

## Feeding Preference of Three Lady Beetle Predators of the Hemlock Woolly Adelgid (Homoptera: Adelgidae)

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**ABSTRACT** In a laboratory study, we tested the feeding preferences of three coccinellid predators of hemlock woolly adelgid, *Adelges tsugae* Annand, an introduced pest of hemlock in the eastern United States. The species tested were *Sasajiscymnus tsugae* Sasaji & McClure (formerly *Pseudoscymnus tsugae*) from Japan, *Scymnus ningshanensis* Yu & Yao from China, and *Harmonia axyridis* (Pallas), a generalist species introduced from Asia that is currently widespread in eastern hemlock, *Tsuga canadensis* Carriere, forests. We measured the feeding preference of each beetle species when given the choice of *A. tsugae* and either 1) *Pineus strobi* (Hartig) on *Pinus strobus* L.; 2) *Adelges laricis* Vallot on *Larix decidua* Mill.; 3) *Adelges cooleyi* (Gillette) on *Pseudotsuga menziesii* (Mirb.) Franco; or 3) *Paraprociophilus tessellatus* (Fitch) on *Alnus serrulata* (Ait.) Willd. We evaluated beetle preference for adults, nymphs, and eggs of each prey species. Generally, when adult or nymphal prey stages were compared, *S. tsugae* preferred *A. tsugae* adults to *P. strobi*, *A. cooleyi*, *A. laricis*, and *P. tessellatus*. *S. ningshanensis* showed less preference between adelgid species, but it did not prefer *P. tessellatus* nymphs. When preferences for adelgid eggs were assayed, *S. tsugae* and *S. ningshanensis* showed no preference between *A. tsugae* and *A. cooleyi* or *P. strobi*, but *S. tsugae* did prefer *A. tsugae* to *A. laricis*. Larvae of *S. tsugae* were unable to survive on *P. tessellatus* nymphs. *H. axyridis* adults readily consumed both *A. tsugae* and *P. tessellatus*, but *H. axyridis* larvae did not complete their life cycle on *A. tsugae*. Our host range tests suggest that *S. ningshanensis* and *S. tsugae* may feed on several species of Adelgidae and that *A. tsugae* is often preferred.

**KEY WORDS** hemlock woolly adelgid, woolly alder aphid, preference testing, *Pseudoscymnus tsugae*

SOME INTRODUCED BIOLOGICAL control agents have been shown in retrospect to exert negative impacts on non-target species (Simberloff and Stiling 1996, Follett et al. 2000, Strong and Pemberton 2000). Prerelease host preference testing can help prevent this by indicating the breadth of a biological control agent's host range. In the past, host range evaluations examined only one potential candidate for introduction in isolation from other candidates, even though a guild of natural enemies may control the pest in its native habitat (Van Driesche and Bellows 1996). We used choice tests and developmental assays to examine the preference of three lady beetle species for the hemlock woolly adelgid, *Adelges tsugae* Annand, versus selected nontarget insect species.

The hemlock woolly adelgid is found in Asia and western North America (Blackman and Eastop 1994). It was first discovered in eastern North America in Virginia in 1951 (Anonymous 1968). Hemlock woolly adelgid now occurs in the Mid-Atlantic states and southern New England on eastern hemlock, *Tsuga*

*canadensis* Carriere, and on Carolina hemlock, *Tsuga caroliniana* Englemann (Orwig and Foster 1998). Hemlock species in western North America are resistant to *A. tsugae*, but hemlock species in eastern North America can be severely injured or killed (Orwig and Foster 1998).

Chemical control of the hemlock woolly adelgid is not feasible in forested areas, and native natural enemies have not suppressed *A. tsugae* populations in North America (Montgomery and Lyon 1996, Wallace and Hain 2000). The most promising control option for *A. tsugae* is classical biological control, or the importation, release, and establishment of non-native natural enemies for control of exotic pests (Cheah and McClure 1996).

Several predatory beetles have been evaluated for biological control of *A. tsugae*. In China and Japan, coccinellids are abundant and widespread natural enemies of *A. tsugae* (Sasaji and McClure 1997, Wang et al. 1998). *Sasajiscymnus tsugae* (Sasaji & McClure) was imported from Japan in 1992, released throughout Connecticut in 1995, and is now established in localized populations throughout Connecticut (McClure et al. 2000). *Scymnus ningshanensis* Yu & Yao was imported from Yunnan province of China in 1998 and is a candidate for release (Yu et al. 2000). The third

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predator evaluated, *Harmonia axyridis* (Pallas), a native of Asia, was released for biological control of arboreal aphids (Hagen et al. 1999) and has been shown to feed on *A. tsugae* (Wallace and Hain 2000).

Environmental organizations, public officials, and land managers are concerned about potential impacts of coccinellids such as *S. tsugae*, *S. ningshanensis*, and *H. axyridis* on nontarget species, especially on the woolly alder aphid, *Paraprociophilus tessellatus* (Fitch). Woolly alder aphid is the primary prey of the butterfly *Feniseca tarquinius* F. This butterfly is the only predaceous lepidopteran in the continental United States, and its larvae depend upon woolly alder aphid and several other woolly species of Homoptera to complete their life cycles (Scott 1997).

There is limited host preference information for the three lady beetle species considered here. The host ranges of *S. tsugae* and *S. ningshanensis* have not been well documented, nor has the preference of *H. axyridis* for *A. tsugae* over other prey. Although considered a primary predator of *A. tsugae* in Japan, *S. tsugae* also was collected on grasses and shrubs at marshy sites in Japan (Sasaji and McClure 1997). Preliminary laboratory tests in New England showed that *S. tsugae* fed on *Adelges cooleyi* (Gillette) and *Pineus strobi* (Hartig) (Cheah and McClure 1996), and it has been reared on *Adelges piceae* (Ratzeburg) (C. Cheah, personal communication). The host range of *S. ningshanensis* has not been reported, but the beetle has been collected only from hemlock and reared on reproductive *A. tsugae* (Wang et al. 2000). *S. ningshanensis* has been shown in the laboratory to respond numerically to increasing densities of *A. tsugae* and in caged field studies to reduce hemlock woolly adelgid populations (Butin et al. 2003). *H. axyridis* is a well-established, generalist predator abundant throughout eastern North America (Hagen et al. 1999) and is considered by some to be a nuisance because it invades homes (Wheeler 1995). *H. axyridis* feeds voraciously on aphids (Hagen et al. 1999) and will feed on many other insects, including selected predators. In the laboratory, *H. axyridis* fed and developed on native lacewings (Phoofolo and Obrycki 1998), native coccinellid species (Cottrell and Yeorgan 1998, Yasuda et al. 2001), and eggs of at least two species of Lepidoptera (Ferran et al. 1997, Abdel-Salam and Abdel-Baky 2001).

For each of the three lady beetle species, we assayed adult feeding preference between *A. tsugae* and the woolly alder aphid. For *S. tsugae* and *S. ningshanensis*, we assayed preference between *A. tsugae* and other adelgid species present in eastern North America. In addition, for *S. tsugae* and *H. axyridis* we examined larval survival on *A. tsugae* versus *P. tessellatus* by using no-choice developmental assays.

## Materials and Methods

### Source of Predators Evaluated

*S. tsugae* adults were obtained from the Phillip Alampi Beneficial Insect Laboratory (Trenton, NJ),

and *S. ningshanensis* adults were obtained from the USDA–Forest Service Insect Rearing Facility (Hamden, CT). *H. axyridis* were field collected as pupae on the University of Massachusetts, Amherst campus, and eclosed 1 wk before the experiment. All predators were maintained at 18°C and a photoperiod of 16:8 (L:D) h on locally collected hemlock infested with ovipositing hemlock woolly adelgid. Lady beetle eggs also were obtained from these stocks, except for *H. axyridis* that were field collected.

### Choice Tests

The test arena consisted of a 9-cm petri dish with moistened filter paper on the bottom. Branch tips of eastern hemlock infested with *A. tsugae* and branch tips of the host plant with the alternate prey item were placed on opposite sides of the dish. Each branch was 2 cm in length. We chose pieces of hemlock and alternate host plants that were similar in size, so that the amount of foliage on each plant did not influence beetle preferences.

In 2001 and 2003, adult *S. tsugae* and *S. ningshanensis* used in the choice tests had eclosed 4–6 wk before testing, and *H. axyridis* had eclosed 1 wk before testing. All beetle species were starved for 24 h, and one beetle was placed in the center of each dish. The initial number of prey items was recorded for each presented prey type. We allowed each beetle to feed for 24 h at 18°C and a photoperiod of 16:8 (L:D) h. After 24 h, we removed the beetles and recorded the number of prey items remaining. Trials were conducted for each of the three lady beetles species for all choice combinations, except where indicated.

In 2001, in addition to the feeding data, we observed the dishes for the first 15 min after a beetle was added and recorded the time spent on each host plant (time spent on the dish was excluded). After the 24-h feeding period, we recorded the location of each beetle before removing it from the petri dish.

**Hemlock Woolly Adelgid versus Woolly Alder Aphid.** In 2001, woolly alder aphids were presented on their host plant, *Alnus serrulata* (Ait.) Willd. Fourth instars of *A. tsugae* were tested versus first instars of *P. tessellatus* so that alternate prey would be of comparable size. We carefully removed excess nymphs with a fine forceps so that 10 nymphs of each prey species were presented in each dish.

**Hemlock Woolly Adelgid versus Other Adelgid Species.** Separate assays were conducted to test beetle preference for adults and for eggs of *A. tsugae* versus other adelgid species found in eastern North America. Other species tested were 1) pine bark adelgid, *Pineus strobi*, on eastern white pine, *Pinus strobus* L.; 2) larch adelgid, *Adelges laricis* Vallot, on European larch, *Larix decidua* Mill.; and 3) cooley spruce gall adelgid, *A. cooleyi*, on Douglas fir, *Pseudotsuga menziesii* (Mirb.) Franco.

**Adelgid Adults.** In 2001, we tested beetle preference for adults of *A. tsugae* versus alternate adelgid species, by using one ovipositing adult of each adelgid species

**Table 1.** Prey consumed by lady beetles (mean ± SE) provided a choice of 10 nymphs each of *A. tsugae* (HWA) and woolly alder aphid (WAA) on their respective host plants for 24 h

Lady beetle	No. trials	No. nymphs consumed		Paired <i>t</i> -test <i>P</i>
		WAA	HWA	
<i>S. tsugae</i>	23	0.82 ± 0.38	2.2 ± 0.42	0.023*
<i>S. ningshanensis</i>	23	0.61 ± 0.20	3.6 ± 0.53	0.000*
<i>H. axyridis</i>	16	6.2 ± 1.2	3.2 ± 0.55	0.029*

\*, significant preference between prey types (*P* < 0.05).

on its host plant. Excess adelgids and their eggs were carefully removed with fine forceps.

**Adelgid Eggs.** In 2003, we tested beetle preference for eggs of *A. tsugae* versus the same adelgid species as in 2001, except larch adelgids were not available when we tested *S. ningshanensis*. We removed ovipositing adults from their branches, leaving only eggs. This was done to avoid error associated with differential oviposition rate between prey species. The woolly wax covering ovipositing adult adelgids was teased aside and the adults were carefully removed with fine forceps from host plants, leaving only eggs. Eggs were counted and excess were removed to provide an equal number of eggs for each of the choices in a dish. After removing adult and excess eggs, we carefully returned the woolly wax to loosely cover the remaining eggs. Generally, each choice consisted of eggs from one individual of each adelgid species. The number of eggs presented per choice ranged from 15 to 100. To obtain an estimate of counting error and loss through damage, we set up controls for each trial as described above, except that adult lady beetles were not added to the dishes. The pre- and post-trial counts of eggs in the control dishes were not significantly different (*P* > 0.05, paired *t*-test), indicating that counting error was minimal; therefore, the control data are not presented.

**Developmental Test**

We performed no-choice assays to examine development of immature lady beetles reared on *A. tsugae* or *P. tessellatus*. One egg of *S. tsugae* or *H. axyridis* was placed in a 60-ml plastic cup with either a 2-cm twig of *T. canadensis* infested with ovipositing *A. tsugae*, or a 2-cm twig of *A. serrulata* infested with *P. tessellatus* nymphs. There were 10 replicates for each predator/prey combination. Infested foliage was changed daily to ensure that beetles received ample prey throughout development. The cups were held in an environmental chamber at 18°C and a photoperiod of 16:8 (L:D)

h. We recorded the number of beetles that survived to adulthood.

**Data Analysis**

$\chi^2$  goodness-of-fit tests were used to analyze feeding and location after 24-h data from choice tests by using adult adelgids and to analyze larval survival data. Paired *t*-tests were used to analyze behavioral data (15-min observations) from choice tests, and the feeding data from choice tests by using woolly alder aphid nymphs and adelgid eggs. Statistical analyses were performed using MINITAB (Minitab Inc. 2000).

**Results**

**Choice Tests**

**Hemlock Woolly Adelgid versus Woolly Alder Aphid.** Significantly more hemlock woolly adelgids than woolly alder aphids were consumed by *S. tsugae* (*t* = -2.97, *df* = 44, *P* < 0.05) and *S. ningshanensis* (*t* = -2.69, *df* = 44, *P* < 0.05) (Table 1). We did notice *S. tsugae* and *S. ningshanensis* biting woolly alder aphids without consuming whole nymphs. Bitten nymphs did die, but we did not count them as eaten. The number of woolly alder aphids remaining in dishes containing *H. axyridis* adults (Table 1) was not significantly different than hemlock woolly adelgids (*t* = 1.53, *df* = 28, *P* > 0.05). *H. axyridis* consumed nearly 70% of the woolly alder aphid nymphs and ≈50% of the hemlock woolly adelgid nymphs.

The behavioral data (Table 2) for dishes containing *S. tsugae*, *S. ningshanensis*, and *H. axyridis* showed that there was no significant difference (*P* > 0.05) between the amounts of time any beetle species spent on hemlock or alder. After 24 h (Table 2), *S. tsugae* and *S. ningshanensis* were found significantly more often on hemlock than alder ( $\chi^2$  > 5.991, *df* = 2, *P* < 0.05 and  $\chi^2$  > 5.991, *df* = 2, *P* < 0.05, respectively), whereas *H. axyridis* was found more often on the dish than on either of the host plants ( $\chi^2$  > 5.991, *df* = 2, *P* < 0.05).

**Hemlock Woolly Adelgid versus Other Adelgid Species. Adelgid Adults.** Feeding by *S. tsugae* was low in the *A. laricis* and *A. cooleyi* trials (Table 3); 0 and 29% of the beetles fed on either host when the non-target host was *A. laricis* and *A. cooleyi*, respectively. In the *A. laricis* trial, *S. tsugae* adults did not consume adults of either prey species. In the *A. cooleyi* trial, only seven of 26 beetles fed, and this was only on *A. tsugae* ( $\chi^2$  = 32.2, *df* = 1, *P* < 0.05). When the pine bark

**Table 2.** Time (mean minutes ± SE) spent by beetles on the prey's host plant during the first 15 min in the choice arena and the total number of beetles on the host plants after 24 h, the end of the test

Lady beetle	Time on plant		<i>t</i> -test <i>P</i>	No. beetles on		$\chi^2$ <i>P</i>
	Hemlock	Alder		Hemlock	Alder	
<i>P. tsugae</i>	3.4 ± 1.2	0.41 ± 0.23	0.020*	15	2	0.000*
<i>S. ningshanensis</i>	2.9 ± 1.1	1.8 ± 0.82	0.43	9	4	0.05
<i>H. axyridis</i>	1.8 ± 0.62	3.8 ± 1.2	0.21	1	0	Counts <5

Time and presence on the dish are not included in analyses. \*, significant preference between prey types (*P* < 0.05).

**Table 3.** Prey consumed by lady beetles provided a choice of one adult of *A. tsugae* and an alternative adelgid species on their respective host plants for 24 h

Lady beetle	Alternative prey species	No. trials	Total no. beetles consuming				$\chi^2$	P
			Neither	<i>A. tsugae</i>	Alternative	Both		
<i>S. tsugae</i>	<i>P. strobi</i>	27	5	14	1	7	12.59	0.001*
	<i>A. cooleyi</i>	24	17	7	0	0	8.20	0.004*
	<i>A. laricis</i>	26	26	0	0	0	0	1.000
<i>S. ningshanensis</i>	<i>P. strobi</i>	27	6	7	9	5	0.30	0.586
	<i>A. cooleyi</i>	26	15	7	3	1	1.73	0.188
	<i>A. laricis</i>	26	18	8	0	0	9.45	0.002*

\*, significant preference between prey types based on  $P < 0.05$ .

adelgid was the alternative, significantly more adults consumed *A. tsugae* ( $\chi^2 = 15.8$ ,  $df = 1$ ,  $P < 0.05$ ). In all trials, *S. tsugae* consumed significantly fewer prey items, including *A. tsugae*, than other lady beetle species ( $F = 6.47$ ,  $df = 1$ ,  $P < 0.05$ ). The behavioral data (Table 4) showed that *S. tsugae* spent significantly more time on hemlock in the *A. cooleyi* and *A. laricis* trials ( $t = 2.69$ ,  $df = 44$ ,  $P < 0.05$ ; and  $t = 2.92$ ,  $df = 44$ ,  $P < 0.05$ , respectively), and there was no significant difference ( $P > 0.05$ ) between the amounts of time beetles spent on hemlock or white pine. After 24 h, *S. tsugae* were found significantly more often on hemlock than other locations in the *A. cooleyi* trial (Table 4) ( $\chi^2 > 5.991$ ,  $df = 2$ ,  $P < 0.05$ ). In the pine bark adelgid trial (Table 4), the numbers of beetles found in each location were nearly uniform ( $\chi^2 < 5.991$ ,  $df = 2$ ,  $P > 0.05$ ).

More than half of the 26 *S. ningshanensis* adults did not feed on adults of either prey species in the *A. laricis* ( $\chi^2 = 33.7$ ,  $df = 1$ ,  $P < 0.05$ ) and *A. cooleyi* ( $\chi^2 = 21.6$ ,  $df = 1$ ,  $P < 0.05$ ) trials (Table 3), but in the *A. cooleyi* trial, beetles that did feed showed no host preference ( $\chi^2 = 5.1$ ,  $df = 1$ ,  $P > 0.05$ ). Beetles equally consumed adults of both adelgid species ( $\chi^2 = 2.36$ ,  $df = 1$ ,  $P > 0.05$ ) in the pine bark adelgid choice test (Table 3). *S. ningshanensis* spent significantly more time (Table 4) on hemlock in the *A. laricis* trial ( $t = 2.31$ ,  $df = 44$ ,  $P < 0.05$ ). However, there was no significant difference between the amounts of time spent on hemlock or the alternate host plant (Table 4) in the *A. cooleyi* or *P. strobi* trials ( $P > 0.05$ ). After 24 h, there was no significant difference in the numbers of *S.*

*ningshanensis* (Table 4) found on hemlock or the alternate host plant species in the *A. cooleyi* and pine bark adelgid trials ( $\chi^2 < 5.991$ ,  $df = 2$ ,  $P > 0.05$ ).

**Adelgid Eggs.** In petri dishes containing *S. tsugae* (Table 5), there was no significant difference between the proportion of *A. tsugae* eggs remaining and the proportion of *P. strobi* ( $t = -0.07$ ,  $df = 18$ ,  $P = 0.94$ ) or *A. cooleyi* ( $t = -0.55$ ,  $df = 18$ ,  $P = 0.59$ ) eggs remaining. In the *A. laricis* trial, *S. tsugae* consumed significantly more ( $t = -2.29$ ,  $df = 18$ ,  $P = 0.038$ ) *A. tsugae* than *A. laricis*, and the lady beetles consumed less than half of all prey species. The proportion prey remaining was significantly higher ( $P < 0.05$ ) in the controls than in dishes containing adult beetles.

The proportion *A. tsugae* eggs remaining (Table 5) in petri dishes containing *S. ningshanensis* was not significantly different from the proportion *A. cooleyi* ( $t = 0.07$ ,  $df = 28$ ,  $P = 0.94$ ) and *P. strobi* ( $t = -0.72$ ,  $df = 28$ ,  $P = 0.48$ ) eggs remaining. The proportion prey remaining was significantly higher ( $P < 0.05$ ) in the control petri dishes than in dishes containing beetles.

#### Development of Immature Lady Beetles

Well-defined differences in ability to survive on adelgid or aphid were observed for *S. tsugae* and *H. axyridis*. Survival of immature *S. tsugae* fed woolly alder aphid was 0% (0/10) compared with 80% (8/10) survival on hemlock woolly adelgid ( $\chi^2 = 15.385$ ,  $df = 1$ ,  $P < 0.05$ ). The proportion *H. axyridis* larvae that completed development on woolly alder aphid was 90% (9/10), significantly higher than the 0% (0/10)

**Table 4.** Time (mean minutes  $\pm$  SE) spent by beetles on the prey's host plant during the first 15 min in the choice arena and the total no. of beetles on the host plants after 24 h, the end of the test

Lady beetle	Alternative prey's host	Time on plant		<i>t</i> -test P	No. beetles on		$\chi^2$ P
		Hemlock	Alternative		Hemlock	Alternative	
<i>P. tsugae</i>	White pine	2.4 $\pm$ 0.8	1.5 $\pm$ 0.7	0.45	11	9	0.53
	Douglas fir	4.5	1.1	0.012*	17	6	0.001*
		$\pm$ 1.2	$\pm$ 0.4				
	Larch	5.3	2.0	0.006*	20	6	0.000*
		$\pm$ 1.1	$\pm$ 0.6				
<i>S. ningshanensis</i>	White pine	1.4	1.1	0.72	10	7	0.30
	Douglas fir	3.0	3.4	0.59	11	13	0.56
		$\pm$ 1.1	$\pm$ 1.0				
	Larch	4.2	1.1	0.026*	22	3	0.000*
		$\pm$ 1.1	$\pm$ 0.7				

Number of trials per beetles tested is shown in Table 3. \*, significant preference between prey types based on  $P < 0.05$ .

Table 5. Number of eggs consumed (mean ± SE) by lady beetles confined for 24 h with an equal no. of eggs in situ of *A. tsugae* and an alternative adelgid species

Lady beetle	Alternative species	No. trials	Eggs consumed		Paired <i>t</i> -test <i>P</i>
			Alternative	<i>A. tsugae</i>	
<i>S. tsugae</i>	<i>P. strobi</i>	10	7.7 ± 2.1	7.9 ± 2.5	0.959
	<i>A. cooleyi</i>	10	10.2 ± 2.4	13.0 ± 2.7	0.434
	<i>A. laricis</i>	10	6.4 ± 1.8	17.1 ± 3.8	0.022*
<i>S. ningshanensis</i>	<i>P. strobi</i>	15	9.0 ± 1.9	13.8 ± 2.8	0.118
	<i>A. cooleyi</i>	15	10.3 ± 1.9	9.6 ± 1.8	0.710

\*, significant preference between prey types based on *P* < 0.05.

survival of those fed hemlock woolly adelgid ( $\chi^2 = 16.36$ , *df* = 1, *P* < 0.05).

Discussion

The two lady beetles imported specifically for biological control of the hemlock woolly adelgid, *S. tsugae* and *S. ningshanensis*, fed very little and could not develop on the woolly alder aphid. Our results indicate that the woolly alder aphid will not be attacked by either *S. tsugae* or *S. ningshanensis*, so the lady beetles should have no impact on *F. tarquinius*. Our assay using prey choices of similar size (first instars of aphids and fourth instars of adelgids) indicates that factors other than size, such as taste, may be involved in determining host preference.

*H. axyridis*, in contrast, preferred woolly alder aphid to hemlock woolly adelgid, and its newly hatched larvae did not survive on the latter. Although *H. axyridis* did not prefer *A. tsugae*, it did consume approximately half of *A. tsugae* eggs offered. Moreover, *H. axyridis* larvae completed development on a diet of woolly alder aphid, but they did not develop past the second instar on a diet of hemlock woolly adelgid. We also noted that *H. axyridis* spent more time on alder than hemlock foliage. In the field, we have observed all stages of *H. axyridis* on the woolly alder aphid and believe that it is a common host in nature, although ants tending the aphid may limit its impact on aphid populations. We also have observed high densities of both *H. axyridis* and its eggs on hemlock foliage heavily infested by hemlock woolly adelgid very early in the season, before appearance of aphids on trees. Thereafter, larval and pupal cases are found in very low numbers. *H. axyridis* was among the most abundant predators of *A. tsugae* in North Carolina and Virginia, but cage exclusion of it and other predators did not significantly affect adelgid populations (Wallace and Hain 2000).

There are a variety of other adelgid species present in eastern North America that are potential alternate prey for these lady beetles. In total, the family Adelgidae contains ≈50 described species in two genera, *Adelges* and *Pineus* (Blackman and Eastop 1994). Five *Adelges* and seven *Pineus* species are reported to have populations in eastern North America. The *Adelges* species, including *A. tsugae*, are not native to this region. *A. cooleyi* is native to western North America and can cause esthetic damage to Engelmann spruce,

*Picea engelmanni* Parry, and Douglas fir when planted as ornamentals and in Christmas tree plantations (Campbell and Balderston 1972). Likewise, *Adelges abietis* (L.), introduced from Europe, causes esthetic damage to introduced Norway spruce, *Picea abies* (L.) Karsten, and native white spruce, *Picea glauca* (Moench) Voss (Mattson et al. 1994). *A. piceae* was introduced from Europe ≈1900 and is a serious pest of balsam fir, *Abies balsamea* (L.) Mill., and Fraser fir, *A. fraseri* (Pursh) Poir (Balch 1952, Arthur and Hain 1984). *A. laricis* is part of a large species complex for which the taxonomy has not been well resolved (Blackman and Eastop 1994). It is thought to be native to alpine Europe (Steffan 1970); however, potential synonymy with other species found in Asia make this uncertain. In eastern North America, it is found on Tamarack, *Larix laricina* (Du Roi) K. Koch and European larch. It is not considered a serious pest on either species.

Of the seven *Pineus* species in eastern North America, two are introduced and the remaining five are considered native. *Pineus boernerii* Annand and *Pineus pineoides* (Cholodkovsky) are introduced species that feed on red pine, *Pinus resinosa* Aiton, and red spruce, *Picea rubens* Sarg., respectively (Underwood 1963, McClure 1982). *P. strobi* is common on the bark and shoots of eastern white pine. *Pineus colorodensis* (Gillette) is found on a variety of pine species across North America (Annand 1928, Doane 1961), and *P. similis* has been reported on several spruce species across Canada (Cumming 1962). Both *Pineus floccus* (Patch) and *Pineus pinifoliae* (Fitch) host alternate between native spruces and eastern white pine (Annand 1928, Lowe 1965). In eastern North America, *Pineus* species are generally innocuous, but they can occasionally produce outbreaks that damage trees, especially in plantations and where trees are grown outside their native range (DeBoo et al. 1964, McClure 1982).

Choice tests within the family Adelgidae did not produce results as unequivocal as the tests between and the woolly alder aphid and the hemlock woolly adelgid. Choice tests with eggs showed that this stage was readily eaten by both *S. tsugae* and *S. ningshanensis*, with little preference for eggs of *A. tsugae* or the alternative adelgid species, except for a nonpreference for the larch adelgid by *S. tsugae*. A peculiarity of the tests with adult adelgid prey is that *S. tsugae* consumption of *A. tsugae*, as well as the alternative host, was low except in the tests with *P. strobi*. *S. tsugae*

preferred *A. tsugae* to *P. strobi* and *A. cooleyi*, whereas *S. ningshanensis*, showed a preference only for *A. tsugae* over *A. laricis*. During the behavioral observations *S. ningshanensis* explored the environment more than *S. tsugae* and were found equally on most alternate host plants and hemlock. In the *P. strobi* trial, equal numbers of *S. tsugae* adults were found on white pine and hemlock, which may be because the white pine twigs had slightly denser foliage than other alternate species tested. Although *S. tsugae* and *S. ningshanensis* may feed on several species of Adelgidae, they pose little threat to nontarget species of concern.

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