

Interactions Between a Native Silkmoth *Hemileuca* sp. and an Invasive Wetland Plant, *Lythrum salicaria*

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ABSTRACT Invasive plants are generally thought to have negative impacts on native communities. Rarely, however, are the impacts of invasive plants on native insects examined, limiting our understanding of the broader effects of invasive plants on native habitats. In this study, I document the use of purple loosestrife, *Lythrum salicaria* L. (Lythraceae), an aggressive wetland invasive, by *Hemileuca* sp. (Saturniidae), a native silkmoth. This buckmoth is a unique ecological variant of the more widespread buck moth, *Hemileuca maia* (Drury), and is of conservation concern in some areas. *Hemileuca* sp. was regularly observed feeding on *L. salicaria* in 2003 and 2004 at two sites in southern Wisconsin. Densities of late instars were as high as 12 individuals/m² and caused significant defoliation of *L. salicaria* with an average 34% loss of foliage relative to undamaged plants. Experimental manipulations of *Hemileuca* sp. caterpillars showed that herbivory could decrease seed production as much as 66%. In a laboratory assay, *Hemileuca* sp. feeding on *L. salicaria* had significantly lower pupal mass and lower survivorship to pupation (24%) relative to larvae feeding on *Salix* foliage (90%). Moreover, in two-choice preference assays, larvae preferred *Salix* over *Lythrum* foliage. Populations of *Hemileuca* sp. were subject to intense parasitism (up to 93%) by a tachinid parasitoid, *Leschenaultia flavipes* (Bigot). This combination of factors suggests there may be significant negative selection on *Hemileuca* sp. feeding on *L. salicaria* and that invaded habitats may be ecological sinks for the native herbivores.

KEY WORDS host shift, novel host, buck moth, *Hemileuca maia* species complex, preference-performance

Invasive organisms are widely regarded as one of the most serious threats to native ecosystems worldwide (Mack et al. 2000). Invasive plants in particular have been shown to significantly alter native ecosystems by reducing diversity of native species, altering disturbance regimes, and changing nutrient and water cycles (Vitousek et al. 1987, Mack and D'Antonio 1998, Windham and Ehrenfeld 2003). In the face of the continued successful expansion of invasive species (McKinney and Lockwood 1999), conservation of native biodiversity will rely on understanding the interactions between native assemblages and exotic species. This issue becomes particularly important when the native communities include rare or endangered species (Wilcove et al. 1998).

One exotic plant that has received significant attention is the recent colonist of North American wetlands purple loosestrife, *Lythrum salicaria* L. (Lythraceae) (hereafter *Lythrum*). *Lythrum* is a Eurasian species that was intentionally introduced in the 1800s on the east coast of the United States. Since the 1930s, this species has experienced a rapid spread into wetlands and is now found throughout the contiguous

United States (except Florida) and nine Canadian provinces (Stuckey 1980, Thompson et al. 1987). Despite *Lythrum's* widespread occurrence and dominance in the vegetation where it occurs, the extent of the negative impacts on native communities has been debated (Anderson 1995). For example, although the incursion of *Lythrum* in wetland habitats has been associated with decreases in native plant species (Gabor et al. 1996, Weiher et al. 1996), the opposite pattern has also been observed (Morrison 2002, Hager and Vinebrooke 2004). Moreover, how *Lythrum* in particular and other invasive species in general, affect local fauna is usually not investigated. Particularly sensitive may be resident insect herbivores that are intimately associated with native plants (Blossey et al. 2001a, Gratton and Denno 2005).

Although habitats invaded by alien plants are often characterized as supporting little biodiversity, native consumers can sometimes use these novel resources (Anderson 1995, Barbour and Kiviat 1997). In North America, numerous native herbivores have been observed feeding on *Lythrum* (Hight 1990, Maddox and Wiedenmann 2003). In an extensive survey of three Canadian wetlands, Diehl et al. (1997) found 41 herbivore species and Hight (1990) collected 60 species

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of insect herbivores on *Lythrum* in east coast wetlands. Barbour and Kiviat (1997) showed that native cecropia moth, *Hyalophora cecropia* (L.), and polyphemus moth, *Antheraea polyphemus* (Cramer), readily feed on *Lythrum* instead of their normal gray dogwood host, *Cornus racemosa* L., although it is not clear whether these herbivores could successfully complete their development on *Lythrum*.

These findings raise the possibility that *Lythrum* may enhance resources for some herbivores, potentially allowing them to become more abundant. In addition, herbivory by native species may depress *Lythrum* populations. There is little empirical data supporting either of these predictions. It is unknown whether *Lythrum* populations, by virtue of their replacement of native species within wetlands, have any impact on populations of native insect species, either positive or negative. Moreover, with the exception of European herbivores intentionally released as classical biological control agents (Malecki et al. 1993, Blossey et al. 2001b), it is also generally thought that native herbivores that can feed on *Lythrum* have minimal impacts, because their populations on *Lythrum* tend to be small (Hight 1990, Diehl et al. 1997, Maddox and Wiedenmann 2003) and *Lythrum* continues to spread (Blossey et al. 2001a).

In this study, I examined how an alien plant species affects a native community by documenting a relatively novel association between a native herbivore of conservation interest, *Hemileuca* sp. (Saturniidae), and the exotic *L. salicaria*. Observations that *Hemileuca* sp. populations reach high densities on *Lythrum* suggested that populations of these moths may benefit from the presence of the exotic plant. In a field experiment, I examined whether *Hemileuca* sp. herbivory can reciprocally affect *Lythrum* and alter seed production, potentially reducing the ability of this plant to spread. In addition, laboratory assays were performed to examine larval performance on and preference for the novel host plant, *Lythrum*, by these native silkmoths.

Background and Natural History. *Hemileuca* sp. (Tuskes et al. 1996, Rubinoff and Sperling 2004) are silkmoths (Lepidoptera: Saturniidae) native to North America that belong to a species complex which includes buck moth, *Hemileuca maia* (Drury), and *Hemileuca nevadensis* Stretch. *H. maia* feeds predominantly on oaks (*Quercus* spp.; Fagaceae) throughout its range (southern United States to the northeast), but it has been shown to feed on other woody plants as well (Tuskes et al. 1996). *H. nevadensis* occurs in the western United States and feeds primarily on willows (*Salix* spp.) and cottonwoods (*Populus* spp.). *Hemileuca* populations from the Great Lakes region have puzzled taxonomists and systematists, because they possess a confusing array of morphological, ecological, and behavioral characteristics that suggest a possible introgression of *H. nevadensis* and *H. maia* in these areas. The ranges of *H. nevadensis* and *H. maia* meet in Wisconsin, making this a zone of possible secondary contact between these species (Tuskes et al. 1996). Populations of *H. maia* from northern Ohio,

New York, and southern Ontario have been collected in wetlands, primarily feeding on buckbean, *Menyanthes trifoliata* L. (Menyanthaceae) (Scholtens and Wagner 1994, Pryor 1998). In Wisconsin, *H. maia* has been collected from swamp birch, *Betula pumila* L., and *M. trifoliata* (Kruse 1998). Based on these unusual host associations, some researchers have suggested that Great Lakes populations are unique (named "Cryan's buck moth" or "bog buck moth") and deserve special conservation consideration (Metzler and Lucas 1990, Legge et al. 1996, Crandall et al. 2000).

The general life cycle of *Hemileuca* sp. is similar to that of most species in the genus. Males of these showy moths are attracted to the pheromone of virgin females (McElfresh et al. 2001) in the fall. After mating, females lay large cylindrical clutches of eggs (≈ 140 eggs per clutch) on small branches of their host plants (Bowers and Stamp 1987). Embryos begin to develop immediately in the fall, but development is suspended by low winter temperatures, and eclosion from the eggs typically does not occur until tree bud-burst in the spring (May–June more northern latitudes). The small black larvae feed on leaves of their host plants in large gregarious clusters during their early instars. As local food resources are consumed, large larvae disperse and feed individually. Larvae go through five instars and can reach lengths of 5–8 cm before moving to the soil to pupate in a loose soil chamber in late August. Adult moths emerge from pupae in October and locate mates.

Materials and Methods

Study Sites. This study focused on two populations of *Hemileuca* sp. in southern Wisconsin: "Rome Pond" site south of the town of Sullivan (Franklin Co., 42.97893° N, 88.57607° W) (2003–2004) and "County Road BB" site south of the town of Oconomowoc (Waukesha Co, 43.09442° N, 88.52025° W) (2004). The Rome Pond site, owned by the Wisconsin Department of Natural Resources (≈ 4 ha), had a heavy infestation of *L. salicaria* with willows (*Salix* spp.) and oaks (*Quercus* spp.) fringing the wetland near an access road. The Wisconsin Department of Natural Resources had repeatedly tried to control *Lythrum* at this site by using the leaf-feeding *Galerucella pusilla* Duftschmid and *Galerucella californiensis* L. (Chrysomelidae) biological control agents, but defoliation by these herbivores was minimal in 2003–2004. The County Road BB site (≈ 5 ha) was upland along the Oconomowoc River and had no evidence of other herbivores except for *Hemileuca* sp.

Census of *Hemileuca* sp. Larvae and Estimates of *Hemileuca* Feeding. In 2003, buck moth populations at the Rome Pond site were censused when late instars were conspicuous (16 July) by haphazardly placing a 0.25 m² quadrat ($n = 30$) along a 100-m transect. The total number of *Lythrum* stems and late instars of *Hemileuca* were counted in each plot. In 2004, at both of our sites, I walked a transect on 8 August and counted the total number of larvae per number of stems examined ($n = 5000$ stems, Rome Pond; $n =$

1,000 stems, County Road BB). Collections of fifth instars from Rome Pond (2003, $n = 155$; 2004, $n = 28$) and County Road BB (2004, $n = 135$) were returned to the laboratory and reared to adulthood to verify species and to determine whether any parasitoids had attacked larvae.

On 17 July 2003, I walked a transect at Rome Pond and haphazardly selected a *Lythrum* plant every 3 m. Plants were then classified as either having no evidence of caterpillar damage or positive evidence of caterpillar feeding damage. Plants were collected until there were 20 in each damage category. Feeding damage from buck moths results in the entire consumption of leaves and is easily distinguishable from damage caused by other herbivores (e.g., beetles and mirids) that are occasionally present at this site. Stems were harvested before they had set seed, so reproductive output was not estimated. For each plant, I measured height (centimeters) and counted the number of leaves. Furthermore, I removed all leaves and dried them at 60°C for 72 h to obtain a dry mass. The relationship between buck moth damage (presence or absence) and 1) leaf number and 2) leaf mass (grams dry weight) with plant height as a covariate was examined by analysis of covariance.

Herbivory Experiment. To further examine the impact of *Hemileuca* sp. on *Lythrum*, I conducted a study at Rome Pond in 2003 in which I manipulated caterpillar herbivory directly. The following four treatment combinations were established in a 2 by 2 factorial design: 1) unbagged plants, no caterpillars; 2) unbagged plants with caterpillars added; 3) bagged plants without caterpillars; and 4) bagged plants with caterpillars added. I haphazardly selected 40 *Lythrum* plants of similar size (≈ 150 -cm height) that had no signs of prior herbivory and randomly assigned the four treatments to these plants ($n = 10$ replicates). For plants that received caterpillars, on 24 July 2003 five fifth instars of *Hemileuca* sp. were placed on the foliage. After 24 h, only $\approx 20\%$ of the caterpillars remained on plants without bags and 1 wk later, there were no caterpillars of the original five caterpillars that were added on unbagged plants. For the bagged plant treatments, a fine mesh bag was placed around the entire plant. After 2 wk, caterpillars were removed from within the mesh bags and the bags were removed from both bagged plant treatments (caterpillars and no caterpillars). After plants flowered and set seed, 14–26 August, plants were cut at the base and returned to the laboratory. For each plant, I measured plant height and biomass of leaves and seed capsules (grams dry weight). The effects of caterpillar and bagging treatments on dependent plant variables were analyzed by two-way factorial analysis of variance (ANOVA). Seed capsule mass was cube root transformed before analyses to normalize variances between treatments.

Larval Performance Assay. To measure larval performance on *Lythrum*, I collected first instars ($n = 20$) from different feeding aggregations on 27 May 2004 from Rome Pond and returned them to the laboratory. Larvae were maintained individually on field-collected *Lythrum* in petri dishes (9 cm in diameter)

lined with moistened filter paper before being assigned to feeding treatments on 10 June. One-half of the larvae were randomly selected to feed on leaves of field-collected black willow, *Salix nigra* Marsh (Salicaceae), whereas the other half were maintained on *Lythrum*. *Salix* was chosen because *Hemileuca* sp. have been observed feeding on marsh willows and a close relative of *Hemileuca* sp., *H. nevadensis*, feeds on willows (Tuskes et al. 1996). Over the ensuing 5 wk larvae were fed new leaves ad libitum every 2 d. As larvae outgrew the petri dishes (approximately fourth instar), they were transferred to 450-ml ice cream containers fitted with a nylon mesh lid. Larvae were removed from rearing containers and weighed (milligrams wet weight) on a microbalance (Mettler-Toledo MT5) every 2–3 d. I noted larval survivorship daily and noted the days to pupation. One day after pupation, I measured pupal mass (milligrams wet mass). Buck moth larvae were maintained in a constant temperature growth chamber (25°C and a photoperiod of 16:8 [L:D] h) for the duration of the experiment. To analyze larval performance on the different host plants, I estimated growth rates of individual caterpillars by fitting a regression line through the log-transformed mass over time (log-mass gained versus time, days 1–30). A *t*-test and Wilcoxon's sign ranks test was used to examine difference in larval performance parameters between the two diet treatments (*Salix* versus *Lythrum*): larval growth rate (milligrams gained per day), time to pupation (days), and pupal mass (milligrams). Survivorship during larval development was examined using Kaplan-Meier curves with censored data (some larvae excluded from the survivorship analysis because of accidental damage during handling) and a log-rank test to examine differences in survivorship between diets (Parmer and Machin 1995).

Larval Feeding Preference Assay. I examined larval preference for *Lythrum* and *Salix* host plants by using a two-choice feeding assay. This experiment was performed with first and second instars ($n = 10$ larvae; 10 June 2004) and third and fourth instars ($n = 20$ larvae; 23 June) collected from Rome Pond. Larvae were placed individually in petri dishes (9 cm in diameter) lined with moistened filter paper and provided with three or four preweighed leaves each of *Lythrum* and *S. nigra* interspersed on the bottom of the dish. Larvae were allowed to feed for 24 h after which leaves of each species were removed and reweighed (milligrams wet weight). To account for changes in leaf mass unrelated to feeding (e.g., desiccation), a set of five dishes with no larvae were established in the same manner as described above and run coincident with the choice experiment. Separately for *Lythrum* and *Salix* leaves in each replicate arena, I calculated the percentage of original mass remaining after the 24 h feeding interval, adjusted by the mass change observed with no herbivory. Under the hypothesis of no preference between host plants, we would expect on average the same relative decrease in leaf mass between the two species. To test this hypothesis, a paired *t*-test was performed using each dish as a replicate set

Table 1. Abundance of *Hemileuca* sp. larvae in southern Wisconsin wetlands and frequency of the tachinid parasitoid *L. fulvipes* emerging from fifth instars

Collection site	Yr	<i>Hemileuca</i> sp.						No. of <i>L. fulvipes</i> emerging from a single <i>Hemileuca</i> sp. caterpillar					
		Abundance ^a	Larvae collected	Adults emerged	Larvae parasitized	Unknown mortality ^b	% parasitism ^c	1	2	3	4	5	6
Rome Pond	2003	0.25	155	28	113	14	80	62	27	16	4	3	1
	2004	0.006	28	17	3	8	15	3	0	0	0	0	0
County Rd BB	2004	0.13	135	7	87	38	93	51	15	12	6	3	0

^a Average number of fifth instars per *Lythrum* stem.

^b Number of larvae or pupae that failed to develop to the next stage with no evidence of parasitism.

^c [(larvae parasitized) / (adults emerged + larvae parasitized)] × 100.

with the percent of *Salix* and *Lythrum* consumed in each dish as the response variables. All statistical analyses were performed with JMP 5.0 (SAS Institute 2003). Means ± SEM are reported.

Results

***Hemileuca* sp. Larval Abundance and Estimates of *Hemileuca* Feeding.** At the Rome Pond site, *Hemileuca* sp. density of late instars was 12.5 ± 2.8 m⁻² (n = 30) in mid-July 2003. As *Lythrum* stem density at this site was 49.5 ± 4.9 individuals/m², this translated to 0.25 larvae per stem. In August 2004, a spot estimate of *Hemileuca* sp. abundance indicated densities of late instars at Rome of 0.006 larvae per stem and 0.13 larvae per stem at the County Road BB site. Collections of late instars from these sites showed variable rates of parasitism (15–93%) by one tachinid parasitoid, *Leschenaultia fulvipes* Bigot (Diptera: Tachinidae). Tachinids were often gregarious with as many as six fly larvae emerging from a single *Hemileuca* sp. caterpillar (Table 1).

Hemileuca sp. herbivory of *Lythrum* was clearly evident at the Rome Pond Site in 2003 and at the County Road BB site in 2004. No other evidence of herbivory from other insects was observed. At Rome Pond in 2003, plants that had evidence of feeding from *Hemileuca* sp. were compared with plants that had no evidence of caterpillar feeding. On average, *Lythrum* with any evidence of *Hemileuca* sp. herbivory had 34% fewer leaves (undamaged, 455 ± 35; damaged, 301 ± 30 leaves per plant; F_{1, 37} = 10.5; P = 0.0025) (Fig. 1) and 28% less leaf mass (undamaged, 8.25 ± 0.65; damaged, 5.82 ± 0.55 g dry weight; F_{1, 37} = 7.97; P = 0.008) compared with plants with no damage. The damage × height interactions were not significant, suggesting homogeneous slopes across both damage categories for both variables (leaf number, P = 0.65; leaf mass, P = 0.85) and were not included in the final analysis.

Herbivory Experiment. The addition of late instars of *Hemileuca* sp. to *Lythrum* had measurable impacts on plant height, leaf mass, and seed production. *Hemileuca* sp. caterpillars reduced plant height ≈10% (Fig. 2A) although this effect was only evident in the open treatments (H × B significant; Table 2). Not surprisingly, leaf mass also was reduced (25%) by the

addition of larvae (Fig. 2B; Table 2), but bagging plants had no additional effect on leaf mass (no bagging effect and no H × B interaction; Table 2). Seed capsule production was almost completely inhibited by the presence of bags over plants for a 2-wk period (Fig. 2C), because *Lythrum* requires open pollination. However, the addition of *Hemileuca* sp. larvae to open plants significantly reduced seed production by 66% (Table 2, herbivory effect).

Larval Performance Assay. *Hemileuca* sp. larval development was similar on *Lythrum* and *Salix* as measured by the rate of mass gain per day (Table 3). Although the time to pupation was also not different between the two diet treatments (≈41 d), pupal mass was about half that of larvae feeding on the *Salix* diet. Lower larval performance on *Lythrum* was most evident in survivorship to pupation, which was significantly lower for larvae feeding on *Lythrum* (0.24) compared with *Salix* (0.90) (Table 3). Most larval mortality occurred between 14–21 d after the start of the experiment.

Larval Feeding Preference Assay. *Hemileuca* sp. larvae (both early and late instars) preferred *Salix* over

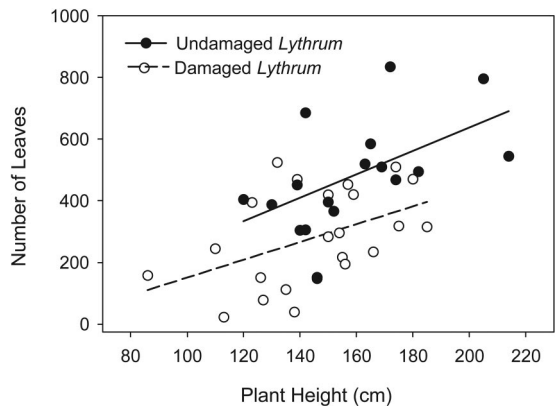


Fig. 1. Effect of *Hemileuca* sp. feeding (undamaged, closed circle and solid line; damaged, open circles and dashed line) on the total number of leaves per *L. salicaria* plant as a function of plant height. Lines are the slopes of the regression equations fitted for damaged and undamaged plants separately.

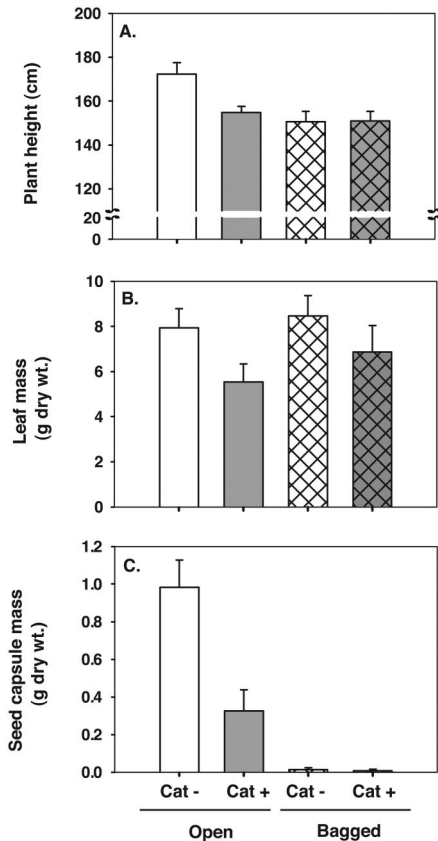


Fig. 2. Mean \pm SEM *L. salicaria* plant height (A), leaf mass (B), and seed capsule mass (C) at the end of the growing season within experimental treatments which manipulated *Hemileuca* sp. herbivory (Cat-, no caterpillars added; Cat+, caterpillars added; white and gray bars, respectively) and bagged treatments (open versus bagged, hatched and unhatched bars, respectively) in a factorial design ($n = 10$ replicates).

Lythrum in two-choice feeding assays (Table 3). Young larvae (first and second instars) consumed on average about twice as much *Salix* as *Lythrum*, although this trend was not statistically significant. The same pattern was seen with later instars (third and fourth), which consumed the same relative quantities of *Salix* but hardly consumed any *Lythrum* (Table 3) over 24 h.

Table 2. Summary of two-way ANOVA (F , P) of the effects of manipulated *Hemileuca* sp. defoliation (herbivory: larvae added versus not added), bagging of plants (bagging: open versus closed), and their interaction ($H \times B$) on *L. salicaria* characteristics measured in August 2003

Effect	Plant ht		Leaf mass		Seed capsule mass ^a	
	F^b	P	F	P	F	P
Herbivory (H)	3.88	0.057	4.48	0.041	10.07	0.003
Bagging (B)	8.62	0.006	0.965	0.333	90.90	<0.0001
$H \times B$	4.25	0.047	0.175	0.679	0.81	0.007

^a Cube-root transformed.

^b For all tests, $df = 1, 35$.

Discussion

Hemileuca sp. in Wisconsin can develop successfully on *L. salicaria*, and in wetland habitats populations can be very abundant on these exotic plants. Throughout the Great Lakes region, populations of buck moths have expanded their ecological range to include wetland habitats and wetland plants, although this study is the first to document an association with *Lythrum*. Legge et al. (1996) suggested that *Hemileuca* sp. in the Great Lakes region are unique, because they are capable of developing successfully on bog buckbean, a feature that is not present in the two putative ancestors of this taxon, *H. maia* and *H. nevadensis*. Because of this unique ecological attribute, several studies have suggested that these moths should be considered for conservation (e.g., Crandall et al. 2000). In New York and Ohio, *Hemileuca* sp. are considered endangered and in Wisconsin, they are considered a species of concern. Recent molecular evidence, however, has cast doubt on the unique evolutionary status of these populations. Using mitochondrial DNA sequence data, Rubinoff and Sperling (2004) showed that *Hemileuca* sp. populations were paraphyletic within *H. maia*, suggesting multiple, recent independent colonizations of wetland habitats and association with wetland plants. Yet, the population-level relationships within the *Hemileuca* sp.-*H. maia* complex are still unresolved and the nature of these novel associations with wetland plants remains an open question.

Novel Host Use in Wetland Habitats. Shifts by herbivores to unusual host plants are sometimes explained by the chemical relatedness of normal and novel host plants (Berenbaum 1990, Wahlberg 2001). Records from Wisconsin, Michigan, Ohio, and New York have found buck moths feeding on hosts in the genera *Salix*, *Populus*, *Betula*, *Spirea*, *Quercus*, *Menyanthes* (Scholtens and Wagner 1994, Kruse 1998, Pryor 1998), and now *Lythrum*. The high tannin levels in *Lythrum* (Rauha et al. 2001) may resemble the chemical profile of host plants of related *Hemileuca*. For example, *H. maia*, feeds on a variety of *Quercus* spp., which are typically high in tannins, although larvae suffer high mortality on nonhost plants such as *Acer* (maple), *Fraxinus* (ash), and *Salix* (Martinat et al. 1997), suggesting some constraints on host use. Occasional feeding on *Lythrum* has been observed in other saturniids such as cecropia moths (Barbour and Kiviat 1997). In general, these findings support the notion that use of

Table 3. Summary (mean \pm SEM) of larval performance and preference laboratory assays for *Hemileuca* sp. feeding on either *Lythrum salicaria* or *Salix nigra*

Parameter	<i>n</i>	<i>Lythrum</i>	<i>n</i>	<i>Salix</i>	Test statistic	<i>P</i> value
Larval performance						
Larval growth rate (log[mg]/d)	10	0.0463 \pm 0.0023	10	0.0499 \pm 0.0014	$t = 1.32$, $df = 18$	0.20
Time to pupation (d)	2	39 \pm 2	7	42 \pm 1	$\chi^2 = 1.83^a$, $df = 1$	0.18
Pupal mass (mg)	2	866 \pm 260	7	1,593 \pm 139	$t = 2.47$, $df = 7$	0.04
Proportion surviving to pupation ^b		0.24		0.90	$\chi^2 = 6.83^c$, $df = 1$	0.009
Two-choice larval preference						
First-second instar (% tissue consumed)	10	15.6 \pm 6.6		33.9 \pm 8.5	$t = 1.65$, $df = 9$	0.13
Third-fourth instar (% tissue consumed)	20	2.9 \pm 3.6		37.8 \pm 5.1	$t = 7.07$, $df = 18$	<0.0001

^a Wilcoxon sign-rank test.^b Calculated from survivorship curves with censored data.^c Log-rank test.

novel plants is not unusual within the Saturniidae, with even localized polyphagy occurring within some taxa (Tuskes et al. 1996). As *Lythrum* continues to dominate many Great Lakes wetlands, the likelihood that these native and exotic species will interact increases.

Nevertheless, a shift into wetland habitats and feeding on wetland plants presents a challenge for *Hemileuca* sp. In the laboratory, larvae developing on *Lythrum* suffer >7 times higher mortality than larvae developing on *Salix* solely because of host plant effects. Legge et al. (1996) found that *Hemileuca* sp. from one population in New York had the ability to develop on *M. trifoliata* and *S. nigra*, but *H. maia* and *H. nevadensis*, close relatives of *Hemileuca* sp. (Rubinoff and Sperling 2004), lacked the ability to develop on *Meynantes*, suggesting that *Hemileuca* sp. populations may be in the process of adapting to wetland plants. In this study, there was no evidence for decreased larval performance on *Lythrum* as evidenced by developmental rate and time to pupation, although pupal mass data suggest that *Lythrum* feeding further decreases larval performance, because pupae weighed significantly less when feeding on *Lythrum* than those reared on *Salix*. However, these data should be interpreted cautiously because there were few larvae that survived to pupation ($n = 2$) and the sex of the emerging adults was not established. For *H. maia* and many other saturniids, male moths are typically smaller and weigh less than females, potentially explaining the differences in pupal mass between the treatments (Martinat et al. 1997). There was significantly higher larval mortality on *Lythrum* and *Lythrum* was not preferred by larvae relative to *Salix* (Table 3). Although high tannin levels in *Lythrum* may encourage feeding by caterpillars, levels of these compounds may be too high to support development. Similarly, decreased amphibian survivorship in the presence of *Lythrum* has been attributed to high tannin concentrations in the plant (Maerz et al. 2005). Evaluating whether other Great Lakes populations of buck moths have the capacity to develop on *Lythrum* and other purportedly ancestral hosts (e.g., *Salix* and *Quercus* spp.) would help determine whether host use patterns

are the result of incidental shifts of generally oligophagous species, or whether there is any evidence of local adaptation to a locally abundant host such as *Lythrum*.

Although laboratory experiments indicate that *Lythrum* is not an ideal host for *Hemileuca* sp. larvae, whether there are negative effects on populations of these native saturniids requires an understanding of how caterpillars forage for food and whether additional plants are used in the field over the course of the growing season. That *Lythrum* is not a preferred host in the laboratory may suggest that caterpillars have the ability to discriminate between different hosts and move to plants that are more suitable for larval development. However, at the field sites examined in this study, early instars were found primarily on *Lythrum* and to a significantly lesser extent *Salix*, whereas late instars were only found on *Lythrum* (C.G., unpublished data), suggesting that host selection in the field may be different than host selection in the laboratory.

Additional mortality from natural enemies also affects *Hemileuca* sp. populations in wetlands. Parasitism from the tachinid *L. flavipes* was as high as 93% during high-density years and may be related to larval abundance (Table 1). *Hemileuca* sp. in general are prey for a variety of natural enemies (Shaw et al. 1987, Stamp and Bowers 1988). Tachinid parasitoids in the genera *Exorista*, *Leschenaultia*, and *Chetogena* are the most common parasitoids from *Hemileuca oliviae* Cockrell, the economically important range caterpillar (Hansen et al. 1982, Fritz et al. 1986). However, the highest parasitism rates observed in *H. oliviae* only reached 54% (Fritz et al. 1986), suggesting that *Hemileuca* sp. may be particularly sensitive to tachinid parasitism. One possible explanation for this pattern is that mortality from natural enemies can vary depending on the larval host plant (English-Loeb et al. 1993). *Hemileuca* sp. feeding on *Lythrum* plants may create a larval host environment particularly permissive for tachinid development. Thus, is it possible that natural enemies may place further constraints on the likelihood of host shifts into wetland habitats (Gratton and Welter 1999). Furthermore, Boettner et al. (2000) found that the introduced tachinid *Compsilura concinnata*, re-

leased for the biological control of gypsy moth, *Lymantria dispar* L., attacked *H. maia*, raising concerns over the effects of introduced biological control agents on native silkmths. The recent spread of gypsy moth into Wisconsin and occurrence of *C. concinnata* in the region (Hoffman 2006) may likewise impact *Hemileuca* sp. populations.

Impact on *Lythrum*. *Hemileuca* sp. can significantly defoliate stands of *Lythrum*, an effect that translates into reduced seed output. These observational and manipulative studies found that the high densities of *Hemileuca* sp. in southern Wisconsin marshes could remove significant amounts of *Lythrum* foliage (Fig. 1). Most strikingly, even a short bout of herbivory (<1 wk) by less than five late instars resulted in the loss of $\approx 25\%$ of leaves with a decrease in seed capsule production of 66% (Fig. 2). It is possible that the timing of the caterpillar damage coincides with a particularly vulnerable window for the plant as it begins to allocate resources to flowering and reproduction. Because seed capsules have 60.0 ± 4.7 seeds ($n = 36$), this level of herbivory translates to a reduction in total seed production from 7,080 to 2,940 seeds per plant. By comparison, Katovich et al. (2001) found that seed capsule number declined 42–95% from *Galerucella* herbivory. This suggests that *Hemileuca* sp. has the potential to damage *Lythrum* plants with similar effects as the biological control agents that are currently being released.

Other native herbivores are assumed to have insignificant impacts on *Lythrum*, because their abundance is deemed too low to impact plants (Hight 1990, Diehl et al. 1997), although there is generally no experimental evidence to support these conclusions. Moreover, it is difficult to compare the relative abundance of *Hemileuca* sp. and their effects on *Lythrum* from this study with that of herbivores from other studies, because absolute densities are usually not recorded. Whether caterpillar defoliation can reduce the spread of *Lythrum* will require long-term monitoring of populations. Because *Hemileuca* sp. population density is highly variable and declined dramatically after high-density years (1.5 orders of magnitude lower at Rome Pond in 2004), I hypothesize that the intensity of feeding on *Lythrum* observed in peak years is likely not sustained over the long term. Since *Lythrum* is particularly tolerant to leaf damage, repeated defoliations are probably necessary to reduce the spread of *Lythrum* (Hunt-Joshi et al. 2004). This suggests that although *Hemileuca* sp. are the only native herbivores that have been documented to significantly impact *Lythrum* reproduction, there is currently no evidence that this will translate to population-level effects for exotic plants.

This study demonstrated that Great Lakes populations of *Hemileuca* sp. use *L. salicaria* within their native wetland habitats. Nevertheless, *Hemileuca* sp. do not perform well on *Lythrum* nor do they prefer these hosts over other plants normally part of their host range. In addition, *Hemileuca* sp. on *Lythrum* suffer high rates of mortality from natural enemies. These findings bring into question whether *Lythrum*

represents a net benefit for these populations, by virtue of providing a copious and competition-free resource, or whether it presents an ecological sink where average population growth rates may decline with the inclusion of this exotic host in the diet. Moreover, the nature of this novel association deserves greater scrutiny, because it is this unique ecological attribute (i.e., the use of unusual host plants), which is cited as the principal characteristic that justifies conservation of these populations. Additional studies should be directed at understanding whether other Great Lakes populations of *Hemileuca* sp. can use *Lythrum*, whether this ability is variable among populations, and whether there is a genetic basis for host use that differentiates it from its hypothesized ancestors *H. maia* and *H. nevadensis* (Rubinoff and Sperling 2004).

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