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Competitor Avoidance Drives Within-Host Feeding Site Selection in a Passively-Dispersed Herbivore

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Abstract

1. Evolutionary theory predicts that ovipositing females that can actively disperse should select hosts that increase offspring performance. However, for organisms that are exclusively passively-dispersed feeding site selection is only possible at the within-host level. This should be particularly important for their offspring which have strong temporal and spatial dispersal constraints within a host. Such constraints will be likely magnified by tissue quality heterogeneity caused by competing herbivores.

2. We investigated within-host feeding site selection of passively-dispersed neonates of a sessile herbivore, the hemlock woolly adelgid (*Adelges tsugae* Annand) when it shares its eastern hemlock (*Tsuga canadensis* Carrière) host, with another sessile herbivore, the elongate hemlock scale (*Fiorinia externa* Ferris). Within-host feeding site selection was studied at the (a) shoot level (with or without *F. externa*) using choice tests and (b) needle level by scoring insect presence in field surveys.

3. *A. tsugae* avoided *F. externa*-colonized foliage in both the choice tests and field surveys. Since *A. tsugae* has no efficient predators or parasitoids in the study area, we conclude that our results are due to the presence of the competing herbivore.

4. Even though *A. tsugae* cannot actively disperse among hosts, we showed that within-host feeding site selection is an important mechanism to minimize the co-occurrence with a competing herbivore that has known negative impacts on *A. tsugae* population densities. Studying within-host feeding site selection in a multiple-species context could assist in understanding and predicting the impact of destructive pests such as *A. tsugae* and the co-evolution with their novel hosts.

Introduction

Evolutionary theory predicts that ovipositing females capable of discriminating between hosts should lay eggs on those hosts that increase the performance of their offspring (Thompson, 1988; Gripenberg *et al.*, 2010). Most studies on herbivore behavior to date have focused on quality differences at the whole-plant level, comparing adult and/or offspring's preference among different genotypes or phenotypes within a plant species and the relationship between preference and offspring performance (Horner & Abrahamson, 1992; van Leur *et al.,* 2008; Kleine & Müller, 2011; Nyman *et al.,* 2011; Soler *et al.*, 2012). Although selecting a high-quality host is an important first step in maximizing the performance of future offspring, assessing multiple hosts is impossible for some organisms such as passively-dispersed herbivores. As a result, the selection of suitable feeding locations for such organisms is only possible at the within-host level. Because of ubiquitous within-plant heterogeneity in food quality (Shelton, 2004) and its potential impact on plant-herbivore interactions (Awmack & Leather, 2002), the ability to select feeding sites within a given host may prove crucial to offspring performance. Evidence shows that herbivores display different preferences between tissues within a host and this can be affected by prior herbivory or other factors extrinsic to the host plant (McAuslane & Alborn, 2000; Anderson & Agrell, 2005; Gómez *et al.,* 2007; 2008). In the case of passively-dispersed organisms, we expect they will be subjected to particularly strong selective pressure to evolve mechanisms to discriminate quality differences within the host plant upon landing. To our knowledge, not much is known about preference of passively-dispersed herbivores and the link to offspring performance.

Within a given host, variation in resource quality (and subsequent herbivore preference) can be driven by ontogenetic differences in the foliage. Young foliage is richer in nitrogen and water content (Mattson, 1980) and usually more palatable than older foliage (Coley & Barone, 1996; Fenner *et al.*, 1999; Gómez *et al.*, 2008). Variation in within-host resource quality can also be affected by the presence of other conspecific or heterospecific herbivores. Feeding by competing herbivores can change host quality via altered resource concentration and composition and/or the induction of defense compounds (Karban & Baldwin, 1997). These changes can be especially important in interactions between temporally-separated herbivore species. Later-arriving herbivores can experience suboptimal growth and development on a host that has suffered prior herbivory (Inbar *et al.*, 1999; Soler *et al.*, 2007) because changes in foliage quality can persist over extended periods of times (Gómez *et al.*, 2010; Underwood, 2012).

Within-host feeding site selection is especially important for herbivores whose active dispersal within a host is constrained by spatial and/or temporal limitations (Burstein & Wool, 1993). Herbivores with limited spatial mobility across all life stages might experience strong intraspecific competition due to limited resource availability. Similarly, time-limited dispersers, such as those that suffer high mortality rates within hours after hatching (Itioka & Inoue, 1991) will be forced to settle in suboptimal feeding sites if a suitable location is not found after an initial habitat discrimination phase is over (Ward 1987). Such spatial and temporal constraints apply to the hemlock woolly adelgid (*Adelges tsugae* Annand). *A. tsugae* is a destructive non-native hemipteran pest introduced to the eastern United States from Japan. It is currently present in 18 states, covering over 45% of the eastern hemlock's range (Morin *et al.*, 2011). In the invaded range, *A. tsugae* feeds exclusively on the native eastern and Carolina hemlocks (*Tsuga canadensis* Carrière and *T. caroliniana* Engelm, respectively), killing its hosts in as little as four years (McClure, 1991). Stands of these long-lived and shade-tolerant conifers create cool and moist microclimates, critical habitat for a wide range of plant and animal species (Orwig *et al.*, 2012). The invasion by *A. tsugae* is devastating hemlock forests and dramatically altering the surrounding forest ecosystems (Orwig & Foster, 1998; Jenkins *et al.*, 1999; Stadler *et al.*, 2005; Cobb, 2010). Because viable *A. tsugae* neonates ('*crawlers*') in the invaded range are wingless, between-host movement of *A. tsugae* occurs via passive dispersal by wind or animals (McClure, 1991; Turner *et al.*, 2011). *A. tsugae* dispersal is also temporally limited since crawlers are only mobile for several days; once they settle and begin feeding, they are sessile for the remainder of their life cycle, including the mature stages (McClure, 1987). Despite the limitations imposed on between-host dispersal, the newly-hatched crawlers are mobile and capable of active within-host dispersal, typically settling on the youngest hemlock foliage (McClure, 1989). Because sessile *A. tsugae* adults must oviposit *in situ*, within-host selection of feeding sites by the newly-hatched crawlers may be crucial for their survival and future fitness.

In its invaded range, *A. tsugae* frequently co-occurs on eastern hemlock with a second non-native hemipteran pest, the elongate hemlock scale (*Fiorinia externa* Ferris). *A. tsugae* and *F. externa* overlap throughout much of their invaded range, and are found in the same hemlock stands and on the same individual trees (Preisser *et al.*, 2008). *F. externa* also feeds preferentially on eastern hemlock and, like *A. tsugae*, continues to expand its invaded range (Preisser *et al.*, 2008; 2011). At low to moderate densities, *F. externa* has minimal impacts on its host (Miller-Pierce *et al.*, 2010; Radville *et al.*, 2011; Gonda-King *et al.*, 2012); at high densities, however, it may be able to kill already-stressed trees (McClure, 1980). There is strong evidence of interspecific competition between *A. tsugae* and *F. externa* (Preisser & Elkinton, 2008). Because *A. tsugae* crawlers are produced mid-summer, 1-2 months after *F. externa* crawlers have settled and begun to feed, *F. externa*-induced changes in host quality could alter *A. tsugae* performance.

This hypothesis is consistent with the results of a previous study showing a 40% decrease in *A. tsugae* population density in trees previously infested with *F. externa* for two years (Miller-Pierce & Preisser, 2012). If this difference in *A. tsugae* performance can alter its settling behavior, a selective advantage will accrue to crawlers capable of detecting and avoiding *F. externa*-infested foliage within a host.

Here we examine tissue selection and distribution of *A. tsugae* crawlers in the presence and absence of *F. externa*. Because crawlers are small, few studies have explored patterns of distribution within or between hosts (but see Evans & Gregoire, 2007, Turner *et al.*, 2011), and to our knowledge no previous studies have addressed active within-host feeding site selection. Because adult *A. tsugae* have no effective predators in the invaded range (Wallace & Hain, 2000; Havill *et al.* 2011), within-tree crawler movement is likely driven by the need to find a permanent feeding site and by the site-specific likelihood of competition with other herbivores. Specifically, we hypothesized that *A. tsugae* prefers uninfested eastern hemlock foliage over *F. externa*-infested foliage. We tested our hypothesis by conducting laboratory choice tests and field surveys.

Materials and methods

Herbivores: *A. tsugae* has two generations a year in its invaded range (McClure, 1987). Briefly, the April-to-June progrediens generation emerges in early spring and settles on previously-produced hemlock foliage, where it produces ~75 eggs/female. In contrast, crawlers from the July-to-April sistens generation settle on newly-produced foliage in mid-summer. They aestivate until late fall, then feed throughout the winter, producing ~300 eggs/female that will become the next progrediens generation. *F. externa* has only one generation in the northern part of the invaded range; *F. externa* crawlers emerge in late spring and are the first herbivores to settle on newly-produced hemlock foliage (Abell, 2010). The mobile *F. externa* crawlers also settle on young foliage and reduce host nitrogen levels (McClure, 1980; Gómez *et al.*, 2012). While *A. tsugae* feeds at the base of hemlock needles by inserting its stylet bundle into ray parenchyma cells at the base of the needle cushion (Young *et al.*, 1995), *F. externa* crawlers settle on the underside of the needles, where they suck fluids from the mesophyll cells (McClure, 1980). Both herbivores' crawlers remain sessile once they settle.

Laboratory choice tests: We conducted choice tests to test whether *A. tsugae* crawlers showed preference for uninfested vs. *F. externa*-infested foliage within the same tree. In April 2012, forty-seven eastern hemlocks naturally infested with *F. externa* were haphazardly selected in the Middlesex Fells Reservation (Winchester, MA). In each tree, two ~5 cm shoots produced during the previous growing season were selected, one collected from an uninfested branch and the other having at least five adult *F. externa* settled on the needles (= 47 replicates). All of the selected foliage was carefully inspected for the presence of *A. tsugae* or any other non-*F. externa* herbivores; there was no evidence of *A. tsugae* or other herbivores on any of the shoots.

In addition to investigate *A. tsugae* preference in naturally-infested trees, we conducted a second set of laboratory choice tests using foliage sources from nursery-purchased trees to control for unknown factors governing *F. externa* infestation in the field. These choice tests were conducted following the same procedure as above but using uninfested and infested foliage (minimum two scale present) from eastern hemlock saplings manually inoculated yearly with *F. externa* in June 2011 and 2012. The saplings were planted in the understory of a mixed conifer-deciduous forest in Kingston, Rhode Island. By enforcing the infestation of *F. externa* on a given set of experimental trees rather than using naturally-infested trees we can rule out the possibility that the *F. externa* foliage used in the choice tests were successfully infested by *F. externa* due to unknown traits of the host rather than by chance and the possibility that *A. tsugae* behavioral patterns in feeding site selection were due to innate differences in preference/survival across hosts (or tissues within hosts) by these two insects. In a subset of those tests (n=30), *F. externa* remained intact on the infested foliage, while in a second subset (n=32) *F. externa* was manually removed from the foliage to determine whether *A. tsugae's* preference is driven by the physical presence of the scale or by *F. externa*-induced changes in the foliage quality.

In all choice tests, the base of each shoot was placed inside an eppendorf tube with a pierced lid filled with deionized water to avoid desiccation. Both tubes were taped to the bottom lid of a 9 cm diameter petri dish. Eastern hemlock foliage with *A. tsugae* egg masses was collected from naturally-infested trees and a small stem fragment with three *A. tsugae* egg masses was placed inside each petri dish touching both shoots (Fig. 1b). The petri dishes were closed and sealed with parafilm and placed on their sides so that the shoots were in an upright position at 21^{o}C and natural light conditions. We inspected each petri dish daily for the presence of *A. tsugae* crawlers. Once *A. tsugae* crawlers were detected, the inoculants were removed and the crawlers allowed to choose between the two foliage types. Seven days after *A. tsugae* crawlers were first detected, the number of *A. tsugae* crawlers on each shoot was counted and the percentage of crawlers on each choice was calculated. A sign test was used to assess whether *A. tsugae* crawlers prefer uninfested foliage by comparing the number of replicates with a higher percentage of crawlers on uninfested versus *F. externa*-infested foliage. The second set of choice tests (experimental trees) was analyzed by using a repeated measures ANOVA on the amount of crawlers present on either choice at the end of the test, using infestation by *F. externa* (uninfested vs infested foliage) as the within-subjects factor and the removal of *F. externa* from the infested foliage (yes/no) as the between-subjects factor.

Field surveys: We conducted three surveys of *A. tsugae* preference in the field. Three hemlock stands were selected based on their moderate densities of naturally-occurring *A. tsugae* and *F. externa* (11-100 insects/m branch) as shown by 2011 field surveys (Preisser *et al.*, 2011). The stands were located in Massachusetts (Belchertown and Hampden; sampled on June 21st, 2012) and Connecticut (Suffield; sampled on July 2nd, 2012). In each site we selected 25 trees infested with both insects. In each tree, we selected two ~5 cm new-growth shoots (i.e., produced during the 2012 growing season) that were infested with at least three *A. tsugae* and three *F. externa* individuals. We counted the number of needles on each shoot with neither insect, *A. tsugae* only, *F. externa* only, or both insects. The results from the two shoots per tree were averaged and the expected distribution of needles in each category analyzed using a 2x2 contingency table. Because there were no statistical differences among sites (Likelihood ratio test; site effect: $\chi^2 = 0.9261$, $P = 0.629$), data from the three sites were pooled in the analysis.

Results

Laboratory choice tests: *A. tsugae* crawlers chose uninfested foliage over *F. externa*-infested foliage from the same tree in both naturally- and artificially-infested with *F. externa* trees. In choice tests using naturally-infested trees, 32 of 47 (68%) choice tests, the majority of *A. tsugae* crawlers were present on the uninfested foliage (one-tailed Sign test $P = 0.015$; Fig 1a). Although there was considerable variation in the percentage of *A. tsugae* crawlers choosing uninfested foliage, 23 of 47 choice tests had between 51-75% of crawlers on the uninfested foliage (Fig 1c). Interestingly, the percentage of *A. tsugae* crawlers on *F. externa*-infested foliage was not correlated with the amount of *F. externa* present on the foliage (Pearson correlation = -0.087, P = 0.561; Fig 1d). In choice tests using foliage from experimentally inoculated trees, *A. tsugae* crawlers also exhibited an overall preference for uninfested foliage (Insect infestation P <0.0001), regardless of whether *F. externa* was left intact on the foliage or manually removed (Insect infestation x Insect removal P = 0.194; Fig 2).

Field surveys: Our field surveys found that *A. tsugae* and *F. externa* co-occurred less often than expected ($\chi^2 = 19.04$, $P < 0.0001$; Table 1). Had *A. tsugae* been randomly distributed with respect to *F. externa*, 3.1% of needles should have contained both insects. Our results show that *A. tsugae* and *F. externa* only co-occurred on 1.8% of needles, meaning that the observed value was 42% lower than expected. Conversely, *A. tsugae* and *F. externa* occurred alone more often than expected if both species were randomly distributed with respect to the other.

Discussion

We found both experimental and survey evidence for active within-host feeding site selection in *Adelges tsugae*. Specifically, we found that *A. tsugae* crawlers preferred foliage that lacks the competing herbivore *F. externa* in both laboratory choice tests and field surveys of naturally-infested trees. The lower preference for *F. externa*-infested foliage was driven by plant-mediated changes on the foliage caused by *F. externa's* attack rather than the physical presence of this insect. This demonstrates that relying on passive between-host dispersal does not preclude *A. tsugae* (and, presumably, many other small-bodied insects) from actively choosing a suitable feeding site within a given host.

Insect performance will inevitably differ across hosts of the same species because of varying genotypic and ontogenetic host quality, which is in turn influenced by abiotic factors such as nutrient availability and by biotic factors such competing herbivores (Cronin & Abrahamson, 1999). While differences in host quality are important for all herbivores, they are perhaps most critical for sessile species that must quickly assess host quality before settling irrevocably in a single location (Ward 1987). In such organisms, the success of newly-hatched juveniles thus depends upon the quality of their natal host or being dispersed to a new suitable host.

Our results showed that *A. tsugae* crawlers could discriminate between *F. externa*-infested foliage at the shoot level (choice tests) and at the needle level (field survey). In the laboratory, 68% of the choice tests had more *A. tsugae* crawlers on uninfested foliage than on *F. externa*-infested foliage from *F. externa* naturally-infested trees. This preference was particularly evident in choice tests conducted on experimentally infested trees, with a known prior history of no infestation, where on average approximately twice as many *A. tsugae* crawlers showed preference for uninfested foliage. In the field, the co-occurrence of *A. tsugae* and *F. externa* on the same needle occurred 42% less often than expected if both insects were randomly distributed with respect to each other. Because *F. externa* crawlers settle on the surveyed newly-produced foliage earlier in the summer than *A. tsugae* crawlers, the most likely explanation for our results is that the presence of settled *F. externa* drives *A. tsugae* preference and settlement through plant-mediated changes in foliage quality. The possibility of apparent competition can also be ruled out since *A. tsugae* has no efficient predators in the invaded range or parasitoids worldwide (Wallace & Hain, 2000; Havill *et al.*, 2011).

Our results showed that *A. tsugae* has a lower preference for *F. externa*-infested shoot regardless of the number of *F. externa* present on the infested shoot. This suggests that the foraging cue *A. tsugae* uses to avoid *F. externa* is not density-dependent. Instead, a presence/absence cue might be used as a longer-range detection mechanism to identify (and subsequently avoid) a broader tree area infested with *F. externa*. This is advantageous because in tree hosts where *F. externa* density is not high, their distribution is initially very patchy within the tree (Preisser, *unpublished data*). Although we found that *A. tsugae* has a lower preference for *F. externa*-infested foliage, we still observed co-occurrence in the field and especially in the laboratory choice-tests. One possible explanation is that *A. tsugae* has not yet adapted to avoid *F. externa*-infested foliage to a larger extent. While *A. tsugae* invaded New England in the late 1980s (McClure & Cheah, 1999), the rapid spread of *F. externa* through this area began in the early 2000s (Preisser *et al.*, 2008); as a result, the co-occurrence of high-density populations of both species is a relatively new event. It is also possible that while *A. tsugae* prefers to settle on *F. externa*-free foliage, it will settle in a suboptimal location rather than incur the risk of increased mortality associated with continued searching for a feeding location.

The fact that *A. tsugae* is obligately asexual in its invaded range (McClure, 1987) might constrain selection for *F. externa* avoidance; since all offspring are clones of their parent, the only source of genetic variation is randomly-occurring mutations in a given individual. The lack of sexual reproduction, and the recombination that results, might limit the adelgid's ability to adapt to avoid a competing herbivore. Despite this limitation, there is some evidence that adelgids in the invaded range have differentiated in response to strong selection; specifically, northern adelgid clones are more tolerant to cold winter temperatures than their southern counterparts (Butin *et al.*, 2005). The authors of this paper suggest that the extremely high rates of adelgid fecundity - a single female can produce >300 eggs in one generation – might produce so many individuals that even 'rare' random mutations could often occur. If avoiding *F. externa* foliage increases *A. tsugae* fitness, as suggested by higher *A. tsugae* population growth rate on uninfested versus *F. externa*-infested trees (Miller-Pierce & Preisser, 2012), mutations that promote *F. externa* avoidance (or quality discrimination in general) could provide a substantial fitness advantage to the clonal line.

Despite being the more recent invader in New England, *F. externa* has now exceeded the northern range of *A. tsugae* and is present in areas that currently lack the adelgid. If *F. externa* can lower *A. tsugae* densities (Miller-Pierce & Preisser, 2012), and therefore tree mortality (Preisser *et al.*, 2008), hemlock stands previously colonized by *F. externa* might derive some benefit from the presence of this second invasive herbivore. Alternately, the ability of *A. tsugae* to efficiently discriminate against *F. externa*-infested foliage within a host might minimize the potential benefits of *F. externa* infestation. Future research should investigate what herbivore induced plant-mediated traits influence within-host feeding site selection and whether they are similar in response to hetero- and conspecific herbivores.

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Contribution of authors

SG designed the project with intellectual contributions from all authors, SG and LGK collected and analyzed the data and all authors contributed to the writing of the manuscript.

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Figure Legends

Figure 1. (a) Percentage of choice tests with the majority of *A. tsugae* crawlers on uninfested foliage (white) or *F. externa*-infested foliage (gray); (b) Typical choice test experimental set-up; (c) Frequency distribution of choice tests with different ranges of *A. tsugae* crawler percentage on uninfested foliage; (d) Correlation between *A. tsugae* crawlers on *F. externa*-infested foliage and number of *F. externa* present on the infested foliage.

Figure 2. Average number (+ standard error) of *A. tsugae* crawlers on uninfested (white) or *F. externa*-infested (gray) foliage sampled from manually inoculated trees in laboratory dual choice tests. *F. externa* was left intact on the foliage in a subset of choice tests (left bars; n=30) and it was manually removed from the infested foliage in a second subset (right bars; n=32).

Figure 1

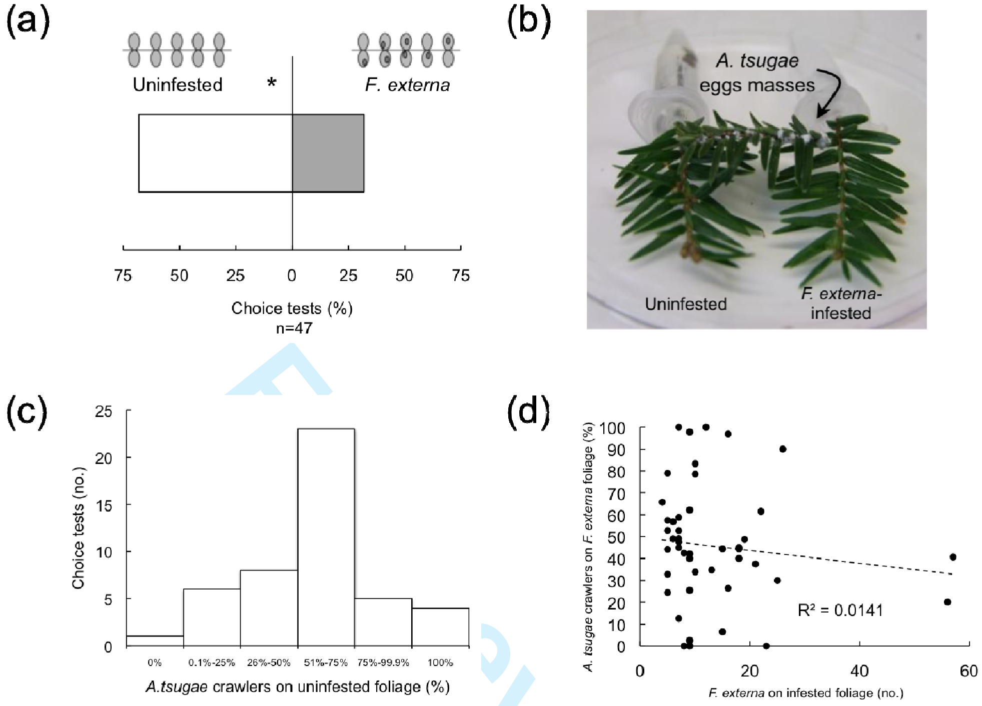
(a)
Uninfested
*
F. externa
75
50
25
0
25
50
75
Choice tests (%)
n=47
(b)
A. tsugae
eggs masses
Uninfested
F. externa-
infested
(c)
Choice tests (no.)
25
20
15
10
5
0
0%
0.1%-25%
26%-50%
51%-75%
75%-99.9%
100%
A.tsugae crawlers on uninfested foliage (%)
(d)
A. tsugae crawlers on F. externa foliage (%)
100
90
80
70
60
50
40
30
20
10
0
R² = 0.0141
0
20
40
60
F. externa on infested foliage (no.)

Figure 2

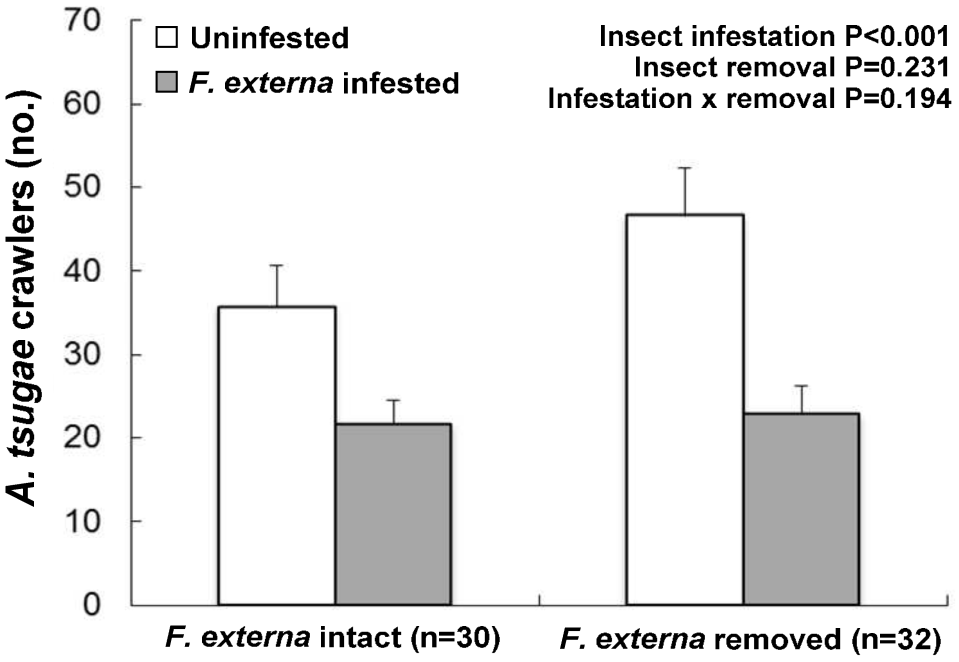
70
60
50
40
30
20
10
0
A. tsugae crawlers (no.)
□ Uninfested
▨ F. externa infested
Insect infestation P<0.001
Insect removal P=0.231
Infestation x removal P=0.194
F. externa intact (n=30)
F. externa removed (n=32)

Table 1. Observed counts of *A. tsugae* and *F. externa* on individual needles of eastern hemlock naturally occurring in the field. Numbers in brackets represent the expected values.

		A. tsugae	
		Absent	Present
F. externa	Absent	1556 (1586)	339 (308)
	Present	408 (377)	43 (73)