Trissolcus japonicus (Hymenoptera: Scelionidae) Causes Low Levels of Parasitism in Three North American Pentatomids Under Field Conditions

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Abstract

Trissolcus japonicus (Ashmead), an Asian parasitoid of Halyomorpha halys (Stål) (Hemiptera: Pentatomidae), was first detected in North America in 2014. Although testing in quarantine facilities as a candidate for classical biological control is ongoing, adventive populations have appeared in multiple sites in the United States, Canada, and Europe. Extensive laboratory testing of T. japonicus against other North American pentatomids and H. halys has revealed a higher rate of parasitism of H. halys, but not complete host specificity. However, laboratory tests are necessarily artificial, in which many host finding and acceptance cues may be circumvented. We offered sentinel egg masses of three native pentatomid (Hemiptera: Pentatomidae) pest species (Chinavia hilaris (Say), Euschistus conspersus Uhler, and Chlorochroa ligata (Say)) in a field paired-host assay in an area with a well-established adventive population of T. japonicus near Vancouver, WA. Overall, 67% of the H. halys egg masses were parasitized by T. japonicus during the 2-yr study. Despite the ‘worst case’ scenario for a field test (close proximity of the paired egg masses), the rate of parasitism (% eggs producing adult wasps) on all three native species was significantly less (0.4–8%) than that on H. halys eggs (77%). The levels of successful parasitism of T. japonicus of the three species are C. hilaris > E. conspersus > C. ligata. The potential impact of T. japonicus on these pentatomids is probably minimal.

Key words: classical biological control, parasitoid, invasive species

Classical biological control, involving the importation and release of a natural enemy from the native range of an exotic pest, has long been considered an ideal management tactic. If successful, the exotic pest may be suppressed to the point where control measures, especially pesticides, can be reduced or eliminated. There are numerous examples of successful introductions resulting in substantial control of the target pest without further intervention (DeBach 1962, Caltagirone 1981, Van Driesche and Hoddlle 2017). However, the potential for imported natural enemies to significantly harm nontarget species has become increasingly controversial (Howarth 1983, 1991; Simberloff and Stiling 1996; Follett and Duan 2000; Louda et al. 2003b; Bigler et al. 2006; Messing and Wright 2006; Van Lenteren et al. 2006). Concerns about these possible nontarget effects have led to stricter regulations regarding the release of nonnative natural enemies (Babendreier et al. 2006). At least 25 countries require host range testing to predict nontarget effects (Van Lenteren et al. 2003), and the granting of approval for release is biased toward natural enemies with narrow host ranges (Louda et al. 2003a).

The brown marmorated stink bug, Halyomorpha halys (Stål) (Hemiptera: Pentatomidae), exhibited rapid population growth in its introduced ranges in the United States and Europe. This success, coupled with the poor performance of indigenous natural enemies (Haye et al. 2015, Herlihy et al. 2016, Ogburn et al. 2016, Abram et al. 2017, Dieckhoff et al. 2017), is consistent with the ‘enemy release hypothesis’ (Ogburn et al. 2016, Heimpel and Mills 2017, Hamilton et al. 2018). Fundamentally, classical biological control seeks to reverse the effects of this phenomenon by restoring the biotic pressure absent in the pest’s invaded range (Hoddle 2004).

Trissolcus japonicus (Ashmead), a scelionid egg parasitoid of H. halys, is considered an important natural enemy in the latter’s native range (Yang et al. 2009, Zhang et al. 2017). When its potential as a biological control agent was recognized, T. japonicus was imported from Asia to quarantine facilities in the United States to assess its physiological host range (Lara et al. 2016, Abram et al. 2017, Hedstrom et al. 2017, Botch and Delfosse 2018, Buffington et al. 2018). Recently, studies of its ecological host range were performed in its native range of northern China (Zhang et al. 2017). Both lines of research revealed a high degree of association between T. japonicus and H. halys, although it also attacks other pentatomid species in multiple genera. However, the relevance of these studies to North American ecosystems is limited by the artificial conditions of quarantine experiments and the differences
between Chinese and North American faunas of Pentatomidae, respectively.

While quarantine studies were underway, adventive populations of *T. japonicus* were found in Maryland in 2014 (Talamas et al. 2015a), the Pacific Northwest in 2015 (Milnes et al. 2016, Hedstrom et al. 2017), and other areas of the mid-Atlantic and Midwest (https://www.stopinmsb.org/biological-control/samurai-wasp-trissolcus-japonicus/). Other recent detections of *T. japonicus* include northern Italy (Sabbatini Peverieri et al. 2018), Switzerland (Stahl et al. 2018), British Columbia, and Canada (Abram et al. 2019b). These adventive populations have generally been welcomed as positive developments in the fight against *H. halys* (Hamilton et al. 2018), and efforts are underway in the United States to expand the distribution of *T. japonicus* within the borders of those states in which it has been detected (K. Hoelmer, personal communication; Jentsch 2017). Pesticidal control measures have had negative side effects, making biological control, especially that involving imported Asian parasitoids, the most promising long-term solution (Leskey et al. 2012).

The establishment of *T. japonicus* in Washington state provides an opportunity to examine its ecological host range in a novel environment, using species not present in its native range. We present here the levels of parasitism of *T. japonicus* on three nontarget pentatomids in field settings where the parasitoid is well established.

**Materials and Methods**

Field paired-host assays were conducted using sentinel egg masses in June–August of 2017 and 2018 at two sites near Vancouver, WA. One was the site where *T. japonicus* was originally detected in western North America (Milnes et al. 2016), and the other site was 5.9 km away. The sites had adventive populations of *T. japonicus*, in that no releases were performed in this area. Both sites contained a mixture of native and introduced vegetation in suburban Vancouver, and included plant hosts (e.g., *Catalpa, Acer, Ailanthus*) of *H. halys*. Vancouver was the location of the first reported find of *H. halys* in the state in 2010 (Zack et al. 2012), and it was well established and abundant at the time this study was initiated. In addition, all three native pentatomid species had been collected in the Vancouver area.

Three native pentatomids (Hemiptera: Pentatomidae) (*Chinavia hilaris* (Say), *Euschistus conspersus* Uhler, and *Chlorochroa ligata* (Say)) and *H. halys* were field-collected in eastern Washington and reared in an insectary at the Irrigated Agriculture Research & Extension Center in Prosser, WA. All species were reared in small insect cages (60 × 60 × 60 cm, BugDorm 6M-610, MegaView Science, Taiwan), held at 24°C, 60–70% relative humidity, and artificial lighting (16:8 photoperiod). Nymphs and adults were kept in separate cages to minimize cannibalism. Colony diets consisted of potted lime bean plants (*Phaseolus lunatus* L.), fresh vegetables (carrots, beans, and corn), hazelnuts, and sunflower seeds. All eggs used in the assay were fresh (as opposed to frozen) and <48 h old at the time of deployment in the field. Egg masses from the colony were transferred to a piece of cardstock on top of double-sided sticky tape. After the eggs were in place, the cardstock was dipped in fine-grained sand to coat the exposed sticky tape surface so that parasitoids did not become entrapped. The initial number of intact eggs was recorded before deployment. The average egg mass sizes for the four species were: *H. halys*, 26.6 ± 0.4 (n = 90); *C. hilaris*, 20.6 ± 1.7 (n = 34); *E. conspersus*, 11.9 ± 0.7 (n = 29); *C. ligata*, 24.4 ± 2.1 (n = 27). No attempt was made to control for egg mass size.

The egg masses were transported to the research sites and deployed on *Acer circinatum* Pursh (Sapindales: Aceraceae) or *Catalpa* sp. (Lamiales: Bignoniaceae). The pieces of cardstock bearing the egg masses were attached to the underside of leaves with an insect pin about 2 m from the ground. The egg masses were placed 3–4 cm apart (similar to a laboratory paired-host assay). In all replicates, the egg mass of the native species was paired with a *H. halys* egg mass. The egg masses were left in place for 2–5 d (x = 3.6 d), then returned to the laboratory to determine egg fate. Predation was categorized using the method of Morrison et al. (2016). Live *H. halys* nymphs and adult parasitoid emergence were recorded daily between 7 and 21 d, and parasitoids were identified to species using the key of Talamas et al. (2015b). Unhatched eggs were dissected after 6 wk, and classified as pentatomid nymphs, unemerged adult parasitoids, or undifferentiated black liquid (aborted eggs, cause undetermined). Pairs were replicated over time as fresh egg masses became available, with 27–34 replicate pairs for each native species.

Only replicates in which parasitoid attack by *T. japonicus* occurred on one or both egg masses in the pair were included in the analysis. Each native pentatomid species was analyzed separately. The effect of year was tested and found to be nonsignificant, and data were pooled in all subsequent analyses. Three variables estimating reproductive (% eggs producing adult *T. japonicus*) and nonreproductive (% unemerged adult parasitoids, % aborted eggs) effects were analyzed (Abram et al. 2019a). We used generalized linear-mixed models with a binomial distribution (logit link) to assess the effects of species (*H. halys* vs. native pentatomid) on each response (SAS Institute 2018). In these models, species was considered a fixed effect and block was considered as a random effect, and each pair was a single experimental replicate. In addition, the proportion of egg masses attacked (as distinct from the proportion of eggs attacked) was calculated, as well as the % successful pentatomid nymph hatch.

**Results**

In total, 152 replicate pairs of egg masses (*H. halys* and native spp.) were deployed in 2017–2018. Eighteen replicates (12%) were missing at the end of the deployment period and could not be retrieved. Of the 134 nonmissing egg mass pairs, 90 (67%) were attacked by *T. japonicus* (and thus included in the analysis). A female wasp was found guarding the egg mass in 34 of the replicates; in all cases, the wasp was identified as *T. japonicus*, and in all but one case, the egg mass was successfully parasitized by this species. Predation was low in this study, ranging from 0 to 4% of eggs (data not shown). The *H. halys* egg mass was attacked in 88 of the 90 replicates (Table 1); in only two replicates was the native species (one *Euschistus* and one *Chinavia*) egg mass attacked but not the *H. halys* egg mass. The numbers of replicates in which both the *H. halys* and the native stink bug egg mass produced adult *T. japonicus* were 9 (*C. hilaris*; n = 34), 2 (*E. conspersus*; n = 29), and 1 (*C. ligata*; n = 27). No other parasitoid species were found during the course of this study, although previous surveys in the area revealed a low incidence of *Trissolcus euschisti* (Ashmead) and *Anastatus reduvii* (Howard) (Hymenoptera: Eupelmidae) (Milnes & Beers, unpublished data). The successful hatch of pentatomid nymphs ranged from 0 to 7% for *H. halys* over the three studies, while hatch rates of the other three species were variable (35% for *C. hilaris*, 32% for *E. conspersus*, and 82% for *C. ligata*) (Table 1).

*Trissolcus japonicus* successfully parasitized *H. halys* eggs at a significantly higher rate (72–81% of eggs) than any of the three
native species by a considerable margin (Fig. 1). Of the three native pentatomids, *C. hilaris* eggs produced the highest percentage emergence of adult *T. japonicus* (8% of eggs, 29% of egg masses) (Fig. 1A), followed by *E. conspersus* (5% of eggs, 10% of egg masses) (Fig. 1B) and *C. ligata* (0.4% of eggs, 4% of egg masses) (Fig. 1C).

The percentage female *T. japonicus* emerging from *H. halys* eggs averaged 92% (*n* = 1,872 adults). The percentage females emerging from *C. hilaris* eggs was 85% (*n* = 41); *E. conspersus* eggs, 75% (*n* = 12); and *C. ligata*, 100% (*n* = 2). However, the low number of adults emerging from the eggs of the native species probably makes these estimates unreliable.

The percentage of unemerged adult parasitoids in the *H. halys* eggs ranged from 2 to 4%, and the percentage aborted eggs from undetermined causes ranged from 3 to 7% (Fig. 2), indicative of the high level of successful attack of *T. japonicus*. For *C. hilaris*, there was a relatively high level (37%) of unmerged parasitoids coupled with a low level (2%) of aborted eggs (Fig. 2A). The reverse was true for *E. conspersus*, with 0.4% unmerged parasitoids, and 33% aborted eggs (Fig. 2B). The rates for both variables for *C. ligata* were low, with 2% unmerged parasitoids and 0.4% aborted eggs (Fig. 2C).

### Discussion

The high rate (>70%) of successful parasitism of *H. halys*, its Asian host, by *T. japonicus* is in stark contrast to the low rates (<8%) on the three North American pentatomid species tested. This parasitoid is not classed as host specific in that it attacks multiple genera and species of pentatomids in its native range as well as in laboratory studies (Hedstrom et al. 2017, Zhang et al. 2017, Botch and Delfosse 2018, Haye et al. 2019). However, the three North American species tested in this study were only marginally in its ecological host range, especially *C. ligata*. Until more extensive data are collected on nontarget effects, these results should only be interpreted in the context of the current study: a mild winter climate with an established population of *T. japonicus* and with abundant numbers of *H. halys*. It should also be noted that all sentinel egg masses were placed ca. 2 m high in a tree canopy, possibly matching an arboreal preference for *T. japonicus* (Herlihy et al. 2016). A positive indicator for biological control is that the rate of parasitism (% egg masses attacked) over the past 4 yr in this area appears to have increased: 0.8% in 2015 (year of original detection of *T. japonicus* in Washington); 12.3% in 2016; 77.8% in 2017; and 65.7% in 2018 (Milnes and Beers, unpublished data). Another positive indicator is that the sentinel egg masses lost some of the chemical cues (Hedstrom et al. 2017, Zhong et al. 2017) during the transfer to cardstock, thus likely underestimating the potential parasitism. Despite the loss of ‘chemical footprints’ left on the oviposition substrate (Hedstrom et al. 2017) as a result of experimental manipulation, clearly a sufficient quantity and quality of cues remained for *T. japonicus* females to find the egg masses at a very high rate. Tognon et al. (2016) found semiochemicals (aldehydes) on the surface of *H. halys* eggs that repelled native parasitoids; these compounds may have the opposite effect on *T. japonicus*.

The high rates of parasitism of *T. japonicus* are also in contrast to those of native hymenopterous parasitoids in the genera *Anastatus* (Eupelmidae), *Telenomus* (Scelionidae), *Trissolcus* (Scelionidae), and *Ooencyrtus* (Encyrtidae). In the comprehensive review of the impact of indigenous natural enemies on *H. halys*, Abram et al. (2017) found that the average percentage successful parasitism of viable (nonfrozen) *H. halys* sentinel egg masses was 1.2% across all studies and habitat types in North America. Similarly, egg predation rates may be high in some regions or habitats, but were generally <15% (Abram et al. 2017).

Overall, this study indicates excellent prospects for biological control of *H. halys* by *T. japonicus* in Washington’s coastal climate. Although our sample size is considerably smaller, the high rate of successful parasitism at our site (53% of *H. halys* eggs producing *T. japonicus* adults when attacked and nonattacked egg masses are included) is slightly higher than that reported in northern China (Zhang et al. 2017), which ranged from 31 to 36% of eggs attacked by *T. japonicus* for sentinel and wild egg masses, respectively. However, our levels are similar to those reported by Yang et al. (2009), who found that parasitism averaged 50%. In both of the Chinese studies, the total impact may be enhanced by (data not shown) nongenetic effects. While these levels of parasitism may not constitute a stand-alone tactic for integrated pest management in specialty crops, it can only be helpful for landscape-scale suppression of this pest (Leskey et al. 2012).

An ongoing problem is that of determining total parasitoid impact versus successful parasitism. A given egg mass may include multiple fates, and differentiating between parasitoid-induced mortality (absent the adult) and natural mortality is problematic. Recent work by Gariepy et al. (2014) and Gariepy et al. (2019) provide molecular tools to determine the cause of nongenetic mortality, or where the adult has emerged and left. However, nongenetic mortality forms an important component of total negative impact, and may in some cases outweigh reproductive effects (Abram et al. 2019a). Given the importance of nongenetic effects, it seems likely that the majority of aborted eggs in our study were also due to parasitoid activity.

These results are generally consistent with those obtained in physiological host range studies performed in quarantine, although there are some noteworthy differences. Studies by Hedstrom et al. (2017) and Botch and Delfosse (2018) found similar patterns of preference of *T. japonicus* for *H. halys* eggs and a moderate ability to parasitize nontarget pentatomids. Interestingly, in the latter study, it was found that rearing *T. japonicus* on native pentatomids slightly reduced their preference for *H. halys* (Botch and Delfosse 2018). As in our study, *C. ligata* was found to be a poorer host for *T. japonicus*.

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### Table 1. Numbers of *T. japonicus* adults produced from sentinel egg masses of *H. halys* and native pentatomids

| Variable                        | *H. halys* | *C. hilaris* | *E. conspersus* | *H. halys* | *C. ligata* |
|---------------------------------|------------|--------------|-----------------|------------|-------------|
| No. of replicate pairs          | 34         | 29           | 27              | 3          | 1           |
| No. of egg masses producing *T. japonicus* adults | 33         | 10           | 28              | 3          | 27          |
| Total *T. japonicus* adults     | 743        | 41           | 547             | 12         | 582         |
| Total *T. japonicus* females    | 687        | 35           | 502             | 9          | 531         |
| % female                        | 92         | 85           | 92              | 75         | 3           |
| % normal egg hatch (nymphs)     | 6.0        | 34.6         | 7.3             | 32.4       | 0.0         |
|                                |            |              |                 |            | 82.4        |
Fig. 1. Percentage eggs producing adult Trissolcus japonicus from its Asian host Halyomorpha halys and three native pentatomid species: A, Chinavia hilaris; B, Euschistus conspersus; C, Chlorochroa ligata. Vertical lines above the bars are standard error of the mean, and horizontal dashed reference lines are 50% of eggs. Letters compare means for % parasitism for H. halys versus C. hilaris (F = 449.09, P < 0.001, df = 1, 33), E. conspersus (F = 240.11, P < 0.001, df = 1, 28) and C. ligata (F = 97.04, P < 0.001, df = 1, 26).

Fig. 2. Percentage eggs classed as unemerged adult parasitoids or aborted eggs (black liquid) from H. halys sentinel egg masses. Vertical lines above the bars are standard error of the mean. Letters compare means for H. halys and A) C. hilaris (unemerged, F = 172.78, P < 0.001, df = 1, 26; aborted, F = 4.37, P = 0.047, df = 1, 26); B) E. conspersus (unemerged, F = 7.15, P = 0.012, df = 1, 28; aborted F = 139.70, P ≤ 0.001, df = 1, 28); C) C. ligata (unemerged, F = 5.19, P = 0.031, df = 1, 26; aborted F = 7.96, P = 0.009, df = 1, 26).
than C. hilaris under quarantine conditions (Hedstrom et al. 2017). In addition, the Hedstrom et al. (2017) study found 0% parasitism of E. conspersus in no-choice tests, and thus was not tested in paired-host assays. However, that study found no significant difference in adult wasp production between C. hilaris and H. halys, while our results indicate that C. hilaris is far less suitable as a host under field conditions than H. halys. Although 39% of C. hilaris eggs in our study exhibited possible or probable nonreproductive effects, only 8% produced adult wasps; this discrepancy between attack and emergence rates represents an evolutionary trap (Abram et al. 2014) for T. japonicus.

The results from a recent study of physiological host range on nontarget European pentatomids (Haye et al. 2019) also contrast with those of our study. Of the 13 species tested, 11 were successfully parasitized by T. japonicus, most at a very high rate. Paired-host tests indicated a higher rate of attack on H. halys in three out of four nontarget species, but with 67–93.9% of eggs producing adult wasps.

Nontarget effects testing uses taxonomic and ecological similarities to guide the choice of species tested (Kuhlmann et al. 2006), regardless of their pest status. In this study, all nontarget species tested are sporadic but locally damaging pests of tree fruits (Beers et al. 1993, McGhee 1997), which are high-value specialty crops in the Pacific Northwest. Any additional biological control effected on these species would be considered a benefit by Washington tree fruit producers and pest managers (T. Smith, personal communication). However, the generally poor performance of T. japonicus on native stink bugs and the existence of a complex of native parasitoids in Washington state exhibiting parasitism rates of up to 63.3% on native egg masses (McGhee 1997) suggest that noticeable impacts of T. japonicus are unlikely. Even under the semiartificial conditions of this test, the attack rate of T. japonicus remained below the level predicted to cause population reduction (50%) in the nontarget species (Van Driesche and Hoddle 2017), although its probable impact on C. hilaris approached this level. Of greater concern is that T. japonicus will negatively impact beneficial species of pentatomids, including Podisus maculiventris (Say). Laboratory tests indicate low levels of successful attack of T. japonicus on P. maculiventris similar to those observed on pest species (Hedstrom et al. 2017, Botch and Delfosse 2018). Further testing may reveal if P. maculiventris is attacked by T. japonicus under field conditions.

The methodology used in this study presents a ‘worst case’ scenario from the perspective of the nontarget effects of T. japonicus on the three pentatomids species tested under field conditions. The unnaturally close proximity of H. halys and native stink bug egg masses increased the probability that T. japonicus females responding to host cues from the H. halys egg mass also encountered the native egg mass. While it is difficult to predict how attack rates might have been affected by these conditions, it seems very likely that spatial and temporal separation of egg mass deployment would further reduce the attack rates of T. japonicus on native pentatomid eggs; future research should address these issues. It is also difficult to predict at this point (early stages of invasion) the extent to which native pentatomids and H. halys will occupy the same habitats in eastern Washington’s shrub-steppe and riparian areas. Oviposition hosts in eastern WA for native pentatomids include weeds and shrubs such as muellen, bitterbrush, and currant (McGhee 1997). If T. japonicus prefers arboreal/wooded habitats as has been suggested (Herlihy et al. 2016), then it is less likely to encounter native pest pentatomid egg masses in other habitats. Any incidental parasitism (both reproductive and nonreproductive) of native pentatomids by T. japonicus would complement the biological control already provided by the native parasitoid complex, serving as a ‘positive non-target effect’ (Haye et al. 2019). Successful reproduction in nontarget species may provide an alternate host for T. japonicus in times of primary host scarcity (Waterhouse 1998, Loch and Walter 1999).

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