2001 FHP TECHNOLOGY DEVELOPMENT PROJECT PROPOSAL

PROJECT STATUS: New, not previously funded.

PROJECT NUMBER: R8-2001-01

PROJECT TITLE: Removing an Imported Predator of Hemlock Woolly Adelgid From Quarantine and Evaluating its Effectiveness as a Biological Control Agent in the Field

SUBJECT: (mark all that apply using 1 for primary category and 2 for secondary categories): Biological Control_1_ Invasive Species_1_ Organism Biology_2_ Other____Rearing Techniques_1_____

STATUS OF SUBJECT SPECIES: non-native noxious

PROJECT OBJECTIVES:

1. To evaluate the efficacy of *Laricobius nigrinus* Fender as a predator of hemlock woolly adelgid (HWA) under field conditions:

    a. Evaluate the success in overwintering and establishment of *L. nigrinus* in eastern hemlock forests infested with HWA.

    b. Determine the potential geographic range for *L. nigrinus* as a predator for HWA.

2. Improve rearing techniques for *L. nigrinus* in a move toward mass rearing.

BRIEF DESCRIPTION OF PROJECT: The project has two major facets:

1. We have received permission to release *Laricobius nigrinus* from quarantine and study it in the field. Experiments will be conducted to determine if the beetle can survive and become established on HWA in eastern North America. In addition, it will be necessary quantify the impact of the predator on HWA population density in the short- and long-term. Short-term studies encompass caged experiments and long-term studies encompass releases without cages.

2. Large numbers of *L. nigrinus* will be needed for releases. Experiments will be conducted to study the laboratory conditions necessary for successful rearing of the beetle. The aim is to develop procedures for its efficient reproduction. Efforts will focus on composition and moisture of the substrate that the beetle uses for pupation and overwintering. Different soil and peat mixtures will be evaluated. The optimal moisture content and techniques for its maintenance will be studied. Various densities of larvae on HWA-infested hemlock will be evaluated to minimize % mortality of developing *L. nigrinus* larvae.

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COOPERATOR INVOLVEMENT:

Name	Role	Time Commitment
Lee Humble	Field collection of *L. nigrinus*	20-40 h/1st year only
Tim Tigner	Identify sites for research plots	20-40 h/2 years
Richard Evans	Identify sites for research plots	20-40 h/2 years

JUSTIFICATION: Biological control is considered the only truly viable management option for use against HWA. Efforts by Drs. Mark McClure (Ct. Ag. Exp. Sta.), Mike Montgomery (USFS), and their colleagues have focused on the evaluation and release of host-specific coccinellids imported from Asia. At Virginia Tech, we have focused our efforts on a Derodontid beetle, *Laricobius nigrinus*, found consistently with HWA in western North America, and more specifically in Victoria, B.C. Canada.

In our previously funded STDP (project no. 08-98-S&PF-PA-04), our objectives were to study the potential of two biological control candidates. One was *Aphidecta obliterata*, a cocinellid imported into North America for balsam woolly adelgid, and *Laricobius nigrinus*, mentioned above. Our work with *A. obliterata* was inconclusive, mostly due to our inability to rear this insect in the laboratory on HWA. This suggested to us that HWA was not a suitable host for this beetle. However, we had much better success with *L. nigrinus*, as we were able to:

a. Develop a continuous lab-rearing procedure for *L. nigrinus*.
b. Provide a complete life cycle of *L. nigrinus*.
c. Determine that in British Columbia *L. nigrinus* and HWA are phenologically synchronous with each other.
d. Determine that *L. nigrinus* prefers to feed and oviposit on HWA when exposed to other adelgid and Homopteran species.
e. Determine that *L. nigrinus* will complete development only on HWA.
f. Observe that *L. nigrinus* larvae and adults feed principally on HWA progrediens eggs. Larvae consumed an average of 226 eggs per larva and to a lesser extent on nymphs, and *L. nigrinus* adults fed at a lower rate than the larvae.

Thus, we consider *L. nigrinus* a viable biological candidate for use against HWA. Until now, all experiments in Virginia have been conducted under quarantine. It is necessary to begin testing this insect under natural field conditions and determine its short- and long-term impact on HWA populations, as well as its ability to adapt to and survive in a new climate. We also need to develop a procedure that allows us to mass-rear the predator in anticipation of mass releases that will occur at a later stage.

URGENCY: Eastern hemlocks in over 25% of their range have been or are currently being destroyed by HWA. There are no chemical or silvicultural treatments available to manage this pest. The only practical option available for suppressing HWA populations in hemlock stands is the use of biological control agents. An ambitious program on biological control is greatly needed. The proposed effort here is an important step towards large-scale release of one promising biological control agent.

NATIONAL FHP TECHNOLOGY DEVELOPMENT PRIORITY (check one):

Priority 1: _XX_ Priority 2: __ Priority 3: __ Priority 4: __

Priority 1: Develop or refine biological control methods for established species (native and non-native) and established pest populations

TECHNICAL COMMITTEE DEVELOPMENT PRIORITY (check one):

Priority 1: __ Priority 2: __ Priority 3: __ Priority 4: _XX_

Priority 5: __ Priority 6: __ Priority 7: __ Priority 8: __

Priority 4: Define/ characterize interactive impacts of native and non-native insects with forest ecosystem structure and function

SCOPE OF APPLICATION: *Laricobius nigrinus* has potential to establish itself throughout the current and future range of HWA. This potential needs to be verified through field experiments. Improvement of rearing procedures will make it possible to mass rear the predator and release it in large numbers at different geographic locations. By the end of the project, we hope to be in a position to release *L. nigrinus* in a number of HWA-infested hemlock stands in the eastern U.S.

RESEARCH BASIS: *Laricobius nigrinus* Fender (Coleoptera: Derodontidae) has been observed in close association with HWA populations on western hemlock, *Tsuga heterophylla* (Raf.) Sargent in British Columbia, Canada (Humble, Canadian Forest Service, pers. commun. 1996), and has a known distribution of British Columbia, western Washington, Oregon and northern Idaho, U.S.A. (Hatch 1962, Lawrence and Hlavac 1979). It is one of four species of *Laricobius* known to occur in North America, all of which feed exclusively on Adelgidae. The others are *L. erichsonii* Rosenhauer, introduced from Europe in the 1950's and 60's for control of balsam woolly adelgid, *Adelges piceae* (Ratz.); *L. rubidus* LeConte, a predator of the pine bark adelgid, *Pineus strobi* (Hartig) (Clark and Brown 1960); and *L. laticollis* Fall, collected from Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, in Washington and British Columbia (Brown 1944).

There are no published reports on the biology and ecology of *L. nigrinus*, or on its relationship with HWA. Because this predator is found with HWA in western North America, where HWA is not considered a pest, the Virginia Tech researchers believed that it merited evaluation as a candidate biological control agent for HWA in eastern United States.

As part of our current STDP (project no. 08-98-S&PF-PA-04), which expires in 2001, we investigated the potential of *L. nigrinus* as a biological control agent for HWA. Results from this project are summarized from Salom et al. (2000):

Life History. We have determined that *L. nigrinus* is univoltine. It becomes active in the fall after undergoing an aestivation period between May and October. This is approximately the same period in which first instar HWA sistens are known to diapause (McClure 1987). In field studies in British Columbia, Canada, where HWA and *L. nigrinus* were sampled for every two weeks from 1998-99, we observed that aestivating *L. nigrinus* adults resumed activity on the second sampling date (11 October) (Fig. 1), the same time that HWA nymphs broke diapause. Egg-laying by *L. nigrinus* adults is shown to be well synchronized with the beginning of egg laying by adult HWA (Fig.

1). Females lay eggs singly within the woolly ovisacs of HWA. The ovipositional period lasts from January to May. Four instars were determined from head capsule measurements using Dyars law (Dyar 1890). All life stages of *L. nigrinus* feed on HWA. Larvae feed primarily on the eggs while adults feed on all life stages. Larvae appear to have well developed mandibles, which they use to grasp prey and suck out body fluids. Mature fourth instars migrate to the soil and lie in a prepupal state for about 10 days before pupating. Pupation period is between 10 and 14 days. Emergent adults remain in the soil in aestivation, resuming activity in early October.

Biology of *L. nigrinus* described from laboratory and field observations is similar to biology described by Franz (1958) for *L. erichsonii*, a European species. However, Franz (1958) reports that emergent adults feed before undergoing aestivation from August to October. *L. nigrinus* is well synchronized with HWA in both activity and reproduction.

Host Suitability Studies in the Lab. In no-choice feeding tests, *L. nigrinus* adults consumed significantly more eggs of HWA than eggs of the balsam woolly adelgid and the pine bark aphid, but not the eastern spruce gall adelgid (Table 1). Larvae reared at 12°C and 12:12 (L:D) photoperiod consumed a mean (± SD) of 225.9 ± 57.1 HWA eggs to complete their development (n=10). In 3-day no-choice oviposition tests, *L. nigrinus* females preferred to oviposit in HWA ovisacs than in other adelgid and non-adelgid species of Homoptera tested (Table 2). No eggs were laid on pepper leaves containing green peach aphid. Similarly, when given a choice in 3-day paired-choice oviposition tests, *L. nigrinus* females preferred to oviposit in HWA ovisacs over other adelgid and non-adelgid Homopterans tested (Table 3). No eggs were laid on host plant cuttings containing pine needle scale (Diaspidae), *Cinara* spp. (Aphidae) and green peach aphid (Aphidae). In larval development tests, *L. nigrinus* completed development on HWA only (Table 4), indicating that its ability to survive on other prey species is very limited. Our results are supported by published reports describing members of the genus *Laricobius* as adelgid specialists (Lawrence and Hlavac 1979).

METHODS:

Objective 1 – To evaluate the efficacy of *L. nigrinus* as a predator of HWA populations:

a. Establishment studies will be conducted in two phases: caged (short-term) and uncaged (long-term) releases. In the first phase, sleeve cage releases will be carried out. Eastern hemlock stands, containing trees infested with HWA at moderate to high population densities will be located and reachable branches used. The cage studies will be conducted in early spring when HWA sistens are laying progrediens eggs. Four trees will be chosen at each of three selected field sites. For each tree, nine lower branches will be studied. We will focus on the outer 0.5 m of each branch. The branches chosen should be similar in health and contain a similar density of HWA. The treatments will include an uncaged branch, a caged branch with no predators, and a caged branch with 2 male and 2 female *L. nigrinus* adults. A fabric cloth with fine mesh to prevent predator escape will be used. Every two weeks, one branch of each treatment on each tree in all the plots will be clipped and placed in a cooler. They will be brought back to the lab and dissected to determine the number of HWA ovisacs, eggs within the ovisacs, live nymphs settled on the twigs, survival of *L. nigrinus* adults, and egg and larval density of *L. nigrinus*. A two week sampling interval is necessary to determine the impact of the predator on HWA as the prey continues to develop. This experiment will take place during the 1st year of the project.

The number of sistens ovisacs, progrediens eggs within the ovisacs, and progrediens nymphs will be compared among treatments using ANOVA. A multi-location randomized complete block design will be used with each tree serving as a block and each stand of four trees serving as a replicate.

In the uncaged release study, two release trees and two control trees no less than 50 m apart will be selected for each of three plots. All the measurements listed above in the caged study will be made before and after releases on both release and control trees. Sampling will take place on each tree every two months for two years. This study will be conducted during years 2 and 3 of the project. In addition, tree branches will be clipped at the mid-crown level and lower branches will be beaten to collect *L. nigrinus*. Collections will be taken from each cardinal direction at lower and mid-crown levels for each release tree. These collections will take place every two weeks in the spring of the year of *L. nigrinus* release and the following year while HWA progrediens are present.

b. To determine the potential geographic range for *L. nigrinus*, the caged release study described above will also be conducted 500 km north of Blacksburg, VA, in the Delaware Water Gap National Recreation Area, in Pennsylvania. This will take place during the 2nd year of the project. All measurements made in the local cage release study will also be conducted at this location. If sufficient beetles are reared, we will attempt to include uncaged *L. nigrinus* releases in this more northern site, and monitor its establishment.

Objective 2 – In the lab, the greatest mortality occurred during the pupal (Table 4) and overwintering adult stages. It is essential that we develop a mass rearing program that minimizes mortality. One area of focus will be to determine the ideal substrate for the pupal and adult overwintering stages. This will be accomplished with a factorial experiment encompassing different substrate treatments and moisture content levels. The substrate treatments will include 100% sterilized soil, 34% soil and 66% peat mixture, 66% soil and 34% peat mixture, and 100% peat. The moisture content levels will be >90%, 70 – 90%, and 50 – 70%.

Another area of focus will be to determine the optimal rearing density for larvae. Too high a density will result in food shortage, and too low a density will result in too much time spent searching for the predators and waste of host material. Current cages used will be examined and perhaps re-designed to meet the objectives of this study. Optimization of the rearing process will be an ongoing effort beginning the 1st year of the project.

MEASURE OF SUCCESS:

Standard of Success: For objective 1, the 1st standard is that *L. nigrinus* survives in the cages. The 2nd standard is that they overwinter successfully at the release sites. The 3rd standard is that they slow HWA population growth on trees they were released on.

For objective 2, the standard will be whether we can reduce mortality (currently about 90% from egg to reproducing adult) in half. Females oviposit an average of 83 eggs in their life and produce about 8 reproductive adults. If we can rear 40 reproductive adults from 83 eggs, it will be a 5-fold increase.

Expected Outcomes: *L. nigrinus* will survive and become established where released. They prefer relatively cool temperatures and should be able to survive in the northern portion of the HWA range. Since they feed predominantly on HWA progrediens eggs and have 1 generation/year, we expect them to have a moderate impact on HWA populations. We also expect to be able to rear larger numbers of the predator, but will ultimately be constrained by facilities and resources unless some type of cooperative effort can be formulated and implemented.

Implementation of Products and Methods: Once the rearing and release procedures are refined, we will work with USDA, Forest Service, Forest Health personnel to develop Environmental Assessments for releasing the predators on public lands. We will also coordinate with state forestry personnel to arrange for more releases. Mass rearing will require additional facilities and resources in order to meet the potential demands.

PRODUCTS: By the end of this project, we hope to demonstrate that the predator has a positive impact on reducing HWA population density and be successful in rearing large numbers of the predator to begin planning large-scale research/operational releases.

PUBLICATIONS: Results will be reported in scientific journals and perhaps technical proceedings in the interim. The natural enemy evaluations may be published in either Entomophaga or Biological Control. Results from the rearing experiments will likely be published in the Journal of Economic Entomology or in Environmental Entomology.

TECHNOLOGY TRANSFER: Any insects available for release will be made available to state agricultural agencies and USDA Forest Service personnel for eventual release in the forest. We plan to ask our cooperators to help us evaluate the impact of the natural enemies. Rearing procedure can be described in detail in a Research Note produced by the USDA Forest Service.

PROJECT DURATION: 3 Years (2001-2003)

LONG TERM BUDGET:

	Item	Requested FHP STDP Funding ($)	Virginia Tech Funding ($)
FIRST YEAR			
Administration	Salary (Two graduate research assistants)	29,700	
	Salom & Kok Salary cost-share		20,000
	Overhead (45%)		17,955
	Travel	4,200	
Procurements	Contracting	1,000	
	Equipment		
	Supplies	5,000	
Year Totals		**39,900**	**37,955**
SECOND YEAR			
Administration	Salary (Two graduate research assistants)	30,100	
	Salom & Kok Salary cost-share		20,400
	Overhead (45%)		18,315
	Travel	4,600	
Procurements	Contracting	1,000	
	Equipment		
	Supplies	5,000	
Year Totals		**40,700**	**38,715**
THIRD YEAR			
Administration	Salary	31,500	20,800
	Salom & Kok Salary cost-share		18,675
	Overhead (45%)		
	Travel	4,600	
Procurements	Contracting		
	Equipment		
	Supplies	5,400	
Year Totals		**41,500**	**39,475**
PROJECT TOTALS		**122,100**	**116,145**

STDP Production Function

Project Number: R8-2001-01

Project Cost: $122,100

Project Objectives:

1. To evaluate the efficacy of *Laricobius nigrinus* Fender as a predator of hemlock woolly adelgid (HWA) under field conditions:

   a. Evaluate the success in overwintering and establishment of *L. nigrinus* in eastern hemlock forests infested with HWA.

   b. Determine the potential geographic range for *L. nigrinus* as a predator for HWA.

2. Improve rearing techniques for *L. nigrinus* in an effort to move toward mass rearing.

Benefits Not Quantified but Considered under the Forest Health Protection Program Analysis:

Avoid Tree Removal/Replacement Costs The establishment of *Pseudoscymnus tsugae* will maintain hemlock species within numerous recreation areas across the eastern United States. This is especially important in areas where hemlocks are the dominant species and there loss would leave the in an unacceptable condition.

Avoid Pesticide Related costs: The establishment of *Pseudoscymnus tsugae* would help eliminate the use of pesticides in control of HWA in recreation and ornamental situations on thousands of acres across the Eastern United States. Currently Forest Health Protection provides in excess of $110,000 annually for chemical control efforts of HWA in the Southern Region.

Avoid Habitat Restoration Costs: The establishment of *Pseudoscymnus tsugae* and subsequent control of HWA could eliminate the need to replace the conifer habitat bordering and protecting thousands of miles of streams and rivers. The loss of this conifer cover in many cases will leave the aquatic habitat in a condition unacceptable for many of the species that occur there. An example of this would be the loss of brook trout habitat due to the rise in water temperatures because of the loss of the hemlock protection.

Maintain Wildlife Habitat: The establishment and control potential of *Pseudoscymnus tsugae* will aid in the maintenance of the fir and hemlock forests that are primary habitat for many species including the northern flying squirrel and the blackburnian warbler.

Avoid Threatened/Endangered Species Listing: The establishment and subsequent control of HWA with *Pseudoscymnus tsugae* will allow both eastern and the rare Carolina hemlock to remain a vital part of the forests of the east. Both hemlock species have potential to become endangered in their natural settings if control methods are not developed and implemented.

Enhance Visual Quality/Recreation: The control of HWA with establishment of *Pseudoscymnus tsugae* will maintain some of the most highly valued and most visited recreational settings found in the eastern United States. Millions of visitors journey to these areas each year and with this comes a great deal of public concern over the demise of hemlocks. In the eastern United States hemlocks are

key species for many of the premier recreation sites. These sites were in most cases located in their current locations due to the immeasurable aesthetic qualities of hemlock.

Assumptions:

For the purposes of this analysis the value of eastern hemlock as a timber species will be utilized. This value is only a small part of the overall importance of eastern hemlock to the forests and landscapes of the eastern United States. Eastern hemlock has numerous imeasurable values that are not easily quantified including aesthetics, recreational, ornamental, and ecological.

- The development of a biological a control (*Laricobius nigrinus*) will ensure that at least 20% of the eastern hemlock forest type can be maintained.

- The entire range of natural eastern hemlock will be infested and lost within 30 years.

- Estimated loss of hemlocks after being infested for 10 years is conservatively 50 percent.

Background Data:

- Number of hemlock hectares is 1.3 million.

- Approximately 325,000 hectares(25%) are currently infested.

- Total cubic foot volume of hemlocks is 12 billion.

- Total cubic feet of hemlock per hectare is 9230.7

- Stumpage value per MCF of hemlocks is $46.87

Data from USDA-FSD-FIA reports

Calculations:

EOV without project = (325,000 hectares)*(50% loss of trees)*(9.2MCF/hectare)*(46.87 per MCF) = 70,070,650 = discounted to 21,604,182

EOV with project = (325,000 hectares)*(50% loss of trees)*(9.2MCF/hectare)*($46.87 per MCF)*(1.2;20% probability of success) = 84,084,780 discounted to 25,925,019

Benefit Attributed to Project: 25,925,019-21,604,182 = $4,320,837

Benefit/Cost Ratio: 4,320,837/238,245 = 18.1

Benefit Attributed to STDP Funds:18.1*$122,100STDP costs = $2,210,010

PNV of Project: $4,320,837 - $238,245 = $4,082,592

PNV of STDP: $2,210,010 - $122,100 = $2,087,910

LITERATURE, CITATIONS, ATTACHMENTS, etc.:

Brown, W.J. 1944. Some new and poorly known species of Coleoptera, II. *Canadian Entomologist* 76:4-10.

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Dyar,H.G. 1890. The numbers of molts of lepidopterous larvae. Psyche.5:420-422.

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McClure, M. S. 1987. Biology and control of hemlock woolly adelgid. Conn. Agric. Exp. Sta. Bull. # 851.

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FIGURES

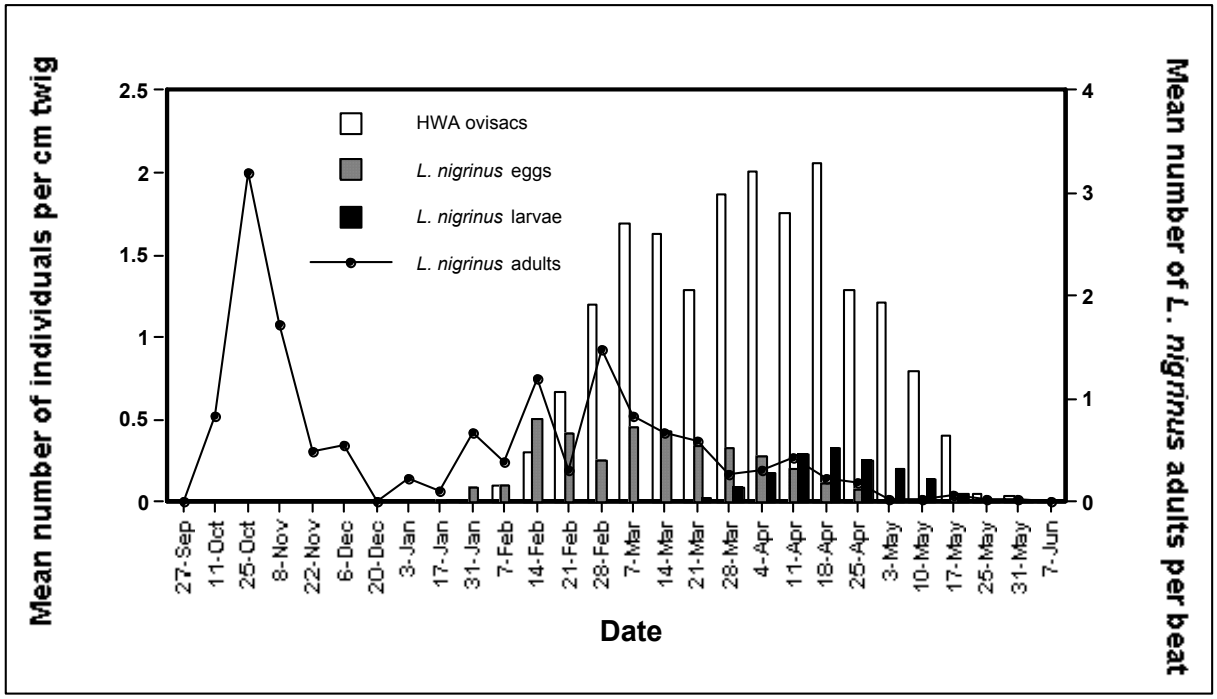

Figure 1. Seasonal abundance of *L. nigrinus* adults, eggs, and larvae and HWA ovisacs between September 1998 and June 1999 in Victoria, BC. CANADA.

Table 1. Mean number of eggs (± SE) consumed by adult *L. nigrinus* in a 3-day no-choice test at 18°C and 12:12 (L:D) photoperiod, 12–15 April 2000.

Host	n	Mean # eggs consumed ± SE
Hemlock woolly adelgid	7	48.28 ± 8.16a[1]
Balsam woolly adelgid	7	6.86 ± 3.40b
Eastern spruce gall adelgid	7	24.71 ± 7.25ab
Pine bark adelgid	7	21.0 ± 4.04b

[1] Means followed by the same letter in the same column are not significantly different at P=0.05 using Tukey-Kramer HSD test.

Table 2. Mean number of eggs laid by *L. nigrinus* females in separate 3-day no-choice tests at 18°C and 12:12 (L:D) photoperiod..

Date	Host	n	Mean # eggs laid ± SE
March 8 – 11, 2000	HWA	11	17.09 ± 2.52a[1]
	pine bark adelgid	11	7.91 ± 1.45b
	balsam woolly adelgid	12	3.08 ± 1.81bc
	Cinara spp.	11	0.17 ± 0.11c
March 20 – 23, 2000	HWA	12	10.91 ± 2.07a
	pine needle scale	12	0.08 ± 0.08b
	green peach aphid	12	0.00 ± 0.00b
April 8 – 11, 2000	HWA	12	8.58 ± 1.59***[2]
	e. spruce gall adelgid	12	0.67 ± 0.31

[1]Means followed by the same letter in the same column are not significantly different at P=0.05 using Tukey-Kramer HSD test.
[2] ***T - test P<0.001.

Table 3. Mean number (± SE) of eggs laid by *L. nigrinus* females in 3-day paired-choice tests conducted between February and April 2000.

Pairwise comparison	n	HWA	BWA	ESGA	PBA	PNS	Cin.	GPA
HWA vs BWA[2]	12	10.1 (± 2.4) *[7]	1.83 (± 1.04)	-	-	-	-	-
HWA vs ESGA[3]	11	7.55 (± 2.43) **	-	0.36 (± 0.20)	-	-	-	-
HWA vs PBA[4]	20	12.25 (± 1.42) ***	-	-	2.25 (± 0.40)	-	-	-
HWA vs PNS[5]	12	17.5 (± 2.02) ***	-	-	-	0 (± 0.0)	-	-
HWA vs *Cinara* spp.[6]	12	12.42 (± 2.24) ***	-	-	-	-	0 (± 0.0)	-
HWA vs GPA[6]	12	9.83 (± 1.92) ***	-	-	-	-	-	0 (± 0.0)

[1] HWA = hemlock woolly adelgid; BWA = balsam woolly adelgid; PBA = pine bark adelgid; ESGA = eastern spruce gall adelgid; PNS = pine needle scale; GPA = green peach aphid.
[2] Test conducted 2-5 March 2000; [3] Test conducted 9-12 April 2000; [4] Test conducted 8-11 March 2000; [5] Test conducted 9-12 April 2000; [6] Test conducted 25-28 February 2000.
[7] *** significant difference P<0.0001, ** significant difference P<0.01, * significant difference P<0.05, using a paired t-test.

Table 4. Percent survivorship of *L. niginus* from egg to adult on various adelgid and non-adelgid hosts.[1]

Life stage	HWA % (n)	BWA % (n)	PBA % (n)	ESGA % (n)	*Cinara* spp. % (n)	PNS % (n)
# of eggs	69	172	149	42	35	50
Instar 1	86.96 (60)[2]	85.47 (147)	68.46 (102)	100 (42)	68.57 (24)	78.0 (39)
Instar 2	79.71 (55)	22.67 (39)	24.16 (36)	0	0	0
Instar 3	69.57 (48)	15.12 (26)	11.41 (17)	-	-	-
Instar 4	57.97 (40)	11.1 (19)	6.71 (10)	-	-	-
Prepupa	42.03 (29)	0	0	-	-	-
Pupa	18.83 (13)	-	-	-	-	-
Adult	17.39 (12)	-	-	-	-	-

[1] HWA = hemlock woolly adelgid; BWA = balsam woolly adelgid; PBA = pine bark adelgid; ESGA = eastern spruce gall adelgid; PNS = pine needle scale; GPA = green peach aphid.
[2] Number at beginning of lifestage