



# Experimental assessment of the biosafety of *Trissolcus japonicus* in New Zealand, prior to the anticipated arrival of the invasive pest *Halyomorpha halys*

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**Abstract** Despite numerous interceptions at the border, the brown marmorated stink bug (BMSB), *Halyomorpha halys* Stål (Hemiptera: Pentatomidae), is not yet established in New Zealand. Nevertheless, a classical biocontrol programme using the egg parasitoid *Trissolcus japonicus* Ashmead (Hymenoptera: Scelionidae) has been initiated in anticipation of its likely arrival. The potential host range of the parasitoid in New Zealand was investigated by importing parasitised BMSB eggs into quarantine from Newark, DE, USA. Egg masses of seven species of Pentatomidae, including one sub-species, were individually exposed to naïve mated female *T. japonicus* in no-choice laboratory experiments. The results showed

that predatory *Cermatulus nasalis nasalis*, *C. nasalis hudsoni* and *Oechalia schellenbergii*, and the phytophagous *Monteithiella humeralis*, *Dictyotus caenosus*, *Glaucias amyoti*, and *Cuspicona simplex* are all within the physiological host range of *T. japonicus*, although not all appeared to be equally susceptible to parasitism. No development or emergence of *T. japonicus* from eggs of the cosmopolitan pentatomid plant pest *Nezara viridula* were observed. The likely ecological consequences of releasing *T. japonicus* in New Zealand are discussed, as is the subsequent decision of New Zealand's Environmental Protection Authority to approve release of the parasitoid once BMSB arrives in New Zealand.

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## Introduction

The brown marmorated stink bug (BMSB), *Halyomorpha halys* Stål (Hemiptera: Pentatomidae), is an invasive temperate/subtropical pest of many horticultural crops. It is native to China, Japan, Korea, and Taiwan, but has successfully established in the USA and Chile, and Europe including Russia (Haye et al. 2015a; Gapon 2016; Faúndez and Rider 2017; Leskey and Nielsen 2018). BMSB is a major economic threat

to New Zealand, potentially jeopardizing multi-billion-dollar export markets for fresh produce (especially kiwifruit and apples). Although not yet known to be present in the country (June 2019), adults have been regularly intercepted at the border in recent years and there remains a high risk of entry and establishment (Duthie 2012).

*Trissolcus japonicus* (Ashmead) (Hymenoptera: Scelionidae) (the ‘samurai wasp’) is a small (1.3–1.8 mm long) oligophagous endoparasitoid of eggs of Pentatomidae (Talamas et al. 2013, 2015a; Kim et al. 2017), which can also parasitise eggs of Scutelleridae (Hedstrom et al. 2017). It is considered to be one of the most effective biocontrol agents of BMSB throughout its native range, frequently parasitising > 70% of egg masses (Yang et al. 2009; Lee et al. 2013; Zhang et al. 2017). *Trissolcus japonicus* overwinters in Korea and Japan as long-lived adults (Kim Hoelmer pers. comm.). Hundreds of species of Pentatomidae and their specialist natural enemies occur naturally in the Palaearctic and Nearctic regions. A few of these natural enemies have been recorded from BMSB in its adventive range, but none has yet been shown to be an effective biocontrol agent (Haye et al. 2015b; Lee 2015; Ogburn et al. 2016; Abram et al. 2017; Dieckhoff et al. 2017). Consequently, *T. japonicus* is considered to be the most promising parasitoid for potential classical biological control programmes in both the USA and Europe (Rice et al. 2014; Milnes et al. 2016; Hedstrom et al. 2017; Zhang et al. 2017). Host-testing trials in quarantine laboratories have demonstrated that some native species of Palaearctic and Nearctic Pentatomidae are attacked by *T. japonicus*, and further definition of the host range and non-target impacts of the parasitoid is ongoing prior to any application to federal or national biosecurity authorities to release it across the USA or in Europe (Hedstrom et al. 2017; Zhang et al. 2017; Haye et al. 2019).

Globally, species in the genus *Trissolcus* only successfully parasitise host eggs from species within the superfamily Pentatomoidea. Field records from Asia, together with laboratory tests in the USA and Europe and molecular phylogeny analysis of the Scelionidae, indicate that hosts of *Trissolcus* spp. are often restricted to the families Pentatomidae (with about 5000 species globally), Scutelleridae and Acanthosomatidae (Yang et al. 2009; Taekul et al. 2014; Talamas et al. 2015a, b). Pentatomoidea are

depauperate in New Zealand, and the superfamily is represented only by 16 species in the families Cydnidae (4), Acanthosomatidae (4) and Pentatomidae (8) (Table 1) (Larivière 1995). Of the Pentatomidae, six species are phytophagous in the Pentatominae and two species and the two sub-species are predatory in the Asopinae (Larivière 1995, Table 1). One species (*Hypsithocus hudsonae* Bergroth) and two sub-species (*Cermatulus nasalis hudsoni* Westwood and *Cermatulus nasalis turbotti* Westwood) are endemic. Three species are native (*Cermatulus nasalis nasalis* Westwood, *Glaucias amyoti* Dallas and *Oeochalia schellenbergii* Guérin), and four species are exotic (*Monteithiella humeralis* Walker, *Dictyotus caenosus* Westwood, *Nezara viridula* L. and *Cuspicona simplex* Walker) (Larivière 1995, Table 1). The New Zealand Acanthosomatidae are endemic. Two species of the Acanthosomatidae, *Rhopalimorpha*, (*R. lineolaris* Pendergrast and *R. obscura* Dallas), are very common and found predominantly on monocotyledons, while *R. alpina* Woodward is known from only a few South Island locations between 1000 and 1300 m.a.s.l. (Larivière 1995). The fourth species of the Acanthosomatidae, *Oncaontias vittatus* F., is the only true forest dwelling pentatomoid in New Zealand, where, unlike temperate forests in the USA and Europe, most native trees are evergreen. Finally, the Cydnidae are small insects that burrow in soil, feeding on roots, stems or fallen seeds (Larivière 1995).

The likely severe economic threat posed to primary industries by BMSB (Duthie 2012) prompted proactive host-range screening of *T. japonicus* in New Zealand to assess the threat it may pose to native fauna. The concept of laboratory host-range testing of a candidate biocontrol agent prior to the arrival of the target pest species is a novel approach. The developmental period within parasitised egg masses of BMSB and longevity of *T. japonicus* females made it feasible to use parasitoids imported directly into New Zealand from a US source for use in experiments, within a containment facility, to measure their responses to potential non-target host eggs, rather than having to establish a captive breeding population of BMSB (which is not present in New Zealand) on which to rear the parasitoid. Knowledge of the potential impacts on non-target species may allow the candidate biocontrol agent to be part of an effective biosecurity response, delivering a timely eradication or management tool that would otherwise not be available. Here, we

**Table 1** Pentatomoidea species in New Zealand—origin, distribution and host preferences, listed alphabetically within family and subfamily, if appropriate (Larivière 1995; Rider 2015)

Species	Biostatus	Distribution in New Zealand	Feeds on
Family: Acanthosomatidae			
<i>O. vittatus</i>	Endemic	Widespread through both N. and S. Islands	Phytophagous. Forest trees and shrubs
<i>R. alpina</i>	Endemic	S. Island: Buller, Fiordland, Nelson	Phytophagous. Alpine sod, most common from 1000 to 1300 m.a.s.l
<i>R. lineolaris</i>	Endemic	Widespread through both N. and S. Islands	Widespread on grasses, rushes, sedges in open habitats
<i>R. obscura</i>	Endemic	Widespread through both N. and S. Islands	Widespread on grasses, rushes, sedges in open habitats
Family: Pentatomidae			
Subfamily: Asopinae (predatory)			
<i>C. nasalis nasalis</i>	Native (Aus) <sup>b</sup>	Widespread through both N. and S. Islands	Insects—including pests in exotic crops
<i>C. nasalis hudsoni</i> <sup>a</sup>	Endemic	Occur only in S. Island above 1200 m.	Insects—in sub-alpine to alpine habitats
<i>C. nasalis turbotti</i> <sup>a</sup>	Endemic	Occur only on Three Kings Islands	Insects—all collected from kanuka or manuka
<i>O. schellenbergii</i>	Native (Aus) <sup>b</sup>	Widespread through both N. and S. Islands	Insects—including pests in exotic crops
Subfamily: Pentatominae (phytophagous)			
<i>H. hudsonae</i>	Endemic	S. Island: Central Otago and Otago Lakes. Restricted, disjunct, sub-alpine to alpine	Shrubs and tussock grass— <i>Hebe odora</i> ; <i>Chionochloa rigida</i>
<i>M. humeralis</i>	Exotic (Aus) <sup>b</sup>	Widespread through both N. and S. Islands	Closely associated with <i>Piptosporum</i>
<i>D. caenosus</i>	Exotic (Aus) <sup>b</sup>	Widespread through both N. and S. Islands	Low plants, grasses, <i>Plantago</i> . Pest of lucerne, blackberries
<i>G. amyoti</i>	Native (Aus) <sup>b</sup>	Widespread throughout N. and S. Islands. Offshore Is. Also occurs in Australia	Closely associated with <i>Coprosma robusta</i> . Pest of vegetables in Queensland, and on privet
<i>N. viridula</i>	Exotic	Widespread in New Zealand South to mid-Canterbury. Offshore is in New Zealand is closely associated with <i>Solanum</i>	Polyphagous cosmopolitan pest. Major pest on many vegetable crops
<i>C. simplex</i>	Exotic (Aus) <sup>b</sup>		Closely associated with <i>Solanum</i> . Pest in exotic crops

<sup>a</sup>Endemic Pentatomidae sub-species in New Zealand

<sup>b</sup>Aus = Also found in, or originated from, Australia

present data from laboratory host-specificity testing of *T. japonicus*, and discuss how its physiological (i.e. fundamental) host-range may be moderated by environmental and ecological limitations to its geographical-range should it be released in New Zealand. We also discuss the decision made by New Zealand's Environmental Protection Authority in August 2018 to approve (with controls) the release of *T. japonicus* upon the arrival of BMSB in New Zealand.

## Materials and methods

### Selection of non-target test species

All species of Pentatomidae in New Zealand were considered to be potential hosts of *T. japonicus* and so were sought for host-testing experiments in containment. The Acanthosomatidae were considered potential 'outgroups' for testing. The terrestrial/subterranean Cydnidae occupy quite different habitats from the other pentatomoids, and have never been recorded as hosts of any *Trissolcus* species. Hence they are not likely to be exploited by *T. japonicus*, and host-testing was not considered to be warranted.

*Monteithiella humeralis*, *D. caenosus*, *G. amyoti*, *N. viridula*, *C. simplex*, *C. nasalis nasalis*, *C. nasalis hudsoni*, and *O. schellenbergii* were collected from the field for host range testing between November 2015 (late-spring) and May 2017 (late autumn). Extensive searches were made for *H. hudsonae* between December 2016 and April 2017. Four of the alpine locations where this pentatomid has been found previously (B. Patrick, pers. comm.) were visited, including one remote site accessible only by helicopter, but despite extensive hand searching and suction sampling, no *H. hudsonae* eggs/nymphs/adults were found and so this species could not be tested within this study. Only a few adults of the alpine *C. nasalis hudsoni* were found, and consequently only a few egg masses were available for testing. The pentatomid *C. nasalis turbotti* was not sought for testing because of its isolated distribution (Three Kings Islands, 55 km from Cape Reinga, the most northern tip of the North Island), which made it inaccessible. Only a small number of nymphs and adults of *R. lineolaris*/*R. obscura* and *O. vittatus* were able to be collected, but only a few eggs of *Rhopalimorpha* spp. were obtained.

Thus, host-testing with acanthosomatids was very limited.

### Shipments of *Trissolcus japonicus* and handling of parasitoids in quarantine

*Trissolcus japonicus* were supplied by the USDA-ARS Beneficial Insects Introductions Research Unit, in Newark, Delaware, USA. Parasitoids used for experiments originated from Beijing, China, and had been reared on BMSB in quarantine in Newark Delaware since 2009. Three shipments of parasitised eggs per mass (with an average 28 eggs per mass) of BMSB, each held separately in a 10-dram (37 ml) snap-cap plastic vial, were air-couriered from Newark to Plant & Food Research's quarantine facility, Auckland, New Zealand, arriving after journeys of 3–7 days, subject to flight schedules and customs/agricultural biosecurity inspection delays. Egg masses were held in a quarantine room at  $20 \pm 1$  °C for emergence of adult *T. japonicus*. Adult parasitoids emerged 12–15 days after arrival, usually over a 3–6 day period. More than 1400 adult *T. japonicus* were recovered, and only a single BMSB nymph emerged from any egg mass (in Shipment 2), which was killed immediately by freezing (Table 2). Males typically emerged first and were allowed to mate freely with their female siblings. Once all females had emerged, and were presumed to have mated, both males and females were removed from the plastic vial and held individually in tubes with a smear of honey as a carbohydrate source until required for testing. Six days after the last parasitoid had emerged, each BMSB egg mass was frozen at  $-20$  °C for at least 48 h and the fate of all BMSB eggs was determined microscopically. Finally, all BMSB egg masses from the USA were destroyed by autoclave to comply with biosecurity requirements.

### Laboratory rearing of New Zealand pentatomids, and preparation of egg masses for bioassays

Laboratory cultures were established from field collections of nymph and adult pentatomid species. As many as 50 insects were reared in clear plastic containers ( $\sim 170$  mm H  $\times$  210 mm L  $\times$  135 mm W), with ventilation grids in the lid (similar to Medal et al. 2012). Each cage was provided with water in wet cotton wool and a folded piece of

**Table 2** Numbers of parasitised BMSB egg masses received from the USA in three shipments from 2015 to 2016, and adult *T. japonicus* emergence in New Zealand

Shipment no.; arrival date in New Zealand	No. BMSB egg masses	Total # BMSB eggs	Dates exposed to parasitism in the USA (*24 h,**96 h)	Total number of parasitoids emerged	Sex ratio (F:M)	Pentatomid species tested (date tests started)
1 23 Nov 2015	18	490	13–18 Nov 2015*	435	2.4:1	<i>N. viridula</i> <i>C. simplex</i> (4 Dec 15)
2 26 Feb 2016	25	702	16–18 Feb 2016*	465	2:1	<i>M. humeralis</i> <i>G. amyoti</i> <i>C. n. nasalis</i> (9 Mar 16)
3 16 Dec 2016	20	558	8 Dec 2016**	502	2.1:1	<i>D. caenosus</i> <i>O. schellenbergii</i> <i>C. n. hudsoni</i> (16 Dec 16)

wax paper as a substrate for oviposition. Cages with *N. viridula* were kept at  $25 \pm 1$  °C L:D 16:8, and all others at  $20 \pm 1$  °C L:D 16:8. The phytophagous species were fed varied diets, according to collection data, published records, and availability of host plants as follows: *N. viridula*—carrots, green beans, fresh sweet corn and a nut-seed mix; *C. simplex*—berries of *Solanum nigrum* L. and *Solanum mauritianum* Scop. (black nightshade and woolly nightshade, respectively) and carrots; *G. amyoti*—Coprosmia fruit (e.g. *Coprosma repens* A. Rich.) and carrots; *M. humeralis*—unripe fruit of *Pittosporum crassifolium* Banks et Sol.; *D. caenosus*—plantain grass seed heads and fresh sweet corn. The predatory taxa (*C. nasalis nasalis*, *C. nasalis hudsoni* and *O. schellenbergii*) were all fed on fifth instar larvae of *Spodoptera litura* F. (Lepidoptera: Noctuidae) (tropical armyworm) from a laboratory culture, at a rate of approximately one larva per adult every two days. Field collected acanthosomatids were held in cages as described above for pentatomids. No breeding culture of acanthosomatids could be established so a continuous supply of eggs for on-going host-testing experiments was not available.

Individual egg masses of pentatomid species were collected from the rearing cages every 1–3 days and examined microscopically. Any egg masses that were > three days old (designated by developed egg-breakers), or with any eggs that had been

cannibalised, were discarded. Each ‘fresh’ egg mass was then removed from the oviposition substrate and mounted onto double sided sticky tape on a  $22.5 \times 70$  mm<sup>2</sup> cardboard strip, taking care to maintain their natural orientation. The remaining, exposed portion of sticky tape was covered with fine white sand (White “Scenic Sand”. Activa® products) to allow unimpeded access for searching parasitoids. The number of eggs in each egg mass was recorded on the cardboard strip and the strips were then placed into 10-dram (37 ml) clear plastic snap-cap vials (the “test arena”). The completed test arena was then held at  $20 \pm 1$  °C for use within 24 h.

#### No-choice, non-target host-testing experiments

In the absence of BMSB, the testing protocols were restricted to no-choice experiments conducted with non-target species only (see Hedstrom et al. 2017). For each replicate, a single naïve, presumably mated female parasitoid was transferred by aspiration or brush into the test-arena, and the tube was then closed, with a smear of honey provided on the vial lid for nutrition. Each parasitoid was briefly observed, and was required to be actively walking around the arena before the replicate was accepted. The vial was then held at  $20 \pm 1$  °C for 24 h when the parasitoid was removed. The egg mass was then examined every 2–5 days and emerged pentatomid nymphs and adult

parasitoids were recorded and removed. The number of egg masses with any successful parasitism, and the number of successfully parasitized eggs per egg mass were recorded. Control egg masses, taken periodically from the laboratory cultures throughout the test period but not exposed to *T. japonicus* females, were held under the same conditions and the emergence of pentatomid nymphs recorded. The fate of any unhatched eggs was determined under a stereo microscope after 20 days (controls) and 35 days (tests). Egg death in control treatments provided an estimate of naturally-occurring mortality rates under experimental conditions in the absence of exposure to *T. japonicus*.

*Trissolcus japonicus* females from shipment 1 were exposed to eggs of *C. simplex* and *N. viridula* within 1–2 days of emergence. In subsequent shipments, the production of 1–3-day-old pentatomid eggs could not be synchronised with emergence of adult *T. japonicus* in sufficient numbers for testing under these conditions. However, pilot experiments with shipment 1 showed that many newly emerged female parasitoids survived being held in the dark at  $13 \pm 1$  °C for up to

seven months. When moved to a light regime at  $20 \pm 1$  °C and held for 2–4 h to acclimatise, they searched for and attacked susceptible host eggs apparently normally. Offspring subsequently emerged within the same time frame as offspring from females held at  $20 \pm 1$  °C and exposed to eggs within 24 h of emergence. Hence female parasitoids emerging from shipment 2 and 3 were held in the dark at  $13 \pm 1$  °C for one day up to three months until required for testing. They were then transferred to the light at  $20 \pm 1$  °C for > 3 h before exposure to a test egg mass. Eggs of *M. humeralis*, *G. amyoti*, and *C. nasalis* were exposed to parasitoids from shipment 2, while those of *D. caenosus*, *O. schellenbergii*, and *C. nasalis hudsoni* were exposed to parasitoids from shipment 3 (Table 2). Between 11 and 70 egg masses of each species were exposed to *T. japonicus* (Table 3). Between three and five egg masses of *R. lineolaris/obscura* (the species could not be determined) were also exposed to *T. japonicus* females, as described above. Since positive-control no-choice tests could not be conducted for *T. japonicus* with BMSB egg masses in quarantine, these control

**Table 3** Parasitism rates and development of parasitoids and nymphs from non-target pentatomid egg masses exposed to a single female *T. japonicus* in no-choice tests

Host	Total egg masses parasitised				Mean % (95% CI) per egg mass of parasitoids and nymph development		
	No. of masses tested	Mean no. of eggs per mass	No. of masses parasitised	% egg masses parasitized (95% CI)	Developed parasitoids	Developed nymphs	Undeveloped parasitized eggs
<i>H. halys</i>	46	27	46	100 (84.8–99.9)a	52.5 (44.9–59.7)a	18.9 (14.4–24.9)c	28.6 (23.4–34.5)c
<i>C. n. hudsoni</i>	11	21	2	18.2 (5.8–52.9)cd	97.8 (24.4–99.9)abcd	0 (0.24–50.9)abc	2.2 (0.04–57.8)abc
<i>C. n. nasalis</i>	42	28	40	95.2 (81.6–98.3)a	82.7 (75.4–87.7)bc	7.9 (5.2–13.4)b	9.4 (6.3–14.2)b
<i>C. simplex</i>	71	11	23	32.4 (22.8–44.3)c	88 (78.6–93.7)c	0.9 (0.2–7.6)a	11.1 (6.3–18.8)b
<i>D. caenosus</i>	26	13	19	73.1 (52.4–85.9)b	71.1 (59.2–81.2)b	4.7 (2.2–13.7)ab	24.2 (15.7–33.5)c
<i>G. amyoti</i>	70	14	67	95.7 (86.7–98.3)a	94.8 (91.3–97.2)d	0.6 (0.2–2.9)a	4.6 (2.5–7.2)a
<i>M. humeralis</i>	19	11	15	78.9 (53.9–90.9)b	83.7 (71.2–92)bc	0 (0.05–12.5)ab	16.3 (8.6–26.4)b
<i>N. viridula</i>	34	60	0	0 (0–19.7)d	nd	nd	nd
<i>O. schellenbergii</i>	36	26	8	22.2 (12.1–39.3)c	74.1 (55.5–96.4)b	8.5 (3.6–24.5)bc	17.4 (8.8–31.7)bc

Within column means for percent egg masses parasitized, as well as for mean percentage of developmental effects, not sharing a letter are significantly different (pair-wise comparisons of fitted means;  $p < 0.05$ ). No data collected are indicated with 'nd'

experiments were conducted in USDA/ARS (Newark, Delaware, USA) laboratories following the methodology described above. Data obtained from these positive controls conducted with BMSB no-choice tests were then used to make comparisons with data obtained from no-choice tests conducted with New Zealand's non-target pentatomids.

### Data analysis

Parasitism rates (total number of egg masses from which at least one *T. japonicus* developed—successful parasitism), as well as the proportions of developed parasitoids, developed pentatomid nymphs and undeveloped pentatomid eggs per successfully parasitised egg mass amongst the non-target species tested and BMSB were analysed using separate logistic regression models (with a logit link function) for each outcome. The logistic regression is appropriate where the response variable is binomial and models the log of the odds of these proportions. Due to evidence of overdispersion, Williams' adjustment was used, with Firth's penalised likelihood accounting for outcomes that were not observed for a given species (Williams 1982). Where overall tests of species were statistically significant pair-wise comparisons of the fitted means were conducted. Fitted means for each species along with the respective 95% confidence intervals were calculated and back-transformed onto the original scale. Similarly, proportions of developed nymphs from apparently unparasitised egg masses of the pentatomid non-target species and negative control masses were analysed using logistic regression models. All analyses were performed with the program SAS 9.4 (SAS Institute Inc., Cary, NC, USA).

## Results

### No-choice, non-target host-testing experiments

Eight taxa (seven species and one sub-species) of New Zealand's non-target Pentatomidae were exposed to *T. japonicus* between December 2015 and May 2017. Parasitoid emergence showed that some of the egg masses of each taxon, except *N. viridula*, were successfully parasitised (Table 3). Parasitism rates of five species (including parasitised BMSB egg masses used as positive control) were above 70%, and were below

35% for two species and the sub-species (Table 3). Percentage parasitism of test egg masses varied significantly between species ( $df = 8$ ,  $\chi^2 = 95.3$ ,  $p < 0.0001$ ). Percentage parasitism of *C. nasalis nasalis* and *G. amyoti* was higher than 95% and did not differ significantly from that of observed in parasitised BMSB eggs (Table 3). No parasitoids developed from any of the few acanthosomatid eggs exposed to *T. japonicus*, so these data were excluded from the analysis.

Mean parasitoid emergence from successfully parasitised egg masses, including *H. halys*, ranged from 52.5 to 97.8% and differed significantly among species ( $df = 7$ ,  $\chi^2 = 94.8$ ,  $p < 0.0001$ , Table 3). Mean emergence of pentatomid nymphs from unparasitised non-target eggs was also observed to vary significantly between test species ( $df = 7$ ,  $\chi^2 = 42.9$ ,  $p < 0.0001$ , Table 3). Similarly, the mean percentage of unhatched pentatomid eggs from successfully parasitised egg masses differed significantly between species ( $df = 7$ ,  $\chi^2 = 67.1$ ,  $p < 0.0001$ , Table 3) and ranged from 2.2 to 28.6% (Table 3).

In the absence of BMSB eggs to test in New Zealand, the test protocol was unable to determine if the lack of attack of an entire non-target egg mass was due to behaviour (e.g. the parasitoid was not interested in searching or the egg mass was not acceptable) or physiology (e.g. the female had no mature eggs to lay or oviposition occurred but all parasitoids failed to develop). Possible parasitoid developmental failure was assessed by comparing the rate of unhatched pentatomid eggs from treated egg masses (i.e. exposed to *T. japonicus* with no parasitoid emergence) with that from control egg masses (i.e. not exposed to parasitoids) (Table 4). For most species there appeared to be little difference, suggesting that the egg mass had been unacceptable to the female parasitoid, but significant differences were observed for *C. n. nasalis* ( $df = 1$ ,  $\chi^2 = 14.4$ ,  $p = 0.0001$ , Table 4) as well as for *C. simplex* ( $df = 1$ ,  $\chi^2 = 15.4$ ,  $p = 0.0001$ , Table 4), suggesting that some of the egg masses of these two species may have been attacked but parasitoids failed to complete development or emergence.

## Discussion

The simplicity of the test arena in our trials allowed accurate replication within laboratories, and hence

**Table 4** Pentatomid development from control non-target egg masses and tested masses from which no *T. japonicus* emerged

Non-target species	Treatment	No. of egg masses examined	Mean no. of eggs per mass	Mean % (95% CI) developed nymphs/mass
<i>C. n. hudsoni</i>	Control	3	21	42.2 (30.8–54.5)a
	Tested	9	21	55.7 (48.5–62.7)a
<i>C. n. nasalis</i>	Control	47	29	83.8 (81.7–85.6)a
	Tested	2	30	62.7 (49.8–74.0)b
<i>C. simplex</i>	Control	72	9	73.5 (70.0–76.8)a
	Tested	48	11	62.8 (58.6–66.9)b
<i>D. caenosus</i>	Control	7	9	55.7 (43.2–67.6)a
	Tested	7	12	48.2 (37.7–58.9) a
<i>G. amyoti</i>	Control	50	14	96.5 (94.8–97.7)a
	Tested	3	12	94.2 (79.8–98.6)a
<i>M. humeralis</i>	Control	30	11	92.1 (88.7–94.5)a
	Tested	4	12	93.5 (81.6–97.8)a
<i>N. viridula</i>	Control	35	54	49.2 (46.9–51.4)a
	Tested	34	60	51.1 (48.9–53.3)a
<i>O. schellenbergii</i>	Control	36	28	93.9 (92.2–95.2)a
	Tested	28	26	96.6 (94.9–97.7)a

Within column means for percent developed nymphs, for each non-target species separately, not sharing a letter are significantly different (pair-wise comparisons of fitted means) at  $p < 0.05$

comparison of responses by *T. japonicus* to New Zealand non-target species with those to BMSB and non-target species in the USA. The removal of all external plant stimuli indicated that the decision by a female *T. japonicus* to attack or ignore an egg mass in the arena was likely to be determined by tactile and chemical cues—either on the surface of the eggs, or on the residual adhesive that attaches them to the oviposition substrate (and to each other). Some egg masses from seven out of the eight species in the New Zealand Pentatomidae were successfully parasitised by *T. japonicus*. The exotic pest *Nezara viridula* was not successfully parasitised by *T. japonicus*. Interestingly, successful parasitism observed on both closely-related *Cermatulus* subspecies was quite different, 18.2% in *C. n. hudsoni* and 95.2% in *C. n. nasalis*. Based on their taxonomic similarity, and possible chemical similarity of host-associated cues, it was expected that the parasitoid would perform similarly on these two closely related hosts. Since both species were tested with batches of parasitoids from two different shipments (see Table 2), this apparent inconsistency could potentially be the results of potential differences in the performance of the

parasitoid batches rather than a true difference in host acceptability in both non-targets.

For two of the non-targets (i.e. *C. n. nasalis*, *G. amyoti*), successful parasitism observed was similar to that of BMSB positive-control egg masses (> 95%). This contrasts with similar experiments in the USA where successful parasitism of non-target egg masses was higher than 50% in only two of seven successfully parasitised non-target species (Hedstrom et al. 2017). In our trials, parasitism levels (i.e. the proportion of pentatomid eggs within an egg mass producing parasitoid off-spring) were higher than 70% for all seven non-target taxa successfully parasitised, whereas parasitism levels of non-target species attacked in the USA experiments was generally low (average of 18%), and the highest parasitism level observed was 47.9% (Hedstrom et al. 2017). These New Zealand data are more similar to those from China, where host range laboratory experiments also found that seven of eight non-target pentatomids were successfully parasitised, with parasitism levels all > 70% (Zhang et al. 2017). Also, data from our trials are very similar to those from Europe, where laboratory no-choice tests found that twelve out of thirteen non-



target species tested were successfully parasitised, with offspring emergence in eleven of these successfully parasitised non-targets, and parasitism levels > 70% in ten of the eleven species (Haye et al. 2019). Nevertheless, the experiments from the USA, China and Europe have included only a small number of the potential species available so the comparisons with New Zealand data are best regarded as preliminary. The absence of successful parasitism of Acanthosomatidae may conceivably have been due to the low numbers tested. Eggs of Acanthosomatidae differed morphologically from the Pentatomidae species tested, in that they were non-operculate and usually laid in a straight line rather than in a cluster, which could potentially make them less suitable for the parasitoids acceptance. However, due to the inability to conduct more replicates with these species, their potential host status remains unknown.

Experience has shown that laboratory-based host specificity tests designed to investigate host ranges of parasitoid biological control agents can be valid predictors of non-target parasitism in the field (Barratt et al. 1997). However, the results must be carefully interpreted as the fundamental (or physiological) host range of a parasitoid deduced from laboratory no-choice tests often overestimates the likely ecological host range of a biological control agent due to the absence of critical ecological or habitat cues (van Driesche and Murray 2004; Haye et al. 2005; Avila et al. 2016; Zhang et al. 2017). Hence while ‘negative’ laboratory results (i.e. no parasitism—resulting from no attack or no development) are powerful indicators of a non-host status in the wild, interpretations of the consequences of ‘positive’ tests is much less certain. In a natural environment, there are many chemical, visual, or habitat cues that determine how and where a female *T. japonicus* will search for hosts or food, how successful it is at both, and when it will disperse to search elsewhere. So, for instance, the way in which a parasitoid species responds to different chemical cues, and the level of specificity to these semiochemicals, may define its ecological range, the risks it may pose to non-target species, and its potential as a safe and successful biological control agent (Conti et al. 2004). Within the genus *Trissolcus*, these field cues may help explain why *T. japonicus* attacks predominantly BMSB in China when apparently suitable species are sympatric with the target pest (Zhang et al. 2017).

Despite the apparently broad physiological host range of *T. japonicus*, there is laboratory evidence from the USA that *T. japonicus* retains a preference for BMSB (Lara et al. 2016; Hedstrom et al. 2017), even a generation after being reared on an alternative host (Kim Hoelmer unpublished data). In addition, *T. japonicus* appears to have a preference for shaded woodland habitats (Talamas et al. 2015b; Morrison et al. 2018), within which they emerge most frequently from BMSB egg masses found at mid-canopy (Quinn et al. 2019). Hence it seems likely that, in New Zealand, *T. japonicus* would be naturally constrained within the geographical range and habitats favoured by BMSB. Of the New Zealand pentatomids that exist within the predicted range of both BMSB (Kriticos et al. 2017) and *T. japonicus* (Avila and Charles 2018), *C. nasalis nasalis*, *O. schellenbergii*, *M. humeralis*, *G. amyoti* live in habitats common to both BMSB and *T. japonicus*, and hence might be attacked by the parasitoid when encountered, while *D. caenosus* and *C. simplex* prefer grass or low shrub ecosystems not generally favoured by *T. japonicus* (Table 1) and would probably escape significant parasitism. The southern regions of the country are climatically unsuitable for BMSB survival (Kriticos et al. 2017), but *T. japonicus* may tolerate a cooler climate than BMSB (Nystrom Santacruz et al. 2017), and a CLIMEX study for *T. japonicus* suggests that the parasitoid may have a wider distribution in the South Island than BMSB (Avila and Charles 2018). If the eventual natural distribution of *T. japonicus* is constrained by that of BMSB, then the rare, high altitude *H. hudsonae* and *C. nasalis hudsoni* will not naturally be exposed to *T. japonicus* attack. Even if individual *T. japonicus* were to disperse or be transported by human activity into the sub-alpine regions beyond the range of BMSB, the low-shrub, treeless environment in which these native pentatomids live would probably limit the survival of *T. japonicus* and its ecological impact on them, as it appears to have a preference for woodland habitats (Talamas et al. 2015b; Morrison et al. 2018).

Release of classical biocontrol agents into New Zealand is strictly regulated and must be approved by the quasi-judicial Environmental Protection Authority (EPA) which implements the Hazardous Substances and New Organisms (HSNO) Act (1976). The purpose of the Act is to protect both agricultural and natural ecosystems by regulating the introduction of new

species that could have adverse effects on the environment (Barratt et al. 2007). For proposed biocontrol agents, the EPA must compare the likely costs of introduction (using economic, environmental, social and cultural criteria) with the likely benefits (which are predominantly economic but may also be social). If the perceived benefits outweigh the costs, then the EPA may approve the release, subject to conditions that may be imposed by either (or both) the EPA and New Zealand's biosecurity authorities under the Biosecurity Act (1993).

Unexpectedly, a self-introduced population of *T. japonicus* was discovered in Beltsville, Maryland, USA in 2014. Populations of naturalized *T. japonicus* have since expanded into at least another ten States in the USA and British Columbia in Canada (Talamas et al. 2015b; Jentsch 2016; Milnes et al. 2016; Ferro 2017; Morrison et al. 2018; Abram et al. 2019). DNA analyses have confirmed that these incursions are distinct from populations held in quarantine facilities, and are likely the result of unintentional introductions of BMSB or other host species egg masses from other parts of the pest's home range (Milnes et al. 2016; Buffington et al. 2018). *Trissolcus japonicus* has also recently arrived in Europe from Asia via unexplained pathways (Stahl et al. 2019; Sabbatini Peverieri et al. 2018). We consider that the accidental arrival of *T. japonicus* into New Zealand is less likely than the incursions into the USA and Europe, primarily because of the very stringent control of live plant material into this country.

In recognition of the potentially vital role to be played by biocontrol in countering a BMSB incursion, an application for approval to release *T. japonicus* into New Zealand was made by an industry led group (i.e. BMSB Council) to the EPA in March 2018, including the host testing information presented here and substantial additional economic and social arguments. In August 2018, the EPA approved the release (EPA 2018) subject to strict conditions—foremost of which was that release could only follow an incursion of BMSB, in accordance with a Response Readiness Plan to be submitted by MPI and the BMSB Council. Details of the application, submissions from interested parties, and decision making process are freely available online (EPA 2018). This is the first approval to release a classical biocontrol agent into New Zealand prior to the arrival of its target pest. It provides the opportunity for inundative biocontrol to

be used as one tool during the early stages of an incursion, when the likelihood of successful eradication is increased through a combination of tools (including, for example, trapping and pesticides) (Tobin et al. 2014; Liebhold et al. 2016). Releasing large numbers of *T. japonicus* could potentially provide a major contribution to successful eradication of a small, localised BMSB population, especially in an area that was technically or socially difficult to access with other management tools. The possible survival of the parasitoid on alternative hosts after successful eradication of BMSB would be one of the factors to consider at the start of the programme. If eradication was subsequently deemed unfeasible then classical biocontrol would become a major strategy for reducing populations throughout New Zealand, and for achieving long-term, environmentally sustainable control. In either event, the early approval of release of a classical biocontrol agent provides the potential for future exciting science opportunities in the early management of exotic pest incursions.

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#### Compliance with ethical standards

**Conflict of interest** The authors have declared that no conflict of interest exists.

**Research involving human and/or animal rights** This article does not contain any studies with human participants or animals (vertebrates) performed by any of the authors.

**Informed consent** Informed consent was obtained from all individual participants included in the study.

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