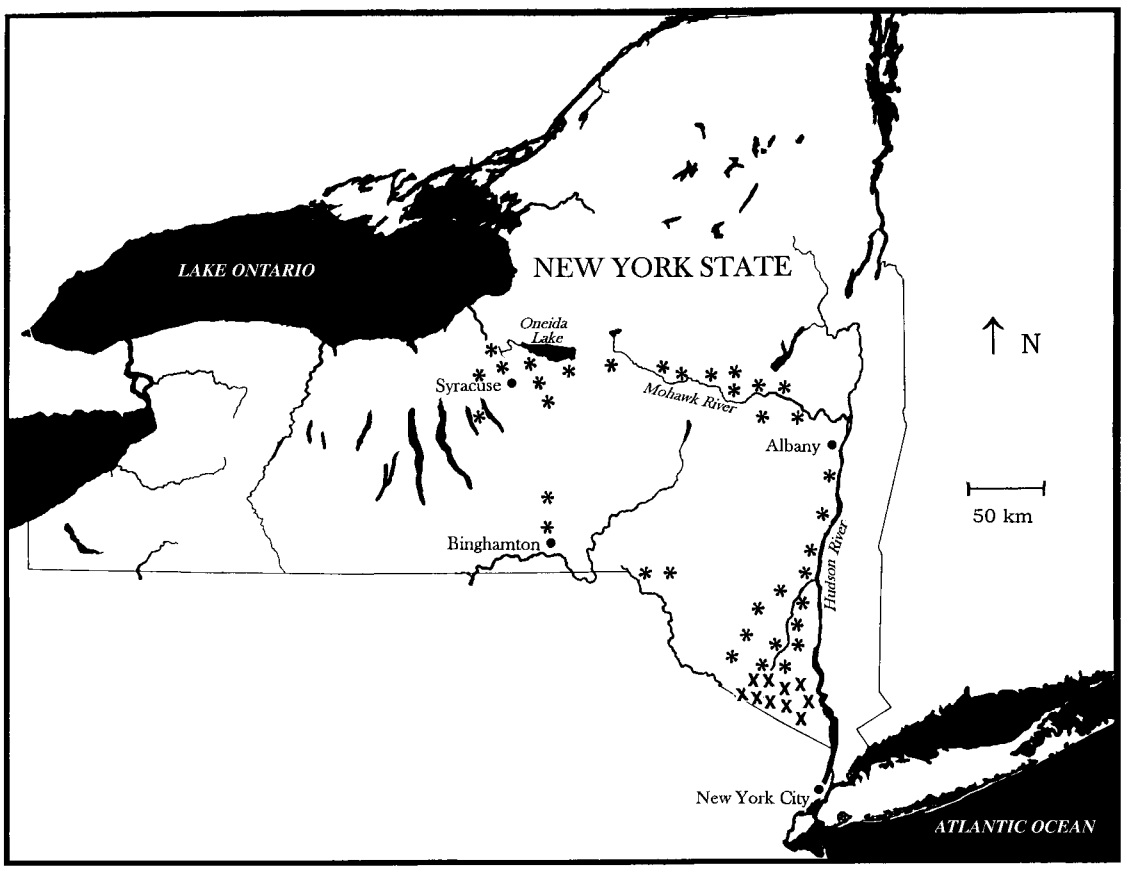

Figure 1. Locations of 46 field sites used in this study. Asterisks (*) indicate sites where 20, 60, 180, or 540 individuals of *G. pusilla* and *G. calmariensis* were released. X's indicate sites where a single female of each species was released.

from 10 to 48 stems/m^2. Each site was isolated from others by at least 10 km. With this separation distance, it was highly improbable that individuals could disperse between sites (see Grevstad and Herzig 1997). Release sites were grouped into 9 blocks by region. Four release size treatments – 20, 60, 180, and 540 individuals – were randomly assigned to the 4 sites within each block.

Anticipating that variability among sites might influence population establishment, I measured the following site characteristics: (1) the area of the stand, (2) the density of *L. salicaria* stems, (3) the height of *L. salicaria* plants early in the growing season, (4) the terminal height of the plants, and (5) the nitrogen content of the leaves. Patch area was determined by approximating the shape of each patch with an appropriate polygon and measuring its dimensions. Stem densities were determined by counting the number of stems in five 1 m^2 quadrats randomly placed within the stand. Stem densities were used rather than plant densities because the number of stems per plant varies greatly among sites; stem density is therefore a better representation of resource concentration. For height measurements, plants were selected 'randomly' along a transect by blindly pointing the meter stick at the ground every two steps and then choosing the nearest plant or stem. Early season heights of 20 plants per site were measured in May of 1995. The terminal heights of an additional 20 plants per site were measured at the end of the growing season in August, 1994. A sample of 30 new but fully expanded leaves were collected from random plants within each patch in late May of 1995. The leaves were dried in a drying oven, ground to a powder, dried again, and analyzed for carbon and nitrogen content using a Carlo Erba® NA 1500 series 2 nitrogen/carbon analyzer.

Rearing and release of insects

The insects used in the releases were reared in a greenhouse on potted plants enclosed in fine mesh fabric bags. Lighting was used to extend the photoperiod to 15 h. Greenhouse temperatures varied with ambient temperatures over a range from 20 °C to 32 °C. The beetles used for the experiment were the second generation produced from parental stock collected in August 1993 from the Tonawanda State Wildlife Refuge in western New York. At this site, field populations of both species were established in 1992 from beetles transferred from Germany (Hight et al. 1995).

At the time of their release, the experimental beetles were of ages between 2 and 12 days since adult eclosion. Each release consisted of a mixture of individuals from many rearing cages. The beetles were transported to the field sites in vented vials containing sprigs of their host plant and were kept in a cooler until they were released.

The beetles were released at the 36 field sites between May 17 and May 22, 1994. To prevent frenzied flight upon liberation, I released them only during the cool of night or morning, or on cool overcast days (< 18 °C). The releases were made by opening the vials and encouraging the beetles onto the plants. I spread the beetles out among a few or many plants (depending on the release size). The two species were released together at each site, but they were placed in different parts of the patch to avoid forcing competition between them. Each release point was marked with a bamboo pole.

One of the consequences of using beetles that had not overwintered is that their fecundity tends to be lower than that of overwintered beetles (personal observation). In addition, the beetles were unmated at the time of release (determined by dissecting a sample of females and examining the spermatheca for the presence of sperm). *Galerucella* do not normally mate until approximately 7 days from adult eclosion. Even older beetles in my colonies were unmated because, unknown at the time, they require > 15.5 h of daylight to break reproductive diapause (personal observation) and I reared them on 15 h of daylight, which was the day length at the time of release. Approximately 2 weeks after their release the beetles began to mate and reproduce as the days lengthened into summer.

Population censuses

One week after the releases were made, I returned to the sites to make qualitative observations. Mainly, I noted the approximate proportion of each species remaining. I did this so that I could determine whether failed establishments could be traced back to immediate dispersal or disappearance from the site, or if it was a more gradual decline.

In late May of the three succeeding years, 1995, 1996, and 1997, I returned to the 36 sites and searched thoroughly for *Galerucella*. At this time of year, the plants are small (10–50 cm) and the adult beetles feed and mate conspicuously near the tops of the stems. Most of the stands were small enough that all of the *L. salicaria* plants at the site could be examined for

presence of beetles. I used a two phase approach to censusing. The first phase consisted of a reconnaissance survey in which I walked slowly back and forth across the site, covering the entire area, and glancing at every plant in my path. I flagged the area(s) within the stand where I found beetles or their damage (usually there was just one such area). In the second phase, I thoroughly examined each plant within that area, recording the number of each species. I also measured the area occupied by the beetles.

At a few of the large stands where populations were well established and dispersed throughout the stand, it was necessary to use transect samples to estimate the total numbers of beetles present. The transects were 1 m wide and crossed the area occupied by the beetles at regularly spaced intervals. The number of transects used varied with the size and shape of the particular patch, but the sampled area was typically 50–100 m^2 and covered 10–20% of the total patch area. In the first census year, I used transects to estimate population size at only one site. In the second year, as the population sizes increased, 5 sites were surveyed in this manner, and in the final year 9 were surveyed this way.

When searching for small populations of just a few individuals, there is the possibility that the entire population will be missed. To test my ability to find *Galerucella*, I set up three 1.84 × 1.84 m screen cages over a natural stand of *L. salicaria* and scattered 20, 60, or 180 *Galerucella* (mixed species) into each cage. I returned the next day to count the beetles, using search intensity similar to that I would use in my surveys.

Statistical analyses

I analyzed the effects of release size and site characteristics on two response variables – population establishment and population growth rate. Multiple logistic regression (using JMP statistical software) was used to determine if release size and site variables influenced whether or not populations established. Logistic regression tests for the dependence of a binomial response variable (in this case 1 = established, 0 = failed) on continuous independent variables (release size, site factors). A population was considered to be 'established' if at least one adult beetle was found during the fourth summer (1997) following the releases. One of the site variables, end-of-season plant height, was correlated with both early-season height and leaf nitrogen level and was therefore omitted from the analyses to avoid confounding these factors. Early-season height and leaf nitrogen levels were not correlated with each other and were therefore retained along with patch size and plant density. The factors to include in the regression model were selected using both forward and backward stepwise procedures. Factors that clearly had no significant effect ($P > 0.10$) were removed from the final regression models. In all of the analyses, forward and backward selection yielded the same model.

I looked for effects of release size and site factors on rate of population growth during the first generation following release (measured as N_1/N_0). A large number of zero values for growth rates precluded use of standard least squares regression. As an alternative, I calculated the median growth rate for all 36 populations (each species separately) and then categorized growth rate responses as being either greater than or less than the median. Then, I used multiple logistic regression, as above, to test the effects of release size and site factors on whether populations grew at a rate above or below the median.

Experiment 2: Single female releases

Using a separate set of releases and slightly different methods, I set out to test the ability of a single female to found a population. Ten additional release sites were selected in Orange County in southern New York State for release of single females (Figure 1). The criteria for selecting these sites were the same as in the above experiment, except that minimum distance between sites was 5 km rather than 10 km. Also, the requirement that the *Lythrum* patch was discrete was relaxed (the abundance of loosestrife in this area made moderate and small sized patches difficult to find). In expansive or sprawling stands, releases were made into one corner or appendage of the stand.

Ten adult females of each *Galerucella* species were collected on June 12, 1994 from the Tonawanda State Wildlife Refuge in eastern New York. At this time of year, female *Galerucella* were gravid with eggs and had presumably mated with multiple males. The beetles were kept overnight in vented plastic vials with a sprig of their host plant, then transferred to the release sites the next two days. One of each *Galerucella* species was released at each site. The release points were spaced two or more meters apart and were marked with a bamboo pole. I initially enclosed each beetle in a fine mesh sleeve slipped over a healthy loosestrife stem. Without this initial enclosure, it would be likely that the beetle would disperse away from the site or perhaps be preyed upon before she had the chance to oviposit.

After the 10-day protection period, I carefully removed the sleeve from the plant to release the beetle and eggs. At this time, I counted the eggs that had been deposited on the stem.

As in the previous experiment, I returned to these 10 sites in late May of 1995, 1996, and 1997 and searched for beetles. If the site was small, I searched the entire site. If it was larger, I restricted intensive searching to an area within a 12 m radius of the release point, and scanned the remaining areas of the stand.

Results

General patterns in colonization dynamics

The four-year time series for the 72 released populations at 36 sites are plotted in Figure 2. One of the striking features of these populations is that population growth rates (measured as the population size in the current year over population size in the previous year, $N(t+1)/N(t)$) varied tremendously among sites and years. The range was from 0/180 in a *G. calmariensis* population to 931/18 in a *G. pusilla* population. At the end of the study period (3 full generations), extant population sizes ranged from 1 to 7083 in *G. pusilla* and from 2 to 876 in *G. calmariensis*.

For all but 1 of the 72 populations, there was a substantial drop in population size between the release year (1994) and the first census year (1995). The one exception was a *G. pusilla* release of 540 individuals near Binghamton, New York. This population more than doubled to 1239 in the first year. The tendency for introduced populations to apparently decline before gradually building up is typical of many biocontrol introductions (Hopper and Roush 1993; Memmott et al. 1998). Part of the apparent decline is certainly due to the fact that even a careful search of the site will not recover 100% of the beetles that are actually there. When I tested my searching efficiency by searching for a known number of beetles in field cages, I found 13 out of 20 beetles, 51 out of 60 beetles, and 95 out of 180 beetles. The weighted mean of these proportions is 0.61 so the population sizes in Figure 2 for years 2, 3, and 4 can be assumed to be roughly 61% of the actual size. The initial drop in population size may also be partly due to dispersal away from the site. When I visited the sites one week after the release, there was already a substantial drop in numbers, especially for *G. calmariensis* where as few as 10% of the number released were found during a brief search of plants near the release point. Finally, from my personal experience rearing *Galerucella* in captivity, I suspect that the released beetles, which did not overwinter, had lower fecundity than the beetles from subsequent generations.

Two additional patterns are suggested from the population trajectories in Figure 2. Populations from larger releases appear to (1) be less likely to go extinct and (2) have higher population growth rates. These patterns are explored further in the following sections.

Population establishment

At the end of the fourth spring of the study period (1997), 12 of 36 *G. calmariensis* populations and 21 of 36 *G. pusilla* populations were still persisting. Only release size and block (or region) met the criteria for entering the multiple logistic regression model. Both of these significantly influenced establishment for both species (Table 1).

For *G. calmariensis* the proportion of populations establishing increased steadily with release size (Figure 3). For *G. pusilla*, a peculiar drop in the proportion of populations establishing occurs from release size of 20–60–180 before a jump to 100% establishment for release sizes of 540 (Figure 3). The initial dip may not be biologically relevant; the points fall within a likely range of sampling error even if the actual relationship is slightly increasing.

None of the measured site characteristics (plant height, plant density, patch area, and nitrogen content) had an effect on establishment. However, a significant block effect suggests that there is some type of regional influence on establishment. Populations tended to do best in the Oneida Lake and Binghamton areas and in the western Mohawk River valley, and they tended to do poorly in the upper Hudson River and Wallkill River valleys.

A few populations appeared to go extinct, but then reappeared in the following year (see Figure 2). Clearly, a small number of *Galerucella* must have been present

Table 1. Results of logistic regression analysis for effect of release size on population establishment.

	Source	df	Likelihood ratio χ^2	*P*
G. pusilla	Release size	1	14.3	0.0002
	Block/region	8	23.4	0.0029
G. calmariensis	Release size	1	28.4	< 0.0001
	Block/region	8	17.7	0.024

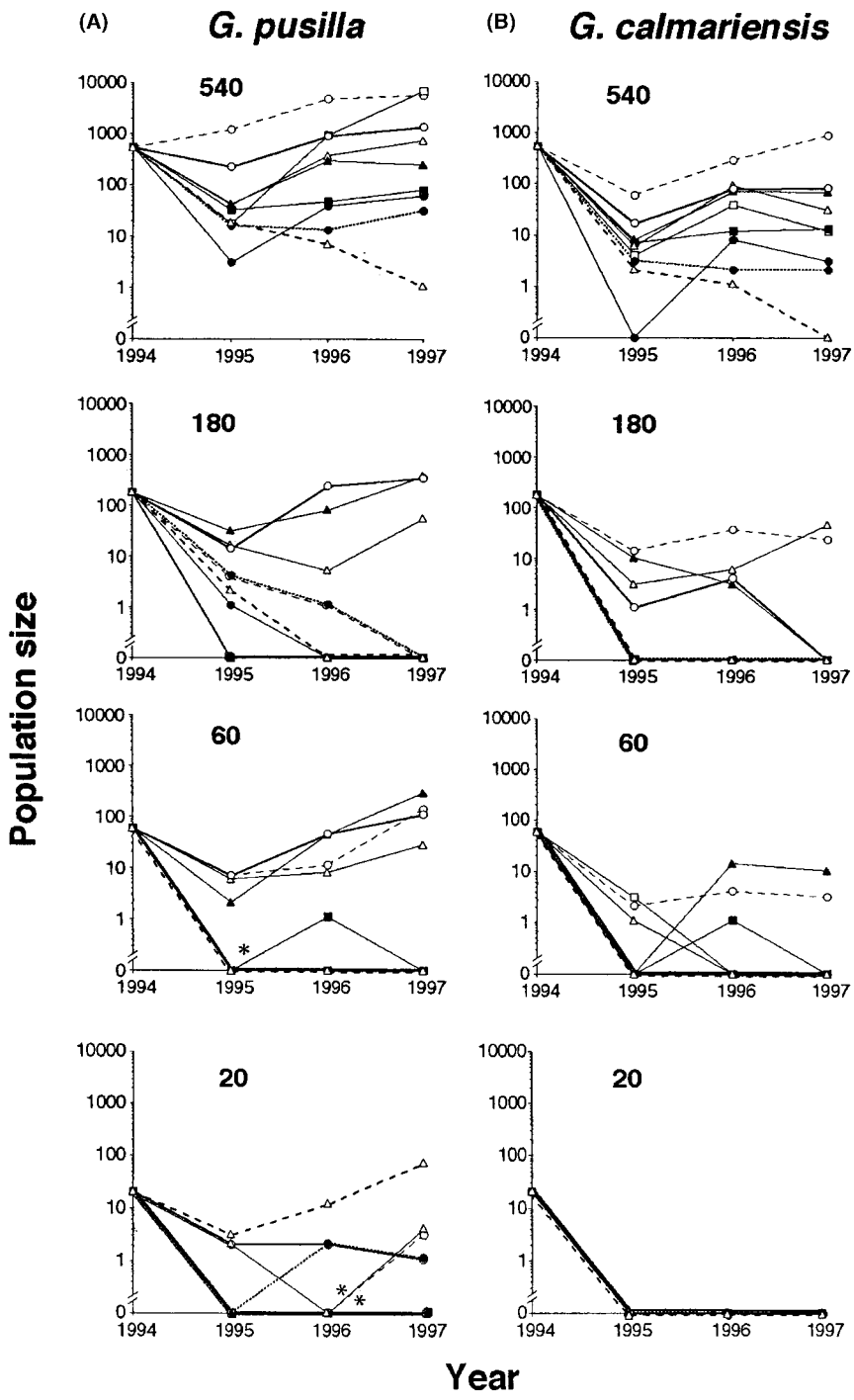

Figure 2. Number of adults of (A) *G. pusilla* and (B) *G. calmariensis* found each year at 36 release sites. The initial number of individuals introduced is labeled above each graph. Matching symbols across treatments indicate populations that are in the same block. Matching symbols within a treatment but between species correspond to populations at the same site. An asterisk signifies a population for which only eggs were found.

but were overlooked. This raises the possibility that some of the populations that were declared extinct at the end of 3 generations were actually persisting with very small numbers. My success in finding individual beetles in the cage trials with known numbers of beetles was 61%. Thus, if there was only one beetle at a site, I could expect to miss it with a probability of 0.39. If there were two beetles, I would miss both with a probability of $(0.39)^2 = 0.15$. With 3 beetles the chance of missing all three drops to 0.059, etc. The probability of erroneously declaring extinctions is reduced further for populations in which no beetles were found more than one year in a row. The probability of missing a population of 2 beetles 2 years in a row is $(0.15)^2 = 0.0225$, and for 3 years it drops to 0.0034. The vanishing nature of these probabilities means that the inaccuracy of the data due to missed populations is likely to be minimal.

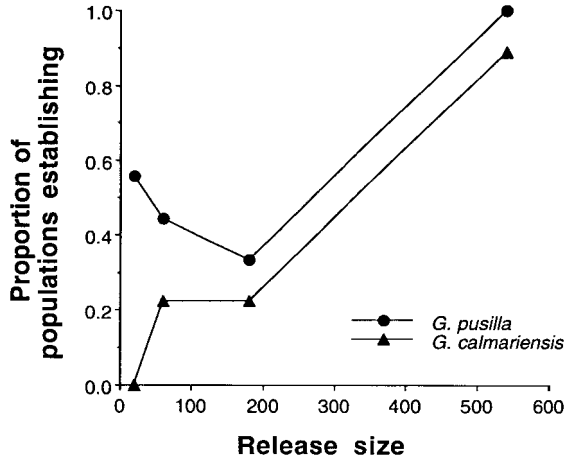

Figure 3. Proportion of *G. pusilla* and *G. calmariensis* populations establishing versus release size.

Population growth rates

In addition to affecting the likelihood of establishment, the number of individuals released had a significant positive effect on growth rates in *G. calmariensis* ($\chi^2 = 23.40$, df $= 1$, $P = 0.000$) and a marginally significant effect in *G. pusilla* ($\chi^2 = 3.9$, df $= 1$, $P = 0.048$ (Figure 4; Table 2)). A significant effect of block on growth rates for *G. calmariensis* again suggests that there is some regional variation in site quality affecting population growth (Table 2). Both species appear to be responding to similar environmental conditions; if one species did well at a particular site, then the other species was also likely to do well, as indicated by a

Table 2. Results of logistic regression analysis for effect of release size on growth rate category.

	Source	df	Likelihood ratio χ^2	*P*
G. pusilla	Release size	1	3.90	0.048
	Block/region	8	22.03	0.005
G. calmariensis	Release size	1	23.40	0.000
	Block/region	8	12.50	NS

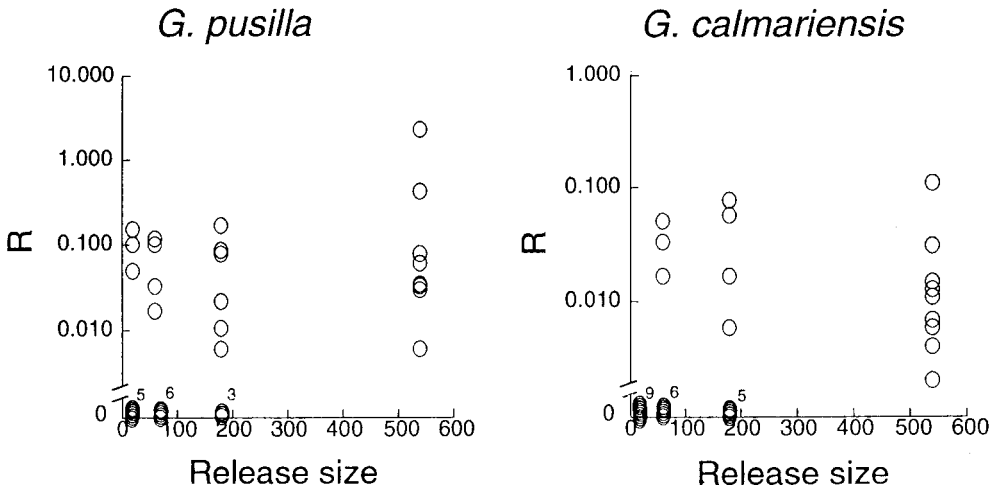

Figure 4. Growth rates during the first year after release (measured as the number of adults released in 1994 divided by the number of adults found in 1995) plotted against the number released.

positive correlation in growth rates for the two species (Figure 5). The correlation is significant even when the potentially confounding effect of release size included as a co-factor ($R^2 = 0.30$, $F = 8.01$, df $= 1$, $P = 0.0079$).

Times to extinction

Of 39 total colonies that went extinct, 28 (72%) went extinct without completing a full generation. Four went extinct during the second year and seven in the third year. All extinctions of the smallest release size occurred in the first year. With increasing release size, extinctions tended to be delayed.

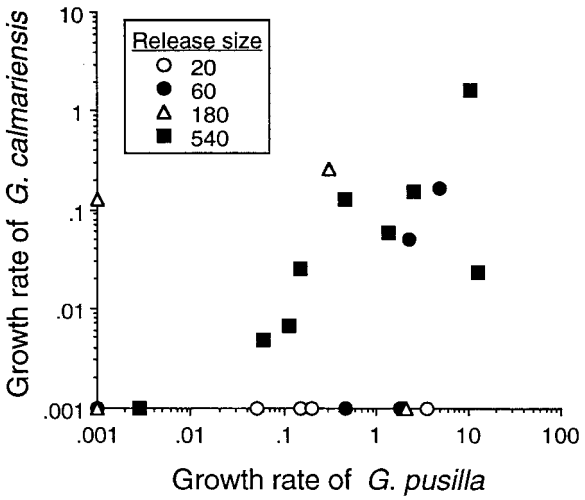

Figure 5. Correlation of growth rates in *G. pusilla* and *G. calmariensis*. Each point represents a pair of populations released at the same site.

Colonization by single gravid females

Most of the colonies initiated by a single female failed to persist beyond the first year (Table 3). One population, known only from eggs (which are not identifiable to species), persisted to the second year only (1995). Two other populations, one of each species, lasted into the third year (1996) before apparently going extinct. Only one population, of *G. calmariensis*, persisted to the end of the study period. The ultimate fate of that population is still questionable since only one adult individual of *G. calmariensis* was found in 1997 after extensive searching. However, additional scattered damage and eggs were found at that site, apparently the result of additional individuals. Assuming that this population is established, the rate of population establishment from one mated female (taking both species together) is 0.05 with 95% binomial confidence limits of 0.0013 and 0.248.

Discussion

This study supports the little tested idea that population establishment is more likely with larger initial colony sizes. For two species of introduced chrysomelid beetles, the chance of establishment (defined as persistence to the beginning of the fourth year after release) increased with the number of individuals released. These experimental results complement previous comparative analyses of past purposeful introductions (Hall and Ehler 1979; Beirne 1985; Hopper and Roush 1993; Green 1997) as well as previous experimental studies that suffered from low replication (e.g. Crowell1972;

Table 3. Number of adult *G. calmariensis* and *G. pusilla* found in 1995–1997 at sites where one gravid female of each species was released in 1994. Also listed are the numbers of eggs laid by each female during the first 10 days after introduction. *Galerucella* eggs found in 1995 at site 1 were not identifiable to species.

Site	*G. calmariensis*				*G. pusilla*			
	Initial eggs	1995	1996	1997	Initial eggs	1995	1996	1997
1	175	(eggs)	0	0	0	(eggs)	0	0
2	248	0	0	0	144	0	0	0
3	230	0	0	0	189	0	0	0
4	307	0	0	0	181	0	0	0
5	225	0	0	0	164	0	0	0
6	234	0	0	0	44	0	0	0
7	275	0	0	0	75	0	0	0
8	267	1	1	0	89	0	2	0
9	225	2	9	1	51	0	0	0
10	169	0	0	0	165	0	0	0

Sheppe 1965; Crowell 1973; Ebenhard 1989) or short monitoring duration (Memmott et al. 1998). These results counter the view that the size of the introduction is of little consequence provided the site is suitable (e.g. Greathead 1971; T.W. Schoener and A. Schoener 1983).

A positive relationship between initial colony size and establishment suggests that demographic factors whose influence depends on population size or density such as demographic stochasticity, Allee effects, and genetics play important roles in determining persistence and that these influences are not entirely swamped by density-independent environmental factors such as climate, site quality, or temporal variability in environmental conditions.

Dependence of establishment on release size does not mean that the outcome of introductions is predictable based on numbers released. One of the most important contributions of this study is to reveal just how stochastic the colonization process can be. Growth rates varied dramatically between sites and years. I found no indication of a 'minimum viable colony size', above which a population is certain (or highly likely) to establish and below which it is doomed. Some very small colonies were succeeded and some large ones failed. At one release site, a population descending from one female *G. calmariensis* persisted into the fourth year (at least) and at a similar site just 45 km away a colony of 540 individuals of the same species went extinct over the same time period.

The two species tended to do well at the same sites, suggesting a common response to site conditions. However, none of the site characteristics that I measured – patch size, plant density, plant height, and leaf nitrogen – had consistent significant effects on population growth or establishment. This is not to say that site conditions were not important. Countless other factors were not quantified, including predators, plant community composition, soil type, drainage, and plant nitrogen levels at other times of the season. There were no obvious patterns matching types of sites with prolific populations. An interesting question to be answered in the future is whether *Galerucella* distributions will always be spatially sporadic, only invading some loosestrife stands, or if more complete occupation of loosestrife sites will arise, perhaps with some sites occupied by 'sink' populations that are supported primarily through dispersal of individuals from more prolific 'source' populations (Harrison 1991).

The greater success of *G. pusilla* in comparison to *G. calmariensis* counters expectations based on their fecundities. Both theory (Crowell 1973; MacArthur and Wilson 1967; Grevstad 1999) and comparative studies (Crawley 1986; Crowell 1973) suggest that higher fecundity should improve the ability of a species to invade. *G. calmariensis*, the inferior invader, laid nearly twice as many eggs in a 10-day period as *G. pusilla*, the superior invader. The lifetime fecundity of *G. calmariensis* is also nearly twice that of *G. pusilla* (measured in greenhouse) (Grevstad 1998). This incongruity may be reconciled by mobility differences between the two species. In previous work, I found that rates of movement among plants and among patches of plants are two times greater in *G. calmariensis* (Grevstad 1998). And I observed much greater drop in numbers of *G. calmariensis* during the first week after release than I did in *G. pusilla*. Thus, dispersal may be preventing *G. calmariensis* from establishing a population at the site of release. However, it is possible that this species successfully colonized other nearby locations, which were not searched.

A final but noteworthy result of this study is the founding of a population by a single *G. calmariensis* individual. Granted, the fate of this population is still uncertain, since I only found one adult individual (plus numerous eggs) in the final year of the experiment. But assuming the population continues to persist, it may be the only clear example of a field release of one individual that has led to a persisting population. Another notable colonization include the successful establishment of a population of lacebugs (*Teleonemia scrupulosa*) for the biological control of the weed *Lantana* camara in Zanzibar from the release of just 2 individuals (Cock 1986). Simberloff (1989) lists several examples of successful insect introductions for which the release stock were reared from one or two individuals (the releases themselves were of greater numbers of individuals). He also lists several successful colonizations from releases of 10 or fewer individuals. That as few as one individual can found an entire population has frightening implications for biological invasions. It renders ominous the task of quarantine officers to prevent importation of not only conspicuous groups of insects but also solitary individuals stowed away in luggage or cargo.

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