
CHAPTER 2. THE EFFECTS OF *COMPSILURA CONCINNATA*, AN INTRODUCED GENERALIST TACHINID, ON NON-TARGET SPECIES IN NORTH AMERICA: A CAUTIONARY TALE

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INTRODUCTION

Classical biological control has long been a principal weapon in the worldwide effort to combat the devastating effects of invasive species. Classical biological control involves locating natural enemies of invasive species in their native range and releasing them in the newly invaded habitat. The premise of classical biological control is that invasive species out-compete native species and become major pest problems in large part because they have become isolated from the suite of natural enemies that keep them in check in their native habitat. There have been many successes worldwide in the classical biological control of both invasive weeds and invasive arthropods. The advantages of classical biological control over any other approach are obvious and well known: the control exerted is typically permanent; it requires little or no further intervention; it is thus highly cost effective compared to mechanical removal or use of chemical pesticides, which must typically be applied repeatedly and are often infeasible in forests or other natural habitats.

Classical biological control of invasive weeds has had a long history of evaluating the host range of candidates for introduction. The obvious reason is that herbivorous natural enemies might become important pests of agricultural crops or other beneficial plants. In contrast, traditionally there has been little concern about the potential impacts on non-target native insects that might be caused by the introduced natural enemies of invasive arthropods. Indeed, the ability of natural enemies to attack native non-target species was viewed by many as a positive attribute (e.g., Culver, 1919; Webber and Schaffner, 1926). Native species might be pests in their own right, or, at the very least, they might provide a host reservoir that would maintain high densities of the natural enemy when densities of the target insect were low.

Until recently, there was little or no evidence that arthropod predators or parasitoids introduced as biological control agents against other invasive arthropods had had any important deleterious effects on non-target species. As a result, several authors have concluded that the technique is generally safe and unlikely to have significant effects on non-target organisms (Coulson *et al.*, 1991; Godfray, 1995). However, as pointed out by Howarth (1991), “absence of evidence is not evidence of absence” of such effects. In the last few years, several studies have elucidated negative impacts by a number of introduced agents (e.g. Obrycki *et al.*, 2000; Henneman and Marmot, 2001). Here we review our work on this topic focusing on the non-target effects of the generalist tachinid parasitoid *Compsilura concinnata* (Meigen), which was introduced to North America in 1906 primarily to control the gypsy moth, *Lymantria dispar* L. We have shown that this species is probably having a severe impact on a number of our native giant silk moths (Saturniidae) (Boettner *et al.*, 2000), which include our largest and most showy native Lepidoptera.

INTRODUCTION OF *C. CONCINNATA* TO NORTH AMERICA

The gypsy moth was introduced to North America in a suburb of Boston, Massachusetts in 1868. (Forbush and Fernald, 1896). By the late 1880s, it had become a serious defoliator in eastern Massachusetts, and this damage triggered a substantial eradication effort based on hand removal of gypsy moth egg masses and widespread application of lead and copper arsenate insecticides to infested trees. Despite this effort, the area infested by gypsy moth continued to expand across eastern New England in the first decade of the 20th century. The eradication effort was then abandoned, and in 1905, the United States Department of Agriculture embarked on a major effort to introduce predators and parasitoids of gypsy moth from its native range in Europe and Asia (Howard and Fiske, 1911). Eventually, ten species of parasitoids were successfully introduced and established on gypsy moth in North America (Elkinton and Liebhold, 1990). One of these species was *C. concinnata*, a tachinid with a very broad host range that has now been recovered from at least 180 species of Lepidoptera and Symphyta (Arnaud, 1978; Boettner *et al.*, 2000; Strazanac *et al.*, 2001). The broad host range of *C. concinnata* was well understood by the individuals involved in its dissemination, but its potential impact on non-target species was not a significant concern (Howard and Fiske, 1911; Culver, 1919; Webber and Schaffner, 1926). Introductions of *C. concinnata* and efforts to release it in other parts of the country against gypsy moth and other target species continued over much of the 20th century (Sanchez, 1996).

EFFECTS OF *C. CONCINNATA* ON GYPSY MOTH POPULATIONS

Despite the establishment of *C. concinnata* and nine other introduced parasitoid species, gypsy moth has continued to spread into southern and mid-western regions of the United States. Frequent outbreaks have continued to occur throughout the introduced range in northeastern North America. Even in its native range in Europe and Asia, where gypsy moth has a richer fauna of parasitoids and other natural enemies, outbreaks and defoliation by gypsy moth occur in many, but not all, regions with forests of appropriate host trees. Few long term studies have been done to document the impact of parasitoids on gypsy moth anywhere in the world, and

their overall role in gypsy moth dynamics remains ambiguous (Elkinton and Liebhold, 1990). A study by Sisojevic (1975) in the former Yugoslavia appeared to show a classic host-parasitoid oscillation between gypsy moth and three tachinid species, of which *C. concinnata* was one. The level of parasitism recorded by Sisojevic and in other European studies was notably higher than that observed for the same parasitoid species on gypsy moth in North America (Elkinton and Liebhold, 1990). The most comprehensive study of parasitism in naturally occurring populations of gypsy moth in North America was conducted by Williams *et al.* (1992). In that study (Figure 1A), there was no hint of any direct or delayed density dependence of parasitism by *C. concinnata* on gypsy moth and overall levels of parasitism by this species never exceeded 20%. Parasitism by other species was also quite low and at best only weakly density dependent. The results of this study confirmed the conclusions drawn by earlier investigators: that parasitoids played a limited or equivocal role in the population dynamics of gypsy moth in North America (Campbell, 1975; Reardon, 1976; Elkinton and Liebhold, 1990).

Research involving experimentally created populations of gypsy moth in our laboratory (Gould *et al.*, 1990) produced quite different results from those of Williams *et al.* (1992). Our study involved collecting gypsy moth egg masses and placing them at densities that ranged from 40,000 to 1.4 million eggs per ha on hectare-sized plots in an oak-dominated forest in western Massachusetts, where the naturally occurring gypsy populations were very low and where there had not been any recent outbreaks of gypsy moth. Following egg hatch, we collected and reared gypsy moth larvae on a weekly basis and recorded parasitoid emergence. In contrast to the results reported by Williams *et al.* (1992), larval parasitism by *C. concinnata* was higher than that due to any other parasitoid or cause of death (including predation on larvae) and it was strongly density dependent (Figure 1B). We have confirmed these results in many subsequent experiments (e.g., Ferguson *et al.*, 1994). It is important to understand, however, that the data collected by Williams *et al.* (1992) (Figure 1A) represents variation in parasitism in

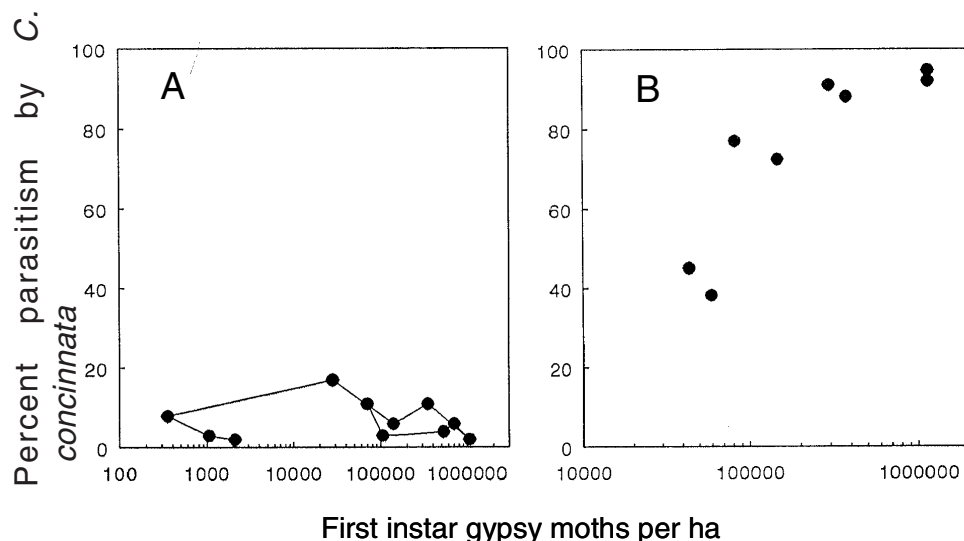


Figure 1. A) A time series of percent mortality caused by *C. concinnata* in a ten year study of gypsy moth in naturally occurring populations (Williams *et al.*, 1992). The solid line connects consecutive generations. Redrawn from Elkinton (2000). B) Percent mortality of gypsy moth caused by *C. concinnata* in a series of experimental populations created with different densities in the same year (Gould *et al.*, 1990).

a single population followed over several years (temporal density dependence), whereas the data from our experiments (Figure 1B) represents variation in parasitism among plots or populations all in the same year (spatial density dependence). Population ecologists have never been clear about the conditions under which spatial density dependence leads to temporal density dependence, but most agree that the latter is required for a natural enemy to stabilize the densities of its host. We do not know for sure why the levels of parasitism recorded in the two studies were so different, but we suspect that it is due to differences in spatial scale. In the hectare-sized, experimentally created populations, we suspect that *C. concinnata* aggregated to the higher density populations from forest areas outside the plots. In naturally occurring populations of gypsy moth, outbreaks and changes in density occur on a much larger spatial scale. The effects of aggregation from low density populations outside the outbreak area might be minimized or confined to the area near the perimeter of the outbreak. On the other hand, perhaps our study shows that *C. concinnata* plays a much more important role than we had realized in suppressing incipient outbreaks of gypsy moth on a small spatial scale.

EFFECTS OF *C. CONCINNATA* ON GIANT SILK MOTHS

The large impact by *C. concinnata* on gypsy moth that we recorded in the experiments reported by Gould *et al.* (1990) made us wonder what impact this species might be having on other native Lepidoptera, particularly those such as giant silk moths (Saturniidae) that finish larval development in late summer. *Compsilura concinnata* is a multivoltine insect (Culver, 1919); it completes a first generation on gypsy moth and two or three subsequent generations on other Lepidoptera whose larvae are present in late summer. This fact may link the dynamics of these different species. The numbers of *C. concinnata* available to attack gypsy moths in the spring will be determined by the abundance of late summer hosts for *C. concinnata*. Similarly, the attack rates by *C. concinnata* on late summer Lepidoptera may be determined by the abundance of gypsy moths.

Cecropia moths, (*Hyalophora cecropia* L.) like other giant silk moths, became notably rarer in the northeastern United States in the late 20th century than they used to be (Schweitzer, 1988; Tuskes *et al.*, 1996). There exist no data to prove this fact, but anecdotal descriptions by collectors of local densities in the 19th century far exceed densities that exist today (Elliot and Soule, 1902; Smith 1908). Several hypotheses have been advanced to account for this decline (Schweitzer, 1988; Tuskes *et al.*, 1996). These ideas include the widespread use of DDT to suppress gypsy moth in the 1960s, the decline of host trees due to urban development, and the deleterious effects on moth mating of mercury vapor street lights. There was no concrete evidence for or against any of these hypotheses, but we considered them unlikely (Boettner *et al.*, 2000). Applications of DDT to forests in the northeast ceased in the 1960s and even at their height never encompassed more than a small fraction of the total forest area. Application of replacement pesticides, such as carbaryl, to forest tracts ended in New England the early 1980s. No resurgence of giant silk moths has been evident. Research on the effects on native Lepidoptera of pesticides applied to forests for gypsy moth control suggests that the impacts are quite ephemeral, rarely lasting beyond the year of application (Sample *et al.*, 1993). As for host availability, different silkmoth species feed on different, but common, deciduous tree species. Despite urban/suburban development, total forest cover in New England has increased over

the past century due to abandonment of agriculture in the region (Foster, 1995). Thus total host availability for silkmoths on a regional basis should have increased, not decreased. Mercury vapor lamps have been used nationwide, yet the decline in silk moths was noted only in the northeast (Tuskes *et al.*, 1996)

Our experience documenting the large impact of *C. concinnata* on experimentally created populations of gypsy moth (Gould *et al.*, 1990) lead us to propose an alternative hypothesis: that populations of giant silk moths have been suppressed by *C. concinnata*. Giant silkmoths have larval stages that last as long as 60 days, and the larvae are present in late summer when those of other Lepidoptera are scarce. We hypothesized that *C. concinnata* densities would be especially high in the northeast, where first generation numbers would build up on highly abundant gypsy moths and then move to attack other species in late summer.

To test this hypothesis, we deployed 500 first instar cecropia moths on trees at the same site in western Massachusetts as our earlier work on *C. concinnata* impact on gypsy moths (Gould *et al.*, 1990). We put them out on understory black cherry trees (*Prunus serotina* L) at a density of five per tree on 100 trees spaced at 5-20 m intervals along four transects across the 64 ha forest. We followed these larvae continually through the entire larval stage in order to get a measure of total larval survival. The initial density per tree of the larvae that we deployed was comparable to the density (two to six eggs) of naturally occurring cecropia moths (Tuskes *et al.*, 1996). In addition, we reared other larvae in the laboratory and placed cohorts of 100 larvae on nearby black cherry trees at five larvae per tree using the same instar as the larvae that we were monitoring in the field for overall survival. Approximately one week later, we retrieved this second group of larvae and replaced them with another laboratory-reared cohort. The retrieved larvae were returned to the laboratory and reared in cups on foliage and monitored frequently for mortality and parasitoid emergence. In this way, we were able to record attack rates by parasitoids instar by instar as the larval stage progressed.

None of the original 500 cecropia larvae that we deployed in the field survived to the pupal stage (Figure 2). In fact, none survived longer than 40 of the approximate 60 days required to complete larval development. The vast majority of this mortality was caused by *C. concinnata*. It caused a cumulative mortality of 81% among the first three instars and was by far the largest cause of death (Table 1). The total mortality caused by *C. concinnata* that we documented would have been even higher had we been able to record attacks on later instars. Unfortunately, our laboratory-reared colony of cecropia larvae became infected with a pathogen so we did not have fourth and fifth instars to deploy. We know from other subsequent research (Kellog *et al.*, 2003) that levels of parasitism by *C. concinnata* on fourth and fifth instar cecropia are even higher than on the first three instars. Thus we conclude that the levels of parasitism by *C. concinnata* in our field populations were at least 81% and were probably a good deal higher.

We wished to compare our results to previous studies of cecropia moth larval survival and found that no such studies existed. The only data on cecropia moth survival and causes of death that we found was of cecropia pupae in Illinois (Marsh, 1937). Using this information along with data on cecropia fecundity and arbitrarily assuming 100% survival of egg and adult stages, we calculated the larval survival needed to maintain cecropia populations at a constant density (dotted straight line in Figure 2). Our observed survival was much less than that. If we had been able to incorporate the actual mortality rates of egg and adult stages, the required level

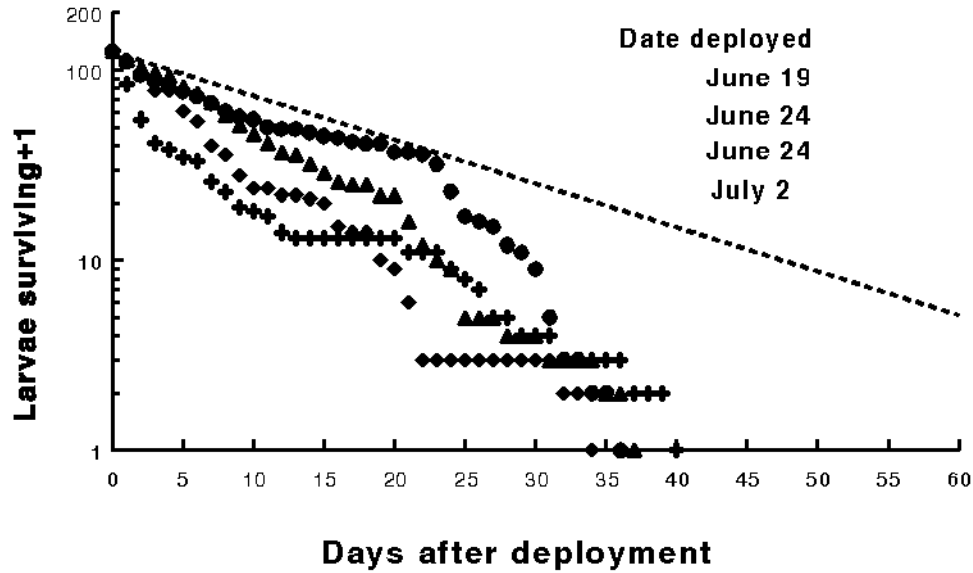


Figure 2. Survivorship curves ($\log_{10}$ numbers plotted vs. time) for deployed *H. cecropia* recorded from daily observations. Dotted line represents an estimate of the required survival for a population to experience no change in density based on data collected by Marsh (1937). Reprinted with permission from Boettner *et al.* (2000).

Table 1. Causes of death for larval cecropia moth and the percentage observed dying at each stage among cohorts of larvae released and recovered from the field. ^a Reprinted with permission from (Boettner *et al.*, 2000).

Stage	Observed Field Mortality				Rearing Mortality		
	No. of larvae deployed	Spiders (%)	Stink bugs: Pentatomid (%)	Days in field	No. of larvae recovered for rearing	Ichneumonid <i>H. fungitivus</i> (%)	Tachinid <i>C. concinnata</i> (%)
1st instar	100	5	4	7	54	1.9	13
2nd instar	100	4	0	5	40 ^b	0	27.5
3rd instar	100	4	0	6	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 One second instar escaped during rearing and is not included in this total.

^c Total percentage mortality calculated as $1 - (1 - m_1)(1 - m_2)(1 - m_3)$ where m_i = the fraction dying during instar *i*.

of survival of larval cecropia for population stability would have to be even higher. Our conclusion is that no cecropia population can long persist if it sustains the level of mortality that we observed in our field experiment. We recognize, of course, that the rates of parasitoid attack are likely to diminish from the levels that we observed as the density of cecropia declines; indeed, that is the only way that cecropia can persist in nature. We point out, however, that declines in attack rates with host density by generalist natural enemies such as *C. concinnata* are not inevitable because the density of *C. concinnata* is unlikely to be linked to that of particular host

species, especially those such as cecropia moth, which are relatively sparse compared to other lepidopteran hosts.

Nevertheless, we have wondered whether aggregation responses by *C. concinnata* may have elevated the levels of parasitism we observed on our experimentally created cecropia populations in a manner similar to what occurred for our experiments with gypsy moth (Gould *et al.*, 1990). The density of five larvae per tree on trees spaced at 5-20 m intervals may be comparable to what occurs in nature for cecropia moth eggs (Tuskes *et al.*, 1996) but is higher than that observed for late instars, at least now that natural densities have declined. To test this idea, we have run follow-up experiments on Cape Cod with the polyphemus moth, *Antheraea polyphemus* (Cramer). We compared *C. concinnata* attack rates on larvae deployed at densities of one per tree vs. five per tree, with trees spaced at least 20 m apart on 12 km transects (Boettner and Elkinton, unpublished). As we hypothesized, attack rates of larvae deployed one per tree were lower than on larvae deployed five per tree, but they were still very high. Overall attack rates by *C. concinnata* on polyphemus larvae in this experiment were even higher than what we had recorded for cecropia moth (Boettner *et al.*, 2000) and on some cohorts reached 100% after only 6-7 days in the field!

EFFECTS OF *C. CONCINNATA* ON OTHER GIANT SILK MOTHS

In a follow-up study to ours, Kellogg *et al.* (2003) deployed luna moth larvae (*Actias luna* L.) in Virginia. Like us, they found that *C. concinnata* dominated the parasitoid fauna emerging from these larvae (accounting for 78% of the parasitoids reared), although the rates of attack were not quite as high as we reported on cecropia in Massachusetts. They also found that up to 47% of the *C. concinnata* that emerged from these larvae were hyperparasitized by trigonalid wasps, a species we have not seen in Massachusetts. Both we and Kellogg *et al.* (2003) also released and recovered single cohorts of promethea moth (*Callosamia promethea* [Drury]). We found 67% parasitism by *C. concinnata* among 117 larvae that were deployed in the field and recovered after 6 or 8 days (Boettner *et al.*, 2000). In contrast, Kellogg *et al.* (2003) found no parasitism by *C. concinnata*, but theirs was a very small sample (18 larvae recovered), so any comparisons with our findings with this species are quite tentative. Finally, we collected 50 naturally occurring pine barrens buck moth larvae (*Hemileuca maia maia* Drury) on Cape Cod, Massachusetts, a species listed as threatened (Boettner *et al.*, 2000). We found that *C. concinnata* had parasitized 36% of them. This finding was very similar to the 30% parasitism reported by Stamp and Bowers (1990) in the closely related *Hemileuca lucina* Edwards, which they collected in central Massachusetts. In all of these examples, *C. concinnata* was causing higher levels of parasitism than any other parasitoid species. Thus, while more intensive studies would be required to elucidate the dynamics of any of these species, it is clear that *C. concinnata* has become a major, if not dominant source of mortality that was superimposed on whatever mortality factors were already governing the dynamics of these species before the introduction of *C. concinnata*. For this reason, we believe *C. concinnata* is the most likely cause of the reported decline of giant silkmoths in the northeastern United States.

CONCLUSIONS

The results of our studies with *C. concinnata* are sobering to anyone concerned with conservation of our native insect fauna. Other studies with other introduced biological control agents are starting to tell a similar story (e.g., Obrycki *et al.*, 2000; Henneman and Marmot, 2001). Perhaps the most striking fact to us is how little we know about the population dynamics and impact of natural enemies for any of our native species. Ours was the first study of its kind on cecropia moth, one of our largest and most showy native Lepidoptera. We know even less about the changes in density and their causes for basically all other native insect species. Even for species such as gypsy moth that have been studied intensively by generations of researchers, our understanding of the impact of particular natural enemies, such as *C. concinnata*, remains very imperfect. The reason for this state of affairs is that research on insect population dynamics is very expensive and difficult. It requires a long-term commitment by investigators and has never been a priority for the state or federal agencies charged with managing our forests and natural habitats.

We believe that the community of scientists involved in biological control introductions must take the lead in establishing guidelines and standards for host range testing to make sure that generalists such as *C. concinnata* are no longer introduced (Simberloff and Stiling, 1996; Strong and Pemberton, 2000; Louda *et al.*, 2003). According to Nechols *et al.* (1992), generalist predators and parasitoids with a wide host range should no longer pass established protocols for United States introductions. However, these protocols are voluntary for biological control agents released to control invertebrates. Despite tighter standards and wider concern about this issue, release of generalist parasitoids with broad host ranges has continued. For example, personnel involved in gypsy moth control (Anonymous, 2000) have continued to release *Pimpla disparis* (Viereck), an ichneumonid pupal parasitoid with as broad a host range as *C. concinnata* (Schaefer *et al.*, 1989). We also believe, however, that we must strike a balance between preventing such introductions and restrictions on introductions or requirements for host-range testing that are so restrictive and expensive that classical biological control becomes infeasible (Van Driesche and Hoddle, 1997). The overall approach of biological control remains the most important weapon we have against many invasive species. We must develop protocols and guidelines that allow us to use this tool more wisely than we have in the past.

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