

Conservation biological control in urban landscapes: Manipulating parasitoids of bagworm (Lepidoptera: Psychidae) with flowering forbs

J.A. Ellis^{a,b}, A.D. Walter^{a,b}, J.F. Tooker^{a,c}, M.D. Ginzel^{a,d}, P.F. Reagel^a, E.S. Lacey^a,
A.B. Bennett^{a,e}, E.M. Grossman^{a,f}, L.M. Hanks^{a,*}

^a Department of Entomology, University of Illinois at Urbana-Champaign, 320 Morrill Hall, 505 South Goodwin Avenue, Urbana, IL 61801, USA

^b Department of Entomology, 131 Smith Hall, Purdue University, West Lafayette, ID 47907, USA

^c Department of Entomology, 501 ASI Building, The Pennsylvania State University, University Park, PA 16802-3508, USA

^d Department of Biochemistry and Molecular Biology, University of Nevada-Reno, Reno, NV 89557, USA

^e Department of Entomology, University of Wisconsin-Madison, 1630 Linden Dr., 237 Russell Labs Madison, WI 53796, USA

^f 346-C Prospect Blvd, Apt 303, Frederick, MD 21701, USA

Received 28 January 2005; accepted 23 March 2005

Available online 20 April 2005

Abstract

We conducted field experiments to test the hypothesis that regulation of herbivorous pests in urban landscapes can be enhanced with forbs that provide floral resources for adult natural enemies. The herbivore was bagworm, *Thyridopteryx ephemeraeformis* (Haworth) (Lepidoptera: Psychidae), which is attacked by a guild of hymenopterous parasitoids. We established host shrubs in common garden plantings, encircling some with flowering forbs, released bagworm larvae on shrubs, and assessed survivorship. The hypothesis was supported: parasitism rates of bagworm were 71% higher in shrubs that were surrounded by flowering forbs than in shrubs that lacked flowers. This study also suggested that white-footed mice and European sparrows were important predators of bagworms. The most abundant parasitoid species was the exotic ichneumonid *Pimpla* (= *Coccygominus*) *disparis* (Vierick), an introduced biological control agent of gypsy moth. In a second experiment, parasitism rates were at least three times higher in shrubs encircled by a high density of forbs compared to those having fewer or no forbs. In a third experiment, parasitism rates exceeded 70% in shrubs that were adjacent to a central bed of flowering forbs, but less than 40% in shrubs that were farther away. We conclude from these studies that flowering forbs have a localized effect on host-searching behavior of female parasitoids, encouraging them to parasitize bagworms in the immediate vicinity. This study provides further evidence that ecological methods of pest management can be integrated into the design of urban landscapes to improve regulation of herbivorous pests.

© 2005 Elsevier Inc. All rights reserved.

Keywords: *Thyridopteryx ephemeraeformis*; Natural enemy; Ichneumonidae; Torymidae; *Itopectis*; *Pimpla disparis*; *Coccygominus disparis*; *Gamburus*; *Monodontomerus*; Gypsy moth; *Peromyscus leucopus*; *Passer domesticus*; Habitat manipulation

1. Introduction

Annual cropping systems are human fabrications, and their inherent ecological imbalance commonly

results in poor regulation of herbivorous pests by natural enemies and pest outbreak (Landis et al., 2000). Regulation can be improved by manipulating the agricultural plant community to favor natural enemies, providing a suitable microclimate, alternative prey, and floral resources for adult natural enemies (reviewed by Heimpel and Jervis, 2005; Landis et al., 2000). Implementation of this form of conservation biological

* Corresponding author. Fax: +1 217 244 3499.

E-mail address: hanks@life.uiuc.edu (L.M. Hanks).

control is complicated by the ephemeral nature of agroecosystems and the severe ecological disturbances resulting from application of pesticides, crop harvest, and soil tillage (Kennedy and Storer, 2000; Landis et al., 2000).

Urban landscapes also are inherently artificial habitats and consequently are prone to outbreak of herbivorous pests (Dreistadt et al., 1990; Frankie and Ehler, 1978; Frankie et al., 1987; Raupp et al., 1992). They are perhaps more amenable to conservation biological control than annual cropping systems, however, because design of the plant community is much more manipulable (in species composition, diversity, and plant density), and also because ecological disturbance may be minimal once plants are established, providing a supportive and relatively stable environment for natural enemies (see Dreistadt et al., 1990; Flanders, 1986; Frankie and Ehler, 1978; Raupp et al., 1992). The association between plant community structure in urban landscapes and abundance and diversity of natural enemies has been well documented (Hanks and Denno, 1993; Shrewsbury and Raupp, 2000; Tooker and Hanks, 2000a), supporting the notion that regulation of pests can be improved through design of the plant community. Such ecological approaches to pest management in urban landscapes have yet to be validated convincingly by formal experimentation, however, and so have not been adopted by the public or green industries charged with maintaining urban landscapes.

In this study, we evaluate the potential for conservation biological control of the bagworm, *Thyridopteryx ephemeraeformis* (Haworth) (Lepidoptera: Psychidae), one of the most important pests of ornamental trees and shrubs in the eastern United States (Johnson and Lyon, 1988). Bagworms are so named because the larvae construct a bag-shaped shelter of silk and leaf fragments (for biology, see Davis, 1964; Moore and Hanks, 2004). Larvae never leave their bag, with only their head and thorax protruding, and enlarge it as they grow. When molting and pupating, they attach their bags to branchlets with a band of silk. Adult males are alate and mate by inserting their genitalia into bags of the vermiform adult females. Females deposit eggs within the pupal exuvia. Eggs overwinter in the maternal bag and neonates usually hatch in early June in the area of our studies (Champaign County, Illinois), and disperse by ballooning (Moore and Hanks, 2004). The bagworm is univoltine (Morden and Waldbauer, 1971).

Although the bagworm is highly polyphagous (Johnson and Lyon, 1988), infestations most commonly arise on *Juniperus* and *Thuja* species (Cupressaceae) in the area of our studies (Ghent, 1999; see Moore and Hanks, 2004). Defoliation by bagworms reduces the aesthetic quality of hosts, and may even kill them (Johnson and Lyon, 1988). Bagworm outbreaks commonly arise in depauperate landscapes, where hosts are isolated in expanses of mulch or turf, but bagworms usually are

rare in natural, park-like settings (Kulman, 1965; LMH, pers. obs.). These characteristic dispersion patterns suggest that bagworm populations are better regulated in habitats that provide a suitable environment for natural enemies.

Vertebrate predators of the bagworm include mice (Cronin, 1989) and a variety of bird species (Berisford and Tsao, 1975b; Haseman, 1912; Horn and Sheppard, 1979; Jones and Parks, 1928; Moore and Hanks, 2000). The guild of arthropod natural enemies of the bagworm was studied by Balduf (1937) in the area of our studies, and he identified 11 species of hymenopteran parasitoids, primarily pupal parasitoids, including ichneumonids, pteromalids, chalcids, eupelmids, encyrtids, and trichogrammatids, as well as parasitic tachinid flies. Parasitoids are important in regulating populations of other bagworm species (Newman, 1980). Predaceous arthropods, including a pyralid caterpillar, apparently play a minor role in regulating bagworm populations (Balduf, 1937; Kulman, 1965).

Adult hymenopteran parasitoids often visit flowers to feed on pollen and/or nectar, and floral resources can enhance longevity and fecundity, and elevate rates of parasitism (reviewed by Heimpel and Jervis, 2005). We hypothesized that parasitoids could be encouraged to kill bagworms by planting flowering forbs in proximity to host shrubs. The research presented here tests this “enemies hypothesis” (sensu Root, 1973) by establishing study plots of arborvitae shrubs, varying the density of flowering forbs around them, releasing bagworms on shrubs, and monitoring their survivorship. We also examined the role of vertebrate predation in regulation of bagworm populations by excluding them with cages from a subset of shrubs. In an independent experiment, we examined the spatial range over which flowering forbs influenced parasitism rates of bagworms.

2. Materials and methods

2.1. Study sites, plants, and sources of insects

The experiments were conducted at the Turf and Horticultural Research Center at the University of Illinois at Urbana-Champaign. The study site for Experiment 1 was a 28 × 36 m turf field bordered by a paved road, plantation of black walnut trees, and mixed-species deciduous woodlot. The site for Experiment 2 was ~150 m away and was a 40 × 8.5 m turf area bordered by mixed-species deciduous woodlot on three sides and an open turf field on the fourth side. The open turf field was the site for Experiment 3, which was ~15 m away from the site for Experiment 2.

Host plants for bagworms were a low-growing ornamental cultivar of arborvitae (*Thuja occidentalis* L. ‘Woodwardii’) that we transplanted with a tree spade

from a small plantation that had been established in 1993 at the Research Center. We thoroughly examined shrubs for bagworms prior to experiments and removed the few that were present.

We selected four varieties of flowering forbs that are commonly planted in gardens and landscapes, that bloom in late summer/early fall when bagworms pupate and pupal parasitoids are active, and that are visited by an abundance and diversity of insects in local plantings (J.A.E., pers. obs.). The forbs were all of the Asteraceae which, in general, are among the most attractive to endemic parasitoids (Tooker and Hanks, 2000b), including Shasta daisy (*Leucanthemum* × *superbum* ‘Alaska’), a compact cultivar of goldenrod (*Solidago canadensis* L. ‘Golden Baby’), a compact aster (*Aster novi-belgii* ‘Niobi,’ ‘Professor Kippenburg’), and treasure-flower (*Gazania rigens* L.). We purchased plants from local nurseries, watered them as needed, and fertilized them (Miracle-Gro, Scots Miracle-Gro Products, Port Washington, New York) at recommended rates about every 3 weeks during the growing season.

Bagworm larvae were reared or collected from populations in urban areas (see below), and we marked their bags with a dot of enamel paint (Testor’s, Rockford, IL) to discriminate them from bagworms that colonized shrubs naturally. We collected the bags at the end of the year and recorded bag length and bagworm sex (adult males had emerged, as evidenced by the pupal case exerted from the bag). We examined bags for evidence of parasitism (small circular exit hole) and predation by vertebrates (large, ragged hole, or bag torn and bagworm absent), and dissected intact bags to determine whether females had survived to oviposit, and otherwise to determine the cause of mortality. We assumed that missing individuals had died, for unknown reasons, because the larvae we released were too old to balloon from plants, and bagworm larvae rarely disperse by walking on the ground except when hosts are defoliated (see Moore and Hanks, 2004). Parasitoid pupae were placed in individual glass test tubes sealed with cotton to rear adults.

2.2. Experiment 1: Influence of flowering forbs on parasitism rate

The field was prepared in March 1999 by plowing soil to a depth of ~0.6 m. In May 1999, we transplanted 32 arborvitae shrubs in a 4 × 8 pattern and 4.5 m centered spacing and surrounded the plantation with a wire fence (90 cm tall, 2.5 cm mesh) to exclude rabbits that would feed on flowering forbs. Each transplanted shrub was surrounded by a bed of hardwood mulch 1.5 m wide that was weeded by hand as needed. These study plots were separated by bare soil, the vegetation suppressed with herbicide (Round-up, Monsanto, St. Louis, MO) applied at the recommended rate every 3 weeks from late May

through October 1999. We pruned shrubs to heights of ~100 cm and diameters of ~80 cm so they would fit within cylindrical cages of hardware cloth (see below).

The experiment included four treatments representing all combinations of two densities of flowering forbs and a cage treatment (with and without) to exclude birds and mice, with eight shrubs randomly assigned to each treatment combination. This experimental design assumes that floral resource plants would have a very localized influence on parasitism rates. Flowering forbs were planted in June around the base of shrubs, with the four forb species assigned randomly to cardinal quadrants, four plants per species positioned 1 m from the trunk and 30 cm apart. Cages were constructed of 1.3 cm mesh hardware cloth with tops attached with wire and were anchored to the ground with steel staples (14 gauge, 15 cm long). Shrubs in the four treatments did not differ significantly in height or diameter (ANOVA $P > 0.05$). We collected 120 bagworm bags in January 1999 from arborvitae shrubs at a private residence in Danville, Illinois (Vermilion County). Bags were stored at ~5 °C to prevent eggs from hatching, then on 1 April 1999 they were placed in individual plastic containers under laboratory conditions (~22 °C) and neonates began emerging on 11 May. Larvae were caged in a glass aquarium and provided fresh arborvitae foliage every 3 days. We transferred four cohorts of 10 bagworm larvae to the top center of each study shrub on 18 and 27 July, and 6 and 16 August 1999, the larvae being 66, 71, 83, and 88 days old, respectively, with bags <1.5 cm long. We collected marked bagworms from shrubs between 22 and 27 October 1999.

We assessed the community of rodents in our study plot by live trapping. On 10 August 2000, we placed traps (aluminum, 14 × 6.5 × 9 cm; Longworth Scientific Instrument, Abingdon, UK) baited with sunflower seeds under the canopy of every other shrub ($N = 16$) and checked them for mice after 2 days. On 7 September 2000, we placed two baited traps on the north and south sides of each of eight randomly selected shrubs and checked them for mice every other day through November.

To further assess the influence of rodents on population densities of bagworms, we conducted another study in the same plantation of shrubs in 2002, but with the cage design improved to exclude mice more effectively. This study was conducted in fall, after adult parasitoids were active, because much of the mortality due to mice appeared to follow harvest of an adjacent corn field (see below). Fourteen shrubs, selected randomly, were trimmed with hedge clippers to fit within cages. We trenched the soil around the base of shrubs so that cages were buried at least 15 cm deep. Soil outside and inside the cages was compacted by foot, and a shallow trough on the outside (~4 cm deep, 15 cm wide) was filled with pea gravel to discourage mice from burrowing under the

cage. We attached aluminum window screening to the outside of the bottom half of the cage to exclude even very small animals, and above that attached a 15-cm wide band of sheet metal flashing to prevent mice from climbing the sides. At the base of seven cages, selected randomly, we cut three holes (10 cm square) at the soil line to allow rodents to enter. All cages were topped with hardware cloth to exclude birds.

On 6 September 2002, we collected bagworms that had tied off their bags to pupate at Mt. Olive cemetery in Mayview, Illinois, ~3 km east of Urbana. Parasitism rates were very low in that population (pers. obs.). A preliminary study on a sample of these bagworms revealed that bags that weighed more than 0.6 g contained female bagworm pupae that were alive, and we used that criterion to select bagworms for the study. We attached 15 bags to the upper branches of each shrub by running a needle and thread through the silk bundle that was the original attachment, and securely tying the thread to a branch. We collected the bags on 3 December 2002 to assess survivorship.

2.3. Experiment 2: Influence of flower density on parasitism rate

We established shrubs in study plots for Experiments 2 and 3 by the methods already described, but the fields were not plowed, plots were separated by turf, and broadleaf weeds were suppressed with herbicide (Millennium Ultra, a combined formulation of clopyralid, 2,4-D, and dicamba; Riverdale Chemical, Glenwood, Illinois) applied at label rates in May 2000. In June 2000, we planted 12 arborvitae shrubs in a 2 × 6 arrangement and 4.5 m centered spacing and fenced the plantation to exclude rabbits. Shrubs also were caged in hardware cloth cylinders to exclude mice and birds, but the cage design was improved over the 1999 design by burying the base to a depth of ~30 cm. In July 2000, we planted around the bases of shrubs the four forb species to establish three densities ($N=4$ shrubs per treatment): no forbs, low forb density (4 plants of each forb species, $N=16$ forbs), and high forb density (16 plants of each species, $N=64$ forbs). Forb species were assigned randomly to quadrants surrounding shrubs and were planted 1 m from the trunk through hardwood mulch.

Bagworm larvae for this experiment, and Experiment 3 (below), were collected on 6 August 2000 from arborvitae shrubs at Mt. Olive cemetery. Larvae were transported immediately to the study plot, their bags were marked with a dot of enamel paint, and 20 were released on each study shrub. We assumed that these larvae were too small to have been parasitized (bag length 2–3 mm), and confirmed this by returning 40 individuals to the lab and placing them in plastic Petri dishes. None of the larvae yielded parasitoids, and dissections revealed no evidence of parasitism. We collected bags from shrubs on

7–11 November (~93 days post-release) to assess survivorship.

2.4. Experiment 3: Spatial influence of flowering forbs on parasitism rate

To study the spatial range over which forbs influence rates of parasitism, we positioned arborvitae shrubs at increasing distances from a 3 × 3 m bed of flowering forbs. In June 2000, we transplanted 24 shrubs in a cross-shaped pattern (aligned with cardinal directions), with the flower bed in the center and six shrubs in each arm. Shrubs were planted at 4.5 m centered spacing with the first shrub in each arm abutting the flower bed. The four shrubs that bordered the flower bed therefore were closer together than the four positioned at the ends of the arms, resulting in decreasing local density of bagworms with increasing distance from the bed. Nevertheless, this test of the influence of flowers on parasitism rate is conservative because any correlation between parasitism rate and bagworm density is likely to be inverse (see Cronin, 1989), resulting in higher parasitism rates at the greatest distances from the flower bed. Each shrub was caged in hardware cloth, with the base buried, to exclude mice and birds. The central flower bed was planted with 20 plants of each of the four forb species, through hardwood mulch, in July 2000. Field collected bagworms (see Experiment 2) were released on 6 August with 20 larvae per shrub. We collected bags on 7–11 November (~93 days post-release) to assess survivorship.

2.5. Statistical procedures

We tested the fixed treatment effects on rates of predation, unexplained mortality, and parasitism by multiple ANCOVA (PROC MIXED; SAS Institute, 2001), with shrubs being replicates and including a density covariate (the number of bagworms used in calculating mortality rates). To calculate predation rate due to mice (see Section 3), we included only data for shrubs that contained at least four bagworms that were either killed by vertebrate predators or parasitoids, or that survived. For parasitism rate, we included only bagworms that were either parasitized or that survived (those killed by mice were excluded because we could not determine whether they had been parasitized or not). Original data were log transformed (linear measurements) or angular transformed (percentages) as necessary to meet ANCOVA assumptions. We confirmed these assumptions were met with the F_{\max} test (homogeneity of variances in error terms) and the G -test (error terms normally distributed; Sokal and Rohlf, 1995). Differences between means were tested with full ANCOVA models, but insignificant interaction terms were eliminated stepwise, starting with highest order interactions, leaving only significant terms (see Milliken and Johnson, 1984).

Differences between pairs of means were tested with the REGWQ means-separation test to control maximum experimentwise error rates (SAS Institute, 2001), and tests were “protected” (i.e., means-separation tests were contingent on a significant overall F ; Day and Quinn, 1989). In all analyses, we confirmed that there were no patterns in the dispersion of residuals indicative of non-linear relationships between variables.

Untransformed means ± 1 standard error are presented throughout except where stated otherwise. Voucher specimens of all species have been submitted to the Insect Collection of the Illinois Natural History Survey (Champaign, Illinois).

3. Results

3.1. Experiment 1: Influence of flowering forbs on parasitism rate

We recovered bags of 519 (~41%) of the 1280 bagworm larvae that were released on shrubs; the remaining 761 bags were missing. Of the bagworms in the recovered bags, 211 (~41%) had survived (including adult males that had emerged), 128 (~25%) were parasitized, 62 (~12%) were dead for unknown reasons, and 118 (~23%) were dead and showed evidence of mouse predation (bag not attached to branchlet and having a ragged hole, or shredded). Rates of predation by mice were significantly influenced by treatment effects (overall ANOVA $F_{3,29} = 3.1$, $P = 0.044$), but averaged higher in caged shrubs than in exposed ones ($30.7 \pm 7.4\%$ and $15.9 \pm 4.0\%$, respectively). This unexpected finding was due to failure of cages to exclude mice, and an apparent preference in mice for caged shrubs. In fact, within some caged shrubs mice had built nests that contained marked bags showing evidence of mouse predation. Predation by mice was not significantly influenced by the flower effect or density covariate ($P > 0.05$). Influx of mice into the study plot, assessed by visual observation of activity, coincided with harvest of a cornfield ~30 m away in fall 1999.

We captured only white-footed mice, *Peromyscus leucopus* (Rafinesque), in live traps within the study plot, with three captured during the August 2000 sample and eight captured during the September through November 2000 period. A nest in one shrub contained the carcass of a *P. leucopus* juvenile.

Bagworm larvae that died by unknown causes had bags that were ~35% smaller than those of other bagworms, averaging 2.2 ± 0.2 cm long compared to 4.1 ± 0.06 cm for parasitized bagworms and 4.3 ± 0.04 cm for survivors (all means significantly different from one another, ANOVA $F_{2,390} = 165$, $P < 0.0001$; REGWQ $P < 0.05$). This finding suggests that individuals killed by unknown agents had died early in development.

Pathogens were the likely cause of this mortality, and can greatly reduce bagworm populations (Berisford and Tsao, 1975a,b; J.A.E., pers. obs.). The rate of unexplained mortality was not influenced by the experimental treatments (overall ANOVA $F > 0.05$).

The proportion of individuals that were missing from shrubs was strongly influenced by treatment effects (overall ANOVA $F_{2,31} = 54.7$, $P < 0.0001$), being nearly twice as high in exposed shrubs than in caged shrubs (78.0 ± 2.0 and $41.0 \pm 2.9\%$, respectively; ANOVA cage term $F_{1,31} = 109$, $P < 0.0001$). This cage effect probably is the result of predation by birds. We suspect that English sparrows, *Passer domesticus* (L.), were important predators because we saw them foraging in exposed shrubs. The flower treatment had no significant influence on this unexplained mortality (ANOVA $P > 0.05$), also consistent with avian predation.

We reared adult parasitoids from 89 of the 128 bagworms that were parasitized; 8 bags contained dead parasitoids that could not be identified and 31 bags had emergence holes of adult parasitoids when collected. Total parasitism rate, including data for unknown parasitoid species, was significantly influenced by treatment effects (overall ANOVA $F_{3,28} = 4.12$, $P = 0.015$). Parasitism rate was ~44% higher in exposed shrubs than in caged shrubs ($46 \pm 5.5\%$ and $32 \pm 5.1\%$, respectively; cage effect $F_{1,28} = 4.31$, $P = 0.048$), suggesting that parasitoid females were hindered by cages to some extent when searching for hosts. Parasitism rate was ~71% higher in shrubs surrounded by flowers than in shrubs without flowers (48 ± 5.1 versus $28 \pm 4.8\%$, respectively; flower effect $F_{1,28} = 6.82$, $P = 0.015$), supporting our primary hypothesis. The bagworm density covariate was not significant ($P > 0.05$).

Parasitoid species included the ichneumonids *Pimpla* (= *Coccygominus*) *disparis* (Vierick) ($N = 49$ individuals), *Itopectis conquisitor* (Say) ($N = 21$), and *Gambrus ultimus* (Cresson) ($N = 18$). Only one parasitoid completed development within individual bags, except for one bag which yielded two adult female *G. ultimus*. The torymid gregarious parasite *Monodontomerus minor* (Ratzeburg) emerged from only one bag. Sex ratios of *P. disparis* and *G. ultimus* were female biased (~82% female in both; $\chi^2 = 17.8$, $P < 0.001$; $\chi^2 = 7.1$, $P < 0.01$, respectively), but nearly even in *I. conquisitor* (~42% female, χ^2 test $P > 0.5$). There was a significant tendency for female parasitoids to emerge from female bagworms, and male parasitoids from male bagworms, in both *I. conquisitor* and *G. ultimus* ($\chi^2 = 9.9$, $df = 19$, $P < 0.025$; $\chi^2 = 26.3$, $df = 13$, $P < 0.001$, respectively). There was no relationship between the sex of *P. disparis* and sex of the host (χ^2 test $P > 0.05$). The three most abundant parasitoid species did not differ in the size of hosts from which they emerged, with bag lengths averaging 4.3 ± 0.09 , 4.2 ± 0.05 , and 4.0 ± 0.1 cm for *P. disparis*, *I. conquisitor*, and *G. ultimus*, respectively (ANOVA $P > 0.05$).

The improved cage design was effective in excluding mice during the 2002 study that focused on mouse predation. There was a highly significant cage effect (ANOVA $F_{1,13} = 16.8$, $P = 0.0015$), with about half the bagworms killed in cages that had entrance holes and very few killed in shrubs that were entirely caged (means $50 \pm 11\%$ and $3 \pm 1.3\%$, respectively). All mortality was attributable to chewing damage by mice. This finding provides further evidence of the potential role of mice in suppressing bagworm populations.

3.2. Experiment 2: Influence of flower density on parasitism rate

Recovery of bagworms in this experiment was incomplete due to misplacement of all bagworms collected from one of the high density shrubs, reducing sample size to three in that treatment. We recovered 170 (~77%) of the 220 bagworms that were released on the 11 other shrubs, and all were attached to shrub branches, suggesting that mice had not entered the cages. We recaptured greater proportions of bagworms in this experiment and Experiment 3 (below) than in Experiment 1, apparently because the cage design was more effective in excluding vertebrate predators.

Of the recaptured bagworms, only 21 (~12%) had been parasitized, yielding only five *P. disparis*, three *I. conquisitor*, seven *G. ultimus*, and six bags with emergence holes of adult parasitoids. Nevertheless, total parasitism rate was at least three times higher in shrubs that were surrounded by the highest density of flowers than in shrubs with a lower density of flowers, or no flowers (mean parasitism rates 25.8 ± 3.6 , 6.4 ± 3.8 , and $8.7 \pm 3.5\%$, respectively; ANOVA $F_{2,10} = 7.41$, $P = 0.015$). The proportion of bags that were missing from shrubs varied from 21 to 26% across treatments, but these differences were not statistically significant (ANOVA $P > 0.05$).

3.3. Experiment 3: Spatial influence of flowering forbs on parasitism rate

We recovered 384 (~80%) of the 480 bagworms that were released in shrubs. All bags were attached to shrub branches, again indicating that mice had been excluded. Of the recovered bags, 200 (52%) had been parasitized, and of those ~85% had parasitoid emergence holes at the time the bagworms were collected. Of the remaining parasitized bagworms, adult *P. disparis* emerged from 8, *I. conquisitor* emerged from 7, and *G. ultimus* emerged from 14. Total parasitism rate was highest in the shrubs that were nearest the central flower bed, and declined linearly with increasing distance (Fig. 1; overall ANOVA $F_{4,23} = 17.2$, $P < 0.0001$; distance covariate $F_{1,23} = 32.1$, $P < 0.0001$). There also was a significant difference in parasitism rate between arms of the planting configuration, being significantly lower for shrubs in the southern

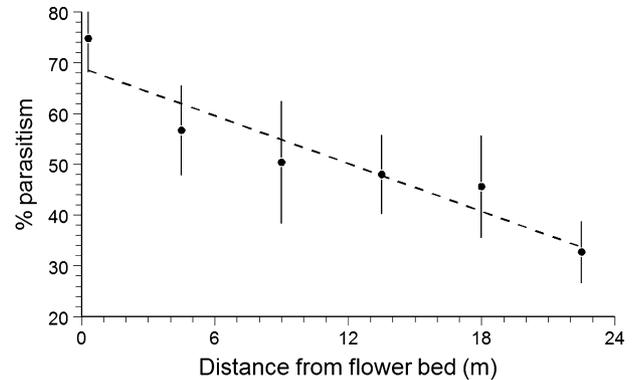


Fig. 1. Relationship between the distance of arborvitae shrubs from a central flower bed and the percentage of bagworms in shrubs that were parasitized. Vertical bars indicate ± 1 SE around means. Best fit regression equation (dotted line): $Y = -1.6X + 69.1$, $r^2 = 0.88$, $P < 0.0001$.

arm than those in the western arm (means $41.2 \pm 6.6\%$ and $73.4 \pm 7.1\%$, respectively; arm effect ANOVA $F_{3,23} = 12.3$, $P = 0.0001$; REGWQ $P < 0.05$; other means intermediate). The proportion of bags that were missing from shrubs varied from 13 to 25% across treatments, but these differences were not statistically significant (ANOVA $P > 0.05$).

4. Discussion

The greater proportion of bagworms missing from shrubs that were not caged in Experiment 1 suggested that English sparrows had an important impact on bagworm density. English sparrows in a colony less than 3 km from the study site have learned to extract bagworms from their bags, allowing them to exploit this convenient resource (see Moore and Hanks, 2000). Different species of birds were apparently important in regulating populations of bagworm in another study (Horn and Sheppard, 1979). Experiment 1 also revealed that mice were important predators of bagworms, further attested to by the greatly reduced levels of mortality when mice were excluded more effectively with the improved cage design. Predation by rodents has been considered in few earlier studies of bagworm (but see Cronin, 1989), and descriptions of damage to bags in some studies suggest that mortality due to rodents was attributed to birds (see Haseman, 1912; Horn and Sheppard, 1979; Kulman, 1965). Tears in the bags of other bagworm species that may have been caused by rodents also have been attributed to birds and lizards (see Gara et al., 1990; Jones and Parks, 1928; Stephens, 1962). The white-footed mouse is an opportunistic species that commonly feeds on insects and can be arboreal (Lackey et al., 1985). Lepidopterous larvae and pupae were common prey of this mouse species in earlier studies conducted near our study sites (Batzli, 1977; Sternburg et al., 1981). The interior of arborvitae shrubs in

our study apparently offered hospitable lodging for mice, stocked as they were with bagworm prey. High rates of vertebrate predation suggest that vertebrates may play an important role in regulating bagworm populations in some situations, as is true for other bagworm species (Stephens, 1962). Nevertheless, it seems unlikely that the public would accept a management strategy for bagworms that involves mice and English sparrows.

Pimpla disparis, the most abundant parasitoid species in the present study, is Palearctic in its natural distribution, and was introduced into the eastern United States in the 1970s and 1980s as a biological control agent of gypsy moth (Schaefer et al., 1989). *P. disparis* was released in Cook County in northern Illinois in 1977 (Schaefer et al., 1989), before gypsy moth was present in the state. Gypsy moth was limited in its distribution in Illinois to northern counties during the present study (Sharov et al., 2002). Thus, *P. disparis* has spread at least 200 km south to Champaign County in advance of its target host. This parasitoid species is highly polyphagous, attacking lepidopterans of at least 14 families, including endemic moths and papilionid butterflies (Schaefer et al., 1989). This polyphagous nature may have assured persistence of this parasitoid even in areas where gypsy moth is scarce (Fuester et al., 1997; Schaefer et al., 1989). Polyphagy may be detrimental, however, if it threatens populations of endemic host species and their parasitoids (see Kimberling, 2004). Nevertheless, the reputation of *P. disparis* as a biological control agent probably will remain unsullied despite its adoption of the endemic bagworm as a host, because bagworm is usually considered as a pest.

Itoplectis conquisitor was a dominant parasitoid in many earlier studies of bagworm (Cronin and Gill, 1989; Gross and Fritz, 1982; Haseman, 1912; Horn and Sheppard, 1979; Kulman, 1965; Sheppard and Stairs, 1976), and can be an important natural enemy of other lepidopteran species (Foltz et al., 1972). In fact, Balduf (1937), who studied natural enemies of bagworm in the area of the present study, reported that *I. conquisitor* was one of the most abundant parasitoids, but collected none of the other parasitoid species that we reared from bagworms. *I. conquisitor* is native to North America, broadly distributed, and highly polyphagous, attacking species in 16 lepidopteran families, as well as hymenopterans of the families Diprionidae, Braconidae, and Ichneumonidae (Arthur, 1963; Krombein et al., 1979).

Gambrus ultimus also is broadly distributed with hosts in six lepidopteran families, including bagworm (Cronin and Gill, 1989; Gross and Fritz, 1982; Sheppard and Stairs, 1976), and may be a parasitoid of other Ichneumonidae (Krombein et al., 1979). The association between parasitoid and host sexes in *I. conquisitor* and *G. ultimus*, reported previously for *I. conquisitor* (Balduf, 1937; Kulman, 1965; Sheppard and Stairs, 1976), probably results from the mother's preference to oviposit

fertilized eggs in the larger female bagworm pupae and unfertilized eggs in the smaller male pupae, as has been described for other hymenopteran parasitoids (e.g., Hanks et al., 2001). The torymid *Monodontomerus minor* is believed to attack bagworm (Horn and Sheppard, 1979; Sheppard and Stairs, 1976), but may be a hyperparasitoid of *I. conquisitor* (Cronin and Gill, 1989; Kulman, 1965).

Parasitism rates of bagworms in the present study ranged from ~25 to 50%, roughly corresponding to average rates of 4–46% reported in earlier studies (Barrows, 1974; Barrows and Gordh, 1974; Berisford and Tsao, 1975b; Cox and Potter, 1988; Cronin, 1989; Gross and Fritz, 1982; Horn and Sheppard, 1979; Kulman, 1965). The greatest parasitism rate in our study (>70%) was reached in shrubs positioned adjacent to the flower bed in Experiment 3, the most extensive contiguous planting of flowers that we have evaluated to date. This parasitism rate greatly exceeds that of these earlier studies, and attests to the importance of considering the spatial influence of floral resources on natural enemies. The absence of density dependence in parasitism rate in Experiment 1 is consistent with earlier bagworm studies (Barrows, 1974; Cox and Potter, 1988; Gross and Fritz, 1982; but see Cronin, 1989).

Our three studies provide strong evidence that flowering forbs have a very localized influence on host-searching behavior of female parasitoids, encouraging them to seek and parasitize bagworms in the immediate vicinity. Spatial limitations in the influence of floral resources on parasitoids could result in reduced parasitism rates where bagworms are on host plants that are taller than the low-growing arborvitae cultivar used in our studies. Floral resource plants enhance regulation of another bagworm species by encouraging its ichneumonid parasitoids (Syed and Shah, 1977). A localized flower effect on abundance has been reported for other parasitoid species (e.g., Rogers and Potter, 2004; Streams et al., 1968; van Emden, 1962) and may result from improved efficiency in host location after adults feed (see Wäckers, 1994; Takasu and Lewis, 1995), or an inclination in females to search for oviposition hosts in the vicinity of floral hosts (a “habitat preference” effect, sensu Vinson, 1976). In fact, adult *I. conquisitor* visit flowers of many plant species (Leius, 1960). The question remains, however, whether greater levels of parasitism may be achievable by providing even more extensive plantings of flowering forbs than we used in our experiments.

Because the parasitoids attack bagworms late in the season, enhanced parasitism rates would do little to reduce feeding damage to host plants. Parasitism could reduce local population densities over time where it is not counterbalanced by immigration of aerially dispersing larvae in spring (Moore and Hanks, 2004). The potential value of parasitoids in regulating bagworm populations suggests that an effective IPM program

would minimize applications of broad-spectrum insecticides, such as by using Bt products for remedial action against bagworm infestations.

This study contributes to a growing body of literature that supports the notion that ecological methods of pest management can be integrated into the design of urban landscapes to combat herbivorous pests (e.g., Hanks and Denno, 1993; Shrewsbury and Raupp, 2000; Tooker and Hanks, 2000a). This management approach could have the benefit of reducing or even eliminating applications of pesticides for controlling herbivorous pests in public places. It requires only the simple manipulation of flowering forbs that already are valued elements of ornamental landscapes. Ecological approaches to pest management promote stewardship of urban environments, a desirable outcome as urban areas are rapidly becoming the primary habitat of human society (United Nations, 2003).

Acknowledgments

We thank M.R. Berenbaum and R.N. Wiedenmann for their comments on an early draft of the manuscript, J.C. Luhman for identifying the parasitoids, M. Rhoads for his generous donation of references, E. Kron, E. Jackson, N. Rauter, and A. Crumrin for technical assistance, and M. Wolf of the Department of Animal Biology for help in live-trapping and identifying mice. We also thank H. Wilkinson, D. Williams, and D. Huffstutler of the Department of Natural Resources and Environmental Sciences for their help in establishing and maintaining arborvitae shrubs and turf, and their Department for use of the land. We also appreciate the many helpful research suggestions and valuable insights into bagworm biology and urban ecology provided by G.P. Waldbauer. The manuscript was considerably improved by the suggestions of an anonymous reviewer. This project was in partial fulfillment of a MS degree for J.A.E. The project was supported by the UIUC Research Board and the National Research Initiative of the USDA Cooperative State Research, Education and Extension Service, Grant Nos. 99-35316-7850 and 2001-35316-11275.

References

Arthur, A.P., 1963. Life histories and immature stages of four ichneumonid parasites of the European pine shoot moth *Rhyacionia buoliana* (Schiff.) in Ontario. *Can. Entomol.* 95, 1078–1091.

Baldof, W.V., 1937. Bionomic notes on the common bagworm, *Thyridopteryx ephemeraeformis* Haw., (Lepid., Psychidae) and its insect enemies (Hym., Lepid.). *Proc. Entomol. Soc. Washington* 39, 169–184.

Barrows, E.M., 1974. Some factors affecting population size of the bagworm, *Thyridopteryx ephemeraeformis* (Lepidoptera: Psychidae). *Environ. Entomol.* 3, 929–932.

Barrows, E.M., Gordh, G., 1974. Insect associates of the bagworm moth, *Thyridopteryx ephemeraeformis* (Lepidoptera: Psychidae), in Kansas. *J. Kansas Entomol. Soc.* 47, 156–161.

Batzli, G.O., 1977. Population dynamics of the white-footed mouse in floodplain and upland forest. *Am. Midl. Nat.* 97, 18–32.

Berisford, Y.C., Tsao, C.H., 1975a. Distribution and pathogenicity of fungi associated with the bagworm, *Thyridopteryx ephemeraeformis* (Haworth). *Environ. Entomol.* 4, 257–261.

Berisford, Y.C., Tsao, C.H., 1975b. Parasitism, predation, and disease in the bagworm, *Thyridopteryx ephemeraeformis* (Haworth) (Lepidoptera: Psychidae). *Environ. Entomol.* 4, 549–554.

Cox, D.L., Potter, D.A., 1988. Within-crown distributions of male and female bagworm (Lepidoptera: Psychidae) pupae on juniper as affected by host defoliation. *Can. Entomol.* 120, 559–567.

Cronin, J.T., 1989. Inverse density-dependent parasitism of the bagworm, *Thyridopteryx ephemeraeformis* (Lepidoptera: Psychidae). *Environ. Entomol.* 18, 403–407.

Cronin, J.T., Gill, D.E., 1989. The influence of host distribution, sex, and size on the level of parasitism by *Itopectis conquisitor* (Hymenoptera: Ichneumonidae). *Ecol. Entomol.* 14, 163–174.

Davis, D.R., 1964. Bagworm moths of the Western Hemisphere. *Bull. U.S. Natl. Mus.* 244, 1–233.

Day, R.W., Quinn, G.P., 1989. Comparisons of treatments after an analysis of variance in ecology. *Ecol. Monogr.* 59, 433–463.

Dreistadt, S.H., Dahlsten, D.L., Frankie, G.W., 1990. Urban forests and insect ecology: complex interactions among trees, insects, and people. *BioScience* 40, 192–198.

Flanders, R.V., 1986. Potential for biological control in urban environments. In: Bennett, G.W., Owens, J.M. (Eds.), *Advances in Urban Pest Management*. Van Nostrand Reinhold, New York, pp. 95–127.

Foltz, J.L., Knight, F.B., Allen, D.C., 1972. Numerical analysis of population fluctuations of the jack pine budworm. *Ann. Entomol. Soc. Am.* 65, 82–89.

Frankie, G.W., Ehler, L.E., 1978. Ecology of insects in urban environments. *Annu. Rev. Entomol.* 23, 367–387.

Frankie, G.W., Brewer, J.W., Cranshaw, W., Barthell, J.F., 1987. Abundance and natural enemies of the spindle gall midge, *Pinyonia edulicola*, in natural and urban stands of pinyon pine in Colorado (Diptera: Cecidomyiidae). *J. Kansas Entomol. Soc.* 60, 133–144.

Fuester, R.W., Sandridge, P.T., Dill, N.H., McLaughlin, J.M., Peiffer, R.A., Taylor, P.B., Sigmon, J.O.D., Newlon, C.J., 1997. Parasitism of gypsy moth (Lepidoptera: Lymantriidae) pupae on the Delmarva Peninsula with emphasis on *Coccygomimus disparis* (Hymenoptera: Ichneumonidae). *J. Econ. Entomol.* 90, 1551–1559.

Gara, R.I., Sarango, A., Cannon, P.G., 1990. Defoliation of an Ecuadorian mangrove forest by the bagworm, *Oiketicus kirbyi* Guiding (Lepidoptera: Psychidae). *J. Trop. For. Sci.* 3, 181–186.

Ghent, A.W., 1999. Studies of ballooning and resulting patterns of locally contagious distribution of the bagworm *Thyridopteryx ephemeraeformis* (Haworth) (Lepidoptera: Psychidae). *Am. Midl. Nat.* 142, 291–313.

Gross, S.W., Fritz, R.S., 1982. Differential stratification, movement and parasitism of sexes of the bagworm, *Thyridopteryx ephemeraeformis*, on redcedar. *Ecol. Entomol.* 7, 149–154.

Hanks, L.M., Denno, R.F., 1993. Natural enemies and plant water relations influence the distribution of an armored scale insect. *Ecology* 74, 1081–1091.

Hanks, L.M., Millar, J.G., Paine, T.D., Wang, Q., Paine, E.O., 2001. Patterns of host utilization by two parasitoids (Hymenoptera: Braconidae) of the eucalyptus longhorned borer (Coleoptera: Cerambycidae). *Biol. Control* 21, 152–159.

Haseman, L., 1912. The evergreen bagworm. *Univ. Missouri Ag. Expt. Stn. Bull.* 104, 308–329.

Heimpel, G.E., Jervis, M.A., 2005. Does floral nectar improve biological control by parasitoids? In: Wäckers, F., van Rijn, P., Bruin, J. (Eds.), *Plant-Provided Food for Carnivorous Insects: Protective*

- Mutualism and its Applications. Cambridge University Press, Cambridge, UK (in press).
- Horn, D.J., Sheppard, R.F., 1979. Sex ratio, pupal parasitism, and predation in two declining populations of the bagworm, *Thyridopteryx ephemeraeformis* (Haworth) (Lepidoptera: Psychidae). *Ecol. Entomol.* 4, 259–265.
- Johnson, W.T., Lyon, H.H., 1988. *Insects That Feed on Trees and Shrubs*. Cornell University Press, Ithaca, New York.
- Jones, F.M., Parks, J.B., 1928. The bagworms of Texas. *Texas Ag. Exp. Stn. Bull.* 382, 36.
- Kennedy, G.G., Storer, N.P., 2000. Life systems of polyphagous arthropod pests in temporally unstable cropping systems. *Annu. Rev. Entomol.* 45, 467–493.
- Kimberling, D.N., 2004. Lessons from history: predicting successes and risks of intentional introductions for arthropod biological control. *Biol. Invasions* 6, 301–318.
- Krombein, K.V., Hurd, P.H., Smith, D.R., 1979. *Catalog of Hymenoptera in America North of Mexico*. Smithsonian Institution Press, Washington, DC.
- Kulman, H.M., 1965. Natural control of the bagworm and notes on its status as a forest pest. *J. Econ. Entomol.* 58, 863–866.
- Lackey, J.A., Huckaby, D.G., Ormiston, B.G., 1985. *Peromyscus leucopus*. *Mamm. Species* 247, 1–10.
- Landis, D.A., Wratten, S.D., Gurr, G.M., 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45, 175–201.
- Leius, K., 1960. Attractiveness of different foods and flowers to the adults of some hymenopterous parasites. *Can. Entomol.* 92, 369–376.
- Milliken, G.A., Johnson, D.E., 1984. *Analysis of Messy Data. Vol. 1: Designed Experiments*. Van Nostrand Reinhold, New York.
- Moore, R.G., Hanks, L.M., 2000. Avian predation of the evergreen bagworm (Lepidoptera: Psychidae). *Proc. Entomol. Soc. Wash.* 102, 350–352.
- Moore, R.G., Hanks, L.M., 2004. Aerial dispersal and host plant selection by neonate *Thyridopteryx ephemeraeformis* (Lepidoptera: Psychidae). *Ecol. Entomol.* 29, 327–336.
- Morden, R.D., Waldbauer, G., 1971. Embryonic development time and spring hatching of *Thyridopteryx ephemeraeformis* (Lepidoptera: Psychidae). *Entomol. News* 82, 209–217.
- Newman, D., 1980. Susceptibilidad de algunos arboles al ataque defoliador del gusano canasta (*Oiketicus kirbyi* Guilding) en el Valle del Cauca. *Investigación Forestal, Carton de Columbia S.A., Informe de Investigación* 63, 1–10. (in Spanish).
- Raupp, M.J., Koehler, C.S., Davidson, J.A., 1992. Advances in implementing integrated pest management for woody landscape plants. *Annu. Rev. Entomol.* 37, 561–585.
- Rogers, M.E., Potter, D.A., 2004. Potential for sugar sprays and flowering plants to increase parasitism of white grubs (Coleoptera: Scarabaeidae) by tiphiid wasps (Hymenoptera: Tiphidae). *Environ. Entomol.* 33, 619–626.
- Root, R.B., 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol. Monogr.* 43, 95–124.
- SAS Institute, 2001. *SAS/STAT User's Guide for Personal Computers*, Release 8e. SAS Institute, Cary, North Carolina.
- Schaefer, P.W., Fuester, R.W., Chianese, R.J., Rhoads, L.D., Tichenor Jr., R.B., 1989. Introduction and North American establishment of *Coccygomimus disparis* (Hymenoptera: Ichneumonidae), a polyphagous pupal parasite of Lepidoptera, including gypsy moth. *Environ. Entomol.* 18, 1117–1125.
- Sharov, A.A., Leonard, D., Liebhold, A.M., Clemens, N.S., 2002. Evaluation of preventive treatments in low-density gypsy moth populations using pheromone traps. *J. Econ. Entomol.* 95, 1205–1215.
- Sheppard, R.F., Stairs, G.R., 1976. Factors affecting the survival of larval and pupal stages of the bagworm, *Thyridopteryx ephemeraeformis* (Lepidoptera: Psychidae). *Can. Entomol.* 108, 469–473.
- Shrewsbury, P.M., Raupp, M.J., 2000. Evaluation of components of vegetational texture for predicting azalea lace bug, *Stephanitis pyrioides* (Heteroptera: Tingidae), abundance in managed landscapes. *Environ. Entomol.* 29, 919–926.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry*, third ed. W.H. Freeman, New York.
- Stephens, C.S., 1962. *Oiketicus kirbyi* (Lepidoptera: Psychidae): a pest of bananas in Costa Rica. *J. Econ. Entomol.* 55, 381–386.
- Sternburg, J.G., Waldbauer, G.P., Scarbrough, A.G., 1981. Distribution of cecropia moth (Saturniidae) in central Illinois: a study in urban ecology. *J. Lepidopterist's Soc.* 35, 304–320.
- Streams, F.A., Shahjahan, M., LeMasurier, H.G., 1968. Influence of plants on the parasitization of the tarnished plant bug by *Leiophron pallipes*. *Environ. Entomol.* 3, 69–72.
- Syed, R.A., Shah, S., 1977. Some important aspects of insect pest management in oil palm estates in Sabah, Malaysia. In: Earp, D.A., Newall, W. (Eds.), *International Developments in Oil Palm*. Incorporated Society of Planters, Kuala Lumpur, pp. 577–590.
- Takasu, K., Lewis, W.J., 1995. Importance of adult food sources to host searching of the larval parasitoid *Microplitis croceipes*. *Biol. Control* 5, 25–30.
- Tooker, J.F., Hanks, L.M., 2000a. Influence of plant community structure on natural enemies of pine needle scale (Homoptera: Diaspididae). *Environ. Entomol.* 29, 1305–1311.
- Tooker, J.F., Hanks, L.M., 2000b. Flowering plant hosts of adult hymenopteran parasitoids of central Illinois. *Ann. Entomol. Soc. Am.* 93, 580–588.
- United Nations, 2003. *World Urbanization Prospectus: The 2003 Revision*. United Nations Dept. of Economic and Social Affairs, Population Division, New York.
- van Emden, F., 1962. Observations on the effect of flowers on the activity of parasitic Hymenoptera. *Entomol. Monthly Mag.* 98, 265–270.
- Vinson, S.B., 1976. Host selection by insect parasitoids. *Annu. Rev. Entomol.* 21, 109–133.
- Wäckers, F., 1994. The effect of food deprivation on the innate visual and olfactory preferences in the parasitoid *Cotesia rubecula*. *J. Insect Physiol.* 40, 641–649.