Effects of a Biological Control Introduction on Three Nontarget Native Species of Saturniid Moths

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Abstract: *Damage to nontarget (native) invertebrates from biological control introductions is rarely documented. We examined the nontarget effects of a generalist parasitoid fly,* Compsilura concinnata *(Diptera: Tachinidae), that has been introduced repeatedly to North America from 1906 to 1986 as a biological control agent against 13 pest species. We tested the effect of previously established populations of this fly on two native, nontarget species of moths (Lepidoptera: Saturniidae),* Hyalophora cecropia *and* Callosamia promethea, *in Massachusetts forests. We estimated survivorship curves for newly hatched* H. cecropia *larvae (n = 500), placed five per tree in the field and found no survival beyond the fifth instar. We simultaneously deployed cohorts (n = 100) of each of the first three instars to measure the effect of parasitoids during each stage of development.* C. concinnata *was responsible for 81% of* H. cecropia *mortality in the first three instars. We deployed semigregarious* C. promethea *in aggregations of 1–100 larvae in the field and recorded high rates of parasitism by* C. concinnata *among* C. promethea *larvae exposed for 6 days (69.8%) and 8 days (65.6%). We discovered a wild population of a third species of silk moth, the state-listed (threatened) saturniid* Hemileuca maia maia, *and found that* C. concinnata *was responsible for 36% (n = 50) mortality in the third instar. Our results suggest that reported declines of silk moth populations in New England may be caused by the importation and introduction of* C. concinnata.

Efectos de la Introducción de Control Biológico Sobre Tres Especies de Polillas Saturniidae Nativas que no Eran el Blanco del Control

Resumen: *Raras veces se ha documentado el daño ocasionado por la introducción de especies para control biológico sobre especies de invertebrados que no son el blanco del control. En este trabajo examinamos los efectos colaterales de la introducción repetida en Norteamérica de la mosca parasitoide generalista* Compsilura concinnata *(Diptera: Tachinidae) entre 1906 y 1986, usada como agente de control biológico contra 13 especies de plaga. Evaluamos los efectos de poblaciones previamente establecidas de esta mosca en bosques de Massachusetts sobre dos especies nativas de polillas (Lepidoptera: Saturniidae),* Hyalophora cecropia *y* Callosamia promethea *que no eran blanco del control. Estimamos curvas de supervivencia de larvas recién eclosionadas de* H. cecropia *(n = 500), colocadas a razón de 5 por árbol en el campo de estudio y no logramos detectar sobrevivientes más allá de la quinta muda. Simultáneamente, desplegamos cohortes (n = 100) de cada una de las primeras tres etapas de desarrollo para medir el efecto del parasitoide en cada estadio de desarrollo.* C. concitan *fue responsable de un 81% de la mortalidad de* H. cecropia *en los primeros tres estadios. También desplegamos conglomerados de 1-100 larvas de la semigregaria* C. promethea *y estimamos altas tasas de parasitismo por* C. concinata *en las larvas de* C. promethea *expuestas por 6 días (69.8%) y por ocho días (65.6%). Descubrimos una población silvestre de una tercera población de polilla de seda Saturniina (* Hemileuca maia maia) *clasificada en el registro estatal como especie amenazada, y encontramos que* C. concinata *fue responsable de un 36% de la mortalidad (n = 50) en el tercer estadio. Nuestros resultados sugieren que las disminuciones reportadas de poblaciones de polillas de seda en Nueva Inglaterra pueden deberse a la importación e introducción de* C. concinata.

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Introduction

Giant silk moths (Lepidoptera: Saturniidae) are among North America's largest and best-known moths (Tuskes et al. 1996). Recently, many saturniid populations appear to be undergoing notable declines in the northeastern United States, and four of these, *Anisota stigma, Cithronia regalis, Eacles imperialis*, and *Hemilueca maia maia*, are classified on several state endangered species lists (Schweitzer 1988; Holden 1992; Tuskes et al. 1996). Schweitzer (1988) summarizes evidence that indicates declines of saturniids in the northeastern United States based on black-light trapping and collections at Yale University's Peabody Museum. Other evidence is largely anecdotal and consists of accounts of densities of saturniid pupae or adults by collectors and researchers which were far higher than anyone has observed in recent decades (Kunze 1906; Smith 1908; Culver 1919; Marsh 1935, 1937, 1941). Tuskes et al. (1996) emphasize that the declines are confined to the northeastern United States.

Various explanations have been proposed for these declines: (1) habitat loss (Tuskes et al. 1996), (2) disruption of mating by mercury vapor lights (Tuskes et al. 1996), and (3) spraying of DDT (Schweitzer 1988; Holden 1992). Evidence for or against each of these hypotheses is meager. Habitat loss could explain the decline of *C. regalis* in that the larvae feed on butternut (*Juglans cinerea)* and black walnut (*J. nigra)* trees, which are valuable as timber and have been logged heavily. Housing construction in the pine barrens on Cape Cod, Massachusetts (Greenbaum & O'Donnell 1987), suggests that habitat destruction could partially explain *H. maia maia* declines. Overall, however, New England saturniid habitat should be expanding. Foster (1995) documents that forest cover in this region has increased from a range of 20–40% during 1830–1890 to a range of 65–85% at present. In addition, Foster supplies evidence that saturniid host plants (*Quercus*, oak; *Acer*, maple; *Betula*, birch; *Pinus*, pine; and *Prunus*, cherry) are becoming more, not less, abundant.

The second hypothesis, disruption of mating from mercury vapor lights, is unlikely to explain the regional decline in silk moths because these lights have been used across the United States without reports of declines in silk moth populations in all regions. Schweitzer (1988) claims that in parts of New England declines occurred prior to the widespread use of streetlights. There exists no hard data for or against the mercury vapor light hypothesis.

The third hypothesis, spraying of DDT, may account for localized declines from the mid-1940s to the early 1960s (Schweitzer 1988), but it does not explain the lack of recovery in the past 40 years since DDT was banned. Other pesticides such as *Bacillus thuringiensis* (Bt) and Diflubenzuron (Dimilin) have supplanted DDT primarily against the gypsy moth in forest settings in the United States in recent decades. Effects of Bt on nontar-get lepidoptera have been found (Sample et al. 1993; Wagner et al. 1996; Hall et al. 2000) and cannot be ruled out entirely. Applications of *B. thuringiensis* against gypsy moths (*Lymantria dispar*), are generally applied shortly after budbreak (the first day tree buds crack open). Wagner et al. (1996) found the early oak-feeding silk moth *Hemileuca maia* susceptible to *B. thuringiensis* applications used against gypsy moths. In North Carolina, Hall et al. (1999), predicted the overall risk to saturniid moths from *B. thuringiensis* applied to control Asian gypsy moths, as ranging from no risk for seven species to moderate-to-high for five species. However, *B. thuringiensis* does not persist long on foliage, and must be reapplied after single rain events. Wagner et al. (1996) claim that because the majority of species of giant silk moths hatch a month later than gypsy moths, *B. thuringiensis* would not likely affect them and may even be beneficial because of the elimination of both competition and early damage to foliage. They also demonstrated that most Lepidoptera rebound quickly the year following *B. thuringiensis* application. Aerial application of *B. thuringiensis* has been widespread in some states, such as West Virginia and Michigan, to curtail gypsy moth outbreaks. In New England states, however, there has been virtually no application of pesticides to forests since the last severe gypsy moth outbreak in 1981 and 1982. Even in states where pesticides were used widely in the past, only a small fraction of the total forest acreage was sprayed. For example, during the height of DDT spraying (1948–1964) in Massachusetts a mean of only 4.5% (SD 7.29) of the total forest area was sprayed (Bliss 1981).

We examined a fourth hypothesis: the introduced generalist parasitoid fly *Compsilura concinnata* caused the regional declines of saturniids (Culver 1919; Simberloff & Stiling 1996). This tachinid was repeatedly introduced to North America from 1906 to 1986 as a biological control agent against 13 different pests (for a detailed list see Sanchez 1996), including one species of saturniid, the range caterpillar (*Hemileuca oliviae).* The majority of these fly releases targeted gypsy moths. Gould et al. (1990) and Liebhold and Elkinton (1989) showed that *C. concinnata* has a dominant effect on artificially created populations of the gypsy moth. Because the gypsy moth is univoltine and *C. concinnata* produces three to four generations a year (Culver 1919; Webber & Schaffner 1926), this parasitoid must attack alternate hosts for up to three of its generations after gypsy moth larvae are no longer available (Weseloh 1984). *C. concinnata* has been recorded killing over 180 different species of native Lepidoptera, Coleoptera, and Symphyta in North America (Culver 1919; Webber & Schaffner 1926; Arnaud 1978; Clausen 1978).

Concerns about the effect of *C. concinnata* on native saturniids were expressed years ago by Culver (1919), who noted that *C. promethea*, which had previously

been common and was still thriving outside the fly release area, was "quite rare" in areas where *C. concinnata* was becoming abundant. Culver also observed that *C. promethea* was heavily superparasitized by the fly in lab trials and that field collections suggested *C. promethea* might be an important host for overwintering *C. concinnata.* Recently, Stamp and Bowers (1990) indicated that *C. concinnata* might be an important source of mortality for the saturniid *Hemileuca lucina* in Massachusetts.

Because current federal regulations do not require monitoring of "nontarget" effects when an arthropod is released to control another arthropod, we have little information about the negative effects of biological control on native invertebrates (Howarth 1991; Miller & Aplet 1993; Howarth et al. 1995; U.S. Congress, Office of Technology Assessment 1993, 1995; Simberloff & Stiling 1996). The shortage of data allowed Godfray (1995) to accurately claim: "We have no evidence of ripple effects through ecosystems after the many deliberate introductions of parasitoids in biological control campaigns." Coulson et al. (1991) stated that even though *C. concinnata* was introduced at the turn of the century and was known to be highly polyphagous, ". . .there is no indication that it has had a profound impact on any native species." We, however, present evidence for such an effect by *C. concinnata* on at least two species of saturniid moths. We measured the effect of *C. concinnata* on larval stages of two species of native saturniids and recovered *C. concinnata* from a state-threatened species. Our results implicate *C. concinnata* as a dominant mortality factor for all three species. From a conservation perspective, the nontarget effects of invertebrate biological control agents are important because once these agents are released, the action is not reversible. Furthermore, introduced parasitoids may spread and affect biodiversity far from the sites of initial release.

Methods

We conducted experiments in Cadwell Memorial Forest in Pelham, Massachusetts (lat 42°22′N, long 72°25′W), in 1995 on *C. promethea* and 1997 on *H. cecropia.* We chose this site for its abundant understory of wild black cherry (*Prunus serotina*) and sassafras (*Sassafras albidum*), the respective host plants for *H. cecropia* and *C. promethea.* The trees used in all studies were understory plants (0.5–2.5 m in height) with a dominant overstory canopy of red oak (*Quercus rubra*). Previous work with gypsy moths at this site indicates that *C. concinnata* was recently abundant (Gould et al. 1990; Ferguson et al. 1994).

H. cecropia and *C. promethea* eggs were obtained from The Butterfly Place in Westford, Massachusetts. To measure parasitism, we reared larvae indoors to ensure they were not parasitized and deployed them on host plants in the field, where they were exposed to parasitoids for a defined period of time. After approximately 1 week, we recovered the larvae and reared them individually in the lab on fresh host-plant leaves, which we replaced daily. Each day we recorded the number of larvae that died and the causes of mortality. All larvae were reared to adulthood because development times of *C. concinnata* vary in different-sized hosts (Weseloh 1984) and because *C. concinnata* has been recovered from both saturniid larvae and pupae. Before the moth eggs hatched, we attempted to remove pathogens from the egg surface by immersing them in 10% formalin for 1 hour, rinsing them with running water for 1.5 hours, and drying them overnight in a fume hood (after Gould et al. 1990; Dwyer & Elkinton 1995). In 1997 we received 500 *H. cecropia* eggs that hatched enroute from Boston and therefore could not be treated with formalin. These larvae were reared in separate containers. In the late instars these succumbed to an unknown disease that we suspect led to the subsequent contamination of our entire indoor colony.

All fly parasitoids were identified to genus by G.H.B. using the key developed by Wood (1987). Worldwide there are only three described species of *Compsilura.* In North America this genus is only represented by one species, *C. concinnata* (Arnaud 1978; Sabrosky & Arnaud 1983; Wood 1987; Poole 1996). Of the other *Compsilura* species, *C. sumatrensis* is found only in Indonesia and *C. samoaensis* is found only in Samoa (J. O'Hara, personal communication). Voucher specimens have been preserved at the University of Massachusetts Insect Collection in Amherst.

H. cecropia Survival in the Field

Survivorship curves provide a starting point for exploring the causes of decline of a species. They are valuable in this regard only if they are supplemented with supporting data on the causes of the observed mortality. Thus, we chose to combine two methods for studying survival of *H. cecropia* larvae. The first, which we refer to as "the direct observation method," has frequently been used by lepidopterists (e.g., Feeny et al. 1985). We placed first instar larvae in the field and observed them daily until they pupated. Mortality factors observed during daily checks were noted, but because cadavers usually disappear after predation or parasite emergence, the source of mortality often could not be identified. For the second method, which we refer to as the cohort method, we left groups of larvae out in the field for only one instar, before bringing them into the lab for rearing. We replaced larvae in the field with fresh larvae of the next instar placed on a new set of trees. We used this method to quantify mortality from parasitoids and disease at each instar by bringing larvae back to the lab before they died or disappeared.

In our direct observation procedure, we deployed five newly hatched *H. cecropia* larvae per tree on each of 25 *P. serotina* trees at four different locations within Cadwell Memorial Forest, for a total of 500 larvae. We chose trees spaced 5–20 m apart along nine separate 150- to 200-m transect lines in a 64-ha section of the forest. Five larvae per tree, placed on both surfaces of the leaves of the host plant, mimicked the natural densities (two to six ova) and location observed by Tuskes et al. (1996). We placed four groups of newly hatched larvae on separate transect lines over a 2-week period (19 June–2 July) to correspond with the natural timing of egg hatch from the Westford, Massachusetts, stock. Surviving larvae were located and counted each day. During the daily visit, we recorded observed acts of predation and parasitism and collected the resulting cadavers. When larvae disappeared, we continued to search for them for 5–7 days before they were considered missing.

To measure losses due to parasitoids, we deployed cohorts of five larvae of the same instar, as we did in the direct observation group, on each of 20 trees ($n = 100$). Survivors were retrieved after each instar or until only 50% remained, at which time 100 of the next instar were deployed on a new transect. We repeated this process with all instars. Retrieved larvae were reared indoors as above. Our intention was to create a life table for all five instars, but a pathogen infected our rearing colony during the last two instars, so only data on the first three instars are presented.

Density Dependence and Short-Term Exposure of *C. promethea* to *C. concinnata*

C. promethea larvae were randomly deployed on 22 July 1995 in Cadwell Forest at differing densities per plant (1, 3, 10, 30, and 100) on 115 understory sassafras trees and were retrieved after 8 days. We chose trees spaced 5–20 m apart along eight parallel transect lines (20 m apart and 300 m long) in a 5-ha area atop Mount Lincoln in Cadwell Memorial Forest. On 24 July more larvae were deployed in the same manner on an additional 135 trees but were retrieved after 6 days. We deployed 1407 larvae. To test for density dependence, we regressed arcsin-square-root-transformed proportions killed by parasitoids versus $\log_{10}$ density (SAS Institute 1988).

Field-Collected *H. maia maia* Reared for *C. concinnata*

In 1998, we located a wild egg mass of *H. maia maia* on Otis Air National Guard Base, Cape Cod, Massachusetts (lat 41°39′N, long 70°34′W). Approximately 200 larvae hatched and fed gregariously on bear oak (*Quercus ilicifolia*). The larvae remained within a 20-m radius of the hatch tree for the first three instars. We noticed a steep decline in numbers of the population during the third instar, so on 23 June 1998 we collected 50 of the

approximately 100 survivors and reared them to monitor for parasitoids.

Results

Survival of *H. cecropia*

In our direct observation method, none of the 500 deployed *H. cecropia* larvae survived to the pupal stage and only 3 survived to early fifth instar (Table 1). Survivorship curves for all four transects were similar, with heavy rain (6.4 cm) causing higher mortality in the first 2 days of the 2 July trial than the first 2 days of the 19 June or 24 June trials. Although direct observation allowed us to quantify overall larval survival (Fig. 1), it was a poor way to determine rates of mortality from the different causes (Table 1). For example, we rarely observed parasitoids in the act of ovipositing and rarely recovered dead larvae, so by this method we attributed only 7 of 500 deaths to parasitoid attacks. Spiders and stinkbugs were often seen in the vicinity of both live and dead larvae, but were rarely caught in the act of predation.

In contrast, our cohort studies revealed high rates of parasitism from *C. concinnata* (Table 2). The combined mortality from *C. concinnata* during the first three instars caused 81% overall mortality and explained most of the unobserved mortality during the second and third instars in the direct observation study (see days 10–30 in Fig. 1). This combined mortality also explained most of

Table 1. Direct observation method: observed causes of death and stage-specific percent mortality for *H. cecropia*, including the number observed dying, dead, or missing at each stage.[a]

	Stage (instar)				
	1st	*2nd*	*3rd*	*4th*	*5th*
No. in stage	500	201	84	32	3
Missing[b]	213	60	39	29	3
Dead unknown[c]	31	16	8	0	0
Spider[d]	48	28	1	0	0
Stink bug: Pentatomidae	7	8	1	0	0
Scorpionfly: Panorpidae	0	1	0	0	0
H. fugitivus (includes three with hyperparasitoids)	0	4	0	0	0
C. concinnata	0	0	3	0	0
Percent dead or missing	59.8	58.2	61.9	90.6	100

[a]*Compiled from daily field observations and analysis of cadavers found.*
[b]*We searched for larvae for 5-7 successive days after the last observation before we considered them missing. Data presented in Table 2 suggest that death from* C. concinnata *accounts for most of the missing second and third instar larvae. We also conducted an extensive search for pupae in late fall and found none.*
[c]*Dead larvae were found and brought back to rear for parasitoids; this category includes only those for which the cause of death was undetermined.*
[d]*Spiders were often observed close to the larvae. These numbers reflect those larvae we saw in the act of predation, in webs, or with spiders close to the cadaver.*
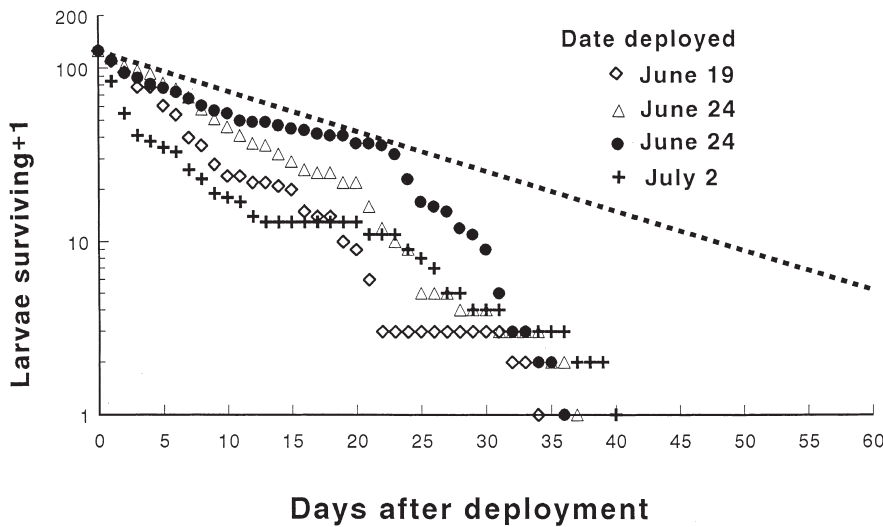
Figure 1. Survivorship curves (numbers plotted on a log scale vs. time) for deployed H. cecropia recorded from daily observations. Dotted line represents an estimate of the required survival for a population to experience no change in density (based on data collected by Marsh 1937).

the mortality categorized as missing in our direct observations during the second and third instars (Table 1). The majority of the cohort mortality (70%) occurred during the third instar, which coincides with the steep decline in the third instars observed during direct observation (days 20–30 in Fig. 1). These data also revealed the instar at which flies would kill *H. cecropia* larvae. We observed that if *C. concinnata* attacked first instar larvae, the hosts died as second instars, whereas larvae attacked as second instars died as either second or third instars and attacked third instars died as third instars.

Experimental Populations of *C. promethea.*

In the course of the study in which differing densities of *C. promethea* were deployed in the field (Table 3), we recovered two species of parasitoids, *C. concinnata* and *Enicospilus americanus* (Hymenoptera: Ichneumonidae). We recovered *C. promethea* larvae from 84 (33.6%) different trees on which the larvae were deployed, and *C. concinnata* were recovered from 58 trees (69%) (Table 3). Density-dependent mortality was not detected (SAS Institute 1988) for either 8 days ($p = 0.1398$, $r^2 = 0.57$) or 6 days ($p = 0.4710$, $r^2 = 0.18$). Of the 117 larvae recovered,

79 (67.5%) died from *C. concinnata*, with an average of 3.5 flies per host (range 1–14). All of the flies emerged from overwintering pupae reared in individual sealed containers.

Effect on Wild Population of *H. maia maia*

One week after sampling third instars from the wild population of *H. maia maia*, we could find no individuals remaining in the field. Of the larvae collected and reared in the lab ($n = 50$), 36% died from *C. concinnata* and one (2%) died from an unidentified hymenopteran parasitoid (unemerged cocoon). Additionally, 13 larvae died of unknown causes late in the final instar; 18 (10 females, 8 males) produced adults. We mated the adults under lab conditions and produced four fertile egg masses (for a total of approximately 800 eggs), which we returned to the site of collection at Otis Air National Guard Base.

Discussion

Effects of *C. concinnata* on *H. cecropia* and *C. promethea*

Our findings, that the combined mortality from *C. concinnata* in the first three instars of *H. cecropia* totaled

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Table 2.   Cohort method: causes of death for larval *H. cecropia* and the percent observed dying at each stage.[a]

| Stage (instar) | No. of larvae deployed | Days in field | Observed field mortality | | Number of larvae recovered for rearing | Rearing mortality | |
			Spiders (%)	Stink bugs: Pentatomidae (%)		Ichneumonid H. fugitivus (%)	Tachinid C. concinnata (%)
1st	100	7	5	4	54	1.9	13
2nd	100	5	4	0	40[b]	0	27.5
3rd	100	6	4	0	40	0	70
Totals[c]	300		12.4	4	134	1.9	81.1

[a] Compiled from daily checks and additionally rearing out the survivors of each instar.
[b] Total percent mortality calculated as $1 - (1 - m_1)(1 - m_2)(1 - m_3)$, where m_i is the fraction dying during instar i.
[c] One second instar escaped during rearing and is not included in this total.

Table 3. Percent mortality and numbers of *C. promethea* larvae deployed at five different densities for 6 days (trial 1) and 8 days (trial 2).

	Number of larvae per tree				
	1	3	10	30	100
Trial 1					
No. of trees	78	23	6	5	3
No. of larvae per treatment	78	69	60	150	300
No. of larvae recovered	15	9	5	23	1
C. concinnata (%)	80.0	77.7	60.0	60.9	100
Trial 2					
No. of trees	81	33	10	2	2
No. of larvae per treatment	81	99	100	270	200
No. of larvae recovered	23	16	6	11	8
E. americanus (%)	4.3	0	16.7	0	0
C. concinnata (%)	52.2	62.5	66.7	90.9	75.0

81%, indicate that *C. concinnata* has become a dominant cause of mortality of the moths in our region. Mortality from *C. concinnata* far exceeded that from any other cause. In fact, it is probable that *C. concinnata* would have an additional effect on the last two instars, considering the high mortality we observed in the fourth and fifth instar of the *C. promethea* study. None of the 500 *H. cecropia* larvae deployed during the life-table study survived beyond 40 days of the 60 days needed to pupate.

Prior to the arrival of *C. concinnata* in Illinois, Marsh (1935, 1937, 1941) studied a high-density population of *H. cecropia* that was "reasonably constant from year to year." We used his data on fecundity and pupal survival to crudely estimate the larval survival required to balance fecundity and maintain a population in perpetuity. The comparison of this information with our survivorship data (Fig. 1) suggests that only one of our four cohorts was surviving near this level, and even this cohort disappeared in the third instar (day 23, Fig. 1). The average larval survival to attain no change in density would have to have been even higher if we accounted for egg mortality, for which neither we nor Marsh (1935, 1937, 1941) have data. The survival rate required for replacement (Fig. 1) thus assumes 100% survival of eggs. Kapraly (1990) found 70.3% mortality of *C. promethea* eggs placed in the field in Ohio (including 12% killed by predators and 19.3% by parasitoids), thus it is unlikely that we would find no egg mortality in the closely related *H. cecropia*. Even if we ignore egg mortality, our experimental population did not come close to surviving, let alone maintaining survival sufficient to sustain future generations. No *H. cecropia* population can persist for long with these levels of larval mortality. Because our studies were all carried out in the understory, future studies should also test the survival of larvae deployed at different heights and microhabitats. Using tethered gypsy moth larvae, Weseloh (1982) presented evidence for

higher mortality from *C. concinnata* within 1 m of the ground than he found in the lower or upper canopy.

It is important to ask whether the densities or spatial scale of our experimental procedures artificially elevated mortality caused by *C. concinnata*. Gould et al. (1990) created artificial populations of gypsy moths of different densities on hectare-sized plots and recorded higher levels of mortality from *C. concinnata* than those recorded in naturally occurring populations of gypsy moth. Our *H. cecropia* densities, however, were more than 100 times lower than the lowest created by Gould et al. and were comparable to those recorded from naturally occurring *H. cecropia* populations (Tuskes et al. 1996). Historic collection records suggest that natural saturniid densities were often much higher than our artificially created populations. For example, Kunze (1906) collected 3000 *H. cecropia*, 600 *Antheraea polyphemus* (Lepidoptera: Saturniidae), and hundreds of *C. promethea* in a two-block area near New York City. Marsh (1935) documented 253 *H. cecropia* cocoons in one tree, 154 in a small thicket, and 19 on one branch of black willow in Chicago.

Our *C. promethea* study also resulted in extremely high rates of parasitism from *C. concinnata* (the lowest for any treatment density was 52.2%). Considering that the larvae were exposed to *C. concinnata* for only 6–8 days of the nearly 2 months needed for larval development, it seems evident that *C. concinnata* is also having a severe impact on *C. promethea*. Our study also shows that *C. concinnata* will attack larger saturniid caterpillars (in this case, fourth and fifth instars), suggesting that this parasitoid has the potential to cause additional mortality in the last two *H. cecropia* instars as well. One *C. promethea* produced 14 *C. concinnata* adults, which is higher than any number of *C. concinnata* we have seen recorded from any published host records. In addition, all of the flies that attacked *C. promethea* larvae emerged from overwintering pupae, supporting the claims of Culver (1919) that *C. promethea* may be an important overwintering host for *C. concinnata*.

Effects of *C. concinnata* on Other Saturniids

To date, 12 species of saturniids have been documented as hosts for *C. concinnata* in North America (Arnaud 1978; Peigler 1994; Tuskes et al. 1996). Unfortunately, the majority of these records lack detailed data that could be used for quantifying mortality. Our results showing 36% mortality by *C. concinnata* on *H. maia maia* in southeastern Massachusetts are similar to the 30% mortality found by Stamp and Bowers (1990) in central Massachusetts for the closely related *H. lucina* (Lepidoptera: Saturniidae). The difficulty with both of these rare species is that it is hard to acquire adequate sample sizes from the field. The findings from these two samples, our own and that of Stamp and Bowers (1990),

suggest that investigations should be conducted on the effects of *C. concinnata* on other saturniids. A measure of percent parasitism based on these single collections has limited value as an estimate of the generational mortality caused by a predator or parasitoid on its host (Van Driesche 1983).

Broader Implications for Biological Control

C. concinnata has been continuously introduced as a biological control agent for 80 years (Sanchez 1996). These releases continued until 1986, despite early knowledge that *C. concinnata* required nontarget hosts for multiple generations each year and that the list of nontarget hosts was large (Culver 1919; Webber & Schaffner 1926; Schaffner & Griswold 1934.). The claim by Coulson et al. (1991) that *C. concinnata* had not profoundly affected any of the 180 nontarget species is not based on any data. We could not find any systematic studies that directly examined the nontarget effects of *C. concinnata.* Howarth (1991) noted that "The absence of evidence, is not evidence of absence." If the effect of a species as common and widespread as *C. concinnata* has never before been documented, we question what other negative effects of biological control have also gone undocumented.

According to Nechols et al. (1992), generalist predators and parasitoids with a wide host range should no longer pass established protocols for introductions in the United States. These protocols, however, are voluntary for biological control agents released to control invertebrates. Once a candidate for introduction as a biological control passes tests in quarantine that prove it is not a plant pest or a hyperparasitoid, it is left to the investigators to determine whether the species should be released. There are, in fact, several recent examples of introductions of generalist predators of invertebrates. For example, the multicolored Asiatic lady beetle (*Harmonia axyridis* [Coleoptera: Coccinellidae]) was introduced to the eastern United States several times prior to 1981 (Wheeler 1995) and in 1999 was still available to the general public in a biological control catalog. This species has now become extremely abundant, overwintering in homes in the northeastern United States. We know of no studies that have examined the effect of this beetle on native aphids or the insects (i.e., ants and harvester butterflies) that depend on specific native aphids for food. Wheeler and Hoebeke (1995) suggested that previous introductions of another coccinellid, *Coccinella septempunctata*, might have caused the disappearance of the once common native coccinellid, *C. novemnotata.*

Concern about preserving native insect fauna in North America is a fairly recent phenomenon, and thus restrictions on introduced natural enemies of insects are a new development. In contrast, because of the obvious need to prevent damage to crops or other beneficial plants, there is a long history of host-range testing of candidate

herbivores for introduction to combat exotic invasive weeds. Nevertheless, host-range testing may not avert problems with introductions. In the late 1960s through early 1970s, for example, a flowerhead weevil (*Rhinocyllus conicus* [Coleoptera: Curculionidae]) was found to be effective at controlling invasive introduced thistles. *R. conicus* was released despite a potential effect on native thistles, in part due to a concern that these invasive thistles might out-compete native thistles. Turner et al. (1987) reported this weevil on 12 nontarget thistles. Louda et al. (1997) found that *R. conicus* had attacked five native thistle species, resulting in reductions of seed production in one species of up to 86%. These studies have added to the debate over biological control as to how best to weigh the potential risks and benefits of introductions (Boldt 1997; Strong 1997; Van Driesche & Hoddle 1997; Louda et al. 1998).

The U.S. Department of Agriculture is preparing changes in the plant pest regulations that will soon appear in the Federal Register. These proposed changes would broaden the scope of the Animal Plant Health Inspection Service (APHIS) to regulate plant pests. This would require risk-benefit analysis for determining the plant pest status of organisms and provide needed protection against introduction of biological controls of plant pollinators (bees). These new regulations will not cover other biological controls of arthropods, including generalists. To broaden these APHIS regulations would require both a mandate and additional funding from Congress. These protocols could be modeled after the New Zealand Hazardous Substances and New Organisms Act of 1996, which requires all new organisms to be approved by the Environmental Risk Management Authority. Van Driesche and Hoddle (1997) provide in-depth discussion of the pros and cons for mandated host-range testing and conclude that some voluntary increases in host-range testing in the United States are needed. However, they cautioned against mandated testing, in part because it would lead to increased costs for biological control.

Introduction of natural enemies—classical biological control—is often the only feasible option for controlling introduced pests. We hope our study is not misinterpreted as a general attack on classical biological control. There are many examples worldwide of introductions of specialist natural enemies that permanently solved major pest problems. These natural enemies can save millions of dollars on controls and prevent environmental damage both from pest organisms and from chemical pesticides used to control the pests. Nonetheless, it behooves the practitioners of biological control to develop guidelines for restricting introductions to organisms with narrow host ranges and rigorous protocols for host-range testing. In addition, studies such as ours that assess the effect of previously released biological control agents on native species are needed to guide decisions about future releases and regulations.

Acknowledgments

Literature Cited

Arnaud, P. H., Jr. 1978. A host-parasite catalog of North American Tachinidae (Diptera). Publication 1319. U.S. Science and Education Administration, Washington, D.C.

Bliss, G. A. 1981. Gypsy moth control. Final environmental impact report 12307-231-100-2-81-C.R. Department of Environmental Management, Division of Forests and Parks, Boston.

Boldt, P. 1997. Response of a *Rhinocyllus* researcher. Biocontrol News and Information **18:**100N.

Clausen, C. P., editor. 1978. Introduced parasites and predators of arthropod pests and weeds: a world review. Handbook 480. U.S. Agriculture Research Service, U.S. Department of Agriculture, Washington, D.C.

Coulson, J. R., R. S. Soper, and D. W. Williams, editors. 1991. Biological control quarantine: needs and procedures. Proceedings of a workshop sponsored by the U.S. Department of Agriculture. Publication ARS-99. Agricultural Research Service, U.S. Department of Agriculture, Washington, D.C.

Culver, J. J. 1919. A study of *Compsilura concinnata*, an imported tachinid parasite of the gipsy moth and the brown-tail moth. Bulletin 766. U.S. Department of Agriculture, Washington, D.C.

Dwyer, G., and J. S. Elkinton. 1995. Host dispersal and the spatial spread of insect pathogens. Ecology **62:**1262-1275.

Feeny, P., W. S. Blau, and P. M. Kareiva. 1985. Larval growth and survivorship of the black swallowtail butterfly in central New York. Ecological Monographs **55:**167-187.

Ferguson C. S., J. S. Elkinton, J. R. Gould, and W. E. Wallner. 1994. Population regulation of gypsy moth (Lepidoptera: Lymantriidae) by parasitoids: does spatial density dependence lead to temporal density dependence? Environmental Entomology **23:**1155-1164.

Foster, D. 1995. Land-use history and four hundred years of vegetation change in New England. Pages 253-319 in B. L. Turner, A. G. Sal, F. G. Bernaldez, and F. di Castri, editors. Global land use change: a perspective from the Columbian encounter. Consejo Superior de Investigaciones Cientificas, Madrid.

Godfray, H. C. J. 1995. Field experiments with genetically manipulated insect viruses: ecological issues. Trends in Ecology and Evolution **10:**465-469.

Gould, J. R., J. S. Elkinton, and W. E. Wallner. 1990. Density-dependent suppression of experimentally created gypsy moth, *Lymantria dispar* (Lepidoptera: Lymantriidae), populations by natural enemies. Journal of Animal Ecology **59:**213-233.

Greenbaum, D. S., and A. O'Donnell. 1987. Losing ground: the case for land conservation in Massachusetts. Massachusetts Audubon Society, Lincoln, Massachusetts.

Hall, S. P., J. B. Sullivan, and D. F. Schweitzer. 2000. Assessment of risk to non-target Macro-moths after *Btk* application to Asian gypsy moth in the Cape Fear region of North Carolina. Publication FHTET-98-16. U.S. Department of Agriculture, Washington, D.C.

Holden, C. 1992. Thousands of insects "enroll" at Yale. Science **256:**313.

Howarth, F. G. 1991. Environmental impacts of classical biological control. Annual Review of Entomology **36:**485-509.

Howarth, F. G., G. Nishida, and A. Asquith. 1995. Insects of Hawaii. Pages 365-368 in E. T. LaRoe, editor. Our living resources. National Biological Service, Washington, D.C.

Kapraly, E. C. 1990. An experimental study of survival and mortality of *Callosamia promethea* (Drury) [Lepidoptera: Saturniidae] eggs in central Ohio. M. S. thesis. Ohio State University, Columbus.

Kunze, R. E. 1906. Stemmed cocoons of *Telea polyphemus.* Entomological News **May:**177-179.

Liebhold, A. M., and J. S. Elkinton. 1989. Elevated parasitism in artificially augmented populations of *Lymantria dispar* (Lepidoptera: Lymantriidae). Environmental Entomology **18:**986-995.

Louda, S. M., D. Kendall, J. Connor, and D. Simberloff. 1997. Ecological effects of an insect introduced for the biological control of weeds. Science **277:**1088-1090.

Louda, S. M., D. Simberloff, G. Boettner, J. Connor, D. Kendall, and A. Arnett. 1998. Insights from data on the nontarget effects of the flowerhead weevil. Biocontrol News and Information **19:**70-72N.

Marsh, F. L. 1935. A regional study of *Samia cecropia* and nine associated primary parasites and hyperparasites: presenting data on the behavior, biology, and interrelationships of these insects. M. S. thesis. Northwestern University, Evanston, Illinois.

Marsh, F. L. 1937. Ecological observations upon the enemies of *Cecropia*, with particular reference to its hymenopterous parasites. Ecology **18:**106-112.

Marsh, F. L. 1941. A few life-history details of *Samia cecropia* within the southwestern limits of Chicago. Ecology **22:**331-337.

Miller, M., and G. Aplet. 1993. Biological control: a little knowledge is a dangerous thing. Rutgers Law Review **45:**285-334.

Nechols, J. R., W. C. Kauffman, and P. W. Schaefer. 1992. Significance of host specificity in classical biological control. Pages 41-52 in W. C. Kauffman and J. E. Nechols, editors. Selection criteria and ecological consequences of importing natural enemies. Thomas Say publications in entomology: proceedings. Entomology Society of America, Lanham, Maryland.

Peigler, R. S. 1994. Catalog of parasitoids of Saturniidae of the world. The Journal of Research on the Lepidoptera **33:**1-121.

Poole, R. W. 1996. Tachinidae. Pages 275-302 in R. W. Poole and P Gentili, editors. Nomina insecta neartica: a checklist of the insects of North America. 3. Diptera, Lepidoptera, Siphonaptera. Entomological Information Services, Rockville, Maryland.

SAS Institute. 1988. SAS/STAT user's guide. General linear models procedure. Release 6.03. Cary, North Carolina.

Sabrosky, C. W., and P. H. Arnaud, Jr. 1983. Family Tachinidae (Larvaevoridae). Pages 1040-1041 in A. Stone, C. W. Sabrosky, W. W. Wirth, R. H. Foote, and J. R. Coulson, editors. A catalog of the diptera of America north of Mexico. Agricultural Research Service, U.S. Department of Agriculture, Agriculture handbook 276 (1965). Reprinted by Smithsonian Institution Press, Washington, D.C.

Sample, B. E., L. Butler, C. Zivkovich, and R. C. Whitmore. 1993. Evaluation of *Bacillus thuringiensis* and defoliation effects on native lepidoptera. Appalachian Integrated Pest Management Technology Transfer, NA-TP-10-93. U.S. Department of Agriculture, Washington, D.C.

Sanchez, V. 1996. The genetic structure of northeastern populations of the tachinid *Compsilura concinnata* (Meigen), an introduced par-

asitoid of exotic forest defoliators of North America. Ph.D. thesis. University of Massachusetts, Amherst.

Schaffner, J. V., and C. L. Griswold. 1934. Macrolepidoptera and their parasites reared from field collections in the northeastern part of the United States. Publication 188. U.S. Department of Agriculture, Washington, D.C.

Schweitzer, D. F. 1988. Status of Saturniidae in the northeastern USA: a quick review. News of the Lepidopterist Society **1:**4–5.

Simberloff, D., and P. Stiling. 1996. How risky is biological control? Ecology **77:**1965–1974.

Smith, J. B. 1908. Notes on some *cecropia* cocoons and parasites. Journal of Economic Entomology **1:**293–297.

Stamp, N. E., and M. D. Bowers 1990. Parasitism of New England buckmoth caterpillars (*Hemileuca lucina*: Saturniidae) by tachinid flies. Journal of the Lepidopterists' Society **44:**199–200.

Strong, D. R. 1997. Fear no weevil? Science **277:**1058–1059.

Turner, C. E., R. W. Pemberton, and S. S. Rosenthal. 1987. Host utilization of native *Cirsium* thistles (Asteraceae) by the introduced weevil *Rhinocyllus conicus* (Coleoptera: Curculionidae) in California. Environmental Entomology **16:**111–115.

Tuskes, P. M., J. P. Tuttle, and M. M. Collins. 1996. The wild silk moths of North America: a natural history of the Saturniidae of the United States and Canada. Cornell University Press, Ithaca, New York.

U. S. Congress, Office of Technology Assessment. 1993. Harmful nonindigenous species in the United States. OTA-F-565. Government Printing Office, Washington D.C.

U. S. Congress, Office of Technology Assessment. 1995. Biologically based technologies for pest control. OTA-ENV-636. Government Printing Office, Washington, D.C.

Van Driesche, R. G. 1983. Meaning of "percent parasitism" in studies of insect parasitoids. Environmental Entomology **12:**1611–1622.

Van Driesche, R. G., and M. Hoddle. 1997. Should arthropod parasitoids and predators be subject to host range testing when used as biological control agents? Agriculture and Human Values **14:**211–226.

Wagner, D. L., J. W. Peacock, J. L. Carter, and S. E. Talley. 1996. Field assessment of *Bacillus thuringiensis* on nontarget Lepidoptera. Environmental Entomology **25:**1444–1454.

Webber, R. T., and J. V. Schaffner Jr. 1926. Host relations of *Compsilura concinnata* Meigen, an important tachinid parasite of the gipsy moth and the brown-tail moth. Bulletin 1363. U.S. Department of Agriculture, Washington, D.C.

Weseloh, R. W. 1982. Implications of tree microhabitat preferences of *Compsilura concinnata* (Diptera: Tachinidae) for its effectiveness as a gypsy moth parasitoid. Canadian Entomologist **114:**617–622.

Weseloh, R. M. 1984. Effect of size, stress, and ligation of gypsy moth (Lepidoptera: Lymantriidae) larvae on development of the tachinid parasite *Compsilura concinnata* Meigen (Diptera: Tachinidae). Annals of the Entomological Society of America **77:**423–428.

Wheeler, A. G., Jr. 1995. Multicolored asian lady beetle, *Harmonia axridis* (Pallas). Regulatory horticulture, entomology circular 173. Pennsylvania Department of Agriculture, Bureau of Plant Industry, Harrisburg.

Wheeler A. G., Jr., and E. R. Hoebeke. 1995. *Coccinella novemnotata* in northeastern North America: historical occurrence and current status (Coleoptera: Coccinellidae). Proceedings of the Entomological Society of Washington **97:**701–716.

Wood, D. M. 1987. Tachinidae. Pages 1193–1269 in J. F. McAlpine, editor. Manual of nearctic diptera. Monograph 28. Volume 2. Biosystematics Research Centre, Research Branch Agriculture Canada, Ottawa, Ontario, Canada.