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Prey Suitability of *Galerucella pusilla* Eggs for Two Generalist Predators, *Coleomegilla maculata* and *Chrysoperla carnea*

Amy P. Wiebe and John J. Obrycki[1]

Department of Entomology, Insectary Building, Iowa State University, Ames, Iowa 50011-3140

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The leaf beetle, *Galerucella pusilla*, is an introduced natural enemy of purple loosestrife, *Lythrum salicaria*, in North America. The suitability of *G. pusilla* eggs for development and survival of *Chrysoperla carnea* and *Coleomegilla maculata* was quantified by measuring preimaginal development, survival, and adult weight. Individual first-instar predators were assigned to one of two diets: *G. pusilla* eggs or a diet of *Ephestia kuehniella* eggs and pea aphids (*Acyrthosiphon pisum*) alternated every 24 h. *Chrysoperla carnea* and *C. maculata* larvae that fed on *G. pusilla* eggs had lower survival rates, longer developmental times, and reduced adult weight. *Galerucella pusilla* eggs were not suitable prey for 95% of *C. maculata* larvae, but 37% of *C. carnea* larvae completed development on *G. pusilla* eggs. Because *G. pusilla* eggs may be utilized by these predatory species as alternative prey during periods of low availability of suitable prey, this predation could affect the biological control of *L. salicaria*.

***Key Words:* biotic interference; biological control; purple loosestrife; prey suitability; *Lythrum salicaria*; *Galerucella pusilla*; *Coleomegilla maculata*; *Chrysoperla carnea*.**

INTRODUCTION

Biotic interference occurs when natural enemies limit the establishment or decrease the effectiveness of introduced natural enemies (Goeden and Louda, 1976). Interference by natural enemies has been documented in several weed biological control projects (Goeden and Louda, 1976; Briese, 1986; Reimer, 1988; Müller *et al.*, 1990; Hill and Hulley, 1995).

Generalist predators and parasitoids have been observed to have greater effects on introduced arthropod natural enemies, when compared with natural enemies with a more restricted host range, because generalists can extend their host range more readily (Goeden and Louda, 1976; Hill and Hulley, 1995). For example, two generalist predators, *Montandoniola moraguesi* (Puton) (Hemiptera: Anthocoridae) and *Pheidole megacephala* (Fabricius) (Hymenoptera: Formicidae), limited the successful control of *Clidemia hirta* (Myrtiflorae: Melastomataceae), a noxious weed, in Hawaii by *Liothrips urichi* Karny (Thysanoptera: Phlaeothripidae) (Reimer, 1988). Also, the carabid *Lebia viridis* Say (Coleoptera: Carabidae) was implicated as the major predator interfering with the establishment of *Altica carduorum* (Coleoptera: Chrysomelidae) for the control of *Cirsium arvense* (Myrtiflorae: Asteraceae), creeping thistle in Canada (Peschken, 1977).

Galerucella calmariensis L. (Coleoptera: Chrysomelidae) and *Galerucella pusilla* Duftschmidt (Coleoptera: Chrysomelidae) have been introduced into North America to control *Lythrum salicaria* (purple loosestrife) L. [Myrtiflorae: Lythraceae], an exotic wetland weed (Blossey *et al.*, 1994; Blossey, 1995; Hight *et al.*, 1995). Since 1994, both *Galerucella* species were released in Iowa wetlands and their establishment was confirmed (Wiebe *et al.*, 2000). Densities of beetles in the field, however, remain lower than expected, given the numbers released (Cortilet, 1998).

The predator complex attacking *Galerucella* species in North America wetlands is poorly known (Nechols *et al.*, 1996; Cortilet, 1998). In New York, arthropod predation was observed to reduce densities of a closely related native species, *Galerucella nymphaeae* L. (Coleoptera: Chrysomelidae), in *L. salicaria* stands (Nechols *et al.*, 1996). Nechols *et al.* (1996) concluded that generalist predators, specifically *C. maculata*, were likely the major predators of *G. nymphaeae* eggs. Predator surveys conducted in Iowa *L. salicaria* stands documented the presence of *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) and *Coleomegilla maculata* DeGeer (Coleoptera: Coccinellidae) (Cortilet, 1998; A. Wiebe, unpublished data). Immature *C. carnea* and *C. maculata* larvae and adults feed on *Galerucella* eggs and larvae in the field (Cortilet, 1998; A. Wiebe, unpublished data). Predation by *C. carnea* and

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[1] To whom correspondence and reprint requests should be addressed. Fax: (515) 294-4431. E-mail: jobrycki@iastate.edu.

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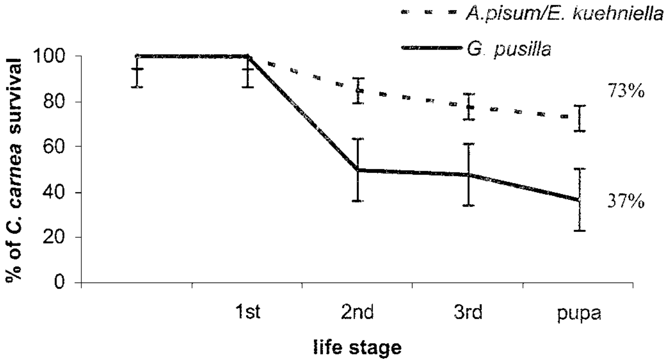

FIG. 1. Survivorship curves of *Chrysoperla carnea* reared on *Galerucella pusilla* eggs and *A. pisum/E. kuehniella* at 24°C, 16 L:8 D. Values plotted are the percentage surviving to each life stage.

C. maculata may be a factor limiting the effectiveness of *Galerucella* spp. for the biological control of *L. salicaria*.

The suitability of prey for polyphagous predators can vary greatly (Hodek and Honek, 1996; Tauber *et al.*, 2000). Many predatory insects appear opportunistic in the field, feeding on a wide range of prey species and plant products, but this behavior may not clearly indicate prey suitability and predator nutritional requirements (e.g., Thompson, 1951; New, 1991; Giles *et al.*, 1994; Strohmeyer *et al.*, 1998; Thompson and Hagen, 1999). Evaluation of the suitability of *G. pusilla* eggs as prey for *C. carnea* and *C. maculata* is needed to determine the extent of the predator–prey relationship in the field (Hagen *et al.*, 1976). In this study, the suitability of *G. pusilla* eggs for larval development and survival of *C. carnea* and *C. maculata* was quantified using three parameters: preimaginal development, survival, and adult size.

MATERIALS AND METHODS

All experiments and rearing of *G. pusilla* were conducted in growth chambers (Model No. 1-30 BLL, Percival, Boone, IA) at 24 ± 1°C with a photoperiod of 16:8 (L:D) h. Adult *C. carnea* and *C. maculata* were collected in Story County, Iowa, in 1998 and 1999, individuals were sexed, and pairs were placed in half-pint paper containers (0.24 liters). A foam cube (0.5 × 0.5 × 0.5 cm) was placed in the containers to act as a oviposition substrate. *Chrysoperla carnea* and *C. maculata* pairs were provided with a 1:1 mixture of honey and Wheast (Qualcepts, Minneapolis, MN) and distilled water. *Coleomegilla maculata* adults were also fed pea aphids, *Acyrthosiphon pisum* (Harris) (Homoptera: Aphidae), because females will not oviposit when only provided the Wheast–honey mixture (Phoofolo and Obrycki, 1997).

The containers were examined for oviposition, and eggs were collected daily. Individual first instars (<24 h old) were placed in glass vials (1.8 cm diameter and 6.5 cm height) and assigned to one of two diets: *G. pusilla* eggs or a diet of *Ephestia kuehniella* (Lepidoptera: Pyralidae) eggs and *A. pisum* alternated every 24 h.

In this study, we wanted to compare development of predators fed *G. pusilla* eggs to predators fed an optimized diet. Optimized predator growth was shown to occur on a mixed diet of insect eggs and aphids (Munyaneza and Obrycki, 1998). This study focused on the larval responses of two predatory species to *G. pusilla*; however, we expect similar responses would occur with *G. calmariensis* eggs. One species was chosen to reduce interspecies variation that could exist. *Coleomegilla maculata* and *C. carnea* larvae were supplied with an excess of prey daily: *A. pisum* (>10 individuals), *E. kuehniella* (.05 g), or *G. pusilla* (>15 eggs). Both *G. pusilla* eggs and *A. pisum* were from laboratory colonies. Frozen *E. kuehniella* eggs were purchased from Beneficial Insectary (Oak Run, CA).

Coleomegilla maculata and *C. carnea* larvae were monitored daily for eclosion or death. The developmental time for each preimaginal stage and adult weight were recorded for each individual. Experiments were replicated three times with 20 individuals in each treatment in each replication.

Previously, Munyaneza and Obrycki (1998) observed that first- and second-instar *C. maculata* did not successfully complete development on *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae) eggs, possibly due to the inability of young larvae to penetrate the chorion with their mandibles. The chorion of *G. pusilla* eggs may be a similar barrier for first- and second-instar *C. maculata*. Therefore, a random sample of *G. pusilla* eggs was inspected daily under the microscope for chorion damage.

Results were analyzed using the general linear model procedure in SAS version 6.12 (SAS Institute, 1985). A two-way analysis of variance (diet vs rep) was used to examine the influence of diet on developmental time, survivorship, and adult weight for each predatory species (SAS Institute, 1985). In addition, nonparametric estimates of survival data were computed by the LIFETEST procedure (SAS Institute, 1985). Survival functions were compared, and chi-square values were estimated by Wilcoxon variance matrix (SAS Institute, 1985). Because replication effects were not significant, adult *C. carnea* characteristics were analyzed by a two-way analysis of variance (sex vs diet) (SAS Institute, 1985). The level of significance for all tests was set at $P < 0.05$. Voucher specimens of *G. pusilla*, *C. carnea*, and *C. maculata* were deposited at the Iowa State Insect Collection, Department of Entomology, Iowa State University, Ames, Iowa.

TABLE 1

Developmental Time in Days (Mean ± SE) of *Chrysoperla carnea* Larvae Reared on *Galerucella pusilla* Eggs and *Acyrthosiphon pisum/Ephestia kuehniella* at 24°C, 16 L:8 D

Diet	1st instar	2nd instar	3rd instar	Total larval	Pupal	Total immature
G. pusilla eggs						
Mean ± SE	4.9 ± 0.3	5.4 ± 0.2	11.1 ± 0.8	24.7 ± 1.0	14.0 ± 1.0	37.4 ± 1.2
(*n*)[a]	(60)	(30)	(29)	(29)	(22)	(22)
A. pisum/E. kuehniella[b]						
Mean ± SE	4.1 ± 0.2	4.0 ± 0.2	5.4 ± 0.5	15.7 ± 6.5	12.6 ± 0.3	27.9 ± 0.7
(n)[a]	(60)	(51)	(47)	(47)	(44)	(44)
df	1	1	1	1	1	1
F	4.84	17.9	45.26	70.51	4.43	57.53
Pr > *F*	0.03	0.01	0.01	0.01	0.04	0.01

[a] Number of individuals that completed life stage. Replication was not significant at $P < .05$; therefore data were pooled for the three replications.

[b] *Acyrthosiphon pisum* was alternated daily with *Ephestia kuehniella* eggs.

RESULTS

Chrysoperla carnea

The percentage of survival of *C. carnea* larvae reared on *G. pusilla* eggs was 37%, whereas the percentage of survival of *C. carnea* larvae fed *A. pisum* and *E. kuehniella* eggs was significantly higher at 73% ($\chi^2 = 13.27$; $df = 1$; $P < 0.0003$; Fig. 1). The greatest decline in survival within a life stage (50%) was during the second instar. In both treatments, a low percentage of individuals pupated (<10%) without forming a silk pupal case. These individuals died during pupation.

Developmental time for *C. carnea* larvae fed *G. pusilla* eggs was significantly longer ($F = 57.53$; $df = 1$; $P < 0.0001$) compared to *C. carnea* larvae fed *A. pisum* and *E. kuehniella* eggs (Table 1). The body mass of female and male *C. carnea* reared on *G. pusilla* eggs was significantly lighter ($F = 19.63$; $df = 1$; $P < 0.0001$), and the length and width of the wings of female and male *C. carnea* reared on *G. pusilla* eggs were shorter ($F = 19.45$; $df = 1$; $P < 0.0001$) (Table 2).

Coleomegilla maculata

The percentage of survival of *C. maculata* larvae reared on *G. pusilla* eggs was 5%, whereas the percentage of survival of *C. maculata* larvae fed *A. pisum* and *E. kuehniella* eggs was significantly higher at 83% ($\chi^2 = 18.45$; $df = 1$; $P < 0.0001$; Fig. 2). High mortality (78%) of *C. maculata* second instars was observed on *G. pusilla* eggs. All larvae that survived to the third instar completed development.

There were significant differences ($F = 1039.69$; $df = 1$; $P < 0.0001$) in developmental times of *C. maculata* fed different diets (Table 3). Total development time of *C. maculata* larvae fed *G. pusilla* eggs was twice the developmental time of *C. maculata* larvae fed *A. pisum* and *E. kuehniella* eggs (Table 3). Developmental time for *C. maculata* fed *G. pusilla* eggs

TABLE 2

Adult Size and Weight (Mean ± SE) of *Chysoperla carnea* Individuals Fed *Galerucella pusilla* Eggs and *Acyrthosiphon pisum/Ephestia kuehniella* Eggs

	Adult mass (mg)		Forewing length (mm)		Forewing width (mm)	
Diet	Female	Male	Female	Male	Female	Male
G. pusilla eggs						
Mean[a]	4.67d	4.52d	3.2e	4.3e	1.2d	1.5d
SE	1.50	0.80	1.5	2.1	0.6	0.8
(*n*)[b]	(8)	(5)	(8)	(5)	(8)	(5)
A. pisum/E. kuehniella[c]						
Mean[a]	8.24f	7.16e	9.7f	8.5f	3.3f	3.7e
(SE)	1.29	1.50	1.1	1.3	0.5	0.5
(*n*)[b]	(22)	(16)	(22)	(16)	(22)	(16)

[a] Letters denote statistical differences for individual adult characteristics of male and female *C. carnea* reared on the two diets at $P < 0.05$.

[b] Number of individuals that completed life stage. Replication was not significant; therefore data were pooled for all replications.

[c] *Acyrthosiphon pisum* was alternated daily with *Ephestia kuehniella* eggs.

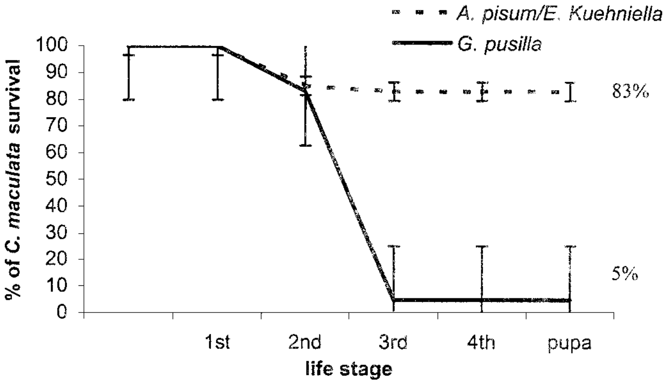

FIG. 2. Survivorship curves of *Coleomegilla maculata* reared on *Galerucella pusilla* eggs and *A. pisum/E. kuehniella* at 24°C, 16 L:8 D. Values plotted are the percentage surviving to each life stage.

TABLE 4

Adult Size and Weight (Mean ± SE) of *Coleomegilla maculata* Individuals Fed *Galerucella pusilla* Eggs and *Acyrthosiphon pisum/Ephestia kuehniella* Eggs

Diet	Adult mass (mg)	Elytra length (mm)	Elytra width (mm)
Galerucella pusilla eggs			
Mean[a]	5.60	3.1	1.8
SE	0.20	0.07	0.03
(*n*)[b]	(3)	(3)	(3)
A. pisum/E. kuehniella[c]			
Mean[a]	12.50	4.4	1.1
SE	0.24	0.07	0.07
(*n*)[b]	(50)	(50)	(50)

[a] Adult characteristics of *Coleomegilla maculata* were not statistically analyzed due to the low number of individuals surviving on *G. pusilla* eggs.

[b] Number of individuals that completed life stage.

[c] *Acyrthosiphon pisum* was alternated daily with *Ephestia kuehniella* eggs.

was longer for second, third, and fourth instars and for total larval development (Table 3). Pupal developmental time for *C. maculata* fed *G. pusilla* eggs was shorter ($F = 86.49$; $df = 1$; $P < 0.0001$) than *C. maculata* fed *A. pisum* and *E. kuehniella* eggs (Table 3).

Adult *C. maculata* reared on *G. pusilla* eggs tended to be smaller than adult *C. maculata* reared on *A. pisum* and *E. kuehniella* eggs (Table 4). Because only three *C. maculata* larvae reared on *G. pusilla* eggs survived to the adult stage, no statistical analysis was conducted as any result would not be biologically significant.

DISCUSSION

Polyphagous arthropod predators are the most common cause of biotic interference (Goeden and Louda, 1976). Various taxa of predators [e.g., Aransae (spiders), Hemiptera, Coleoptera, Mesostigmata (mites), and even vertebrates] have been shown to reduce the success of some weed biological control projects (Goeden and Louda, 1976; Harris, 1991; Hill and Hulley, 1995).

Both *C. carnea* and *C. maculata* occur in Iowa wetlands where *Galerucella* species have been released (Cortilet, 1998; Wiebe, unpublished data). Evidence of predation of *G. pusilla* eggs and *G. nymphaeae* by *C. maculata* larvae and adults and *C. carnea* larvae has been documented in loosestrife stands (Nechols *et al.*, 1996; Cortilet, 1998; A. Wiebe, unpublished data). *Galerucella pusilla* egg predation by both manibulate predators (coccinellids and carabids) and predators possessing piercing mouthparts (true bugs, lacewing larvae, and spiders) (A. Wiebe, unpublished data) was observed.

The nutritional requirements of the generalist predators, *C. maculata* and *C. carnea*, have been extensively studied (e.g., Andow, 1990; Munyaneza and Ob-

TABLE 3

Developmental Time in Days (Mean ± SE) of *Coleomegilla maculata* Larvae Reared on *Galerucella pusilla* Eggs and *Acyrthosiphon pisum/Ephestia kuehniella* at 24°C, 16 L:8 D

Diet	1st instar	2nd instar	3rd instar	4th instar	Total larval	Pupal	Total immature
G. pusilla eggs							
Mean ± SE	4.1 ± .2	4.8 ± 0.9	8.0 ± 0.9	14.3 ± 4.2	36.3 ± 2.2	4.0 ± 0.6	40.3 ± 1.8
(*n*)[a]	(60)	(5)	(3)	(3)	(3)	(3)	(3)
A. pisum/E. kuehniella[b]							
Mean ± SE	3.9 ± 0.1	2.9 ± 0.1	3.3 ± 0.1	5.3 ± 0.2	15.8 ± 0.2	5.1 ± 0.1	20.94 ± 0.2
(*n*)[a]	(60)	(51)	(50)	(50)	(50)	(50)	(50)
df	1	1	1	1	1	1	1
F	0.51	19.56	218.29	272.92	900.29	86.49	1039.69
Pr > *F*	0.48	0.01	0.01	0.01	0.01	0.01	0.01

[a] Number of individuals that completed life stage. Replication was not significant at $P < .05$; therefore data were pooled for the three replications.

[b] *Acyrthosiphon pisum* was alternated daily with *Ephestia kuehniella* eggs.

rycki, 1998; Phoofolo and Obrycki, 1998; Tauber *et al.*, 2000). *Chrysoperla carnea* has a wide range of suitable prey, including eggs and early instars of numerous moth and beetle species, aphids, and other soft-bodied insects (Obrycki *et al.*, 1989; Zheng *et al.*, 1993a,b; Cox, 1996; Tauber *et al.*, 2000). Likewise, the range of suitable prey for *C. maculata* includes aphids, mites, insect eggs, and other soft-bodied insects (Hazzard and Ferro, 1991; Giles *et al.*, 1994; Munyaneza and Obrycki, 1998).

Galerucella pusilla eggs were acceptable prey for both *C. maculata* and *C. carnea*. Neither predator species completely rejected *G. pusilla* eggs as prey. The chorion of *G. pusilla* eggs exposed to *C. maculata* and *C. carnea* larvae showed evidence of feeding under microscopic examination where larvae penetrated the egg chorion of *G. pusilla*.

There was, however, variation in survival on *G. pusilla* eggs between the two predatory species. Thirty-seven percent of *C. carnea* individuals reached maturity when fed only *G. pusilla* eggs. Total developmental time for *C. carnea* fed *G. pusilla* eggs was longer than *C. carnea* fed *A. pisum* and *E. kuehniella* eggs. However, total developmental time of *C. carnea* fed *G. pusilla* eggs in this study was only slightly longer (1–2 days) than developmental times of *C. carnea* observed when fed six different prey diets (Obrycki *et al.*, 1989).

While *C. maculata* feeds on a wide array of prey, its effective host range may be much narrower. Hazzard and Ferro (1991) and Munyaneza and Obrycki (1998) observed extended developmental time and increased mortality for *C. maculata* larvae when fed *L. decemlineata* eggs. Similarly, Munyaneza and Obrycki (1998) observed a low percentage of survival for selected populations of *C. maculata* exposed to novel prey items. Only 5% of *C. maculata* individuals reached maturity when fed only *G. pusilla* eggs. *Galerucella pusilla* eggs may lack one or more essential nutritional elements needed for the development of most *C. maculata* larvae (Thompson and Hagen, 1999).

Evans *et al.* (1999) demonstrated the benefits of a mixed diet consisting of suitable and nonsuitable prey for two coccinellid species, *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) and *C. transversoguttata* Brown (Coleoptera: Coccinellidae). A suitable diet (one that supports complete development) supplemented with nonsuitable prey (only a source of energy and nutrients) increased fecundity (Hodek and Honek, 1996; Evans *et al.*, 1999). *Coleomegilla maculata* fed a mixed diet of suitable and nonsuitable prey had shorter developmental times and larger adults (Phoofolo and Obrycki, 1997). Mixed diets, including suboptimal prey, have been shown to benefit generalist predators (Evans *et al.*, 1999). Alternative prey items such as aphids are readily available in loosestrife stands. In times of prey scarcity, *Galerucella* eggs could sustain *C. maculata* and *C. carnea* larvae.

Coleomegilla maculata adults have been observed feeding on *Galerucella* eggs in the field (Wiebe, unpublished data; Cortilet, 1998) and laboratory (Sebolt, 2000). Some essential nutrients needed for *C. maculata* larval development may not be required for adult nutrition and reproduction; therefore *G. pusilla* eggs may be suitable prey for the adults.

Predation of *G. pusilla* and *G. calmariensis* has not been quantified in other midwest states. A comparison of predation levels between sites where *Galerucella* outbreaks have occurred in other midwestern states and Iowa wetlands could explain the differences in beetle densities observed.

Landscape features such as nearby habitats and water proximity may differ among *Galerucella* release locations in Iowa and other midwestern states and help to explain the occurrence of outbreak populations. Unlike Michigan and most of Minnesota, row crops dominate the Iowa landscape. Most *Galerucella* release sites in Iowa are in close proximity to row crops. Illinois, Michigan, and Minnesota wetlands may border alternate habitats such as forest, grazing lands, or urbanized areas. Prey may be more abundant in these alternate areas.

In Iowa, egg predation increased from the first generation to the second generation. Agricultural fields in Iowa later in the summer may not provide adequate prey or moisture for generalist predators. Wetlands usually dry out in Iowa during the first month of the summer. If wetlands in other midwestern states are wet for longer periods of time, this may deter predators from entering.

Another factor that may influence predation of *L. salicaria* is the composition of the predatory fauna. Predatory fauna can be compared within the region. The most common predatory arthropod families found in Iowa were Coccinellidae, Carabidae, and Lycosidae. In Michigan, Araneae and Coccinellidae were also abundant (Sebolt, 2000). In Manitoba, however, Coccinellidae were not prevalent (Diehl *et al.*, 1997). The predominant predatory species found was the stinkbug *Apoecilus bracteatus* Fitch (Hemiptera: Pentatomidae) (Diehl *et al.*, 1997). This difference in predatory fauna among sites may offer some explanation as to the variability in *Galerucella* densities.

All of these factors can influence *Galerucella* establishment and population densities. Evidence from this study and others suggest biotic interference is a possible explanation for lower beetle densities in Iowa. A combination of factors, however, may be responsible for differences among Iowa wetlands and other midwestern wetlands.

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