

# CHAPTER 2: SIMULATIONS OF POPULATION DYNAMICS OF HEMLOCK WOOLLY ADELGID AND POTENTIAL IMPACT OF BIOLOGICAL CONTROL AGENTS

Joseph S. Elkinton<sup>1</sup>, Robert T. Trotter<sup>2</sup>, and Ann F. Paradis<sup>1</sup>

<sup>1</sup>Department of Plant, Soil and Insect Sciences, University of Massachusetts-Amherst, MA

<sup>2</sup>U.S. Forest Service, Northern Research Station, Hamden CT

## ABSTRACT

The hemlock woolly adelgid (*Adelges tsugae*) is a small invasive Hemipteran herbivore that threatens the continued presence and abundance of hemlock in eastern North America. Efforts to control the adelgid have focused on the introduction of classical biological control agents. These biological controls include six different species of predatory beetles, two of which have established. Of these predatory beetle species, *Laricobius nigrinus* has the most potential to alter the dynamics of hemlock woolly adelgid, because it has been recovered in large numbers at multiple release sites in eastern North America. However, establishment does not guarantee the predators will maintain the density of the adelgid at levels sufficiently low to prevent hemlock damage and death. Here we present results of a simulation model in which the potential impact of the introduced predator *L. nigrinus* is explored in the context of what is known about the dynamics of hemlock woolly adelgid in the absence of predators.

## INTRODUCTION

The hemlock woolly adelgid (*Adelges tsugae* Annand) was first documented in eastern North America near Richmond, Virginia in 1951 (Gouger 1971). Since then, the adelgid has moved through natural stands of hemlock and now infests at least 17 states from Georgia to Maine (<http://na.fs.fed.us/fhnp/hwa/maps/distribution.shtm>). The rapid growth

and expansion of adelgid populations, and the resulting decline in hemlock health and abundance has prompted research into the biology, ecology, and management of this forest pest over the last 30 years.

Research on the biology of the hemlock woolly adelgid in North America has shown the annual life-cycle of hemlock woolly adelgid (hereafter HWA) to consist of two generations, both of which reproduce asexually (McClure 1989) on members of the genus *Tsuga*. The overwintering sistentes generation begins development in the fall after a summer aestivation period. Development continues through the winter, with adults maturing and laying eggs in early spring. These eggs hatch after a short development period to produce progredientes crawlers. These crawlers then settle on the previous year's growth and mature in June. Some individuals in this generation become sexuparae that disperse and settle on spruce (*Picea* spp.). Sexuparae in the native range of China and Japan initiate a sexually reproducing generation on spruce, but McClure (1989) showed that none of the North American species of spruce trees are suitable hosts. The progredientes which do not develop into sexuparae continue to develop into adults, and lay eggs that hatch in June. The crawlers of the new sistentes generation settle primarily on new (current year) hemlock growth and enter a summer aestivation phase that lasts until October, whereupon they resume development and feeding. Development is completed the following March.

In eastern North America, HWA has very few known natural enemies, and those that have been observed are not believed to have any significant impact on HWA populations (Montgomery and Lyon 1996; Wallace and Hain 2000). There are no known parasitoids that attack any species in the family Adelgidae. Little is known about the potential or actual impact of pathogens, and the dynamics of the invaded system are largely driven by the interaction of HWA and its hemlock host as shown by McClure (1991) who provided the first comprehensive account of the population dynamics of HWA. Using artificially established populations on uninfested plantation trees and recently infested forest trees in Connecticut in 1986-1989, McClure showed that the HWA populations built to densities

as high as 25 per cm of hemlock twigs in as little as one year after the initial infestation (Fig. 1a). As a result, trees produced little or no new growth the following year. This reduction in new growth forced the crawlers to colonize 1-2 year old growth where survival of nymphs was much lower relative to new growth. Additionally, the proportion of nymphs which became sexuparae instead of progredientes nymphs increased. Because sexuparae are unable to reproduce in North America, population densities declined dramatically in the second year (Fig. 1). The lower HWA densities allowed the trees to partially recover, leading in turn to an increase in HWA densities. This caused a second precipitous decline in hemlock growth that ended in the death of all the trees and HWA.

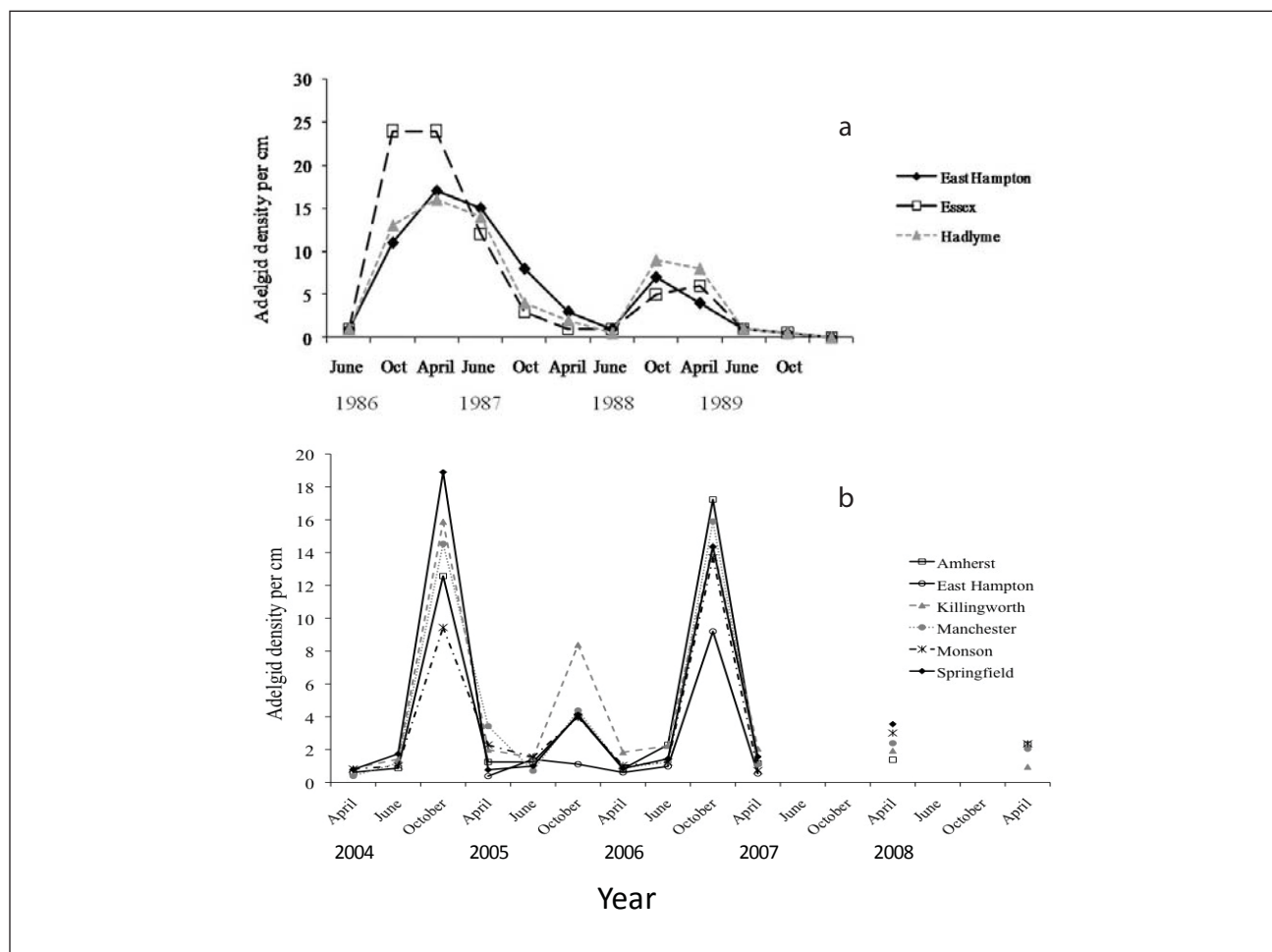


Figure 1. (a) Fluctuations in density of HWA at three naturally infested forest sites studied by McClure (1991) in Connecticut from 1986-1989 (figure redrawn from McClure 1991); (b) Six sites studied by Paradis (2011) in Massachusetts and Connecticut 2004-2008 using methods designed to be comparable with McClure's original studies. In 2008 and 2009 only the April counts of adult sistentes were made.

The pattern of hemlock death four years (or even two years) after infestation has been described by many observers in the southern Appalachians, an area which has recently been invaded by HWA. In northern New England, however, hemlock trees have been known to host infestations of HWA for ten years and continue to survive (Orwig and Foster 1998, Orwig et al. 2002, Paradis 2011). Several investigators have shown that overwintering mortality is much higher in northern compared to southern states (e.g. Trotter and Shields 2009) due to colder winter temperatures (Paradis 2008).

Paradis (2011) (Fig. 1b) conducted a study of naturally established HWA populations in Massachusetts and Connecticut between 2004 and 2008 that was designed to be comparable with previous work by McClure (Fig. 1a). Her purpose

was to gain insight as to why very few hemlock trees were dying from HWA at these northern sites. Like McClure, Paradis (2011) (Fig. 1b) recorded declines in the production of new growth by infested hemlocks at high HWA densities. In contrast to McClure's results, however, some new growth was produced even on highly infested trees, and none of the 60 trees in her study were dead after six years. Paradis also investigated various factors that might explain the apparent stability of HWA densities in her study sites, and found that higher sistentes densities increased mortality and decreased fecundity in the progredientes generation (Fig. 2). Overwintering mortality varied from year to year depending primarily on winter temperature, and was not consistently density dependent (Paradis et al. 2008).

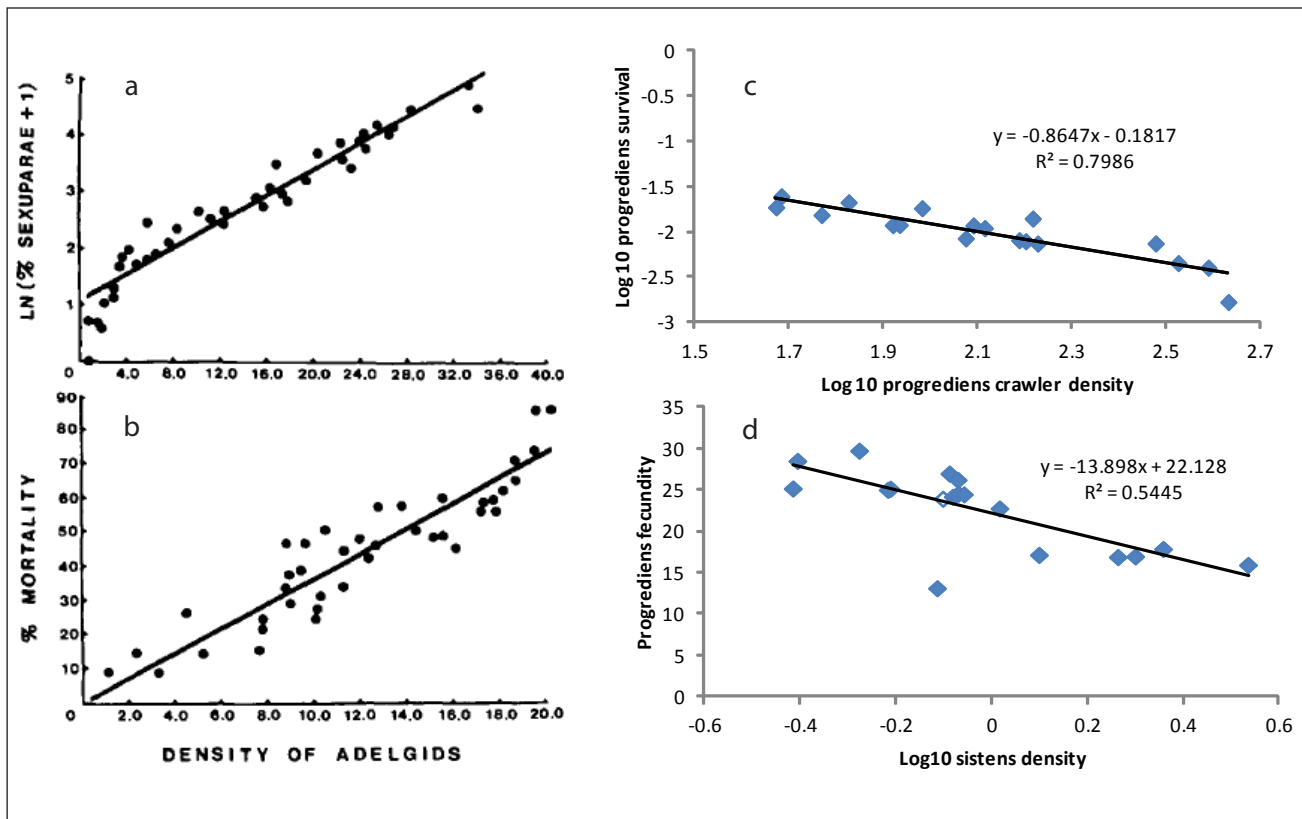


Figure 2. Density dependent a) production of sexuparae; b) mortality in the progredientes stage from McClure 1991; c) density dependent survival of progredientes; and d) progredientes fecundity recorded by Paradis (2011). Figure 2b plots mortality versus density of progredientes whereas Figure 2c plots survival versus density. They presumably represent the same process in the two different studies.

It is clear from the yearly variation in HWA density (Fig. 1) that some factor(s) limit the growth of HWA populations; this limitation is presumably caused by interaction of HWA with its hemlock host (McClure 1991). Both McClure (1991) and Paradis (2011) found density-dependent mortality among immature progredientes (Fig. 2). McClure attributed at least part of this mortality to density-dependent production of sexuparae (Fig. 2a), which disperse to settle on spruce. However, because none of the North American spruce species are suitable for HWA, none of these adelgids survive. Paradis (2011) also showed that sistentes density is negatively correlated with the fecundity of the following progredientes generation (Fig. 2d). Paradis (2011) found no evidence for density-dependent mortality in any other life stage, or for density-dependent changes in sistentes fecundity.

In the absence of native predators and parasites, the natural enemies of HWA in the invaded range appear to be the two predatory beetle species *Sasajiscymnus tsugae* and *Laricobius nigrinus* Fender. Both have been successfully introduced in the eastern United States as part of the ongoing biological control effort against HWA. The long-term impact of these releases is not yet known, though it appears unlikely that *S. tsugae* has a measurable impact on HWA population densities. Although the beetle was released in the mid 1990s (Cheah et al. 2004) at three of the sites that Paradis (2011) studied, intensive sampling for the beetles by Paradis (2011) did not recover any *S. tsugae* at these sites. Although *S. tsugae* has been recovered at sites many years after release, in the northeastern states it is rarely if ever abundant enough to significantly affect HWA densities.

In contrast, the predatory beetle *Laricobius nigrinus* (Derodontidae) was imported from the Pacific Northwest and has been recovered in large numbers at many release sites throughout the eastern United States (Mausel 2007, Mausel et al. 2008). It is by far the most promising biological control agent released against HWA so far, yet we still do not know how much of an impact it is having on HWA densities or dynamics. For this reason we concentrate our simulation efforts on this species.

## SIMULATION

Data collected by Paradis (2011) (Fig. 1b), was used to parameterize simulations of HWA population densities. We began by constructing a simulation of the system in the absence of any predators based on generalized (averaged) values of sistentes and progredientes survival and fecundity. The data consist of information collected from eight locations, with 3-5 years of data for each location (Table 1).

These data provided the basic values needed to generate an empirically-based simulation of HWA dynamics. We constructed our model using two parallel approaches. In the first, a flow model was built to describe the population dynamics of the adelgid over the course of multiple life-stages and generations using Stella (V9.1 IE systems). For verification, a similar model was constructed in MS Excel®. In Stella we built a flow model using the following basic structure:

$$SA_{(t+1)} = (PA_{(t)} * PF_{(t)}) * SS_{(t+1)}$$

$$PA_{(t+2)} = (SA_{(t+1)} * SF_{(t+1)}) * PS_{(t+2)}$$

in which SA = Density of Sistentes Adults,  
PA = Density of Progredientes Adults,

**Table 1. Average values of density, mortality and fecundity of HWA life stages recorded by Paradis (2011) (Fig. 1b).**

	Density: HWA per cm			Mortality: proportion dying				Fecundity	
	OW sistens	Progred adults	Immature sistentes	OW sistens	Progredientes	Sistens crawlers	Prewinter sistentes	Sistentes	Progredientes
Mean	2.21	1.33	10.60	0.52	0.99	0.64	0.75	146.97	22.54
Std. dev	0.90	0.43	5.41	0.27	0.01	0.13	0.15	29.77	4.85

SF = Sistenter Fecundity, PF = Progredientes Fecundity, SS = Sistenter Survival Rate, and PS = Progredientes Survival Rate. Based on this set of relationships, and using the above parameters, our simulated HWA populations grow exponentially. This behavior was expected, since any population with constant rates of mortality and fecundity will either grow or decline exponentially, and no doubt this behavior describes the growth of HWA populations when they first colonize a tree or stand. Such populations soon reach the carrying capacity represented by the available hemlock foliage and the densities are subsequently governed by the density-dependent processes described above. We thus incorporated density-dependent progredientes survival (Fig. 2c) and fecundity (Fig. 2d) into our

simulation. The result is a population system that stabilizes at around two adult sistenter per cm of hemlock twig, but that exhibits the expected variation in density of different life stages evident in Figs. 1a and 1b. If we add a modest amount of annual variation in overwintering mortality, drawn at random from a normal distribution with a mean and standard deviation equal to that recorded by Paradis (2011) (Table 1), we generate fluctuations in simulated densities (Fig. 3a) similar to those observed by McClure (1991) (Fig. 2a) and Paradis (2011) (Fig. 1b). These results give us confidence that our simulation has captured the essence of HWA dynamics in the absence of predators, at least in the northeastern US where McClure and Paradis conducted their studies.

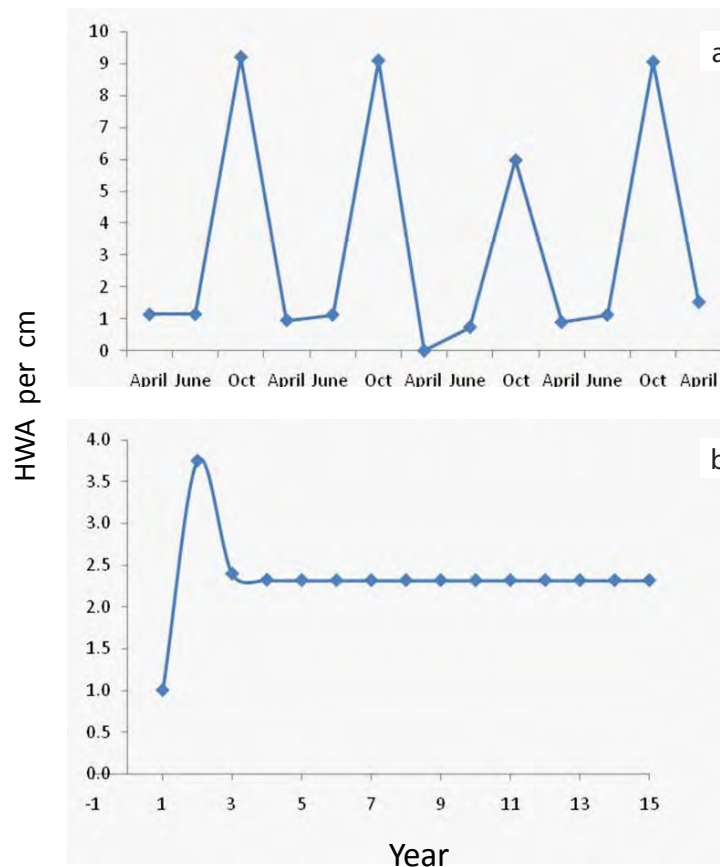


Figure 3. Our simulated time series of HWA density incorporating mean values of fecundity and survival of HWA life stages recorded by Paradis (2011) (Table 1) and density-dependence in progredientes survival (Fig. 2c) and fecundity (Fig. 2d). In Figure 3a we plot HWA densities at 3 times per year as in Figure 1 and we add variation in overwintering mortality recorded by Paradis (2011). In Figure 3b, we plot only one life stage per year (the overwintering adult sistenter) and we remove the variation in overwintering mortality. Otherwise they are the same simulation.



Although the population shown in Figure 3a demonstrates the fundamental stability evident in this system caused by the density dependence in mortality and fecundity discussed above, the stability is partially obscured by the inclusion of variable HWA overwintering mortality. This is highlighted if we remove this variation and plot only one life stage per year (overwintering sistentes, Fig. 3b) rather than the three life stages plotted in Figures 1 and 3a. As Figure 3b shows, the system stabilizes at an equilibrium value of approximately 2.1 sistentes per cm. Although instructive with regards to evaluating the fundamental parameters responsible for long-term population dynamics, it is important to remember that this simulation represents an idealized system. In natural settings, annual fluctuations still occur, and sometimes result in tree death (McClure 1991).

With these results in hand, we simulated the impact of predation by *L. nigrinus* on the eggs produced in early spring by the overwintering sistentes generation. This was accomplished by reducing the survival of HWA progredientes eggs (eggs laid by sistentes). We were surprised to learn that the removal of even 80 or 90 percent of these eggs had negligible effects on the subsequent density of the next generation in our simulation (Fig. 4a). This result occurred because the density-dependent mortality in the progredientes crawler stage (Fig. 2b,c) decreased as egg predation increased, offsetting the population decreases that would otherwise have occurred.

On further reflection, we realized that this result depends on the actual cause and timing of the mortality evident in this stage. If most or all of it is due to density dependent production of sexuparae (Fig. 2a) as McClure (1991) suggests, then the density dependence presumably occurs when the eggs are laid, rather than after the progredientes hatch. If that is true, then egg predation occurs after sexuparae production. If we incorporate this into our simulation, then egg predation has a profound effect on the equilibrium density (Fig. 4b), because it is now preceded instead of followed by the compensating density-dependent

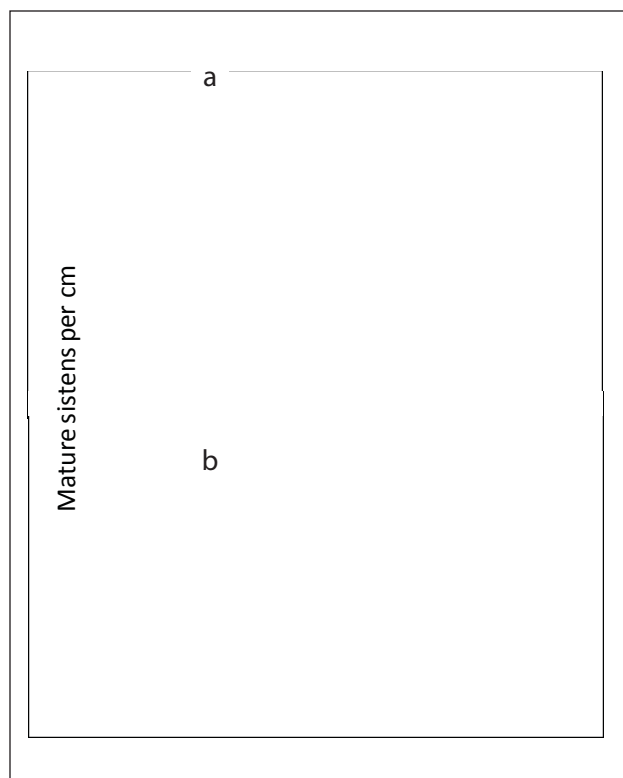


Figure 4. Simulated effect of predation on HWA eggs produced by overwintering sistentes a) after or b) before density dependent mortality occurring in the progrediens generation as in Figure 2a,b,c.

mortality. Alternatively, it seems likely that the response of the hemlock host is involved in some way that is not well understood in causing the density dependent mortality evident in Figure 2, as McClure (1991) suggested. Recent work by Radville et al. (2011) shows that HWA attack induces a systemic hypersensitive response in hemlocks. If the host response causes the mortality documented in Figure 2 and it occurs in response to HWA density during the overwintering sistentes stage, then the mortality may occur whether or not the egg densities are reduced by predation. The resulting effect would be like Figure 4b. If, on the other hand, the host response occurs when the immature progredientes settle, then the effect of egg predation would be compensated as in Figure 4a. The experiments by Radville et al. involved inoculating hemlock foliage with progredientes crawlers and their results thus suggest the latter

conclusion (Fig. 4a). These considerations make it clear that understanding the exact cause and timing of the mortality evident in Figure 2 should be a high research priority. We have initiated experiments designed to accomplish this need.

Thus far we have only considered the effects of constant rates of egg predation on HWA densities. In nature, egg predation rates presumably vary with density of *L. nigrinus* and we know from Mausel et al. (2008) that density of *L. nigrinus* increases with the density of HWA (Fig. 5). Furthermore, we know that adult *L. nigrinus* feed on late-instar sistentes in autumn. Incorporating these effects into our simulation also has profound effects on the equilibrium density, including the version of the simulation where egg predation precedes (Fig. 4a) rather than follows (Fig. 4b) progredientes mortality. In this version of our simulation, we make assumptions about the number of eggs and late instar sistentes consumed per beetle and allow beetle density to vary according to Figure 5. In Figure 6, we show the effects of varying the

number of late-instar sistentes eaten per beetle. The resulting dynamics are complex. As the numbers of sistentes eaten per beetle increases, the mean HWA density declines, but the amplitude of the density fluctuations increases. As the number of HWA eaten per beetle increases, the HWA density progresses from equilibrium (10 sistentes per beetle), to damped oscillations, to evident two- and four-year cycles, and eventually extinction, which occurs when the fluctuating densities overlap zero. This behavior is reminiscent of the progression from equilibrium, to damped oscillations, to cycles with periods of  $2n$ , and finally to chaos first explored by May (1974) with the discrete logistic model. This behavior was demonstrated subsequently in many other models. Whether our system is chaotic under particular parameter values is difficult to answer and of little practical importance. We present these results, not because we believe it to be an accurate description of the impact of *L. nigrinus* on HWA dynamics, but because it illustrates the complex dynamics that even simple models such as ours can exhibit.

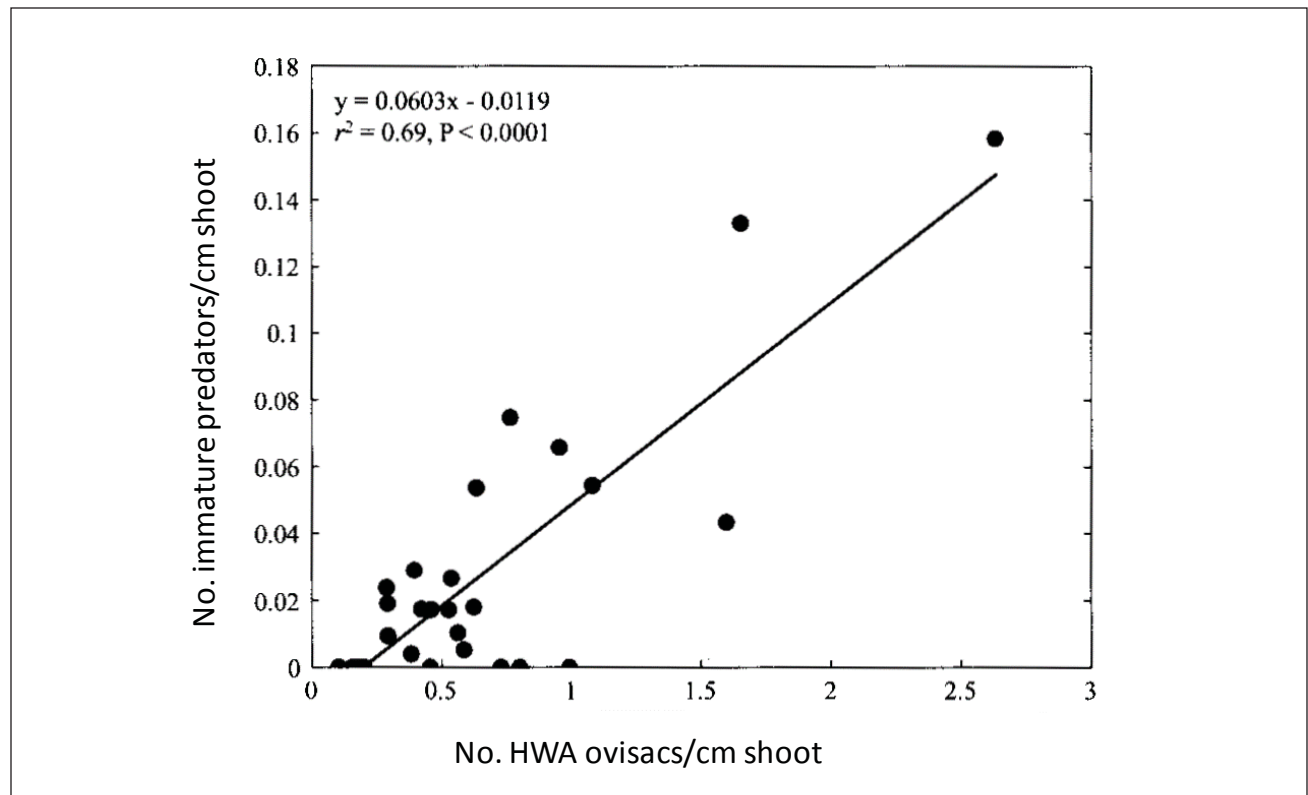


Figure 5. Increases in density of *L. nigrinus* as a function of HWA density recorded by Mausel et al. (2008).

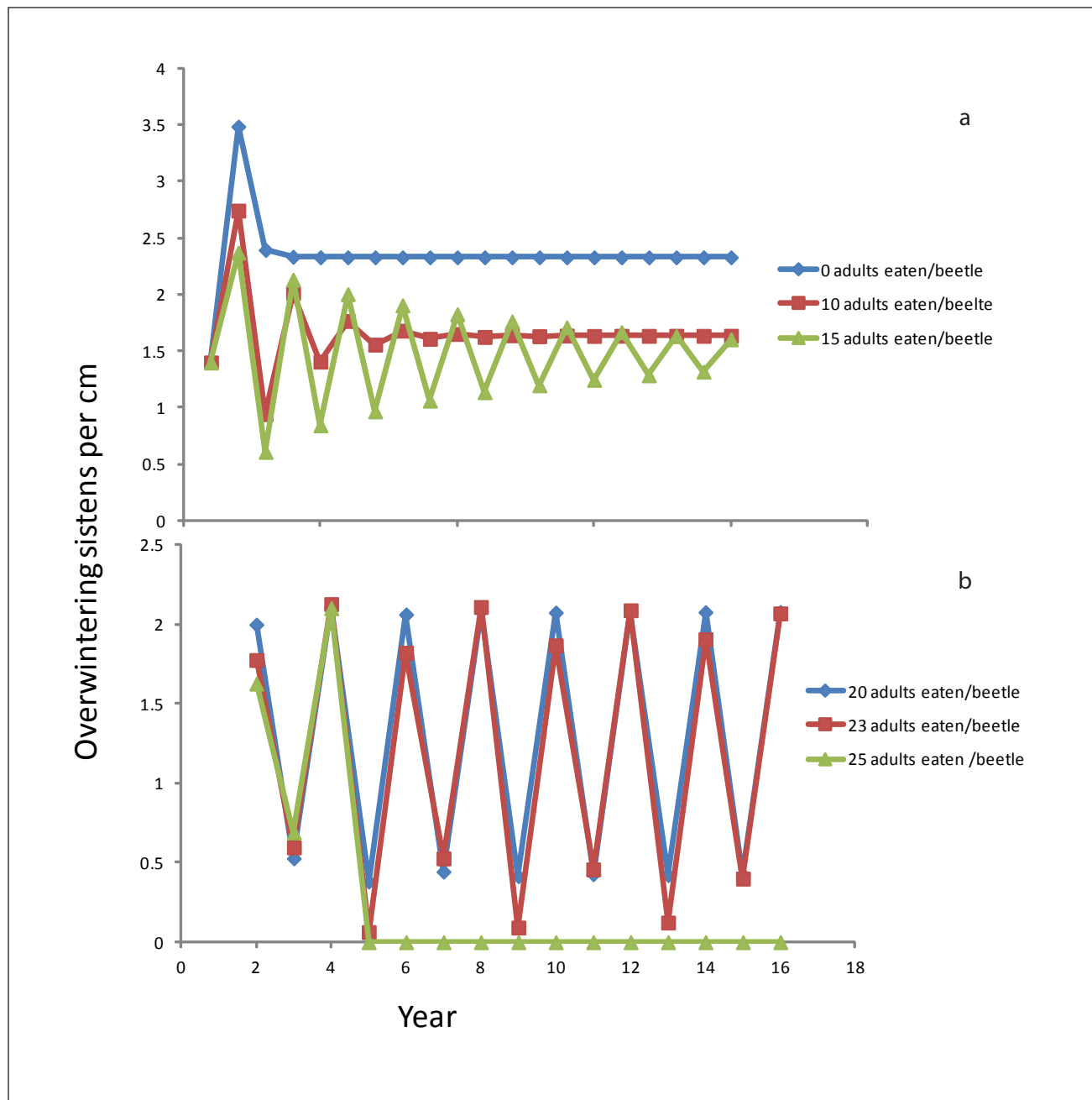


Figure 6. Variation in simulated HWA density as a function of numbers of late-instar HWA consumed by each individual adult *L. nigrinus* in the autumn.



## DISCUSSION AND CONCLUSION

We are tempted to add more and more details to our model, incorporating various other factors that we already know affect HWA population dynamics. We might include host tree effects and factors influencing survival and fecundity of other life stages. We might also include the impact of elongate hemlock scale, *Fiorinia externa*, another invasive species co-infesting hemlock in the eastern US that Preisser and Elkinton (2008) have shown has a significant impact on HWA. We are mindful however, of the rather sorry history of complex simulations in forest entomology. The Gypsy Moth Life System Model (Sharov and Colbert 1994) for example, was constructed in the 1980s and 1990s at great expense and incorporated much of what was known about gypsy moth population dynamics. It was one of several such models, all of which were soon abandoned, because they were too complex to understand and they yielded little insight into the dynamics of the system (Liebhold 1994, Sharov 1996). Rather, models that incorporate minimal to intermediate complexity (Liebhold 1994, Logan 1994, Sharov 1996) have been shown to yield the most insight. The art of building such models is to know what to put in and what to leave out. It is our belief that any useful model of HWA dynamics must include the strong density dependent mortality in the absence of predators (Fig. 2) documented by McClure (1991) and Paradis (2011). These effects involve the interaction of HWA with its hemlock host, as McClure (1991) described, but they continue to govern the system even in the absence of tree mortality, as Paradis (2011) has shown.

Our simulation suggests that the impact of biological control agents on HWA can be counter-intuitive and can only be understood in the context of the rest of the population dynamics of the system. For example, our simulations revealed that very high rates of predation can have almost no effect on mean HWA densities, if they are followed by other compensatory density-dependent mortalities. These findings underscore the importance of introducing biocontrol agents that prey on multiple life stages, and the importance of the timing of predation.

Finally, we believe our simulation shows the importance of understanding the various factors that affect mortality and fecundity of different life stages of a pest population system undergoing biological control and can suggest critical experiments that need to be done to understand these effects. As additional information on the biology of the controls becomes available, our ability to estimate their potential impact should continue to improve.

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# **IMPLEMENTATION AND STATUS OF BIOLOGICAL CONTROL OF THE HEMLOCK WOOLLY ADELGID**

## **Technical Coordinators**

Brad Onken

Forest Health Protection, U.S. Forest Service  
180 Canfield Street, Morgantown, WV 26505

Richard Reardon

Forest Health Technology Enterprise Team, U.S. Forest Service  
180 Canfield Street, Morgantown, WV 26505